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INVITED REVIEW

Genetic consequences of habitat fragmentation in plant populations: susceptible signals in plant traits and methodological approaches

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Abstract

Conservation of genetic diversity, one of the three main forms of biodiversity, is a fundamental concern in conservation biology as it provides the raw material for evolutionary change and thus the potential to adapt to changing environments. By means of meta-analyses, we tested the generality of the hypotheses that habitat fragmentation affects genetic diversity of plant populations and that certain life history and ecological traits of plants can determine differential susceptibility to genetic erosion in fragmented habitats. Additionally, we assessed whether certain methodological approaches used by authors influence the ability to detect fragmentation effects on plant genetic diversity. We found overall large and negative effects of fragmentation on genetic diversity and outcrossing rates but no effects on inbreeding coefficients. Significant increases in inbreeding coefficient in fragmented habitats were only observed in studies analyzing progenies. The mating system and the rarity status of plants explained the highest proportion of variation in the effect sizes among species. The age of the fragment was also decisive in explaining variability among effect sizes: the larger the number of generations elapsed in fragmentation conditions, the larger the negative magnitude of effect sizes on heterozygosity. Our results also suggest that fragmentation is shifting mating patterns towards increased selfing. We conclude that current conservation efforts in fragmented habitats should be focused on common or recently rare species and mainly outcrossing species and outline important issues that need to be addressed in future research on this area.

Keywords: conservation genetics, habitat fragmentation, mating systems, meta-analysis, plant genetic diversity, rarity status

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Introduction

The development of human civilization throughout the last two centuries has resulted in the transformation of vast natural areas into anthropogenic landscapes, resulting in a process of habitat fragmentation that alters the structure, distribution, and functioning of natural ecosystems (Saunders *et al*. 1991). Immediate consequences of this process include habitat loss, the formation of remnant habitat patches of varied forms and sizes, a reduction of population sizes, and an increase in the degree of isolation of the remaining populations immersed in an anthropogenic matrix (McGarigal & Cushman 2002; Fahrig 2003). These persistent phenomena are well recognized as the main current driving forces of biodiversity loss in terrestrial ecosystems across the planet (Sala *et al*. 2000).

Studies of fragmentation effects in plants have largely concentrated on population demographic processes,

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especially evaluating plant reproductive dynamics in fragmented habitats (Hobbs & Yates 2003; Ghazoul 2005; Honnay *et al*. 2005; Aguilar *et al*. 2006). However, within the last decade there has been an increased interest in assessing the genetic consequences of habitat fragmentation in plants as stated by initial and recent reviews on this subject (Young *et al*. 1996; Lowe *et al*. 2005; Ouborg *et al*. 2006; Honnay & Jacquemyn 2007). The expected genetic consequences of fragmentation, which creates small, discrete, and isolated populations, are based on traditional island biogeography and metapopulation theories (MacArthur & Wilson 1967; Levins 1969). Thus, habitat fragmentation is expected to erode genetic variability and to increase interpopulation genetic divergence of plant populations due to increased random genetic drift and inbreeding, and reductions in gene flow (e.g. Young *et al*. 1996; Sork *et al*. 1999; Lowe *et al*. 2005).

The most immediate effects of fragmentation on the genetic composition of plant populations depend on two factors: the effective population size within fragments and the patterns of genetic variability of the original populations previous to fragmentation (Nason *et al*. 1997; Hamrick 2004). Once a continuous forest is cleared and subdivided into small patches, from a metapopulation viewpoint, the distribution of genetic variability within and between the remaining populations in the landscape will depend on the spatial scale of fragmentation relative to the spatial scale of the pre-existent breeding neighbourhood (Nason *et al*. 1997; Hamrick 2004). Some hypotheses have been proposed to address the effects of habitat fragmentation on plant population genetics. As an immediate result, the genetic variation of populations is reduced due to genetic bottlenecks; specifically, a lower proportion of polymorphic loci and a reduction in the number of alleles per locus are expected within the fragments (Nei *et al*. 1975; Ellstrand & Elam 1993; Young *et al*. 1996). If fragmentation conditions persist over successive generations, decreased heterozygosity due to random drift and increased inbreeding are expected resulting in the accumulation of deleterious recessive alleles, lowering the fecundity of individuals, increasing seed/seedling mortality, and reducing the growth rate of individuals, eventually driving populations to extinction (e.g. Lande 1988; Young *et al*. 1996). The loss of genetic variation may reduce a population's ability to respond to future environmental change, such that the probability of extinction is increased or, at best, opportunities for evolution are limited (Caro & Laurenson 1994; Young *et al*. 1996; Nason *et al*. 1997; Booy *et al*. 2000).

The hypotheses concerning the negative impact of fragmentation on genetic diversity are the basis for the conservation genetic paradigm (Ouborg *et al*. 2006). The field of conservation genetics is relatively recent, and one of its main concerns is to develop basic and applied knowledge to create tools and strategies for conserving the genetic resources and the evolutionary potential of species (Amos & Balmford 2001; Ouborg *et al*. 2006; Pertoldi *et al*. 2007). In order to develop such tools for effective conservation efforts, it is crucial to arrive to generalizations of plant genetic response patterns of plant species to habitat fragmentation.

Nevertheless, the empirical evidence from the literature provides inconsistent results to support these hypotheses, implying that not all fragmentation episodes necessarily result in genetic erosion of plant populations (e.g. Young *et al*. 1996; Collevatti *et al*. 2001; Lowe *et al*. 2005; Kettle *et al*. 2007). In this regard, quantitative statistical approaches are especially useful tools to integrate and synthesize the body of evidence from published literature (Arnqvist & Wooster 1995). Quantitative reviews such as meta-analysis allow us to reach general conclusions about a domain of research despite the apparent contradictory response patterns of individual studies (Gurevitch & Hedges 2001). This is accomplished by treating individual published results as if they were subjected to sampling uncertainty; thus, we are able to obtain not only the magnitude and direction of each effect (regardless of their *P* values), but also the variability of effects among individual studies (Hedges & Olkin 1985; Arnqvist & Wooster 1995; Gurevitch & Hedges 2001). Consequently, we can estimate the average magnitude of the effect across all studies, test whether the effect is significantly different from zero, and examine potentially causative differences in the effects among studies (Gurevitch & Hedges 2001).

Particular life-history traits of plants may confer different vulnerability to fragmentation effects. Because genetic erosion in fragmented habitats should be more pronounced after several generations, it is expected to find stronger negative effects on the adult generation of short-lived species compared to long-lived species (Young *et al*. 1996); or more precisely, in any plant population subjected to fragmentation conditions for several generations. Similarly, the ability of plants to reproduce clonally, via vegetative spread, may also buffer the genetic effects of fragmentation as a result of delaying the time between generations (Honnay & Bossuyt 2005). Also, the ploidy level of plants may influence the effects on genetic diversity due to fragmentation; as theory predicts, autotetraploids are less subject to the loss of genetic diversity by genetic drift than diploids (Bever & Felber 1992; Moody *et al*. 1993). Finally, the mating system of plants determines the spatial distribution of genetic variation within and among populations (Loveless & Hamrick 1984). Outcrossing plants typically show higher genetic variation within populations, whereas in selfing plants most of the genetic variation is found among populations (Loveless & Hamrick 1984; Hamrick & Godt 1989). Sudden decreases in effective population sizes due to habitat fragmentation would then have stronger negative effects on within-population genetic diversity of outcrossing

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species. The fewer individuals remaining after fragmentation, the more severe the genetic bottleneck, which will have particularly large effects on the maintenance of rare alleles (Nei *et al*. 1975).

Likewise, some ecological processes, especially pollination and seed dispersal of plants, can shape the level of demographic and genetic connectivity among populations in fragmented habitats (Nason *et al*. 1997; Nathan & Muller-Landau 2000; Tewksbury *et al*. 2002; Hamrick 2004). The ability of vectors to move pollen and seeds through the fragmented landscape will determine the potential of plant species to offset the effects of genetic drift. In animal-pollinated or animal seed-dispersed plants, the level of genetic connectivity among fragments will depend on vector distribution, abundance, composition, and behaviour (Nason *et al*. 1997), attributes of pollinators and seed dispersers that are usually affected by habitat fragmentation (Didham *et al*. 1996; Graham 2001; Aizen & Feinsinger 2003; Griscom *et al*. 2007). Therefore, animal-pollinated and animal seed-dispersed plant species are expected to show decreased genetic connectivity due to habitat fragmentation compared to abiotically pollinated and abiotically seed-dispersed plants (Nathan & Muller-Landau 2000; García *et al*. 2007). The rarity of species can also determine susceptibility to genetic erosion. Naturally rare species, defined by their narrow geographical range, restricted habitat specificity or small local population sizes (*sensu* Rabinowitz 1981) are usually genetically less diverse than more widespread or common species (Karron 1987; Hamrick & Godt 1989; Ellstrand & Elam 1993). Then, common species may be more susceptible to lose genetic variation due to habitat fragmentation compared to rare species. Including rarity in models is problematic because authors do not uniformly assess rarity; species categorized as rare are not always *naturally* rare, but rather *recently* rare as a consequence of anthropogenic disturbance and habitat fragmentation (Gitzendanner & Soltis 2000). Thus, this categorization usually overlaps with the conservation status of the species (i.e. recently rare species are typically threatened or endangered). Once common and now rare species are expected to show stronger effects on genetic diversity than naturally rare species, as the former have suffered recent (i.e. in non-*evolutionary time*) decreases in regional or local abundance of populations (Huenneke 1991; Gitzendanner & Soltis 2000).

Certain characteristics of published studies may also influence the sensibility to find fragmentation effects. The ability to find fragmentation effects on genetic parameters may be different when using allozymes vs. DNA-based genetic markers. Specifically, because DNA-based genetic markers such as microsatellites have higher mutation rates (and consequently higher levels of variation), they may have higher resolution to detect changes in inter- and intra-population genetic variation compared to allozymes. Also, fragmentation effects on genetic erosion may not be detected on adult individuals of long-lived woody species, but may be detected in their progeny. Thus, in species of long generational time, the type of tissue used by authors to measure genetic diversity (either from adult or progeny) may determine the magnitude of fragmentation effects. Finally, the time elapsed since fragmentation occurred should be an important factor to assess genetic erosion in plants. Effects are expected to be stronger in plant populations subjected to fragmentation conditions for larger periods of time, where a few or several generations have passed.

In this paper, we conduct a quantitative review to assess the overall effects of habitat fragmentation on plant population genetic parameters and test the predictions of the conservation genetic paradigm. Specifically, we determined (i) the overall magnitude and direction of fragmentation effects on the genetic variability of plant populations; (ii) whether longevity, ploidy level, mating system, clonal growth, type of pollen and seed dispersal vector, and rarity status of plants determine differential susceptibility to genetic erosion in fragmented habitats; (iii) whether different methodological approaches used by the authors determine the ability to find fragmentation effects; and (iv) whether there is a relationship between time elapsed in fragmentation conditions and the magnitude of fragmentation effects in genetic parameters.

Methods

Literature search

We surveyed the literature through different databases using a combination of 'fragment*' AND 'genet*' AND 'plant' as keywords. Searches were conducted in the Science Citation Index and Biological Abstracts databases and also in the main editorials (Blackwell Science, Springer-Verlag, and Elsevier) and scientific societies that group the most relevant indexed journals of ecological genetics and conservation biology. We obtained a large number of papers that were examined for suitability in the meta-analyses. Considering that habitat fragmentation produces three main outcomes in the landscape (namely habitat loss, decreased population sizes, and increased isolation among populations), we included studies using any of these measures of fragmentation, which were statistically compared to assess whether any one of them had particularly stronger effects on genetic parameters. Thus, we included studies conducted in real habitat fragments, in natural plant populations of different sizes and/or degrees of isolation. We also considered a few studies evaluating the effects of fragmentation due to selective logging on genetic parameters. This type of disturbance introduces changes in population density of adult trees, a measure of population size (Kunin 1997; Lowe

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et al. 2005), without necessarily creating habitat fragments. We excluded articles that exclusively analysed correlations among population size and genetic variability without any explicit mention to the effects of habitat fragmentation (see Leimu *et al*. 2006). We included only studies that correlated genetic variability with population size as an indirect assessment of habitat fragmentation effects.

As measures of genetic variability, we considered expected heterozygosity (H_E), percent polymorphic loci (P), number of alleles (A), and inbreeding coefficient (F_{IS}). In cases where heterozygosity was not given (typically in studies using random amplified polymorphic DNA or amplified fragment length polymorhphism), we used molecular variance or gene diversity and analysed these parameters together with expected heterozygosity. These four genetic parameters were not necessarily evaluated all together in each study, thus sample sizes for each meta-analysis differed. In several studies, we were able to calculate inbreeding coefficients from observed and expected heterozygosity values ($F_{IS} = H_E–H_O/H_E$). Whenever available, we also included measures of outcrossing rate (OR) in fragmented habitats.

For each plant species studied, we gathered information on several life-history traits and ecological aspects as well as on the methodology used by the authors of each study as potential predictors of the genetic responses to habitat fragmentation. We determined: (i) the longevity associated to the different life forms (woody long lived, herbaceous perennial or herbaceous short lived); (ii) whether vegetative reproduction occurred; (iii) the ploidy level (polyploid or diploid); (iv) the mating system, whether a species was mainly outcrossing (which included strictly self-incompatible species, as well as self-compatible species with a predominant outcrossing mating system) or selfing (including species with predominant selfing mating system and some self-compatible species with mixed mating system with clear capability of selfing) as explicitly declared by the authors; (v) pollen dispersal vector (biotic or wind); (vi) seed dispersal vector (biotic or abiotic); (vii) rarity (common, naturally rare or recently rare). We also evaluated the type of genetic marker (allozyme or DNA based) and the plant tissue used for each study (either from adult individuals or progenies). We further searched in each paper for information regarding the time elapsed in fragmentation conditions; this included rough estimates given by authors (expressed as a *few decades or centuries*, *more than* or *between* certain amount of time) and also more precise dates or time periods elapsed. With this information, we created three categories (less than 50 years, between 50 and 100 years, and more than 100 years) to compare the magnitude of effect sizes. Furthermore, within the group of publications where authors gave a more precise date of when fragmentation started, we searched for the approximate lifespan of each species. We found information on lifespans in the same or different publications for 35 out of 47 species. For some species, we used genus-level lifespan information. For the remaining 12 species, we conservatively assigned a tabulated lifespan for woody and non-woody perennials following Ehrlén & Lehtilä (2002). For these species, we calculated the number of generations under fragmentation conditions by dividing the time period of fragmentation by the lifespan of the species, and ran correlation analyses between the number of generations and the effect sizes for H_E and F_{IS}. Based on theoretical grounds, these two genetic parameters are expected to be correlated with the number of generations under fragmentation conditions, showing stronger negative effects as more generations pass by. All the species' information was obtained from the same article, from other publications on the same species, or by contacting the authors. However, not every species' characteristic was available, thus predictor variables within a meta-analysis do not necessarily share the same sample size.

Seven articles evaluated the effects of fragmentation on genetic parameters in two species simultaneously and we included each of these species in the same analysis. Because the magnitude and sometimes direction of the responses of each species to habitat fragmentation within the same study were quite different, it is reasonable to assume that the effects are independent for each species (Gurevitch & Hedges 2001).

Data analysis

We used a categorical meta-analytical approach due to the large majority of studies evaluating population genetic parameters of plants in contrasting conditions (i.e. fragmented vs. non-fragmented). We obtained the mean value ($\bar{X}$) and standard deviations (SD) of each genetic parameter (H_E, A, P, OR, and F_{IS}) from plant populations (n) in each of the two conditions (fragmented and continuous habitats) in each published study. These data were taken either from text, tables or graphs (data from graphs were scanned using Datathief II software available online).[1] For each study, the magnitude of the effect of fragmentation on each of the genetic parameters (d_i) was estimated as the unbiased standardized mean difference (Hedge's d) between the mean value of the genetic parameter in fragmented and continuous habitats:

$$d_i = \frac{\bar{x}^F - \bar{x}^C}{SD^{FC}} J$$

where $\bar{X}^F$ is the mean value of a given genetic parameter in fragmented habitats, $\bar{X}^C$ is the mean value of the same genetic parameter in continuous habitats, SD^{FC} is the pooled standard deviation, of both groups and J is a term

[1] http://www.nikhef.nl/~keeshu/datathief/

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that corrects for bias due to small sample size (see Gurevitch & Hedges 2001). The effect size d can be interpreted as the difference between the genetic diversity of plants in fragmented habitats and continuous conditions, measured in units of standard deviations. Thus, large differences and low variability generate the largest effect sizes (Gurevitch & Hedges 2001). For each genetic parameter, the overall weighted mean effect size estimate (d^*_{++}) was calculated as:

$$d^*_{++} = \frac{\sum_{i=1}^{n} w_i d_i}{\sum_{i=1}^{n} w_i}$$

where d_i is the effect size of the ith study and w_i is the weight (reciprocal of the sampling variance) of the ith study.

Positive values of the effect size (d) for H_E, A, P, and OR, imply positive effects of habitat fragmentation on these parameters whereas negative d values imply negative effects of fragmentation on these parameters. The interpretation of effect sizes for inbreeding coefficients is exactly the opposite: positive values of d imply negative effects of habitat fragmentation (i.e. higher inbreeding) whereas negative d values imply positive effects of fragmentation (i.e. lower inbreeding). For studies using correlational approaches to evaluate fragmentation effects (typically using population size as the independent variable), we calculated the mean value, standard deviation and sample size by pooling the data points for the lower-half (used as fragmented condition values) and higher-half values (used as non-fragmented condition values) of the continuous independent variable.

We used MetaWin 2.0 (Rosenberg *et al*. 2000) to run the analyses and bootstrap re-sampling procedures as described in Adams *et al*. (1997) to calculate confidence intervals of effect sizes. An effect of habitat fragmentation was considered significant if the 95% biased-corrected bootstrap confidence intervals (CI) of the effect size (d) did not overlap zero (Rosenberg *et al*. 2000). Confidence intervals based on bootstrapping methods are generally wider than standard CI, which implies that re-sampling estimates of CI are more conservative (Adams *et al*. 1997). Data were analysed using random-effect models (Raudenbush 1994). This model assumes that differences among studies are due to both sampling error and random variation, which is usually the rule in ecological data (Gurevitch & Hedges 2001). The heterogeneity among effect sizes was assessed with Q statistics. Specifically, we examined the P values associated with $Q_{between}$ statistics, which describe the variation in effect sizes that can be ascribed to differences between the categories of each predictor variable (i.e. species' life history and ecological traits, and studies' methodologies). We also used these statistics to compare the effect sizes between studies that used different factors of analyses (e.g. fragment size, logging, population size) to evaluate habitat fragmentation. Within the species used for the meta-analyses, we found few congeneric species (Table S1, Supporting information). We re-ran analyses using data pooled by congeneric species and found no difference in magnitude or direction of effects compared to the analyses performed using all the species as independent data points. We also tested for potential interactions among predictor variables by measuring their pairwise level of dependence with chi-squared tests.

Quantitative reviews of published studies have the intrinsic problem of potential publication bias. That is, studies showing significant results may have a greater probability of publication than those showing non-significant results. We explored this possibility graphically (weighted histograms and funnel plots), and by calculating weighted fail-safe numbers. If the fail-safe number is larger than $5n + 10$, where n is the number of studies, then publication bias may be safely ignored (i.e. results are robust regardless of publication bias; Rosenberg 2005).

Results

Sample of studies

From the literature search, we obtained 101 publications from 28 international indexed journals throughout the period of 1989–2008 that evaluated the effects of habitat fragmentation on plant population genetic parameters (Appendix S1, Supporting information). These studies measured at least one parameter of genetic variability on 102 unique plant species to conduct the meta-analyses, which yielded 101 data points for expected heterozygosity (H_E), 77 data points for number of alleles (A), 57 data points for percent polymorphic loci (P), 18 data points for outcrossing rate (OR), and 62 data points for inbreeding coefficients (F_{IS}). Although the species included in this review comprise a wide sample of plants with different biological and ecological attributes, there is some bias in these characteristics and also in the approaches used by authors to study genetic consequences of habitat fragmentation. Herbaceous perennial and woody long lived (shrubs and trees) represent 53% and 40% of the studied species, respectively, while herbaceous short-lived species comprised only 7% of the studied species. There are larger proportions of insect pollinated species (72%) and abiotically seed-dispersed species (77%). Diploid species are also a majority (84%). Although self-compatible (54%) and self-incompatible (46%) plants are approximately equally represented in the sample, within self-compatible plants there is a high number of mainly outcrossing plants as declared by the authors. Hence, there is a higher proportion of mainly outcrossing species (75%) compared with selfing plants (25%). Species without the capability of vegetative reproduction are slightly

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more represented (61%). Common species represent 48%, whereas naturally and recently rare species represent 25% and 27% of the sample, respectively. We found no significant pairwise associations among any of these predictor variables (not shown), which indicate they can be considered statistically independent. Most of the studies evaluate the effects of habitat fragmentation on the genetic variability of adult individuals (72%), using mainly allozymes (60%) as genetic markers.

A comparison of the different factors of analysis used by the authors as measures of habitat fragmentation showed no significant differences in the effect sizes for H_E ($Q_{between} = 1.35$; $P = 0.493$), A ($Q_{between} = 1.68$; $P = 0.441$), P ($Q_{between} = 2.05$; $P = 0.162$), and F_{IS} ($Q_{between} = 0.76$; $P = 0.652$). That is, fragmentation effects on each of these genetic parameters are comparable whether considering fragment size, degree of isolation, habitat loss, population size, or density of conspecifics (i.e. logging) as factors of analysis.

Weighted histograms showed unimodal distributions with the highest frequency around zero (not shown) and funnel plots of effect sizes vs. sample sizes showed no skewness (not shown), which indicates no bias in reporting results (cf. Aguilar *et al*. 2006 for details of interpretation). Similarly, the calculated weighted fail-safe numbers for each meta-analysis were larger than $5n + 10$ [H_E: $2249.4 > (5 * 101) + 10 = 515$; A: $2805.4 > (5 * 78) + 10 = 400$; P: $1444.2 > (5 * 57) + 10 = 295$; OR: $168.3 > (5 * 18) + 10 = 100$; F_{IS}: $1306.6 > (5 * 62) + 10 = 320$], reinforcing the robustness of these results.

Habitat fragmentation and genetic variability

Overall weighted-mean effect sizes of habitat fragmentation on H_E, A, and P were negative and significantly different from zero (Fig. 1). The OR, which was only consistently assessed in 18 studies, also showed an overall negative weighted-mean effect size (Fig. 1). Habitat fragmentation showed non-significant overall effects on F_{IS} (Fig. 1), despite the small positive value implying a slight trend of increasing inbreeding due to habitat fragmentation.

From the evaluation of all predictor variables associated with the species' life history and ecological attributes for each of the genetic parameters, we present only the results that showed significant P (< 0.05) values of $Q_{between}$ statistics in text and figures. We found that fragmentation effects were significantly different for H_E between common, naturally rare and recently rare species ($Q_{between} = 23.18$; $P < 0.001$). On average, common and recently rare species showed strong, negative and significant effects of fragmentation on H_E, whereas naturally rare species showed non-significant effects on H_E (Fig. 2a). The same trend was found for A and P, although the heterogeneity among effect sizes was only marginally significant (for A: $Q_{between}$

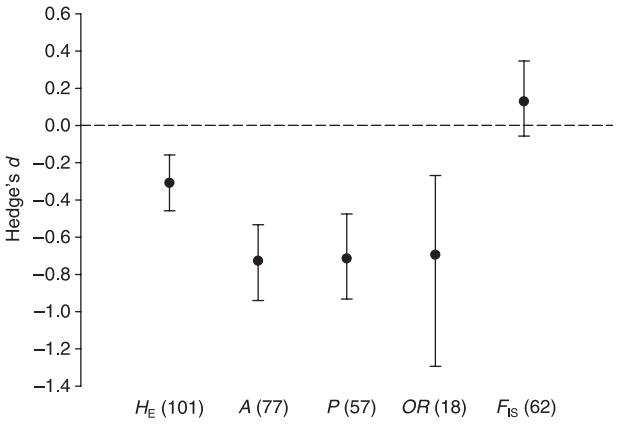

Fig. 1 Overall weighted-mean effect sizes and 95% bias-corrected confidence intervals of habitat fragmentation on expected heterozygosity (H_E), number of alleles (A), percent polymorphic loci (P), outcrossing rate (OR), and inbreeding coefficient (F_{IS}). Sample sizes for each meta-analysis are shown in parenthesis; dotted line indicates Hedge's $d = 0$.

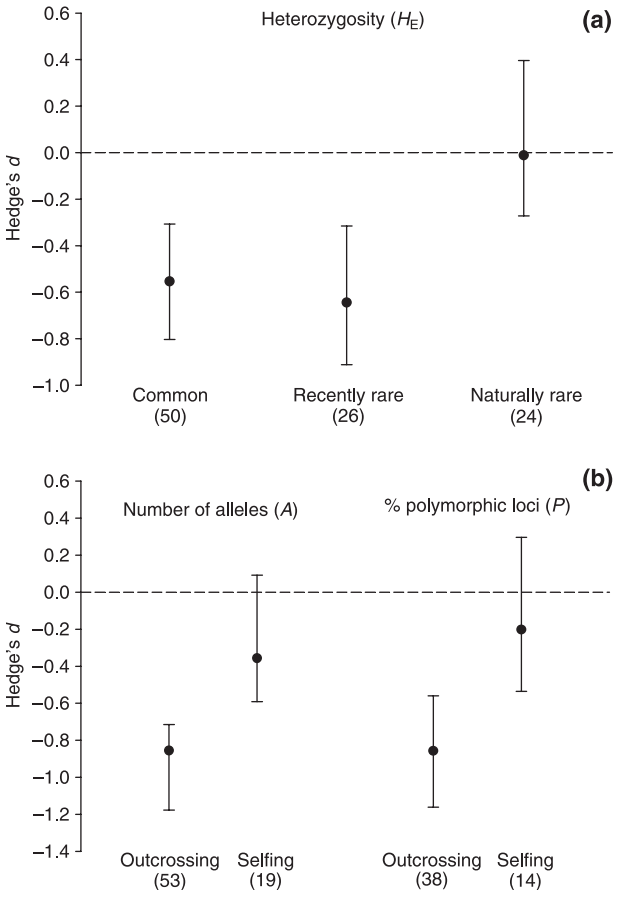

Fig. 2 Weighted-mean effect sizes and 95% bias-corrected confidence intervals of habitat fragmentation on (a) H_E of plant species with different categories of rarity (common, recently rare, and naturally rare) and on (b) A and P of plants with different mating systems (outcrossing and non-outcrossing) showing statistically significant heterogeneity ($Q_{between}$). Sample sizes of each category are given in parentheses. Dotted line shows Hedge's $d = 0$.

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Fig. 3 Weighted-mean effect sizes and 95% bias-corrected confidence intervals of habitat fragmentation on inbreeding coefficient (F_{IS}) of studies evaluating adult and progeny tissues. Sample sizes of each category are given in parentheses. Dotted line shows Hedge's $d = 0$.

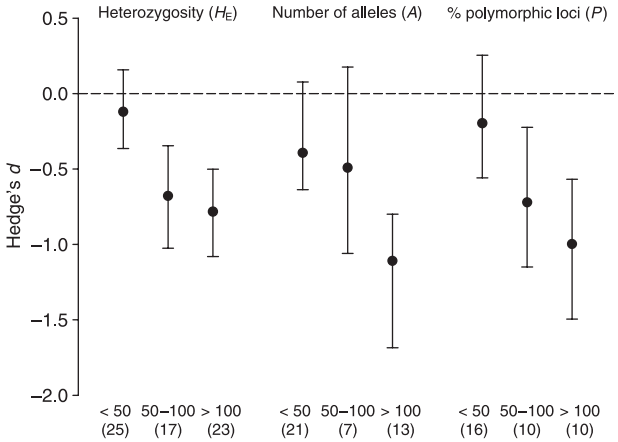

Fig. 4 Weighted-mean effect sizes and 95% bias-corrected confidence intervals of habitat fragmentation on H_E, A, and P of plant populations subjected to different time periods in fragmentation conditions: less than 50 years (< 50), between 50–100 years (50–100), and more than 100 years (> 100). Sample sizes of each category are given in parentheses. Dotted line shows Hedge's $d = 0$.

= 4.72; $P = 0.094$; for P: $Q_{between} = 5.01$; $P = 0.081$). Furthermore, for A and P, there were significant differences in mean effect sizes between outcrossing and selfing species ($Q_{between} = 14.96$; $P = 0.028$ and $Q_{between} = 9.17$; $P = 0.05$ for A and P, respectively). Outcrossing species showed stronger negative effects of fragmentation on A and P compared to selfing species (Fig. 2b). A similar but marginally significant trend was observed for H_E, [$d_{outcrossing\ (n=69)} = -0.57$, $d_{selfing\ (n=24)} = -0.22$; $Q_{between} = 3.24$; $P = 0.071$]. In the case of inbreeding coefficients, none of these predictor variables showed significant heterogeneity, implying that fragmentation not only does not have an overall effect on inbreeding, but also no particular life-history trait is showing susceptibility to fragmentation (not shown). Surprisingly, fragmentation effects on inbreeding were only studied in one short-lived species, which precluded the formal comparison between short- and long-lived species. None of the other life history (life form, vegetative growth capability, and ploidy level) and ecological traits (pollination and seed dispersal vector types) evaluated as predictor variables showed significant heterogeneity in effect sizes of fragmentation on these genetic parameters (not shown).

The use of different genetic markers (allozymes vs. DNA based) did not significantly alter the magnitude of effect sizes for each of the genetic parameters evaluated in fragmented habitats (not shown). Furthermore, effect sizes of fragmentation on H_E, A, and P were also homogeneous among studies sampling adult or progeny tissues (not shown). For inbreeding coefficients, on the contrary, there was a significant difference in mean effect sizes between studies evaluating adult and progeny tissues ($Q_{between} = 16.80$; $P = 0.012$; Fig. 3): progenies showed a significant positive overall mean effect size value while adults showed a non-significant mean effect size (Fig. 3). This result implies that progenies generated in fragmented habitats (which comprised mostly non-established seeds) presented higher inbreeding coefficients than progenies produced in continuous habitats; whereas for adult individuals no difference in mean F_{IS} values were observed between fragmented and continuous habitats. Depending on the parameter evaluated, between 53% and 64% of the studies gave at least rough information on the time elapsed in fragmentation condition. Overall, species subjected for more than 100 years in fragmentation conditions had significantly stronger effects on H_E ($Q_{between} = 17.72$; $P = 0.009$), A ($Q_{between} = 6.68$; $P = 0.05$), and P ($Q_{between} = 15.57$; $P = 0.018$; Fig. 4) compared to species evaluated in fragmented systems of less than 50 years, which showed non-significant mean effect sizes on these three genetic parameters (i.e. CI's overlapping zero value; Fig. 4).

Finally, we were able to estimate the number of generations elapsed in fragmentation conditions for 47 and 35 case studies evaluating H_E and F_{IS}, respectively. We log-transformed the number of generations and ran correlations with the effect sizes of fragmentation on these two parameters. We found a significant negative correlation between the number of generations elapsed and the species' effect sizes for H_E ($r = -0.36$, $P = 0.012$, Fig. 5). That is, the more generations elapsed in fragmentation conditions for any given plant population, the stronger negative magnitude of effect sizes on H_E. In the case of fragmentation effects on inbreeding coefficient, we found a non-significant positive correlation with the number of generations ($r = 0.29$, $P = 0.102$, $n = 35$), suggesting a trend of higher inbreeding as more generations pass by in fragmentation conditions.

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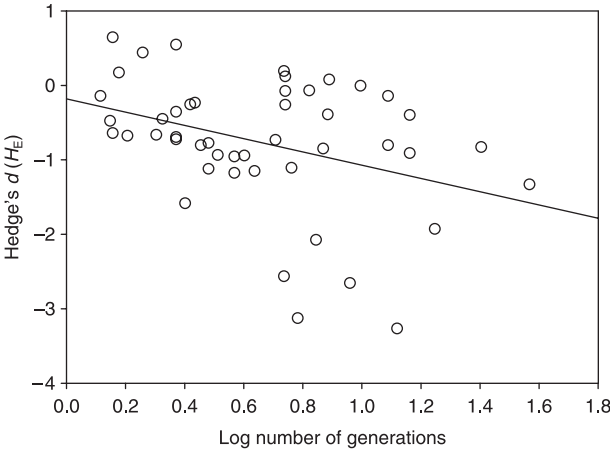

Fig. 5 Correlation between the log-transformed number of generations of plant populations in fragmented habitats and the effect sizes of fragmentation on H_E for 47 plant species. Correlation coefficient $r = -0.36$, $P = 0.012$.

Discussion

Anthropogenic habitat fragmentation is a recent phenomenon in evolutionary time but a pervasive feature of modern landscapes (Fahrig 2003). Plant populations that remain in habitat fragments are confronted with modified environments of reduced area, increased isolation, and new ecological boundaries, potentially affecting their biotic and abiotic interactions (e.g. Fahrig 2003; Ewers & Didham 2006). The genetic consequences of fragmentation on plant populations have been studied for over two decades and no clear response patterns have emerged from the literature. Recently, two reviews have focused on the relationship between genetic diversity and population size (Leimu *et al*. 2006; Honnay & Jacquemyn 2007), one of the immediate possible demographic consequences of habitat fragmentation. Nevertheless, fragmentation is a complex process that involves several different factors simultaneously (McGarigal & Cushman 2002; Fahrig 2003; Ezard & Travis 2006; Leblois *et al*. 2006; Ouborg *et al*. 2006); thus analyzing solely reductions of population size may not fully reflect what is happening in real fragmented scenarios. Population size per se may not be very important for animal pollinators and seed dispersers, whereas the degree of population isolation or the matrix characteristics surrounding the fragments may have more influence on their foraging behaviour (Kunin 1997; Ricketts 2001), affecting their ability to maintain gene flow among fragmented populations. These different factors, which often interact in diverse ways, are difficult to separate in observational or non-experimental designs, the rule in fragmentation studies. Authors tend to focus on one factor and do not usually control for the others (Leblois *et al*. 2006; Ouborg *et al*. 2006; but see e.g. Prober & Brown 1994; Honnay *et al*. 2007). Thus, the cause of reduced genetic diversity in fragmented habitats should not be adjudicated to one single factor, but rather to the interacting effects of, at least, population size, degree of isolation and matrix characteristics (Ezard & Travis 2006).

In this review, we explicitly focused on fragmentation studies and arrived at a conclusive generalization: habitat fragmentation decreases the genetic diversity of plant populations. The vast majority of studies were conducted on adult populations of long-lived species in relatively recently fragmented systems, which indicates the effects observed on genetic diversity, especially on *A* and *P*, are probably mainly the result of genetic bottlenecks, the most immediate consequence of fragmentation (e.g. Young *et al*. 1996; Nason *et al*. 1997; Oostermeijer *et al*. 2003; Lowe *et al*. 2005). These species and studies' characteristics may also be the reason for the absence of overall significant effects on inbreeding coefficients (i.e. most sampled adults have probably established before fragmentation took place) and the comparatively smaller mean effect size observed on H_E, which may be mostly due to the overall reduction in number and frequency of alleles (Barret & Kohn 1991; Nason *et al*. 1997). In a closer examination of the subset of studies that provided dates of fragmentation events, it was clearly observed that time and, more precisely, the number of generations elapsed under fragmentation conditions, are crucial in determining stronger genetic diversity reductions in plant populations, especially in heterozygosity, which may take a number of generations to become apparent (Young *et al*. 1996; Lowe *et al*. 2004, 2005). Studies conducted in more than 100-year-old fragmented systems presented significantly stronger negative effects on genetic diversity (Fig. 4). This notion was more specifically supported by the significant correlation between the estimated number of generations for a subset of species and the magnitude of negative fragmentation effects on H_E (Fig. 5), primarily as a result of random genetic drift (e.g. Young *et al*. 1996; Young & Clarke 2000; Lowe *et al*. 2004).

Gene flow and mating patterns in fragmented habitats

The amount of gene flow among remnant populations is a key element that will ultimately determine the genetic consequences of habitat fragmentation (Sork *et al*. 1999; Frankham *et al*. 2002; Hamrick 2004; Sork & Smouse 2006). Moderate or even relatively low levels of gene flow via pollen or seeds between fragmented populations can significantly alleviate the loss of genetic diversity by preventing the effects of genetic drift (e.g. Sork *et al*. 1999; Couvet 2002). In this regard, we found no evidence of any particular pollinator or seed dispersal vector type (either biotic or abiotic) to confer differential susceptibility to the loss of genetic diversity. Although this result does not give

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us information about the patterns of gene flow per se in fragmented habitats, it does indicate there is no obvious type of vector able to conduct consistently extensive gene flow between fragments within the studies analysed.

In the present review, we were not able to evaluate contemporary gene flow due to the current paucity of this kind of study and the difficulty of generating effect size measures from gene flow parameters. However, the results observed for outcrossing rates and inbreeding coefficients may indirectly support the possibility of disrupted gene flow and/or changes in mating patterns of fragmented plant populations. Outcrossing rates in fragmented populations showed a significant overall decrease compared to populations in continuous habitats (Fig. 1), suggesting that fragmented plant populations are suffering changes in mating patterns towards increased selfing. Moreover, inbreeding coefficients will increase immediately in the first generation of progenies if mating patterns are biased towards higher selfing or mating among related individuals (e.g. Young *et al*. 1996; Lowe *et al*. 2005; Kettle *et al*. 2007). Precisely, we found that progenies in fragmented habitats presented significant mean higher inbreeding coefficients than progenies in non-fragmented habitats (Fig. 3), indicating adult individuals in fragmented populations are mating more frequently among related individuals and/or through autogamous pollination.

In addition to reduced heterozygosity due to random genetic drift in populations that remain fragmented for several generations, heterozygosity erosion is more severe when inbreeding accompanies fragmentation (e.g. Young *et al*. 1996; Nason *et al*. 1997; Young & Clarke 2000). The few species subjected to fragmentation conditions for many generations presented quite strong negative effect sizes on H_E (Fig. 5), probably as a result of both drift and increased inbreeding. In the hypothetical scenario of anthropogenic fragmentation ceasing and landscapes remaining as they are today, the effects on genetic diversity of plants will still be much stronger in the future than we have estimated here if mating patterns continue shifting towards selfing.

Mating systems

Self-incompatible (SI) and mainly outcrossing self-compatible species, which contain most of their genetic variability within populations, suffered greater losses of alleles and polymorphic loci than non-outcrossing self-compatible and selfing species. For self-incompatible species in particular, this may result in the loss of low-frequency self-incompatibility alleles (S) (Wright 1965; Nei *et al*. 1975). In genetically controlled self-incompatibility systems, sharing of even a single S allele can prevent mating between individuals (De Nettancourt 2001). Thus, SI plants surviving in small, isolated populations may experience mate limitation due to reduced S allele diversity so that the effective population size is further reduced (Byers & Meagher 1992; Glémin *et al*. 2008). Such synergism between genetic and demographic processes has great potential to influence population viability of these species (Young & Clarke 2000; Glémin *et al*. 2008). In fact, animal-pollinated SI species are also strongly negatively affected in terms of effective pollination service and seed production by habitat fragmentation (Aguilar *et al*. 2006), thus these species are exceptionally vulnerable to fragmentation as a consequence of both, ecological and genetic mechanisms. These results represent a clear example of how genetic erosion can have short-term impacts on individual fitness and population viability (e.g. Cascante *et al*. 2002; Fuchs *et al*. 2003).

Rarity status

Our results support the initial hypothesis regarding the rarity status of plants: because common species have comparatively higher levels of genetic variability than naturally rare species, they are expected to lose more diversity due to recent fragmentation processes. Whether rarity is a cause or a consequence of evolutionary and ecological processes is still an open question (Rabinowitz 1981; Gitzendanner & Soltis 2000). In this regard, naturally and recently rare species may represent different timescales and origins of disturbance, which affect the genetic characteristics they possess in the present (Karron 1987; Ellstrand & Elam 1993; Gitzendanner & Soltis 2000; Oostermeijer *et al*. 2003). If this is true, it would be important to distinguish in the system under study whether habitat fragmentation is a consequence of natural phenomena, and thus occurred through evolutionary time, or whether is the result of anthropogenic activity, occurring in recent ecological times. While evolutionary fragmentation may be a more gradual and slower process that may also 'have an end', ongoing ecological fragmentation is a much faster increasing, non-random process (Saunders *et al*. 1991; McGarigal & Cushman 2002; Fahrig 2003). Given the ubiquitous nature of anthropogenic habitat fragmentation in today's landscapes, the results presented here are important and of interest to conservation biology as they situate common species in potential risk of genetic erosion, which is counterintuitive to current conservation principles that almost exclusively emphasize efforts on rare or threatened species (Honnay & Jacquemyn 2007; Gaston & Fuller 2008).

Conservation implications and future directions

Conservation of genetic diversity within populations has direct implications not only for ecosystem functioning but also for providing resilience in the face of environmental change (Luck *et al*. 2003; Reusch & Hughes 2006). The

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controversy about whether ecological and demographic factors are more important than genetic factors in driving species to extinction (Lande 1988; Frankham *et al*. 2002) has been recently quantitatively assessed: most taxa are not driven to extinction before genetic factors affect them adversely (Spielman *et al*. 2004), an assertion also supported by further research on plants in fragmented habitats (e.g. Endels *et al*. 2007). Thus, revealing which plant traits are more susceptible to suffer genetic erosion in fragmented habitats is crucial to detect lowered evolutionary potential, compromised reproductive fitness, and elevated extinction risks of wild populations, which should help generate criteria to prioritize conservation efforts (Young *et al*. 1996; Young & Clarke 2000; Amos & Balmford 2001; Lowe *et al*. 2005). Our results indicate that such efforts should be directed to common or recently rare species and mainly outcrossing species. Strictly self-incompatible, animal-pollinated species are at even greater risk due to their additional reproductive impairment in fragmented habitats (Aguilar *et al*. 2006).

Despite these unequivocal signals of susceptibility in plants, there is a clear gap in the literature of plant population genetics in fragmented habitats that precluded us making further generalizations. Such is the case of the poor representation of short-lived species as study targets and the dearth of studies evaluating contemporary gene flow via pollen and seeds on plant species with different life forms coupled with ecological information on the biotic dispersal vectors. Also, special attention should be given to the study of established progenies (seedlings and saplings) in fragmented habitats. Most of the progeny tissue evaluated up to now comes from non-established seeds (personal observation) and their genetic composition may differ markedly from that of the progeny that is actually being recruited in fragmentation conditions if they are subjected to selective pressures shaped by seed predators and herbivores (e.g. Cascante *et al*. 2002) and/or if they come from seed banks of previous reproductive episodes (Mandák *et al*. 2006; Honnay *et al*. 2008). Increasing these types of studies may allow us to determine whether gene flow mediated by animals is in fact changing and how changes in mating patterns will affect the genetic diversity of future generations of plant populations. Including precise measures and information on the history and characteristics of fragmented systems is particularly important, not only to determine timescales of fragmentation but also to test for possible fragmentation thresholds below which genetic variation is lost (e.g. Prober & Brown 1994; Ezard & Travis 2006). These approaches imply the merging of population genetics, plant–animal interaction ecology, and landscape ecology, a multidisciplinary endeavor that will provide knowledge-based tools for conserving the evolutionary potential of species and for managing ongoing anthropogenic modified landscapes.

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The authors share research interests in the ecology, evolution and genetics of plant reproductive dynamics. They have been evaluating the effects of forest fragmentation and other anthropogenic disturbances on pollinators, sexual reproduction and the genetic structure of flowering plants. They are interested in generating basic and applied knowledge in ecology and conservation biology of plant-animal interactions and their role in preserving the genetic diversity of plant populations in human-altered landscapes. Other research interests involve the study of hybridization processes between genetically modified plants with native relatives, the role of pollinators as ecological service providers for human well-being, and the conservation of tropical and subtropical dry forests.

Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1 List of 102 unique plant species included in the meta-analyses. For each species, we provide the botanical family, the genetic parameters evaluated in the study, the molecular marker used, the compatibility system, mating system, pollination vector, seed dispersal vector, ploidy level, vegetative growth capability, life form, type of rarity, studied tissue, time elapsed in fragmentation conditions and the source publication where information was obtained.

Appendix S1 List of complete references of the studies included in the analyses.

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RESEARCH ARTICLE

The Role of Scent Marking in Mate Selection by Female Pumas (*Puma concolor*)

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Abstract

Mate selection influences individual fitness, is often based on complex cues and behaviours, and can be difficult to study in solitary species including carnivores. We used motion-triggered cameras at 29 community scrapes (i.e. scent marking locations used by multiple individuals) and home range data from 39 GPS-collared pumas (*Puma concolor*) to assess the relevance of communication behaviours for mate selection by female pumas in California. Female pumas visited community scrapes irregularly and visitation bouts appeared to be correlated with oestrus. Female pumas on average selected from 1.7 collared males, and selection was based on multiple cues that varied among the different time periods measured (i.e. the female's visitation bout and in 90 days previous to the consorting event). Female mate selection over the course of a visitation bout was based on frequency of the male visitation, mass, and age. In the 90 days previous to consorting, the number of scrapes a male created was the most important contributor to selection, which was likely related to his residency status. We also found that at least 14% of females mated with multiple males, thus possibly confusing paternity. Our findings provide a mechanistic understanding of how female pumas use scent and auditory communication at community scrapes to select dominant resident males to mate with.

Introduction

Reproductive success is essential for individual traits to transfer to, and hence modify, future generations [1], and therefore behaviours associated with reproduction are an important source of adaptation and evolution. How individuals select mates is complex and often involves multiple cues that vary among species [2,3], necessitating the development of species-specific behaviours and signals to advertise for and communicate with potential mates [4,5,6,7]. In order to understand the adaptive significance of behaviours used for mate selection, it is necessary to understand each cue and its associated function. However, the challenges associated with observing cues involved in mate selection of cryptic mammals such as solitary carnivores in natural environments have historically prevented detailed study of these behaviours [8,9].

Competing Interests: The authors have declared that no competing interests exist.

Reproductive strategies in solitary carnivores are expected to vary between males and females. In these species, males are commonly polygynous and often significantly larger than females. Males are thought to compete with other males for territories that encompass the home ranges of multiple females and are believed to attempt to mate with every reproductive female residing within their territory [4,7,8,10,11]. Conversely, female solitary carnivores tend to overlap with few potential mates [8,12,13], and may primarily rely on carefully assessing cues to select a mate that best enhances survival of their offspring [2]. A key aspect of female mate selection is thought to be the body mass of potential mates. Larger mass in male carnivores appears to be selected for across generations as an indicator of greater fitness and physical dominance, both of which can be expressed via larger territories [8,9]. However, recent advances in our understanding of mate selection suggest that female selection is more complex than simplistic assessments of male ornamentation or mass [9].

The spatiotemporal dispersed structure of populations of solitary carnivores requires indirect methods to advertise for potential mates and communicate with competitors. Many solitary carnivores are thought to therefore communicate with competitors through indirect cues (i.e. scent marking and vocalizations) rather than through direct contact [8,13,14]. Felids are generally considered to have a poor sense of smell when compared to canids and ursids [8], but nevertheless, the most commonly observed form of indirect communication in solitary felids is scent marking [4,8,14]. Scent marking (e.g. via sprayed urine) potentially allows male felids to advertise their presence and residency status to other males and females whose home ranges they overlap [4,8,14,15]. Female solitary carnivores can then potentially visit scent marking areas used by multiple males and simultaneously assess potential mates.

Pumas (*Puma concolor*) are solitary, territorial felids, and primarily communicate through scent marking [8,16]. Pumas breed throughout the year [8,16], however, research suggests that parturitions in some areas peak in summer and early autumn [8,17,18]. For populations that experience peaks in parturitions, mating behaviour is also expected to peak (i.e. an additional 3 months earlier). Nevertheless, the potential for mating to occur throughout the year suggests that scent marking and other communication behaviours associated with mate selection, too, must occur throughout the year. Mate selection in pumas might be further complicated due to aggressive behaviours, including those causing injuries or death, of males towards females not in oestrus [8].

Scraping, where a puma uses its hind feet to create a mound of substrate material and then sometimes urinates or defecates on the mound (S1 Video), is the most frequently observed communication behaviour in pumas [8,19,20]. Following Allen et al. [20], we define scent marking areas where scrapes are concentrated or clumped ($\geq$ 3 in 9 m^2) as 'community scrapes.' Community scrapes are often used by multiple individual pumas, most frequently by resident males [20]. Pumas have been observed to display other behaviours at these scrape areas, including olfactory investigation, the flehmen response, and caterwauling (S2 Video) (Table 1) [20]. Male communication at community scrapes may be primarily to advertise for mates, but is also likely to deter competitors [20]. In contrast, the most frequent communication behaviours displayed by female pumas at community scrapes are investigative and may be used for the assessment of potential mates [20]. Although recent research has begun to explain how scraping and associated behaviours are used by pumas for intraspecific communication e.g., [8,19,20], we do not currently understand their functions in female mate selection.

We monitored a puma population that included 39 marked individuals (20 females and 19 males) in California from 2011–2013 to better understand female mate selection strategies. Pumas are difficult to observe due to their cryptic nature, so we deployed motion-triggered video cameras at known community scrapes to record communication behaviours, visitation rates, and to assess the relevance of communication behaviours for mate selection. We

Table 1. The definitions of behaviours exhibited by pumas at community scrapes, based on Allen et al. [20].

Behaviour	Definition
Caterwauling	A loud, reverberant call. Most frequently given by females.
Flehmen Response	Where the puma picked up its head and curled back its upper lip, sometimes arching its neck backwards, in order to expose its vomeronasal organ.
Olfactory Investigation	Where the puma is using its olfactory sense to investigate cues and signals, noted by the pumas nose within one head length of a scrape or other cue.
Scraping	Where the puma clawed in substrate with their hind feet and then sometimes urinated and/or defecated on the scraped mound of material.

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formulated the following three hypotheses: 1) Due to differences in mating strategies, patterns in visitation would vary between male and female pumas. We expected male pumas to visit regularly to advertise for females and mark for territorial ownership. We expected females to be irregular in visitation, avoiding community scrapes when raising kittens, and visiting when in estrus; 2) Because reproductive females generally mate once every two years, we expected that female pumas will make fewer forays to community scrapes outside of their core home ranges than males. Successful females generally mate once every two years, so less of their time is spent seeking out mates, and may be more likely to choose the resident male to improve safety of their dependent kittens from infanticide. In contrast, male pumas are expected to seek opportunities to mate with every available female, including making forays out of their home range to search for females, and being drawn outside of their home range by the caterwauling of females; 3) Females will select male pumas based on perceived residency (in order to avoid infanticide later), which males advertise by the frequency of their visitation to community scrapes. Because mass and age are related to residency in male pumas (Logan and Sweanor 2001), females may also indirectly select for those characteristics.

Materials and Methods

Study area

Our study area is 1,700 km^2 in the Santa Cruz Mountains of California, including parts of Santa Cruz, San Mateo, and Santa Clara counties (Fig 1). The study area is bounded by the Pacific Ocean to the west, the city of San Jose to the north, the city of Santa Cruz to the south and Highway 101 to the east. An arterial highway (California Highway 17) bisects the study area. Vegetation characteristics and climatic conditions in the study area have been described in detail elsewhere [20,21].

Ethics statement

Our protocols for the capture of pumas adhered to the guidelines outlined by the American Society of Mammalogists [22], and were approved by the Institutional Animal Care and Use Committee of the University of California, Santa Cruz (Protocols Wilmc0709 and Wilmc1101), and the Wildlife Investigations Lab of the California Department of Fish and Wildlife. Puma capture and handling protocols have been described in Wilmers et al. [21], and no pumas were ever killed/sacrificed as part of research methods. Pumas were not endangered, and permission to handle pumas was granted through a Memorandum of Understanding and Scientific Collecting Permit #11968 with the California Department of Fish and Wildlife.

Our research was carried out on a combination of public and private land. In each case, we approached the property owner for permission to access their property before entering. Public

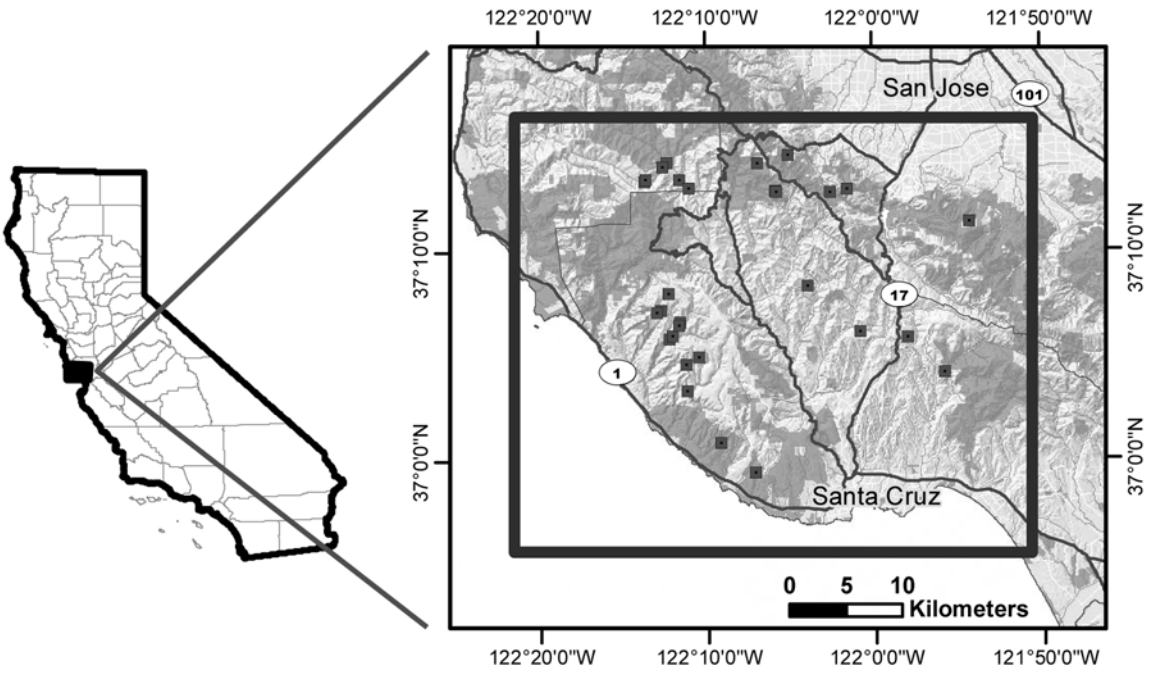

Fig 1. A map of the study area, showing the location of monitored community scrapes. The study area included areas in Santa Cruz, San Mateo, and Santa Clara Counties and the cities of Santa Cruz and San Jose in California.

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properties that required permits were California State Parks, the city of Santa Cruz, Midpeninsula Regional Open Space District, Penninsula Open Space Trust, and Santa Clara County Parks.

Field methods

We monitored behaviour of pumas at community scrapes between May 2011 and July 2013 using motion-triggered video cameras with infrared flash (Bushnell TrophyCam, Overland Park, KS). We concurrently captured and placed GPS-enabled collars (Model GPS Plus 1D, Vectronics Aerospace, Berlin, Germany) with unique identifiers on 39 pumas (females = 20, males = 19) residing in our study area. The collars were generally set to collect waypoints every 4 h, and had a mean fix rate of 76.1 (± 4.1 SE) %. The pumas with collars were monitored for a mean of 1.71 (± 0.26 SE) years. We defined community scrapes as scrape areas used for communication by >1 puma (confirmed through camera data), that were not associated with either kill or bedding sites [20]. The community scrapes we found were typically characterized by an abundance of scrapes in a small area ($\geq$ 3 in 9m^2) [20]. The community scrapes were also used by other carnivores for scent marking, including coyotes (*Canis latrans*), bobcat (*Lynx rufus*), gray foxes (*Urocyon cinereoargenteus*), and striped skunks (*Mephitis mephitis*). We identified areas that potentially contained community scrapes using an algorithm that identified areas visited by collared pumas multiple times but with at least 7 days in between consecutive visits (to eliminate kill sites) [21]. We also identified additional scrapes in areas not occupied by collared pumas during opportunistic site investigations. To date we have documented 299 community scrapes through field visits, and placed motion-triggered cameras at community scrapes at dispersed sites that appeared to have regular activity. We placed 1 camera at each community scrape, approximately 3 m from the scrape itself. We programmed cameras to record 60 s videos at each trigger with a 1 s delay before becoming active again in order to

maximize recording time. We visited the community scrapes to maintain the cameras every 1–3 months, based on battery type and memory card capacity.

When possible, we identified the individual puma recorded in videos and placed them into demographic classes based on age (mature > 3.5 years or immature < 3.5 years) and sex (male or female). Demographic information, including mass and age, was readily available for collared individuals documented on cameras (n_{male} = 8, n_{female} = 13). We used the mass acquired from the capture closest to the visit, and determined age by measuring gum line recession during capture [23] and adjusting the age in half year increments following the initial capture date. For individuals without collars (n_{male} = 2, n_{female} = 22, $n_{unknown}$ = 4), when possible, we identified sex and age class through the type and position of genitals and external physical characteristics [24,25]. Identifying individuals in species that lack definite markings is often unreliable e.g., [26]. We thus attempted to use what appeared to be unique spotting patterns on the inside of the upper leg or other distinct features including scarring, kinks in their tail, and old injuries [27,28]. In cases where an individual was not readily identifiable we did not use their identity in the statistical analyses. Due to the difficulty in identifying individuals, and our large number of females without collars, data on female visitation rates should be interpreted with caution.

We removed immature pumas and mature females traveling with kittens from our analyses, as they were less regular visitors and tend to act as non-participants in mating behaviours [20]. To ensure spatio-temporally independent samples and minimize pseudo-replication, we pooled the data from cameras placed at community scrapes < 1 km apart. We had one exception where the scrapes were separated by a lake and cliff that, based on GPS data, substantially increased the travel time of pumas. We removed from our analyses any community scrapes we monitored for < 3 months, and excluded any periods with camera malfunctions from our visitation samples. This resulted in 30 distinct community scrape areas monitored during this study.

We monitored these 30 community scrapes for a mean of 501 days ± 38 SE (range 125–791), and watched each video that met our previously listed criteria (676 visits by mature males and 179 visits by mature females traveling without kittens). For each visit, we recorded the date and time, length of visit to the closest second (averaged for pooled samples), and number of scrapes created (averaged for pooled samples). We also recorded events of consorting with pumas of the opposite sex, and behaviours possibly associated with mate selection, including scraping, olfactory investigating, caterwauling, and flehmen response (see Table 1 for definitions).

Statistical analyses

We used program *R* version 3.1.0 [29] for all statistical analyses. In each analysis we considered $p < 0.05$ to represent statistical significance. The data used in these analyses is available using the doi address: doi:10.5061/dryad.6d5h2.

We first tested for differences in visitation between male and female pumas using the 'days until next visit' as our variable, with a mixed-model analyses of variance (ANOVAs) within the *nlme* package [30]. We measured days until next visit as the number of days for the same individual to return to the same community scrape. We compared male visitation to two categories of female visitation, first comparing male visitation to all female visitation. Second, because female visitation occurred in shorter visitation bouts, we compared male visitation to females during their visitation bouts. We defined visitation bouts as repeated visits by an individual female with ≤ 60 days between visits, based on a natural break in the data [31,32]. In our analysis we used days until next visit as our dependent variable, sex of the pumas as the independent

variable, and used the individual puma id as a random effect to account for variation among individuals.

Based on GPS location data, we estimated 95% local convex hull (LoCoH) home ranges [33] using the LoCoH tool in ArcMap (v. 10.1, ESRI, 2012). We separated locations into two yearly monitoring periods (from July 2011-June 2012 and July 2012-June 2013), and included any collared adult puma with a minimum of three months of monitoring during a given period, resulting in a mean of 1120 points (± 107 SE) to calculate each home range. We then documented each foray outside of the 95% home range during each monitoring period, where we considered a foray to be the presence of 2 or more continuous GPS locations $>$ 1 km outside of the yearly 95% LoCoH home range ($mean_{female}$ = 37.9 km^2 ± 3.3 SE, $mean_{male}$ = 115.7 km^2 ± 13.2 SE). We used a two-tailed t-test assuming equal variances to test for differences between male and female pumas, after first testing the data for normality and homoscedasticity. Finally, we determined the number of male pumas each female overlapped with during each annual monitoring period using the 95% LoCoH home ranges.

We determined which male characteristics and behaviours best predicted being selected as a mate by female pumas. We compared variables of behaviours exhibited during visitation (total number of scrapes created, mean number of scrapes created per visit, number of visits, and mean duration of visits) and physical characteristics (mass during most recent capture, and age) between two different time periods: during female visitation bouts to determine what is important while a female is actively selecting a mate, and in the 90 days previous to the consorting to determine the potential role of advertisement and other aspects prior to female arrival. We choose a 90-day period prior to mating as it coincides with the known gestation duration of pumas [8]. We included all females that consorted with $\geq$1 male in the analysis. We defined consorting as traveling with a male (n = 16) (S3 Video) or visiting scrapes within two hours of each other (n = 7) (where we considered it likely that the individuals met despite the event not being captured by our cameras based on associated GPS data). We used whether a male was selected as our dependent variable, and used the visitation behaviour and physical characteristics as our predictor variables. We used a stepwise AIC procedure in the *MASS* package [34] to determine the best model. The combination of all possible variables was used, and in a stepwise process each variable was eliminated until the best model based on AIC scores was arrived at for both time periods.

Results

Patterns in visitation

Visitation by females at community scrapes (S4 Video) occurred in short visitation bouts (n = 40) or single visits (n = 28). Visitation bouts had a mean duration of 31.8 (± 5.1 SE) days, and included a mean of 3.7 (± 0.4 SE) visits per bout. Females had a mean of 11.8 (± 1.5 SE) days between visits during a given visitation bout. The visitation bouts of females occurred throughout the year, and were separated by large gaps in time (mean = 367 ± 62 SE days).

Mature male and female pumas varied in their patterns of visitation to community scrapes. In contrast to females, visitation by males at community scrapes (S5 Video) was characterized by regular visits throughout monitoring periods that averaged 17.7 (± 2.1 SE) days between visits. Visitation of females during their visitation bouts was 1.5 times more frequent than male pumas ($F_{1, 650}$ = 13.4, $p < 0.0001$), while male visitation was twice as frequent as females overall (mean = 33.2 days ± 8.9 SE, $F_{1, 657}$ = 2.9, p = 0.0959). In essence, male pumas visited regularly throughout the year, while females visited less frequently overall, but visited more frequently during short visitation bouts.

On three occasions we documented on camera an individual male at a community scrape outside of its 95% LoCoH home range for the first time during a female visitation bout. On these occasions, the males arrived during the visitation bout, and then after the female visitation bout ended the male's visitation to the community scrape decreased in frequency and eventually ended. This suggests that these male pumas moved out of their normal territory to take advantage of the temporal presence of a female pumas in oestrus, who possibly advertised their presence across long distances by caterwauling. We documented females exhibiting caterwauling (S2 Video) during 28.2% of visitation bouts. Our spatial analysis found that males made 6.7 (± 1.3 SE, range 2–12) forays outside of their home range during yearly monitoring periods. This was significantly more than the 2.0 (± 0.4 SE, range 0–5) annual forays made by females ($t_{18} = 4.3$, $p = 0.0004$).

Female mate selection

We documented 23 incidents of consorting with mates (Video 5) by 17 female pumas. Females who consorted with a male selected from a mean of 1.7 (range = 1–3) males based on video data. This was similar to the number of males a female's home range overlapped with; from July 2011 to June 2012 each female monitored with GPS collars overlapped with 1.7 males with GPS collars (range 1–3), and from July 2012 to June 2013 each female monitored with GPS collars overlapped with 2.0 males with GPS collars (range = 0–3) (Fig 2). Of the 17 females we recorded consorting with a male, 2 (12%) consorted with 2 different males during a visitation bout.

All of the males selected of known age (n = 8) were between the ages of 3 to 7 years old. During a female's visitation bout, model selection results suggested that the best model included additive effects of the number of visits, mass and age ($AIC_w = 0.54$), which had more than twice the support of any other models we considered (Table 2). In the time period 90 days before the consorting event, model selection results found that a single predictor variable associated with visits, the total number of scrapes created ($AIC_w = 0.56$), was the best model and performed twice as well as any other model we considered (Table 2).

Discussion

Our objective was to increase our understanding of mate selection strategies used by female pumas based on behaviours we recorded with video cameras at community scrapes and GPS location data that allowed us to consider aspects of the spatial distribution of the population. Our results suggest sex-specific differences in mate selection strategies, with males potentially attempting to mate with every female they encounter and females actively selecting their mates. We found that females varied from males in visitation rates of and behaviours displayed at community scrapes, and appeared to use multiple cues to select mates. These results support previous suggestions that community scrapes effectively function as "billboards" e.g., [8] where individual males advertise their reproductive status and females select from potential mates. Community scrapes thus appear to play an integral role in communication and mate selection in pumas.

Female pumas apparently used multiple cues in their selection of mates, as is common in other mammals [3], and supported our hypothesis that females would select for the dominant resident males. During female visitation bouts, females selected males based on their number of visits, mass, and age. In the period 90 days previous to consorting, the total scrapes made by a male were the most important aspect of that male being selected. These patterns imply that while females prefer larger and older (>3 years) males (which are likely correlated, and an indication of dominance [8,9]), frequent community scrape visitation and scent marking can

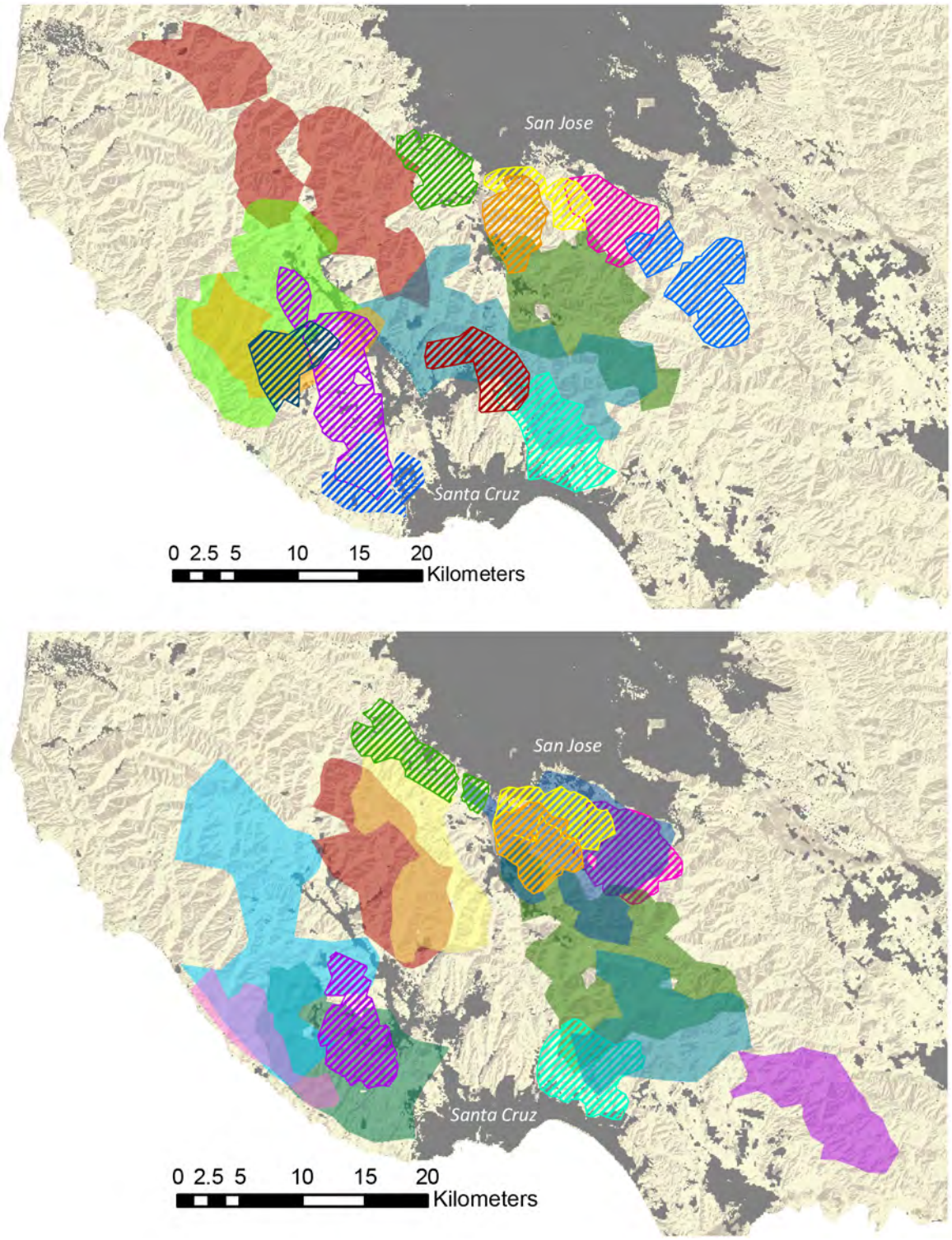

Fig 2. A map showing the overlap among pumas using 95% LoCoH home ranges in the study area. The upper map shows the overlap in our first time period (July 2011 to June 2012), and the lower map shows the overlap in our second time period (July 2012 to June 2013).

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Table 2. Predictors of female mate selection, represented by the best models during the female's visitation bout, and 90 days previous to consorting with males. We determined the best models using combinations of variables[1], and for each model we report the variables of the best model and the C-statistic score, the AIC score, and the AIC_w weight for each of the best 3 models.

Time Period	Model	C	AIC	ΔAIC	AIC_w
During	VSTS + MASS + AGE	0.81	34.5	0	0.54
	VSTS + MDUR + MASS + AGE	0.8	35.8	1.3	0.28
	TSCR + VSTS + MDUR + MASS + AGE	0.8	36.7	2.2	0.18
90 days	TSCR	0.72	32	0	0.56
	TSCR + MDUR	0.81	33.5	1.5	0.27
	TSCR + MDUR + AGE	0.77	35.3	3.3	0.11

[1] TSCR = The total number of scrapes made, MSCR = The mean number of scrapes made, VSTS = The number of visits made, MDUR = The mean duration of visits, MASS = The mass of the male, AGE = The age of the male.

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greatly improve mating opportunities for males. In addition to increasing the probability of an encounter with a female in oestrus, frequent visitation to a community scrape also serves to advertise their residency. The apparent use of these physical and temporal cues during a female's visitation bout suggest that females may evaluate physical characteristics and dominance when selecting mates. The importance of scraping activity prior to consorting events also suggests that females select the resident, and hence dominant, male. The male puma that scrapes the most is likely to be the dominant male in the area, as juvenile pumas rarely scrape [8,20], and it is resident males who most frequently visit and scent mark in a given area. Mating with the dominant male likely reduces the risk of infanticide e.g., [8]. The use of the these multiple cues likely allows females to evaluate mate quality, reduce errors in selecting suboptimal mates, and may also allow for individuals to select traits they deem most important to the survival of their offspring e.g., [3, 35].

Female pumas differed from males in their visitation and mate selection strategies, and appeared to be influenced by a complex set of cues and behaviours at community scrapes. Our results supported our hypothesis, by indicating that although visits to community scrapes by females occurred over the entire year, visits of individuals were likely correlated with oestrus bouts, with frequent visitation occurring over short time periods that potentially overlapped with 2 oestrus cycles (mean = 32 days). Our data for female pumas was predominantly based on individuals without collars, and is hence less exact, but the irregularity in female visitation rates was in contrast to males who regularly visited community scrapes to advertise their presence through scent marking. Scrape visitation was predominately a male activity, and male pumas exhibit vigilance through regular visiting and advertising their presence for prospective mates as well as territorial rivals [8,20]. The use of community scrapes is thus an important mechanism for communication with potential mates in spatially dispersed populations of solitary felids, and could possibly be more important for males to advertise dominance in species with spatially clumped populations.

Female pumas appeared to consort with one of the dominant resident males that overlapped their home range, which were also likely the males they were most familiar with. This highlights the importance of access to females in male territoriality and its role in intraspecific competition. Mass of males is an important adaptation for competition, and is often correlated with age, and hence residency. It is an important competitive advantage in confrontations, as larger males can prevent the access of smaller males to females either through fighting or intimidation. Aggressive disputes are relatively infrequent among resident male felids due to the potential for serious injury [8,36,37], but access to reproductive females may temporarily

outweigh risks associated with interactions with other males [12,37], reinforcing the importance of large mass in male solitary felids.

Although most solitary carnivores regularly visit and scent mark areas to maintain a territory, our findings suggest that attempts to exclude other males through scent marking are apparently not completely successful in spatially dispersed populations. We recorded 3 incidents on video where non-resident males consorted with females that were visiting community scrapes that previously had been used by only one male. Our analyses of forays outside of the home range documented that forays by male pumas are more common than previously thought, and were more frequent than forays by female pumas, supporting our hypothesis. Female pumas caterwauling may be the cause of these incidents of temporary territorial transgressions, as the function of caterwauling (S2 Video) is thought to be to advertise from a distance [8], and is likely a mechanism to alert males to the presence of females to which they would otherwise be unaware. Although we documented caterwauling at 28.2% of female visitation bouts, this is likely an underestimate because our cameras monitored only a small part of the area potentially used by pumas during courtship and mating. It is unknown if female pumas use caterwauling to advertise their presence to all males or a specific individual. Because males continue to scrape while consorting with a female, we expect that females are able to discern between trespassing males and territorial males that had previously been scraping. Therefore, in the instances where females select a trespassing male, the opportunity to increase the genetic diversity of their offspring may be more important than residence or familiarity.

We documented that female pumas are sometimes polyandrous, as we recorded two female pumas consorting with more than one male during visitation bouts (14.2% of the consorting documented). A genetic analysis of kittens in the study area showed a similar pattern with two sires in one of eight litters tested (12.5% of litters) (Wilmers, unpublished data). Other mammals have shown increased reproductive success associated with polyandry [38], and the same may be true of pumas. Sperm competition plays an important role in mate selection in species with confirmed polyandry [9], but there are other adaptive benefits of confusing paternity. Because many male felids, including pumas, frequently kill unrelated kittens in order to induce ovulation in females and increase their own reproductive success, mating with multiple males may decrease the probability of infanticide [8,39,40]. Polyandry also allows for greater genetic diversity in the offspring of the female, limits risk of genetic incompatibility or defects, and increases the survival probability of at least one kitten in the case of resource uncertainty [41].

Supporting Information

S1 Video. Scraping behaviour by a mature male puma.
(MP4)

S2 Video. A subset of a female visit, highlighting caterwauling.
(MP4)

S3 Video. A mature male and mature female consorting at a community scrape.
(MP4)

S4 Video. A female visiting a community scrape.
(MP4)

S5 Video. A typical male visit to a community scrape.
(MP4)

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Author Contributions

Conceived and designed the experiments: MLA CCW HUW. Performed the experiments: MLA PH. Analyzed the data: MLA JS. Contributed reagents/materials/analysis tools: CCW HUW MLA. Wrote the paper: MLA HUW CCW JS PH LME.

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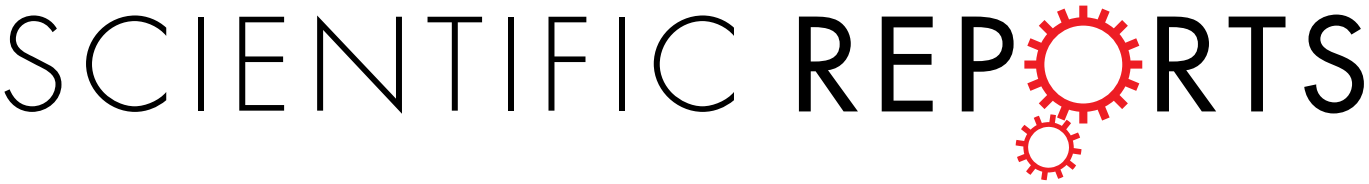

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Evaluating the responses of a territorial solitary carnivore to potential mates and competitors

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Successful communication is critical to the fitness of individuals and maintenance of populations, but less is known regarding the social contexts and reactions to scent marking by other individuals in solitary carnivores, including pumas. We evaluated the responses of resident male pumas to visitation and scent marking by potential competitors (other male pumas) and potential mates (female pumas) by capturing and marking 46 pumas (*Puma concolor*), and documenting scent marking behaviours using motion-triggered video cameras. By comparing resident male puma visitation rates and communication behaviours in response to either male or female visitors, we found that their visitation and communication behaviours were best explained by the combination of visitation by both competitors and potential mates. Resident males returned to scent marking sites more quickly and increased their rate of flehmen response after visitation by a females, while they increased their rate of visitation and duration of visits in response to other males. Male pumas also visited less frequently in summer and autumn when female visitation rates were lower, but males created nearly twice as many scrapes during these visits. This study suggests that advertising for mates when scent marking may sometimes overshadow the importance of deterring competitors and claiming territory.

Communication is an integral element of animal behaviour, and scent marking is one of the most frequent forms of communication for many mammal species. As secondary sexual characteristics, scent marks are considered reliable indicators of an individual's health and viability as a mate[1,2]. Due to their spatially dispersed populations, solitary carnivores rely on scent marking as an indirect method of conspecific communication (e.g. ref. 3–6). The predominance of communication via scent marking has led to many explanations regarding the function of this behaviour in solitary carnivores. The main functions are thought to include asserting dominance[7,8], selecting mates[4,9,10], and maintaining territories[3,11–13]. Scent marking may also be used to determine the identity and relatedness of individuals[14], to mark and defend food resources[15,16], and to possibly avoid infanticide[6]. Given the many different purposes attributed to scent marking, understanding the dynamics influencing this behaviour will help us understand its use in social contexts.

The two most important functions of scent marking in solitary carnivores may be to advertise their reproductive status to potential mates and to assert dominance and maintain territories over their competitors. For solitary carnivore species with a defined breeding season, scent marking increases during the breeding season[4,5,11,17], which suggests that scent marking plays an important role in advertising for potential mates. However, scent marking also occurs throughout the year[3,4,6,12,18], suggesting it has an on-going role in maintaining territories, and may therefore play an essential role in social organization stability. Many communication systems, including among solitary carnivores, are mark-countermark systems, whereby one individual marks, and another then marks in response[3,12]. The infrequency of encounters among solitary carnivores makes it more likely for individuals to respond when they come across intraspecific communication attempts, whether through investigation, scent marking, or another response. The utilities of scent marking in solitary carnivores could be further understood by determining how they respond to competitors and potential mates.

In contrast to the majority of carnivore species, many large felids breed throughout the year[17,18]. This makes them ideal species to discern the relative importance between scent marking purposes, including whether individuals react more strongly to visitation and scent marking by potential mates or by potential competitors. Like other solitary felids, pumas are territorial[18,19], and communicate most frequently through scent marking[18,20,21].

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Male pumas actively compete for territories that encompass resources, including access to potential mates, and scent mark throughout their territories[19]. Some puma populations, including in our area, show a birth pulse in summer[22], with a related peak in mating season in late winter or spring.

The most frequent form of scent marking by pumas is scraping[18,20,21] (Supplementary Video 1), which is concentrated in areas called 'community scrapes' (e.g. ref. 20) or 'shared scrapes' (e.g. ref. 18). We use the term 'community scrapes' hereafter. These are defined as a location in which multiple pumas create scrapes in a small area ($\geq$3 scrapes in 9 m^2) that is not associated with a kill or resting site[20]. Male visitation and scent marking at community scrapes occurs regularly throughout the year[10,18]. In contrast, female visitation occurs in short bouts of activity that can be at any time of the year, which most likely correlate with breeding and estrus[10,18]. Pumas also exhibit other communication behaviours at community scrapes such as olfactory investigation (Supplementary Video 2), the flehmen response (Supplementary Video 3), body rubbing (Supplementary Video 4), and caterwauling or other vocalizations (e.g. ref. 10,20,21,23). Little research has been conducted as to which stimuli elicit communication behaviours, or how these behaviours and their frequency are affected by interactions with potential mates and competitors.

We monitored a puma population with 46 marked individuals from 2011–2014 in order to better understand how male pumas respond to visitation and scent marking by male competitors and potential female mates. We deployed motion-triggered video cameras at community scrapes to record communication behaviours. Our specific objectives were to: 1) determine whether seasonal variation occurred in visitation and scent marking of male pumas at community scrapes. We hypothesized that if visitation and scent marking were based on competitors they would not vary throughout the year, while if they were based on potential mates than visitation rates would be most frequent and the most scrapes would be created in spring to coincide with the perceived peak in the mating season. 2) Determine how male visitation and behaviours changed in response to visitation by possible mates and competitors. We hypothesized that male pumas would visit and exhibit behaviours more frequently after a recent visit by both potential mates and competitors. Additionally, we hypothesized that if potential mates drive male communication, their visitation and display of behaviours would increase in response to visitation by potential mates rather than to visitation by competitors. 3) Determine whether male pumas display stronger responses to visitation by potential mates, competitors, or whether it is a combination of both. We hypothesized that while visitation and scent marking is likely affected by the combination of both, the function of visitation and scent marking may be more affected by potential mates, as they may be the rarest resource in a male's territory.

Results

We monitored 28 community scrape areas for a mean of 596 ($\pm$45 SE) days. We recorded 724 visits by mature males, and 198 visits by mature females traveling without cubs. We used the 533 visits by the 11 known (collared) mature males in our analyses.

Seasonal Variation in Visitation. Male visitation behaviours varied among seasons; including the days until next visit ($F_{3, 445} = 3.17$, $p = 0.02$), the number of scrapes created ($F_{3, 519} = 5.60$, $p < 0.01$), and the duration of visits ($F_{3, 519} = 3.00$, $p = 0.03$). The days until next visit for males in spring was nearly 2 times more frequent than in summer ($p = 0.01$) (Fig. 1a). In summer, males created 35% more scrapes than in spring ($p = 0.02$), and 30% more than in winter ($p = 0.01$). In autumn, males created 13% more scrapes than in spring ($p = 0.04$) and 9% more than in winter ($p = 0.01$) (Fig. 1b). The duration of male visits in summer was 25% longer than in spring ($p = 0.05$), and marginally longer than in winter (19%, $p = 0.08$) (Fig. 1c).

A post hoc test showed that the seasonal mean for days until next visit had strong inverse correlations with both the number of scrapes made during visits ($r^2_{1, 3} = 0.94$, $p < 0.01$), and visit duration ($r^2_{1, 3} = 0.93$, $p = 0.04$). The inverse relationship between the number of scrapes created and days between visits suggests that male pumas create more scrapes during seasons with less frequent visitation (Fig. 2). The inverse relationship between the visit duration and days between visits suggests that males spend longer durations at the scrape during seasons with less frequent visitation.

Influences on male visitation and behaviours. Male days until next visit and visit duration increased in response to visitation by other pumas, while their number of scrapes created did note vary significantly (Table 1). The mean time between visits for male pumas was 37% more frequent when another male was present within 28 days ($F_{1, 447} = 12.09$, $p < 0.01$), and 34% more frequent when another male was present within 7 days ($F_{1, 447} = 7.34$, $p = 0.01$). The mean time between visits for males was 29% more frequent when a female was present within 28 days ($F_{1, 447} = 18.80$, $p < 0.01$), and also 29% more frequent when a female was present within 7 days ($F_{1, 447} = 15.68$, $p < 0.01$). Duration of visit was significantly influenced by visits within 7 days by other males, increasing by 31% when another male was present ($F_{1, 455} = 4.33$, $p = 0.04$), but females did not have a significant effect (Table 1). The responses of male pumas to visitation by competitors and potential mates suggest that both are important driving factors in their visitation.

For the display of behaviours, the display of flehmen response and body rubbing increased significantly in response to visitation by other pumas, while scraping and olfactory investigation did not (Table 2). Flehmen response increased in response to female visitation in both time periods, increasing by 9.4% when a female was present in the previous 28 days ($X^2_{1, 463} = 11.37$, $p < 0.01$, $phi = 0.17$), and by 13.1% when a female was present in the previous 7 days ($X^2_{1, 463} = 14.74$, $p < 0.01$, $phi = 0.19$). Flehmen response also increased 8.3% in response to male visitation in the previous 7 days ($X^2_{1, 463} = 5.29$, $p = 0.02$, $phi = 0.12$). Body rubbing increased 9.8% in response to male visitation in the previous 28 days ($X^2_{1, 463} = 10.52$, $p < 0.01$, $phi = 0.16$), but was not significantly influenced by visits by females (Table 2).

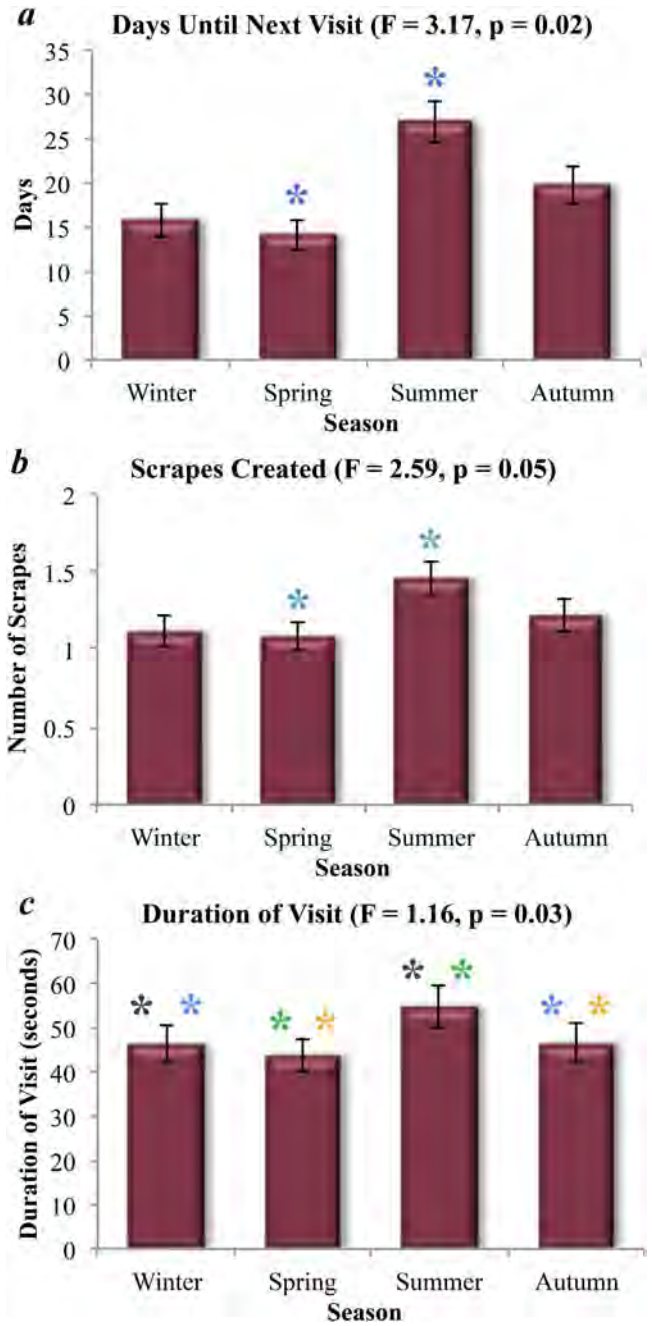

Figure 1. The seasonal means for 3 aspects of male puma behaviour: days until next visit (*a*), number of scrapes created (*b*), and duration of visit (*c*). For each behaviour we report the mean, the standard error represented as error bars, as well as the F score and p-values from our ANOVA, and significant differences from our post hoc Tukey HSD tests with asterisks of the same colour.

Comparative effects of competitors and potential mates. We compared the potential influences on days until next visit, the visit duration, body rubbing and the display of flehmen response by male pumas. Among the five models we tested, the model combining female and male visitation was the clearly the top model for all the variables we tested; all other models were implausible (Table 3). These top models supported our hypothesis that both competitors and potential mates were important drivers of male puma behaviour.

Discussion

Due to their spatially dispersed populations, scent marking is an important mechanism for communicating with potential mates and competitors among solitary carnivores. We analysed the use of scent marking behaviours at community scrapes by male pumas to determine whether they exhibited stronger reactions through visitation or communication behaviours to either potential mates or by competitors. Our results support previous theory that has suggested that scent marking is multi-purpose and used for both competitors and potential mates. Based on

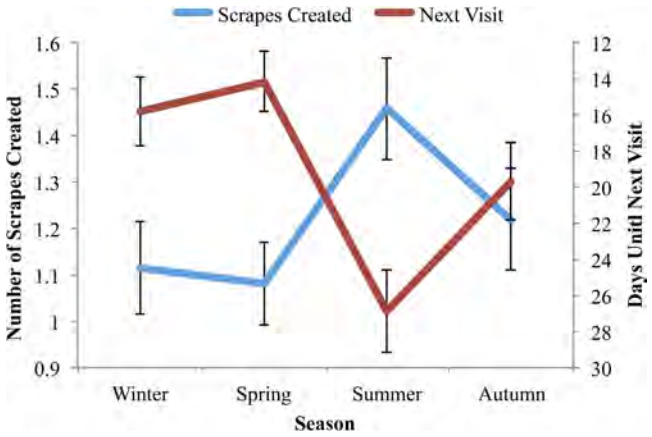

Figure 2. The days until next visit and scrapes created by male pumas during each season. Each variable is represented as its mean value for the season, with error bars representing the standard error. The values have a significant inverse relationship, suggesting that male pumas create more scrapes in seasons with less frequent visits.

Variable	Sex	Days	Mean (±SE)		*F*	*p*	*d*
			Present	Not Present			
Days Until Next Visit	Male	28	13.1 (2.1)	20.8 (1.3)	12.09	**<0.01**	0.32
		7	12.8 (2.5)	19.4 (1.3)	7.34	**0.01**	0.32
	Female	28	14.0 (2.2)	19.8 (1.2)	18.80	**<0.01**	0.42
		7	13.6 (2.6)	19.1 (1.2)	15.68	**<0.01**	0.49
Scrapes Created	Male	28	1.46 (0.12)	1.23 (0.15)	2.53	0.11	0.16
		7	1.54 (0.14)	1.26 (0.15)	2.23	0.14	0.18
	Female	28	1.25 (0.12)	1.34 (0.16)	0.01	0.95	0.01
		7	1.20 (0.14)	1.33 (0.16)	0.03	0.87	0.02
Duration of Visit	Male	28	58.2 (5.1)	48.0 (5.3)	1.44	0.23	0.12
		7	63.7 (6.2)	48.8 (5.2)	4.33	**0.04**	0.25
	Female	28	53.6 (5.0)	50.7 (5.8)	2.35	0.13	0.15
		7	56.4 (6.0)	50.4 (5.7)	1.92	0.17	0.17

Table 1. The influences of visitation by male and female pumas on visitation behaviours of male pumas. Visitation behaviour variables include the days until next visit, the number of scrapes created, and duration of visit (in seconds). We tested the influence of whether females and other males had been present in two time periods: the previous month (28 days) and the previous week (7 days). We report the mean, standard error, p-value (significant values in bold), and effect size as Cohen's d scores.

visitation to community scrapes, we found that potential mates sometimes created a stronger response than competitors for male pumas. The best model explaining male puma visitation and scent marking behaviours, however, was the combination of potential mates and competitors. We also found seasonal variation in both visitation and the number of scrapes created by male pumas, and this may be due to the seasonal visitation patterns of female pumas.

The combination of potential mates and competitors was clearly the best explanatory model for each variable we tested. Solitary carnivores rely upon scent marking for intraspecific communication; including scent marking to advertise for potential mates[4,9,10], and demonstrating the use of an area to maintain territories from competitors[3,11–13,18]. Our results suggest that scent marking is used for multiple purposes, but our results suggest there may be differences in how male pumas react to visits by potential mates and competitors. Future research to determine how potential mates and competitors affect the functional use of scent marking could increase our understanding of behavioural ecology.

Female pumas are less frequent visitors to community scrapes[10], and we found that when females visit, male pumas show a larger increase in their visitation rate than they do for male puma visits. Male solitary carnivores often compete for territories with food, mates, and other resources, but spatial and temporal unpredictability may make potential mates the most limited resource for which males compete (e.g. ref. 24). Female pumas can be in estrus at any time of year, and likely visit community scrapes at these times in search of breeding opportunities[10,18]. Female pumas often select the males that visit most frequently to breed with[10], making it important for a male to be the dominant resident in order to maximize his exposure to community scrapes when a receptive female is present. Scent marking to define a territory may be helpful for many resources, but complete exclusion is seldom achieved[10]. Since the currency for winning the ultimate evolutionary game is successfully producing offspring, securing potential mates could be a more important reason for holding a territory than food or other resources.

Behavior	Sex	Days	%Displayed		X^2	p	phi
			Present	Absent			
Scraping	Male	28	81.5%	76.1%	1.47	0.23	0.06
		7	81.5%	77.2%	0.49	0.49	0.04
	Female	28	77.1%	78.3%	0.03	0.86	0.01
		7	76.7%	78.2%	0.02	0.88	0.01
Body Rubbing	Male	28	15.9%	6.1%	10.52	**<0.01**	0.16
		7	12.3%	8.8%	0.61	0.43	0.05
	Female	28	6.9%	10.5%	1.11	0.29	0.06
		7	5.8%	10.2%	1.13	0.29	0.06
Investigating	Male	28	89.8%	88.7%	0.04	0.84	0.02
		7	91.4%	88.6%	0.28	0.60	0.03
	Female	28	90.3%	88.5%	0.16	0.69	0.03
		7	88.4%	89.2%	0.01	0.97	0.10
Flehmen Response	Male	28	10.8%	6.5%	2.17	0.14	0.08
		7	14.8%	6.5%	5.29	**0.02**	0.12
	Female	28	14.6%	5.0%	11.37	**<0.01**	0.17
		7	18.6%	5.5%	14.74	**<0.01**	0.19

Table 2. The influences of visitation by male and female pumas on the display of four behaviours (scraping, body rubbing, investigating, and flehmen response) by male pumas. We tested the influence of females and other males in two time periods, whether the other puma had been present in the previous month (28 days) and if they had been present in the previous week (7 days). For each behaviour we report the percent of visits where the behaviours were displayed, the p-value, and an effect size as *phi* coefficients.

Variable	Model	AIC	ΔAIC	AIC_w
Days Until Next Visit	Male* Female* Season	141.44	10.05	0.01
	Male + Female + Season	137.95	6.56	0.04
	Male + Female	131.39	0.00	**0.95**
	Female* Season	341.63	210.24	0.00
	Female	319.76	188.37	0.00
	Male	358.10	226.71	0.00
Duration Of Visit	Male* Female* Season	88.76	27.32	0.00
	Male + Female + Season	71.13	9.69	0.01
	Male + Female	61.44	0.00	**0.99**
	Female* Season	160.88	99.44	0.00
	Female	136.70	75.26	0.00
	Male	198.53	137.09	0.00
Exhibiting Body Rubbing	Male* Female* Season	66.56	11.84	0.00
	Male + Female + Season	69.77	15.05	0.00
	Male + Female	54.72	0.00	**1.00**
	Female* Season	140.33	85.61	0.00
	Female	132.61	77.89	0.00
	Male	176.14	121.42	0.00
Exhibiting Flehmen Response	Male* Female* Season	50.23	5.28	0.06
	Male + Female + Season	49.46	4.51	0.09
	Male + Female	44.95	0.00	**0.85**
	Female* Season	119.76	74.81	0.00
	Female	122.74	77.79	0.00
	Male	165.88	120.93	0.00

Table 3. AIC models comparing the influences on the visitation and behaviours of male pumas. Variables include the days until next visit (in days), and duration of visit (in seconds), and whether they displayed body rubbing, and the flehmen response. For each variable, we first tested five models to determine which was the best explanatory model, and then tested just male visitation versus female visitation. For each model we report the components of each model, the AIC score, the ΔAIC score, and the AIC weight (AIC_w).

Contrary to our hypothesis, the number of scrapes created during a visit was apparently not a direct response to either potential mates or competitors. Instead, the number of scrapes created was inversely correlated with

visitation, as male pumas created more scrapes during seasons when they visited less frequently. Scent marking is used in some species as a secondary sexual signal to advertise an individual's health and viability as a mate[1,2]. In pumas, frequent visitation and scent marking, as a sign of dominance and territory ownership, is an important aspect of mate selection[10]. The increased number of scrapes could be a dishonest signalling behaviour (e.g. ref. 25) to over-represent their visitation and compensate for less frequent visitation during these seasons. By creating more scrapes during seasons with less frequent visitation, male pumas may be able to over-represent their actual visitation for mates, and therefore increase their chances of reproductive success. The greater number of scrapes were also created during the seasons with the hottest seasons, and male pumas may also be leaving more scent to compensate for it drying out. However, this does not explain why visitation is less frequent during these seasons. The seasonal changes in visitation may impact other aspects of puma ecology. For example, many male mammals lose weight during the breeding season because they prioritize securing mating opportunities over acquiring food[26,27]. Once the breeding season has past, individuals increase their foraging rate to recoup lost energy stores. We see similar shifts in puma foraging ecology where pumas in California increase their kill rates in summer and autumn[28]. If the same pattern applies to pumas, they may compensate for periods with lower energy acquisition by spending summer and autumn hunting more frequently, and visiting scrapes less frequently as an energy-saving measure.

In a social context it may be important to distinguish between the functional purposes of scent marking from the proximate frequency of scent marking. A key aspect of scent marking is for defining territories[3,11,12], but the frequency with which a male must scent mark for maintaining boundaries is yet unknown. Scrapes are a combination of two forms of scent marking, with a physical scrape to help other pumas locate the scent, and urine to convey their messages[20]. Urine is also composed of multiple elements, including pheromones, and it is unknown how frequently the separate components need to be refreshed in order to attract mates. This may be a factor that necessitates the frequent visitation and scraping to community scrapes, with increases in visitation in the seasons when females are most likely to be present.

Visitation and the behaviours displayed by males were influenced by visitation of both females (visitation rate and flehmen response) and other males (visitation rate, duration of visits, flehmen response, and body rubbing). The strongest response, as measured by effect size, was in how quickly a male returned after a female visited ($d = 0.49$). Male pumas also increased their display of flehmen response after visitation by potential mates and competitors, which likely enables the male to investigate fresh scent more thoroughly. Males only exhibited more frequent body rubbing when another male was present within 28 days. It may be that body rubbing deposits scent in either larger quantities or in a way that persists longer in the environment. It may be effective in exhibiting their long-term presence to other males for territorial purposes, but may have limited utility to advertise for mate selection by females due to a lack of pheromones (e.g. ref. 29). Alternatively, body rubbing may disrupt or dampen the signals left by other males.

Methods

Study Area. Our study area encompassed 1,700 km^2 in the Santa Cruz Mountains of California, including parts of Santa Cruz, San Mateo, and Santa Clara counties (Fig. 3). The boundaries of the study area included the Pacific Ocean to the west, Highway 84 and the city of San Jose to the north, the city of Santa Cruz to the south, and Highway 101 to the east. The highways and cities, including California Highway 17 that bisected the study area, were a major source of mortality for pumas in our study[30], and also acted as barriers to movement; hence, these sites often formed the edges of puma home ranges. Vegetation characteristics and climatic conditions in the study area are classified as Mediterranean and have been described in detail elsewhere[30].

Field Methods. We monitored puma behaviour at community scrapes between May 2011 and January 2014 using motion-triggered video cameras with infrared flash (Bushnell TrophyCam model and TrophyCam HD model, Overland Park, KS). We initially found community scrapes by searching prominent landscape features and areas commonly used by pumas. We then developed a custom algorithm based on our algorithm for identifying kill sites with GPS data[30]. The algorithms identified potential community scrapes by locating clusters of $\geq$3 GPS locations where the locations were recorded more than 7 days apart from each other[30]. We documented 299 community scrapes during field investigations, and placed cameras at active community scrape sites. We programmed cameras to record a 60 s video for each time the camera was triggered, with a 1 s refractory period. To ensure spatially independent samples and also to avoid pseudo-replication, we pooled the data from cameras placed at community scrapes $<$1 km apart, except in cases where two scrapes were separated by a substantial travel barrier (e.g. an impassable ravine, river, etc.). We excluded any periods with camera malfunctions from our visitation samples.

Concurrent with camera deployment, we captured and placed GPS-enabled collars with unique visual identifiers on 46 pumas, and the capture methods we used are described in detail elsewhere[30]. All animal capture and handling, and experimental procedures were carried out in accordance with approved guidelines from the Independent Animal Care and Use Committee at the University of California, Santa Cruz (Protocols Wilmc0709 and Wilmc1101). When possible, we identified the individual pumas recorded in videos using unique collar identifiers, and subsequently placed the pumas into age and sex classes as: mature male, mature female, immature male, or immature female. For individuals without collars we determined the sex from visible characteristics including the position of the genitals. We removed immature pumas and mature females traveling with kittens from our analyses, as they tend to act as non-participants in mating behaviours[20].

We quantified aspects of each video that met our qualifications, including the date and time, duration of visit to the closest second (averaged for pooled samples), and number of scrapes created (averaged for pooled samples). We also documented whether behaviours associated with intraspecific communication were displayed, including:

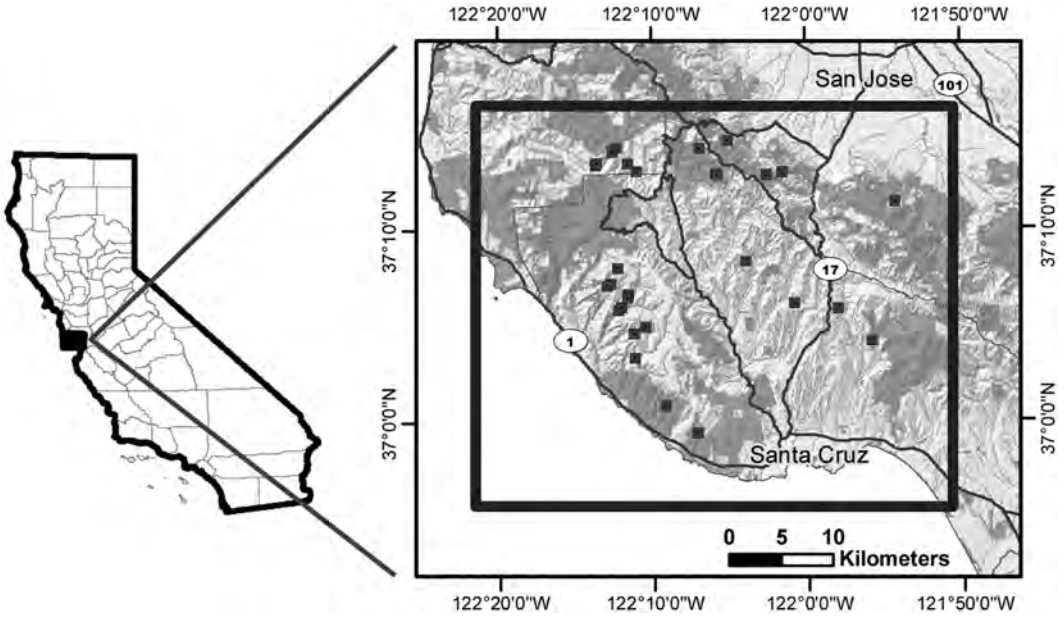

Figure 3. A map of the study area, created using ArcGIS (v. 10.1, ESRI, 2012, http://www.esri.com), which included areas in Santa Cruz, San Mateo, and Santa Clara Counties in California. The study area is outlined by the thick black line, within the greater context of major highways, and the cities of Santa Cruz and San Jose, and the location of each community scrape area monitored is noted.

scraping (where the puma clawed in substrate with their hind feet and then sometimes urinated and/or defecated on the scraped mound of material; Supplementary Video 1), olfactory investigation (where the puma used its olfactory sense to investigate cues and signals, as noted by the pumas nose within one head length of a scrape or other cue; Supplementary Video 2), flehmen response (where the puma picked up its head and curled back its upper lip, sometimes arching its neck backwards, in order to expose its vomeronasal organ; Supplementary Video 3), and body rubbing (where the puma rubbed its cheek or shoulder on the ground or an object, or rolled back and forth on the ground; Supplementary Video 4).

Statistical Analyses. We used program *R* version 3.1.3[31] for all statistical analyses, and following *R* guidelines we cited any associated packages used in analyses. In each analysis, we considered $p \leq 0.05$ significant.

We wanted to determine whether seasonal variation occurred in visitation and scent marking of male pumas at community scrapes. We used mixed model analyses of variance (ANOVAs) to test for variation among seasons for 3 behaviours: 'days until next visit', 'number of scrapes created per visit', and the 'duration of visit'. We first tested each data set for normality with a Shapiro-Wilk test and for variance equality with a Levene's test[32]. Each data set lacked normality, and we therefore log transformed the data to meet the assumptions of the ANOVA, and then performed the ANOVA using the *nlme* package[33]. We used each of the behaviour variables as our dependent variables in the models, used season (based on the calendar year) as our fixed predictor variable, and included puma identity as a random effect to account for variation among individuals. When we found significant differences we used a post hoc Tukey's HSD test[32] using the *multcomp* package[34] to determine where the significant differences occurred. We then performed post hoc analyses to determine whether the 'days until next visit' by male pumas was correlated with either the 'number of scrapes created per visit' or the 'duration of visit' among different seasons. In each analysis we used the seasonal means of each variable to perform linear regressions.

Next, we wanted to determine how male visitation and behaviours were influenced by the visitation of possible mates and competitors. First, we determined the influence of visitation by potential mates (females) and competitors (other males) for three aspects of visitation for male pumas: 'days until next visit', 'number of scrapes created per visit', and the 'duration of visit'. We modelled each of the variables using a mixed model ANOVA, using the *nlme* package[33]. We used the behaviour variables as our dependent variables in the models, used a categorical predictor of presence or absence of other pumas (first other males, then females) for two time periods: one month (28 days) and one week (7 days) as our fixed predictor variable, and included the individual puma as random effects. We then calculated post hoc effect sizes using Cohen's *d* score, and considered scores of 0.20 small effects, 0.50 medium effects, and 0.80 large effects[35]. Second, we determined the influence of recent visitation by potential mates and competitors on the display of four communication behaviours of male pumas: 'scraping', 'olfactory investigation', 'flehmen response', and 'body rubbing'. We compared the proportion of visits each behaviour was displayed based on the presence of other pumas (first other males, then females) in the previous month using a chi-square test[32]. We then calculated post hoc effect sizes for each behaviour by calculating *phi* coefficients, using the *vcd* package[36]. We considered scores of 0.10 small effects, 0.30 medium effects, and 0.50 large effects[35].

Last, we used model selection to determine whether male pumas display stronger responses to the visitation of a) potential mates, b) competitors, or c) a combination of both. We considered six models that included various

permutations of male and female activity and season (Table 3). We used these models for each of the variables that we found to have a significant relationship in at least one time period (days until next visit, duration of visit, display of body rubbing, display of flehmen response). For our two continuous data sets (days until next visits and the duration of visit) we used a mixed model linear regression, after first log transforming the data to meet the assumptions of the test. For our 2 binomial data sets (display of body rubbing and flehmen response) we used a Generalized Linear Model with a binomial distribution and a logit link. We used the visitation and behaviour variables as our dependent variables in the models, the number of days since the last visit by male and female pumas as our fixed predictor variable, and the identity of the individual male puma as a random effect. Because the behaviours of male pumas are likely to be only influenced by relatively recent visits, we set our cut off for visits by other pumas at 50 days, roughly 3 times the mean 17.7 days between visits for male pumas[10].

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Author Contributions

M.L.A. and C.C.W. conceived and designed the experiments. M.L.A. performed the experiments and statistical analyses. C.C.W. and M.L.A. acquired funding for the project. M.L.A., V.Y. and C.C.W. wrote and revised the manuscript.

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THE CARBON BUDGET IMPACT OF SAGEBRUSH DEGRADATION

by

Andrew Connor Austreng

A thesis

submitted in partial fulfillment

of the requirements for the degree of

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ABSTRACT

More than 20,000 km^2 of sagebrush (*Artemesia* spp.) ecosystems within the Great Basin have been replaced, often following wildfire, by the nonnative winter annual cheatgrass (*Bromus tectorum*). At a field site in the central Snake River Plain of southern Idaho, the impact of this invasion on the soil carbon (C) reservoir has been evaluated and the potential soil C benefits of bunchgrass (*Agropyron cristatum*) seeding was assessed. Using a large soil C dataset (n = 850), differences in total organic carbon and root biomass were quantified in immediately-adjacent sagebrush, cheatgrass, and bunchgrass communities. Statistical significance was determined by employment of nonparametric analysis using bootstrap resampling and the two-population Kolmogrov-Smirnov test for statistical significance. Replacement of sagebrush by cheatgrass following fire has resulted in a 50% loss in below-ground carbon (56 to 29 Mg C ha^{-1}, over a 27 yr period), with decreased root-C accounting for 20% of the total below-ground carbon loss. Bunchgrass seeding immediately following the fire reduced the amount of C lost to sagebrush degradation by 30% (31 vs. 40 Mg C ha^{-1}). There is a positive relationship between above-ground biomass and below-ground soil carbon, however C loss is an order of magnitude greater in below-ground compared to above-ground C pools (27 vs. 3 Mg ha^{-1}). Observed changes in soil structure, in particular the loss of large soil aggregates, and altered soil moisture conditions may contribute to the observed soil carbon loss. Extension of these results to the entire Great Basin, suggest the total below-

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LIST OF ABBREVIATIONS

C	Carbon
TC	Total Below-ground Carbon
TOC	Total Below-ground Organic Carbon
TIC	Total Below-ground Inorganic Carbon
SOC	Soil Organic Carbon
R_b	Below-ground Root Biomass
TN	Total Nitrogen
K-S test	Two-population Kolmogrov-Smirnov Test for Significant Difference
BREB	Bowen Ratio Energy Balance
POM	Particulate Organic Matter
SOM	Soil Organic Matter
AM Fungi	Vesicular Arbuscular Mycorrhizal Fungi
O-	Occluded in Macroaggregates

CHAPTER ONE: INTRODUCTION

1.1 Degradation and Reclamation of the Sagebrush-steppe Ecosystem

The sagebrush-steppe ecosystem (*Artemisia* spp.) is one of the most expansive in the U.S., covering approximately 480,000 km^2 and distributed across 13 states (Connelly, Knick, Schroeder, & Stiver, 2004). Healthy sagebrush-steppe ecosystems (sagebrush) are important social and economic resources that support a diversity of wildlife and livestock grazing (Mack et al. 2000). However, during the last century sagebrush-steppe communities of the Great Basin and elsewhere have been dramatically affected by climate change and anthropogenic activities where, often following wildfire or other disturbance, invasion by the nonnative winter annual, cheatgrass (*Bromus tectorum*), is widely observed (Bradley 2009). Cheatgrass invasion reduces ecosystem function by diminishing resources such as livestock grazing and wildlife diversity. This ecological shift is challenging to remediate because, once established, cheatgrass is more fire prone, limiting the ability of more slow growing sagebrush to compete (DiTomaso 2000). Accordingly, cheatgrass infestation has been a cause of ecosystem degradation throughout the Intermountain West, specifically within the Great Basin (Bradley 2009; Connelly et al. 2004). A qualitative survey conducted by the U. S. Bureau of Land Management (BLM) in 1991 that spanned 400,000 km^2 (Idaho, Oregon, Nevada, Utah, Washington), estimated that cheatgrass has displaced over 11,000 $km^2$of sagebrush habitat and become a major understory component in a further 57,000 km^2 of BLM-managed public lands (Pellant 1994). More recently, Bradley & Mustard (2005) analyzed

satellite imagery and mapped over 20,000 km^2 of cheatgrass monocultures within the Great basin, whereas Bradley (2009) mapped 760,000 km^2 of land in the western U.S. at risk of cheatgrass invasion under current climatic conditions.

One promising solution to cheatgrass degradation of sagebrush ecosystems involves introducing species other than sagebrush that are more effective competitors (M. Pellant, 2010, personal communication). One such strategy that has shown success is seeding certain bunchgrass species such as Crested Wheatgrass (*Agropyron cristatum*) either immediately following fire or after active removal of cheatgrass. Once bunchgrass is established, it may then be possible to reintroduce sagebrush (M. Pellant, 2010, personal communication).

The goal of this research was to quantify changes in below-ground carbon storage associated with: (1) cheatgrass degradation of sagebrush ecosystems and (2) cheatgrass remediation via bunchgrass seeding. This was done in an effort to provide the framework for a long-term approach to mitigate CO_2 emissions while simultaneously improving the health of cheatgrass-degraded sagebrush ecosystems.

1.2 Previous Research

1.2.1 The Soil Carbon Reservoir: Functional Pools and the Influence of Vegetation

There are large differences in the physiology of plant species, implying that a change in species dominance can greatly affect the degree to which carbon (C) is introduced and retained in soils. Consequently, a shift in the dominant plant life form can alter the size and nature of the underlying soil C reservoir. Such physiological shifts are apparent in plant communities that represent degradation and improvement of disturbed

sagebrush (cheatgrass and bunchgrass, respectively), where senescence of cheatgrass, bunchgrass, and sagebrush occurs in late spring, early summer, and late summer, respectively. Cheatgrass allocates much of its resources to seed and shoot production while generating a dense and shallow root system (Upadhaya, Turkington, & McIlride 1986), whereas sagebrush and bunchgrass dedicate more resources to producing deeply penetrating perennial root systems (Caldwell, White, Moore, & Camp 1977; Dahlman & Kucera 1965; Hooker et al. 2008). These differences reflect the timing and duration of CO_2 fixation, as well as the allocation of that carbon, and thus the size of the soil C reservoir.

Carbon derived from living and dead roots is extremely important to below-ground C fluxes (Jackson, Mooney, & Schulze 1997). Living roots contribute carbon in the form of sugars and organic acids through rhizodeposition, whereas dead roots are incorporated into the soil matrix by bacterial decomposition (Stevensen 1994). Roots tend to be more resistant to decomposition than above-ground litter because of high lignin content (Lorenz & Lal 2005) and, consequently, increased root input promotes C storage. In addition, some researchers have documented variability in root turnover rates with depth (Gill, Burke, Milchunas, & Lauenroth 1999; Ares 1976; Dahlman & Kucera 1965); this is an important distinction because the residence time of root-derived C may vary with depth due to changing soil temperature and moisture regimes (Gill, Burke, Milchunas, & Lauenroth 2002).

Carbon respiration is equally critical in determining the size of the soil C reservoir and can be largely influenced by vegetation (Lorenz & Lal 2005). Both the composition and timing of inputs for above- and below-ground material are important to carbon

mineralization rates. Similarly, higher soil moisture and temperature can enhance respiration rates while being influenced by vegetation (Wedin & Tilman 1990, Gill et al. 1999).

There are specific functional pools within the soil C reservoir, each having unique dynamics and residence times (Lorenz & Lal 2005; Christensen 1992; Stevensen 1994; Gill & Burke 1999). An accurate description of the C budget impact of vegetative shifts therefore requires quantification of specific C pools. Total carbon (TC) within soils includes total inorganic carbon (TIC) and total organic carbon (TOC). TIC consists of carbonates that are deposited by processes of soil formation, whereas TOC represents all organic carbon that is the product of biological activity in any stage of decay (Christensen 1992). TOC can be classified as either root-C or soil organic carbon (SOC). In this study, root-C represents various types of plant residue within soil that is greater than 250 µm, including roots and other partially decomposed material, whereas SOC is a metabolic product of root-C. SOC typically has longer soil residence times in soils (Brady & Weil 2008; Stevenson 1994).

The development of soil structure can strongly influence the nature and degree of soil carbon sequestration (Six, Bossuyt, Degryze, & Denef 2004). Soil macroaggregates (>250 µm) can form within soils, physically preserving root-C and SOC. Within macroaggregates, metabolized organic C becomes encrusted with clay particles and microbial products, forming very stable microaggregates (250 -53µm). Eventually, these microaggregates break down into less stable silt- and clay-sized organo-mineral complexes (Six et al. 2004). Stable isotope and radiocarbon studies have corroborated the theory that soil C residence times are negatively correlated to SOC aggregate sizes

(Christensen 1992; Gill & Burke 1999; Del Galdo, Six, Peressottis, & Cotrufo 2003; Marzioli et al. 2010; and others), although whether or not this trend is due to organic recalcitrance or physical exclusion is still debated (McCarthy, Ilvasky, Jastrow, Mayer, & Perfect 2008). Therefore, in order to accurately describe changes in SOC storage and dynamics, it is important to investigate changes in the distribution of SOC within soil aggregates.

1.2.2 Soil Carbon Investigation within Sagebrush-steppe Ecosystems

Several researchers have attempted to quantify C budget changes associated with shifts in species dominance of semi-arid ecosystems (Gill & Burke 1999; Potter, Torbert, Johnson, & Tischler 1999; Chen & Stark 2000; Norton, Monaco, Norton, Johnson, & Jones 2004; Hooker et al. 2008; Rau, Johnson, & Blank 2011) (Table 1). In comparing the SOC content of near surface soils (0-10 cm), Hooker et al. (2008) reported cheatgrass to have significantly higher SOC content compared to sagebrush soils, whereas Gill et al. (1999) found higher soil carbon content within shrubs (*Atriplex confertifolia*) compared to cheatgrass. Norton et al. (2004) found no significant differences in near surface C between sagebrush-steppe and cheatgrass soils. Norton et al. (2004) also observed the most variability in OC content of cheatgrass soils compared to the shrub-grass-interspace soils in sagebrush, as proposed by Chen and Stark (2000). This lack of scientific consensus on the impact of cheatgrass invasion on the soil C reservoir may be attributable to: (1) variability in stand age, (2) level of cheatgrass encroachment, (3) contrasting concentrations of antecedent soil carbon, and (4) differences in experimental design. Potter et al. (1999) found SOC to be linearly correlated with stand age in reclaimed grasslands, and Rau et al. (2011) showed the level of cheatgrass invasion to be inversely

correlated with OC content. Importantly, Rau et al. (2011) concluded that replacement of perennial grasses with cheatgrass could result in a net loss of 6-9 Mg C ha^{-1} for sagebrush ecosystems, while also predicting loss of sagebrush to cause a further decline in SOC content.

Potter et al. (1999) documented a significant decrease in SOC when grasslands were degraded by cultivation (inversion tillage) and that subsequent restoration of these grasslands produced a linear increase in SOC storage (447 kg C ha^{-1} yr^{-1}). Similarly, Del Galdoet al. (2003) used ^{13}C stable isotope signatures to show that forestation of cultivated lands significantly increased SOC within distinct aggregate sizes. The results of these studies are potentially relevant as several researchers have likened the effects of cheatgrass invasion to cultivation for agriculture (Norton et al. 2004; Schimel 1986). In this study, we quantify differences in below ground carbon with cheatgrass invasion, demonstrating, for the first time, dramatic declines in soil carbon content.

CHAPTER TWO: MATERIALS AND METHODS

2.1 Introduction

Key components of our research approach included (1) locating a site with homogeneous properties of climate, soil, and stand age, (2) designing efficient field and lab methods that facilitate the processing of large quantities of samples, (3) accurately quantifying distinct C pools, and (4) using statistical analyses to quantify uncertainty of observed trends.

2.2 Study Site

2.1.1 Site Location

Kuna Butte, located in the western Snake River Plain of Southern Idaho (43°27'55"N, 116°28'55" W, elevation 915 m; Figure 1), is public land administered by the Bureau of Land Management (mean temp and precipitation is 11 °C and 280 mm yr^{-1}, respectively). The soil (70 to 90 cm total depth) is a loamy, mesic shallow Xerollic Duragid, with parent material of loess over basalt bedrock (Barker, McDole, & Logan 1983), providing relatively flat topography. Approximately 20 cm of duripan lies above bedrock, providing an ideal boundary condition for quantifying C pools.

Covariates between vegetative stands are minimal at Kuna Butte, owing to a juxtaposition of the three plant communities representing each stage of sagebrush alteration (initial condition, cheatgrass-degraded, and partially reclaimed). Importantly,

the vegetative stands representing stages of sagebrush alteration (cheatgrass and bunchgrass) have been established for equal and extended periods of time, potentially long enough to affect soil C stores; this conjecture is based on the work of Potter et al. (1999) who documented differences in soil C of reclaimed agricultural soils after six years of growth.

2.1.2 Site History

Kuna Butte experienced a wildfire in the spring of 1983, which consumed a large portion of sagebrush, except for an area that was excluded from fire due to the presence of a small dirt road (Figure 2). In late fall of 1983, a 25 m wide strip of Fairway Crested Wheatgrass (*Agropyron cristatum)* was drill seeded (4.5 lbs·seed·acre^{-1}) beginning near the road. The spring of 1984 revealed that the seeded area had high germination and growth rates, and cheatgrass (*Bromus tectorum*) dominated the adjacent unseeded area (Johansen 1984). The path of crested wheatgrass (bunchgrass) seeding was well pronounced at the time of this study, forming a sharp transition between bunchgrass and cheatgrass communities, indicating that neither grass species has invaded the other since establishment. Conversely, cheatgrass has remained present in sagebrush interspaces, occupying approximately 80% of sagebrush interspace during the time of this study.

2.2 Field Methods

2.2.1 Soil Sampling for Total Carbon (TC), Total Organic Carbon (TOC), Soil Organic Carbon (SOC), and Below-ground Biomass (Rb)

Along four 30 m long transects (15 m in each vegetation type) orientated perpendicular to species community boundaries, soil cores were extracted at a 1 m

spacing. The four sampling transects crossed the species boundaries in the following manner: cheatgrass/bunchgrass (C/B), cheatgrass/sagebrush (C/S), sagebrush/bunchgrass (S/B), and cheatgrass/bunchgrass (C/B 2). Due to the presence of the road, the two transects including sagebrush were discontinuous. Accordingly, each half of the C/S and S/B transects began more than 10 m from the road to avoid potential disturbances. This sampling scheme was designed to compare the effects of species dominance and natural variation of plant biomass and soil carbon, but also to investigate changes in soil carbon with respect to distance from species boundary.

All samples were collected from July to early September of 2010 using a 7 cm sand auger (AMS, 300.41). This auger provided the ability to remove and retain roots, allowing estimation of below-ground biomass in each plant community. The upper 3 cm of soil was sampled using a bulb planter to isolate elevated C content from litter incorporation. Following removal of the upper 3 cm of the soil profile, samples were collected at 5 cm increments to a depth of 18 cm and every other 5 cm increment was retained for analysis thereafter. Sampling depth did not exceed 58 cm because this was approximately the depth at which duripan was encountered. Samples were stored in plastic bags and frozen at -10 °C until analysis.

2.2.2 Soil Sampling for Aggregates Containing of Soil Organic Carbon

Soil aggregate samples were collected within the same transects established for soil carbon samples. A 7 cm sand auger (AMS, 300.41) was used to remove the upper 0-5 cm of soil and a 5 cm diameter slide hammer (AMS, 404.61) was used to collect a continuous 10 cm sample from 5-15 cm. This depth increment was chosen for aggregate sampling because it was deemed to be actively influenced by root exudation and assumed

to be deep enough so that influence of above-ground processes are insignificant. All samples were stored at 10 °C until analysis could be carried out.

2.2.3 Soil Sampling for Bulk Density and Grain Size

Four soil pits, each located throughout the study site and within contrasting plant communities (Figure 2), were excavated by hand to allow field classification of soil properties following USDA protocols (SSDS 1993). Samples were collected from pit walls with a 5 x 10 cm diameter slide hammer (AMS, 404.61) for laboratory analysis of grain size and bulk density. All samples were centered at the same depth increments as those for soil carbon analysis, excluding the 0-3 cm increment. If compaction of samples was evident, the sample was discarded and another was collected.

2.2.4 Quantification of Canopy Cover

Canopy cover was estimated in an effort to quantify potential differences between sample locations but within plant communities. However, cheatgrass communities were not included in estimation of canopy cover because little to no bare ground was present within transects and all populations were assumed to be monocultures representing 100% canopy cover. Canopy cover was estimated by linearly classifying ground cover as either bare ground, beneath canopy, or invaded by cheatgrass, at a resolution of 5 cm along each transect. Additionally, the number of soil cores taken beneath canopy for each transect was documented.

2.2.5 Sample Collection of Above-ground Biomass

Above-ground biomass was estimated for each plant community following U.S. Department of the Interior protocols (Habich 2001). For cheatgrass and bunchgrass, three

9 m^2 plots representing the range in biomass for each species was selected for destructive harvest. For sagebrush communities, six 6.25 m^2 plots were selected as being representative and cut to the soil surface. A wood chipping device was used to homogenize biomass and to ease transport and weighing for sagebrush populations. All samples were subsequently dried until no further decrease in mass was observed and weighed to determine moisture content. Biomass was estimated on a mass per unit area basis for entire stands. Dried biomass samples were frozen (-10 °C) until analyzed for carbon content.

2.3 Laboratory Methods

2.3.1 Homogenization and Subsampling

Samples collected via sand auger were used for quantification of multiple below-ground C pools (TC, TOC, TIC, root-C, or SOC). Samples were first removed from frozen storage, weighed, dried at 90 °C for 24 h, and reweighed for determination of gravimetric moisture content. Samples were then placed in a standard blender used in food preparation to aid in the breakdown of cemented soil clods and to improve homogenization of roots and organic matter. Samples were then passed through a 2 mm (10 mesh) sieve to remove and quantify rock fragments, and to ensure that roots were small enough to allow adequate homogenization. The entire sample passing the 2 mm sieve (including root-C) was then further homogenized by overturning and pouring the sample into “cones” five times (after Schumacher, Shines, Burton, & Papp 1990). The sample was then split in half using a standardized 17 mm riffle splitter (W.S. Tyler, SS-

50). Half of the original sample (average 200 g) was used in analysis of TC, TOC, TIC, and SOC, whereas the remaining half was used in quantification of root-C.

Allowing root-C to be incorporated into soil samples, as in this study, is atypical for many soil C studies. However, since the main goal of this study was to quantify the total below-ground organic carbon, it was appropriate and efficient to include all below-ground organic C pools in a single analysis. Incorporation of root-C within a soil sample allows processing of many more samples, providing the ability to generate a more robust dataset.

2.3.2 Processing of Laboratory Duplicates

Laboratory duplicates were generated for every 10th sample processed. Duplicates were generated by homogenizing and splitting the initial sample into four subsamples via riffle splitter (average mass 100 g). Two of the four subsamples would be used as root-C duplicates and the remaining two were used for TC, TOC, and TIC duplicates. Since duplicates were generated during the first step of sample preparation, they represent the combined error of all lab processing.

2.3.3 Analysis of Total Carbon (TC), Total Organic Carbon (TOC), Total Inorganic Carbon (TIC), and Total Nitrogen (TN)

Half of the original soil sample (splitting described previously) was further homogenized by overturning the sample three times and randomly removing a 10 g subsample after each repetition. The final subsample, which was a combination of three 10 g subsamples (~ 30 g total mass), was again homogenized by overturning, and a final 10 g sample was removed for grinding. The 10 g sample was then ground via mortar and pestle to pass a 125 µm (120 mesh) sieve. This sieve size was chosen based on replicate

analysis and by visual confirmation that all roots and organic matter was indistinguishable. The sample was then dried at 105°C for 24h and concentrations of TC and nitrogen were determined for a 60 mg sample using a Thermo Electron Flash EA 1112 CN analyzer (CE Elantech, Inc., Lakewood, NJ).

Because significant concentrations of carbonates are present throughout soil profiles in this area (Barker et al. 1983), all samples required pretreatment for removal of carbonates in order to quantify TOC. Approximately 300 mg of ground sample (120 mesh) was treated with 3 mL of 0.73 M H_2SO_3 and dried at 105 °C as described by Nelson & Sommers (1996). According to Heron, Barcelona, Andersen, & Christensen (1997), this ratio of solids to acid is sufficient to remove approximately 7% TIC by weight. Approximately 60 mg of pretreated sample was then analyzed for carbon and nitrogen concentrations using a Thermo Electron Flash EA 1112 CN analyzer (CE Elantech, Inc., Lakewood, NJ) and results were reported as wt. % TOC. Because TC and TOC were both quantified using the same pulverized sample, TIC could be calculated as TIC = TC – TOC.

2.3.4 Quantification of Below-ground Biomass (Rb) and Root-Carbon

Quantification of root biomass (R_b) and, accordingly, organic carbon present as root biomass (root-C) was achieved through modification of a root flotation method outlined by Al-Khafaf (1977). This method consisted of the following steps: (1) half of the original soil sample (splitting described previously) was further homogenized, split, and mass (m) was determined, Accordingly, 25% of the original sample was used in quantification of R_b (average mass 100 g). This subsample size was chosen based on efficiency requirements and on the work of Schroth & Kolbe (1994), in their

investigation of subsample sizes needed to accurately represent root mass within soil cores. In short, they concluded that 5-10% of a total sample was needed to adequately estimate plot scale (70 m^2) root mass in a groundnut field using combined soil cores. (2) Approximately 100 g of soil was weighed and added to a 500 mL graduated cylinder containing a solution of 4% (wt/wt) $(NaPO_3)_6$ for deffloculation of clays. (3) The cylinder containing the soil solution was placed on a 250 µm (60 mesh) sieve that was partially submerged in DI water within a plastic tub. (4) 50 mL of 50% $CaCl_2$ solution was then added to the soil solution to flocculate clays and increase the solution density to approximately 1.1 $g \cdot cm^{-3}$, causing the flotation of roots. (5) DI water was then added to completely fill the cylinder so that roots could be flushed onto the 250 µm sieve. Because flocculation was extremely rapid, some roots were quickly buried in soil and further agitation of the soil solution was repeated until no roots floated to the surface. (6) The material remaining on the sieve was rinsed, dried at 70 °C for 24-hr, and R_b mass (z) was determined at a precision of 0.1 mg. R_b was then calculated as $R_b = 100 \cdot z \div m$. R_b samples were then ground to pass a 120 mesh sieve and analyzed for carbon concentrations using a Thermo Electron Flash EA 1112 CN analyzer (CE Elantech, Inc., Lakewood, NJ). Root-C was then calculated as root-C= R_b x weight % Root-Carbon ÷ 100.

Quantification of R_b and root-C via root flotation was performed on samples ranging from 0 to 38 cm depth. Samples taken from deeper in the profile were not able to be processed by this method because they contained extremely low concentrations of roots, possibly due to the presence of carbonates. A subset of samples taken from the 43-48 and 53-58 cm depth intervals were handpicked for roots to verify that an insignificant

amount of R_b and, accordingly, root-C was present at these depths. Additionally, the root flotation method was validated using 12 samples that were homogenized and split (as previously described), creating replicate samples. R_b content of replicate samples was then quantified in one of two ways: either root flotation, or handpicking of roots.

2.3.5 Physical Fractionation of Soil Aggregates

Soil samples collected via slide hammer were fractionated by aggregate size according to the wet sieving procedure outlined by Elliott (1986), consisting of the following steps: (1) field moist samples were removed from cold storage (4 °C) and passed through a 4.75 mm (4 mesh) sieve and subsampled. (2) Gravimetric moisture content was determined (dried 105 °C, 24 h) and the dry weight of each subsample (*i*) was calculated (~50 g). (3) The sample was slacked for 5 min. on a 250 µm (60 mesh) sieve and (4) floating roots were removed by vacuum. (5) The sieve was then moved with a slight angle at a 3 cm amplitude for 50 repetitions during a 2 min period; the remaining material was backwashed into an aluminum pan and classified as small macroaggregates. (6) Material passing the 60 mesh sieve was poured onto a 53 µm (270 mesh) sieve and the wet sieving procedure repeated; the material remaining on the sieve (microaggrgates) was backwashed into an aluminum pan, whereas all passing material was classified as silt + clay. (7) Aluminum pans containing DI water and aggregates were dried at 105 °C. (8) Dry mass of each size fraction (*d*) was determined and the mass percentage of aggregate fractions (*Z*) were calculated as $Z=100 \times d \div i$. (10) SOC content (*f*) was determined on each fraction after acidification (0.73 M H_2SO_3) using a Thermo Electron Flash EA 1112 CN analyzer (CE Elantech, Inc., Lakewood, NJ). (9) Percent of total SOC (*w*) within each aggregate size was then calculated as $w = f \times Z \div 100$.

The composition of macroaggregates was determined using the microaggregate isolation methodology described in Six, Elliott, & Paustian (2000). Physical fractions occluded in macroaggregates were classified as occluded particulate organic matter (*O*-POM), occluded microaggregates (*O*-microaggregates), or occluded silt and clay (*O*-silt+clay).

2.3.6 Quantification of Bulk Density and Grain Size

Samples collected via slide hammer from soil pits excavated throughout the field site (Figure 2) were used for quantification of bulk density and grain size distribution. Dry bulk density and gravimetric soil moisture was calculated by combining oven-dried soil mass (105°C, 24 hr) determined after removal of gravel and the known volume of the soil corer. Grain size distributions were calculated using a combination of dry sieving and hydrometer analysis, as outlined in ASTM D422-63.

2.3.7 Analysis of Carbon Content of Above-ground Biomass

Carbon content of above-ground biomass was determined for the three plant communities (cheatgrass, bunchgrass, and sagebrush) for a 20 g subsample. Samples of dry biomass were removed from frozen storage and finely ground using a standard coffee grinder. Pulverization was continued by hand until samples passed a 125 µm (120 mesh) sieve. Approximately 10-20 mg of pulverized sample was analyzed for carbon content using a Thermo Electron Flash EA 1112 CN analyzer (CE Elantech, Inc., Lakewood, NJ) calibrated using aspartic acid and peach leaves.

2.4 Statistical Analyses

2.4.1 Non-Parametric Analysis

The Lilliefors goodness-of-fit test for composite normality was used to determine if the data respected normally. The Lilliefors test calculates the empirical cumulative distribution function (ECDF) for a sample population and applies a 2-sided goodness-of-fit test using a normally distributed CDF with mean and standard deviation calculated from the sample population (Lilliefors 1967). The largest difference between the two distributions is quantified and compared to a table of critical values to determine a *p*-value for the comparison. If the *p*-value is sufficiently low (≤ 0.05), the null hypothesis of normality is disproved and the sample population can be viewed as non-normal. The Lilliefors test is included in the MATLAB statistics package and was applied to the data. Approximately 40% of the sample populations tested (depth x vegetation type) did not appear to respect normally (Table 2), and therefore nonparametric statistical analyses were used to examine all data.

2.4.2 Bootstrap Sampling to Quantify Uncertainty in Mean Values

A bootstrap sampling routine was coded in MATLAB and used to determine the uncertainty in estimating the true mean carbon values (reported as 95% range) at each depth increment and within each vegetation type. Bootstrap sampling operates on the postulation that a set of samples can be viewed as one realization out of an infinite number of possible sample sets taken from a study site (Martínez & Martínez 2008). By resampling a dataset with replacement (bootstrapping), it is possible to choose the same

sample more than once or not at all during subsequent realizations. This permits quantification of the variability of a statistic of interest for a given dataset. For each bootstrap simulation, a mean is calculated and stored and the true mean is estimated by calculating the mean of all bootstrap simulations and the uncertainty in this estimate is reported as the 95% range of the means calculated from all 100 simulations. A similar strategy has been demonstrated by Poussartet al. (2004) to be applicable for quantification of differences in soil carbon between two populations, specifically when data non-normality is observed.

2.4.3 Two-Population Kolmogrov-Smirnov Test (K-S test) for Significant Difference

The two population Kolmogrov-Smirnov test (K-S test) is used to determine if, given the variability of soil carbon values, one population can be deemed to have significantly greater below-ground carbon. Similar to the Lilliefors test, the K-S test compares two ECDFs generated from each of the sample populations while making no assumptions about the underlying distribution of the data. The null hypothesis of the K-S test is that the two populations being tested are from the same distribution. If the largest distance between the two ECDFs is larger than a critical value, the null hypothesis is disproved and the test concludes that the samples are from two distinct populations ($p \leq 0.05$). The K-S test is included in the MATLAB statistics package and was applied to each of the datasets of below-ground carbon (vegetation type x depth) in a two-by-two fashion.

In addition to applying the K-S test to the entire sample population, the results of the K-S test were investigated for varying population sizes. A bootstrap routine that applied the K-S test to increasing sample sizes was coded into MATLAB and 1000

simulations were preformed for each comparison and for a given sample size. For each sample size, the bootstrap routine simulated 1000 alternative datasets (realizations) for cumulative TOC to a depth of 38 cm using data from two vegetation types. A K-S test was applied to each of the 1000 realizations and an average *p*-value was calculated for a given sample size (modified from Poussart, Ardo, & Olsson 2004). Lower depth increments (43-48 and 53-58 cm) were not included in this analysis because fewer samples were collected at these depths due to obstructions. Due to the low variability in TOC at these depths (Figure 11, Table 7), it was assumed that their exclusion would not affect the results.

CHAPTER THREE: RESULTS

3.1 Laboratory Duplicate Analysis of Total Carbon (TC), Total Organic Carbon, and Below-ground Biomass (R_b)

A total of 67, 68, and 52 laboratory duplicates were analyzed for TC, TOC, and R_b, respectively (Table 3). The mean difference in laboratory duplicates was 8.2 (5.4% median) and 11% (8% median) for TC and TOC, respectively, where the largest differences generally occurred at low concentrations. R_b duplicates produced mean and median differences of approximately 19 and 16%, respectively. In addition to laboratory duplicates, the accuracy of the root flotation method was investigated using 12 replicate samples that were handpicked to determine R_b content. Linear regression of the two methods produced an R^2 value of 0.95 (Figure 3).

3.2 Bulk Density, Grain Size, and Gravimetric Moisture Content

Bulk density averaged approximately 1200 $kg \cdot m^{-3}$ throughout the site and no trends with depth or vegetation were observed (Figure 4). Depth-averaged grain size was approximately 18, 56, and 26 % for sand, silt, and clay, respectively, corresponding to a silt loam textural class. Clay content increased to a profile maximum of 37 % within the 13-18 cm depth increment (Figure 5; Table 4) and decreased with depth thereafter. Depth-averaged gravimetric moisture content indicated higher summertime moisture contents under cheatgrass and lower values under sagebrush for two consecutive years (Figures 6 and 7).

3.3 Above-ground Biomass

Above-ground biomass increased in the order where: cheatgrass<bunchgrass <sagebrush, corresponding to 1.7, 2.9, and 8.4 $Mg \cdot ha^{-1}$, respectively. Carbon content was 46, 43, and 50 wt. %, corresponding to above-ground C storage of 0.8, 1.3, and 4.2 $Mg \cdot ha^{-1}$ for cheatgrass, bunchgrass, and sagebrush, respectively (Figure 8; Table 2).

3.4 Canopy Cover of Sampling Transects

Canopy cover in areas sampled within cheatgrass communities was approximately 100% for replicate sample populations throughout the study site, with the exception of CB2, which contained significant cover (~20 %) of Rush Skeleton weed (*Chondrilla juncea*). Similarly, canopy cover within replicate bunchgrass communities was similar, estimated as ranging from 42 to 50% within transects (Figure 9), likely due in part to the drill seeding method used in bunchgrass establishment. In contrast, replicate canopy cover in sagebrush populations varied from 28 to 40% for S and CS transects, respectively.

3.5 Below-groundTotal Inorganic Carbon (TIC)

Total inorganic carbon (TIC) averaged 32, 46, and 57 $Mg \cdot ha^{-1}$ for cheatgrass, bunchgrass, and sagebrush, respectively, but was not significantly different between plant communities (Table 5). There was a significant difference in TIC within the 53-58 cm depth interval for all three vegetation types, with TIC increasing where: cheatgrass < bunchgrass < sagebrush (Figure 12). The uncertainties in estimating TIC were relatively large due to the additive error produced when combining measurements of TC and TOC.

3.6 Below-ground Total Organic Carbon (TOC)

Below-ground total organic carbon (TOC) was significantly reduced in cheatgrass. Cumulative TOC averaged 29, 41, and 56 Mg C·ha^{-1} for cheatgrass, bunchgrass, and sagebrush, respectively. The results of the K-S test and the bootstrap routine indicated that greater TOC within sagebrush relative to cheatgrass was significant for all depths, with the exception of the 18-28 cm interval (Figure 10, Table 6). The cumulative TOC decrease in cheatgrass relative to sagebrush represented approximately 27 Mg·ha^{-1}, corresponding to a 50% decrease. The largest differences in TOC were between sagebrush and cheatgrass and occurred in the upper 18 cm of soil, where this decrease accounted for 63% of the total loss in TOC. Mean values of TOC for bunchgrass were significantly greater than cheatgrass at all depths below 8 cm (Figure 10, Table 6); excluding the upper 8 cm of the soil profile, this corresponds to a cumulative increase of 9 Mg·ha^{-1} (53%) TOC. Increased TOC in bunchgrass relative to cheatgrass was approximately equal at all depths below 8 cm as the two populations had similar depth distributions of TOC.

The trends reported for TOC were reproducible for both grass communities at locations separated by approximately 200 m (Figure 11, Figure 2). In contrast, replicate sagebrush populations, “S” and “CS”, separated by approximately 35 m displayed similar depth distributions of TOC, but exhibited significant differences in TOC content (49 vs. 64 Mg·ha^{-1}, respectively).

3.7 Below-ground Biomass (R_b) and Root-Carbon (C)

Root biomass (R_b) averaged 11, 22, and 31 Mg·ha^{-1} for cheatgrass, bunchgrass, and sagebrush, respectively (Table 8). R_b content within sagebrush and bunchgrass

communities was significantly greater than cheatgrass at all depths below 3 cm, whereas bunchgrass and sagebrush were statistically indistinguishable at all depths (Figure 13, Table 6). R_b content in the upper 0 to 3 cm of the soil profile accounted for approximately 65, 51, and 61 % of total profile R_b in cheatgrass, bunchgrass, and sagebrush communities, respectively, while accounting for 70% of the error in estimating total profile R_b. R_b content was below detection level for all depths below 38 cm.

Trends with depth were reproducible for replicate populations where, specifically, sagebrush replicates display a decrease in TOC and a parallel decrease in R_b within the "S" population relative to the "CS" population (Figures 12 and 15). C content of R_b samples (n = 47) averaged approximately 27 wt. % and was not significantly different between communities. Accordingly, root-C and R_b depth distributions are similar, but differ in magnitude by a factor of 0.27.

3.8 Soil Organic Carbon (SOC)

Total profile SOC averaged 23, 33, and 44 $Mg \cdot ha^{-1}$ for cheatgrass, bunchgrass, and sagebrush, respectively (Figure 15; Table 9). Importantly, because R_b content was found to be insignificant at depths exceeding 38 cm, SOC was assumed to equal TOC for depths ranging from 38 to 58 cm. This model appears reasonable as the distribution of SOC with depth remains uniform for depths exceeding 38 cm.

3.9 SOC Content of Aggregate Fractions

Soil macroaggregates (> 250 µm) were present at significant levels (22% soil mass) in sagebrush communities only; cheatgrass and bunchgrass had no detectable quantity of macroaggregates (Figure 16, Table 10). Conversely, microaggregate

concentrations (53 – 250 µm) were similar in all three plant communities and accounted for approximately 50% soil mass. Silt+clay sized particles (< 53 µm) represented 45% of soil mass in both grass communities, and accounted for 27% soil mass in sagebrush. The remaining proportions of soil mass were characterized by sand fractions.

Cumulative SOC of all size fractions after acidification and root removal corresponded to 0.25, 0.32, and 0.81 wt. % for bunchgrass, cheatgrass, and sagebrush, respectively; these values of SOC were roughly equivalent to those previously determined by subtracting root-C from TOC (Figure 16). SOC content of macroaggregates within sagebrush populations was approximately 3 g kg^{-1}, which corresponded to approximately 36% of total SOC for sagebrush. For sagebrush, microaggregates occluded within macroaggregates contained 18% (1.5 g kg^{-1}) of the total SOC, whereas occluded silt+clay and POM accounted for the remaining 7 (0.6 g kg^{-1}) and 11% (0.9 g kg^{-1}), respectively.

Average SOC concentrations of free microaggregates corresponded to 1.2, 1.6, and 3.6g kg^{-1} for cheatgrass, bunchgrass, and sagebrush, respectively. SOC concentration of the silt+clay fraction was equivalent for bunchgrass and sagebrush (1.6 g kg^{-1}) but was less for cheatgrass populations (1.3 g kg^{-1}).

Carbon/Nitrogen (C:N) ratios were calculated for non-occluded size fractions within vegetation type. C:N ratios were positively correlated with aggregate size for all vegetation types (Table 11). Additionally, C:N ratios increased in the order where: cheatgrass< bunchgrass< sagebrush for all aggregate sizes, although this trend was not statistically significant.

3.10 Total Nitrogen (TN)

Total nitrogen (TN) was determined to be 6, 6, and 8 $Mg \cdot ha^{-1}$ within cheatgrass, bunchgrass, and sagebrush populations, respectively (Figure 17). The depth distribution of TN was similar to TOC for all three vegetation types. Both cheatgrass and bunchgrass had low variability in TN but were indistinguishable at all depths, whereas sagebrush had significantly greater TN at all depths with higher variability.

3.11 Sample Sizes Required to Demonstrate Significant Differences in TOC

Cumulative TOC values (0-38 cm) obtained from each community indicated that, to reach a *p*-value less than 0.05, 24 soil cores would be needed from each population to distinguish differences in cheatgrass compared to sagebrush (Figure 18). The results also indicate that at least 36 soil cores would be needed from each population for statistical distinction of bunchgrass from either sagebrush or cheatgrass at a *p*-value less than 0.05, which was more than obtained in this study. Application of the K-S test to discrete depth increments using the current data set (Table 6) indicates that the additional samples required may be confined to the upper 8 cm of soil when comparing cheatgrass to sagebrush, whereas intermediate depths would require additional samples when comparing bunchgrass to sagebrush.

CHAPTER FOUR: DISCUSSION

4.1 Rates of Change in the Carbon Budget

Part of an established sagebrush community was lost to wildfire in the spring of 1983, 27 years prior to this study; the burned area was immediately converted to either a cheatgrass or crested wheatgrass monoculture. Rates of C loss may be on the order of 1 Mg C ha^{-1} yr^{-1}, twice the rate of C gain in restored grasslands (447 kg C ha^{-1} yr^{-1}) reported by Potter et al. (1999). The initial rate of C loss may be enhanced in bunchgrass communities at Kuna Butte due to the soil aeration caused by drill seeding. However, the loss rates may decrease non-linearly in grass communities as labile C becomes limited during establishment and, subsequently, plant-derived inputs begin to offset losses.

4.2 Loss of Total Inorganic Carbon (TIC) Following Sagebrush Degradation

The significant decrease in TIC concentration at depth (53-58 cm) in cheatgrass (Figure 12) is in contrast to the results of Chen & Stark (2000), where they documented a trend in TIC where: sagebrush < bunchgrass < interspace soils. They attributed this trend to increasing respiration and organic acid production in bunchgrass and sagebrush, which could dissolve and prevent carbonate precipitation. However, increased photosynthesis would also correspond to an increase in evapotranspiration and, consequently, carbonate precipitaiton, producing the trends in soil moisture and TIC at Kuna Butte (Figures 6 and 7). Alternatively, differences in TIC at depth could also be due to decreased profile thickness or an underestimation of coring depth in sagebrush. The former was

investigated via soil pits and determined to be unlikely while the latter is improbable as underestimation of coring depth would likely be random in all plant communities.

Greater TIC in shallow sagebrush soils, although not statistically significant, may be due to increased capture of aeolian carbonates caused by denser ground cover in sagebrush communities (see Norton et al. 2004). Alternatively, Emmerich (2003) documented 15% annual variation in TIC of shallow grass- and brushland soils, indicating that significant cycling of TIC does occur and may be dependent on vegetation. Our estimated C losses from sagebrush degradation do not include TIC pools due to lack of any specific mechanism.

4.3 Changes in TOC Distribution: Pool and Depth Allocation

Our results indicate that both sagebrush and bunchgrass had higher concentrations of root-C in the subsoil; this was also documented by Hooker et al. (2008). This implies higher C input at lower depths within sagebrush and bunchgrass communities where rates of decomposition can be reduced due to lower soil temperatures, anaerobic conditions, and pH changes (Lorenz & Lal 2005). This claim was supported by Gill et al. (1999) who used ^{14}C labeling to identify decreasing SOC decomposition rates with depth.

The second peak in SOC at the 13-28 cm depth observed in grass communities (Figure 16) corresponds to increased clay content (Figure 5). A similar distribution of SOC was documented by Gill et al. (1999) within a shortgrass-steppe ecosystem and also corresponded to increased clay content. This correlation suggests that higher clay content contributes to SOC stabilization, likely due to greater occlusion (Lorenz & Lal 2005; Six et al. 2004).

The relative contribution of root-C and SOC to TOC was not markedly different between communities for specific depths, or throughout the entire profile (Table 12); both root-C and SOC decreased across the entire profile. This indicates that C loss following sagebrush degradation was not limited to near surface soils or a specific C pool. The observation of declining carbon across the entire profile is in contrast to previous studies that documented significant differences to exist only within shallow soils (Hooker et al. 2008; Norton et al. 2004; Gill et al. 1999). The observation of proportional declines in SOC and root-C also suggests changes in both root-C input and SOC stabilization.

4.4 Potential Mechanisms for TOC Loss Following Sagebrush Degradation

4.4.1 Decreased Input Quantity

Using annual root turnover rates of 1 and 0.5 yr^{-1} for cheatgrass and bunchgrass, respectively (Gill & Jackson 2000), our observed values indicate annual root-C inputs of approximately 3 Mg C·ha^{-1} for both grass communities, whereas a root turnover rate of 0.3 yr^{-1} for sagebrush (Caldwell et al. 1977) corresponds to an input of 2.4 Mg root-C·ha^{-1}·yr^{-1}. Accounting for the cheatgrass presence in sagebrush at Kuna Butte (~60% areal cover) increases our estimate of root-C input to 5.6 Mg ha^{-1}·yr^{-1} for sagebrush; these results are higher than those reported by Gilmanov, Svejcar, Johnson, Angell, & Nicanor, (2006), who used Bowen ratio-energy balance (BREB) instrumentation to calculate annual respiration and primary production in a sagebrush-steppe of southeastern Idaho (annual precipitation 283 mm, 40% canopy cover); average primary productivity and respiration was reported as 4.4 and 3.7 Mg C·ha^{-1}·yr^{-1},

respectively; using a root/shoot ratio of 4, as calculated in this study, their results correspond to a root-C input of 3.3 Mg $ha^{-1} \cdot yr^{-1}$.

We did not distinguish between living and dead roots or plant residue in determining root-C. Estimates of annual root-C input may therefore be overestimated due to inclusion of dead plant material in root-C estimates. Greater than 50% of all root-C is located within the upper 3 cm of soil for all three plant types (Table 8); this may be an artifact of litter incorporation into the shallow subsurface, however studies have reported between 50 and 80% of total root biomass within the upper 10 cm of soil (Rau et al. 2011; Hooker et al 2008; Gill et al. 1999; Dahlman 1965, and others). Other studies in similar environments have quantified root-C by removing roots using sieves ranging from 2 to 4 mm (Gill & Burke 1999; Gill et al. 1999; Hooker et al. 2008; Norton 2004; Svejcar & Sheley 2001, and others) while average root diameters are documented to range from 0.1 to 0.3 mm (Hooker et al. 2008; Gill et al. 2002). This discrepancy may indicate an underestimation of root-C in past studies; Rau et al. (2011) reported root-C to be 25% of those reported for sagebrush. In addition, the shallow subsurface boundary condition at Kuna Butte may produce higher concentrations of root-C in near surface soils.

4.4.2 Decreased Quality of Inputs

Higher TOC content may be produced by greater recalcitrance of sagebrush roots; however our observed C:Nfor R_b (mean of 25) are similar to those of Svejcar and Sheley (2001), who reported no significant differences in C:N of R_b for sagebrush and cheatgrass. In contrast, Hooker et al. (2008) documented significantly higher C:N in bunchgrass roots while also reporting higher lignin, a chemically recalcitrant compound (Lorenz & Lal 2005), in sagebrush roots compared to bunchgrass. Their results may

provide the mechanism for documenting a higher accumulation of root-C in the subsurface of sagebrush and bunchgrass compared to cheatgrass soils. Alternatively, researchers have shown root turnover to be positively correlated with diameter (Gill et al. 2002) and, although not quantified in this study, we observed larger root diameters within bunchgrass and sagebrush communities. Additionally, Norton et al. (2004) reported cheatgrass to have no roots larger than 1 mm in diameter, whereas sagebrush-steppe ecosystems had significant quantities of roots in the 1-2 mm class size, suggesting that sagebrush communities have lower root turnover and potentially longer residence times of root-C.

4.4.3 Differences in C Mineralization

Lower soil C content may be produced by higher rates of carbon mineralization. Increased mineralization of SOC could be caused by cheatgrass invasion and may be the result of: (1) production of less recalcitrant root-C, corresponding to shorter residence time in soils, (2) modifying edaphic factors such as temperature and moisture which can influence kinetics of decomposition, or (3) decreased occlusion of organic matter by loss of soil aggregate stabilization.

Soil moisture can often limit bacterial respiration of soil organic matter (Lorenz & Lal 2005; Gill et al. 1999). We observed an inverse correlation between soil moisture and SOC, with the highest summer soil moisture observed in cheatgrass, followed by bunchgrass, with sagebrush exhibiting the lowest summer soil moisture contents (Figures 6 and 7). Increased soil moisture in grass communities (bunchgrass <cheatgrass) is likely due to cessation of evapotranspiration upon plant senescence, which is earliest in cheatgrass followed by bunchgrass and sagebrush. Lower surface temperatures from

canopy cover may explain greater near surface soil moisture in bunchgrass and sagebrush communities (Figure 9). These results are similar to those of Prater, Obrist, Armone, & DeLucia (2006) who reported higher soil temperature and moisture in cheatgrass compared to sagebrush and bunchgrass. Gill et al. (1999) were also able to positively correlate decomposition rates to the amount soil moisture available for respiration. At Kuna Butte, we documented similar but unequal distributions of SOC within both grasses, but the same distribution was not documented for root-C; this disconnect may indicate greater decomposition rates in cheatgrass, possibly due to higher soil moisture availability. The inverse correlation between root-C and soil moisture also explains the loss of both root-C and SOC following sagebrush degradation.

Our third hypothesis, loss of aggregate stabilization, was documented within cheatgrass by the loss of macroaggregates. Although not definitive, these findings indicate the likelihood that hypotheses 2 and 3 are correct in that decreased SOC stabilization is likely due to both increased soil moisture and decreased aggregation in degraded sagebrush ecosystems.

4.5 The Role of Soil Structure in Carbon Preservation

4.5.1 Macroaggregates

Sagebrush degradation caused a loss of physically occluded POM with a corresponding decrease in SOC and root-C. This is in agreement with mechanistic models of aggregate dynamics where aggregate formation can be largely dictated by root dynamics (Brady & Weil 2008; Gregory 2006; Six et al. 2004; Angers & Caron 1998), and higher SOC content can enhance macroaggregate stability (Brady & Weil 2008; Six

et al. 2004; Christensen 1992, and others). The trends in R_b at Kuna Butte are similar to Tisdall & Oades (1982), who showed that conversion of grassland to arable cropping caused a decrease in SOC and macroaggregates, where they attributed this loss to decomposition of roots and fungal hyphae. Additionally, the larger diameters of sagebrush roots may correspond to slower decomposition rates (Gill et al. 2002) as well as decreased disruption of aggregate structure (Gregory 2006; Angers & Caron 1998).

Concentrations of fungal hyphae may not be ubiquitous between plant communities. Both sagebrush and bunchgrass are obligate symbionts with vesicular arbuscular mycorrhizal (AM) fungi, whereas cheatgrass is merely a facultive symbiont and, accordingly cheatgrass often has low AM fungal populations compared to bunchgrass and sagebrush communities (Ypsilantis 2003). This is an important distinction because, in addition to the work of Tisdall and Oades (1982), several researchers have demonstrated that AM fungi can dramatically affect soil aggregation by excreting glomalin and producing hyphae that act as a support structure for aggregates (Brady & Weil 2008; Gregory 2006; Angers & Caron 1998).

Wetting-drying dynamics have been shown to influence the formation of soil aggregates by promoting fragmentation (Six et al. 2004, Angers & Caron 1998), whereas the stability of aggregates has been shown to increase with decreasing soil moisture due to greater cohesion (Horn, Taubner, Wuttke, & Baumartl 1994). This is also consistent with the results from Kuna Butte, where macroaggregates were found only within sagebrush communities that had the lowest soil moisture. We propose that the presence of macroaggregates within sagebrush could be due to (1) decreased soil moisture, (2) higher concentrations of roots, (3) concentrations of AM fungi, or (4) root exudates.

The greater degree of soil aggregation (macroaggregates) beneath sagebrush communities likely contributes to the overall health and productivity of soil by increasing aeration, infiltration, and reducing compaction (Brady & Weil 2008), but may also be promoting increased SOC storage. Treseder, Egerton-Wardurton, Allen, Cheng, & Oechel, (2003) found that SOC content quickly increased within macroaggregates following CO_2 fertilization of a shrubland; they credited this to AM fungi acting as conduits for SOC deposition within macroaggregates. This process could result in increased deposition of labile C within physically protected macroaggregates, promoting lower C turnover and, potentially, long term C storage. The loss of large-scale soil aggregation following sagebrush replacement by cheatgrass is likely an important driver of observed declines in soil carbon content.

4.5.2 The Composition of Macroaggregates in Sagebrush

The SOC associated with *O*-microaggregates represents a very stable fraction of SOC (Six et al. 2004) that is lost following sagebrush degradation; nearly 20% of sagebrush SOC is contained within this fraction (Figure 16). The decrease in the silt+clay soil fraction (Table 10) and the existence of *O*-microaggregates may suggest less destabilization of microaggregates in sagebrush. Additionally, the existence of *O*-POM demonstrates increased physical protection of labile C in sagebrush.

4.5.3 Free Microaggregates

The decreased SOC content within free microaggregates of grasses accounted for approximately 40% of the total SOC lost following sagebrush degradation (Figures 17 and 18). Current models for microaggregate formation specify the formation of microaggregates within macroaggregates (Six et al. 2004). If these models describe microaggregate formation at Kuna Butte, microaggregates within grass communities may be remnants of sagebrush; suggesting that greater SOC content within bunchgrasses relative to cheatgrass may be due to slower decomposition of microaggregate SOC, possibly due to lower soil temperature and moisture relative to cheatgrass. Alternatively, if microaggregates are formed independently of macroaggregates, as proposed by Tisdall and Oades (1982), the intermediate SOC content of microaggregates within bunchgrass (Figure 16) may be due to greater preservation of SOC within microaggregates. Importantly, the fraction of soil characterized by microaggregates was not different between communities (Table 10), but rather, the SOC content of microaggregates decreased where sagebrush >bunchgrass >cheatgrass. Changes in vegetation may therefore alter the input of SOC associated with microaggregates without affecting their formation or stability in soil.

The results of recent studies are generally in agreement that microaggregate fractions have some of the longest turnover times of SOC (McCarthy et al. 2008; Six et al. 2004; Del Galdo et al 2003; Christenson 1992, and others). SOC preservation within this fraction may therefore facilitate long term C storage and should be considered an important metric when determining the relative ability of vegetation to promote long term storage of atmospheric CO_2. The decreased SOC concentration of microaggregates within

cheatgrass communities should then be regarded as a reduction in long term C storage capacity due to sagebrush degradation.

4.6 Upscaling Results

Our results indicate that the 20,000 km^2 of Great Basin vegetation displaced by cheatgrass monocultures (Bradley & Mustard 2005) represent significant C emissions. If the C losses documented in this study are to the entire Great Basin, approximately 60 Mt C has been lost to cheatgrass invasion. In addition, Bradley (2009) estimated that an additional 760,000 km^2 within the Great Basin is at risk of cheatgrass invasion under current climatic conditions; with a predicted future emission of more than 2 Gt C. Conversely under the same scenario, bunchgrass seeding following fire may prevent the loss of nearly 700 Mt C.

Importantly, the current study used a sagebrush-cheatgrass community to quantify baseline C content, but the initial loss of perennial herbaceous vegetation in sagebrush interspace may represent an additional loss of C (see Rau et al. 2011) and, consequently, we may have underestimated total C emission associated with cheatgrass degradation of natural sagebrush-steppe ecosystems. At Kuna Butte, bunchgrass seeding prevented the loss of 9 Mg $C \cdot ha^{-1}$ in the subsurface following the abatement of sagebrush. These results corroborate the projection of Rau et al. (2011), where their results suggest replacement of bunchgrasses with cheatgrass in sagebrush interspaces would cause a loss of 6-9 Mg $C \cdot ha^{-1}$.

CHAPTER FIVE: CONCLUSIONS

We quantified below-ground C loss associated with conversion of a sagebrush ecosystem to contrasting grass monocultures. Our study led to four main results: (1) In contrast to previous studies, we demonstrated that conversion of sagebrush ecosystems to cheatgrass monocultures caused a 50% loss in below-ground TOC (30 Mg C·ha^{-1}). (2) Bunchgrass seeding immediately following fire reduced the amount of TOC lost to sagebrush degradation by 30%. The significantly greater TOC in subsurface soils of bunchgrass corresponded to a 9 Mg C·ha^{-1} reduction in the amount of C lost after sagebrush degradation for depths between 8 and 58 cm. (3) Significant differences were observed within specific C pools beneath different plant communities. Because we documented significant losses within multiple pools of C, namely root-C and SOC, we cannot solely attribute the C lost following sagebrush degradation to either decreased C input, or greater decomposition of more labile C compounds. (4) Loss of macroaggregate stability following sagebrush degradation inhibits physical protection of labile C inputs, which would increase the proportion of SOC metabolized by soil biota. SOC content within microaggregates decreased following loss of sagebrush, where cheatgrass communities had the lowest concentrations of SOC within microaggregates. The inverse correlation between soil moisture and microaggregate SOC suggests that sagebrush degradation may stimulate greater decomposition stable C fractions.

Future work should focus on accurately characterizing the decomposability of specific C pools for each stage of sagebrush alteration. This could be accomplished via fractionation and laboratory incubations and would serve to address uncertainties regarding the stability of various C pools; this may provide an indication of the state of equilibrium of these ecosystems. The use of radiogenic C isotopes to estimate C pool turnover times may also prove useful in identifying either decreased stabilization or input as being the dominant mechanism for C loss following sagebrush degradation. In addition, the C budget consequences of decreased fire return intervals characteristic of cheatgrass communities should be investigated; such results may further indicate the need to prevent cheatgrass degradation of sagebrush ecosystems.

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APPENDIX A

Figures

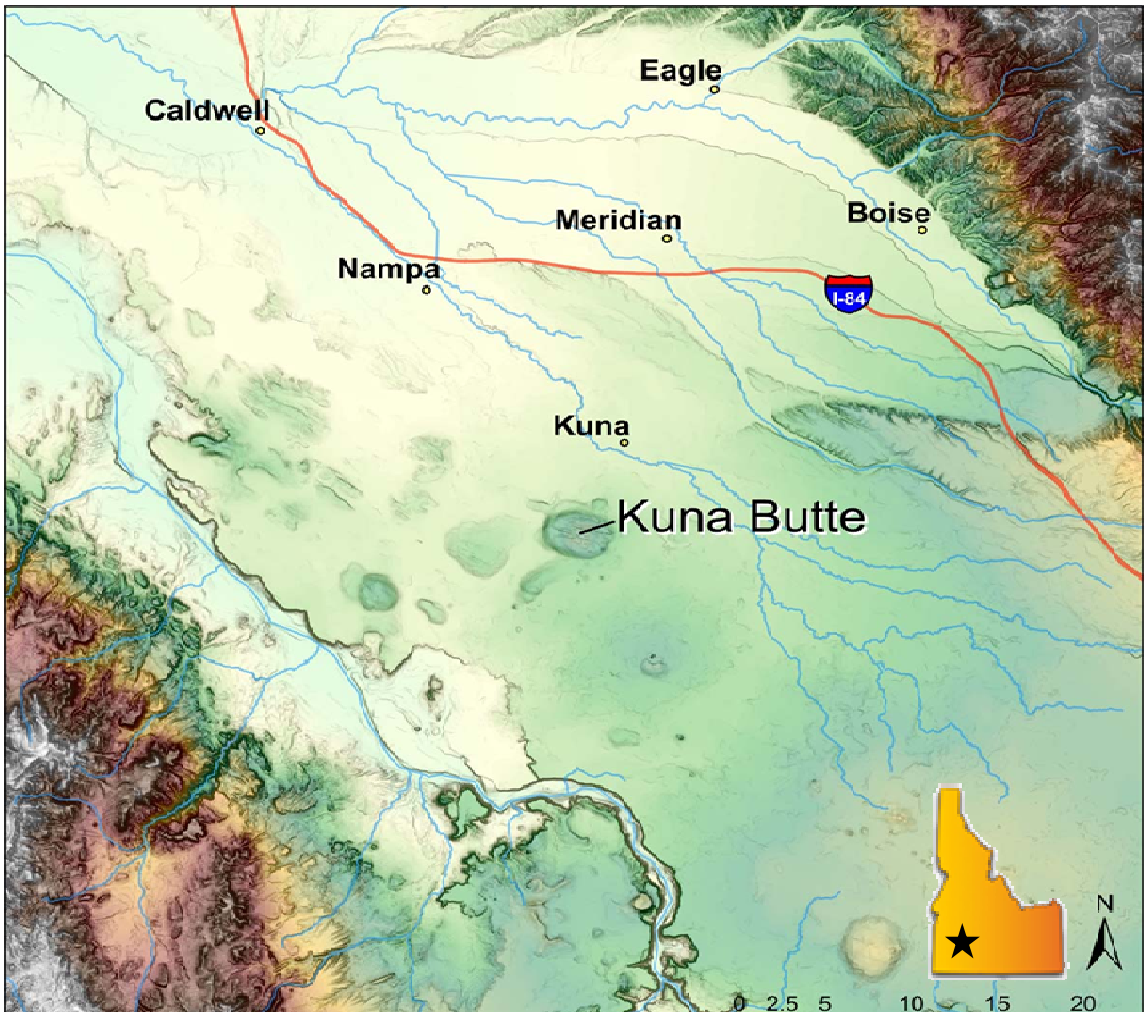

Figure A.1: Map showing the location of Kuna Butte



Figure A.2: Location of transects and soil pits at Kuna Butte. Letters indicate vegetation type and transect label where C, B, and S corresponds to cheatgrass, bunchgrass, and sagebrush, respectively. Lines and circles designate transects and soil pits, respectively.

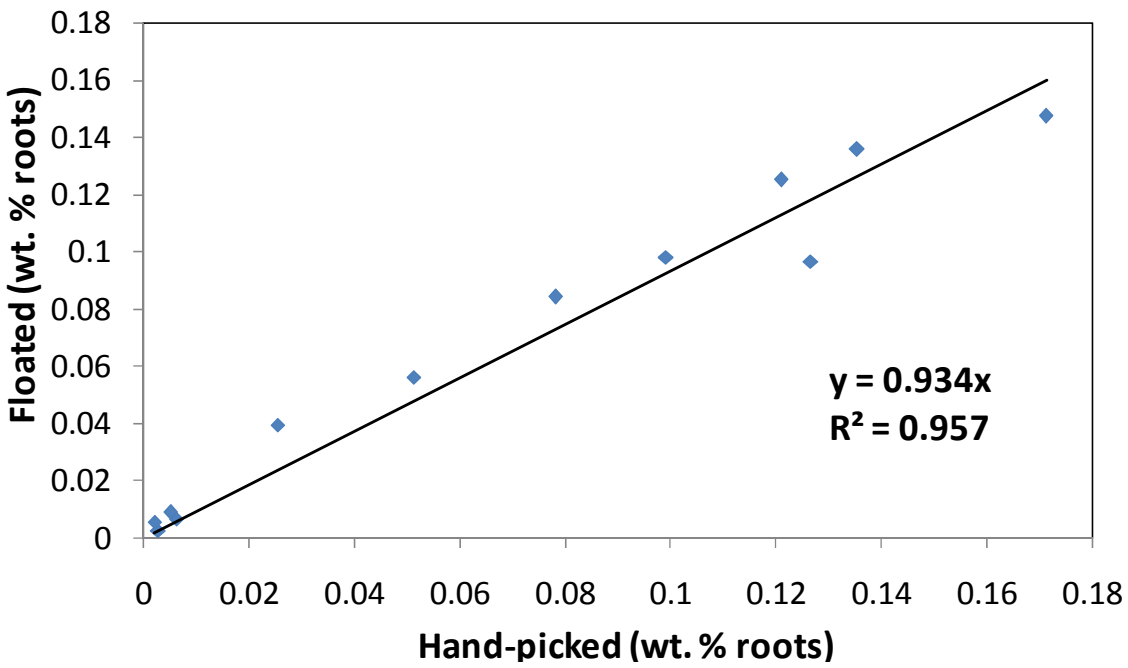

Figure A.3: Qualification of root flotation method used for quantifying R_b and root-C. R_b content was quantified by both handpicking and root flotation of replicate samples to compare values.

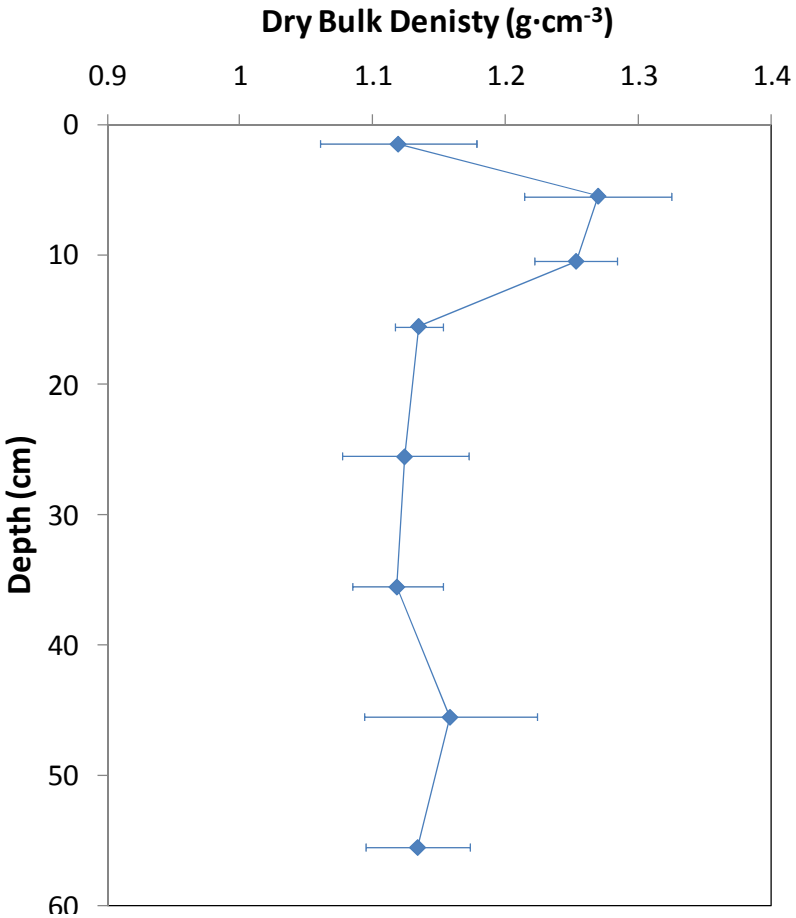

Figure A.4: Depth distribution of dry soil bulk density. Error bars are +/- one standard error (*n* = 4). See Figure 2 for sampling locations.

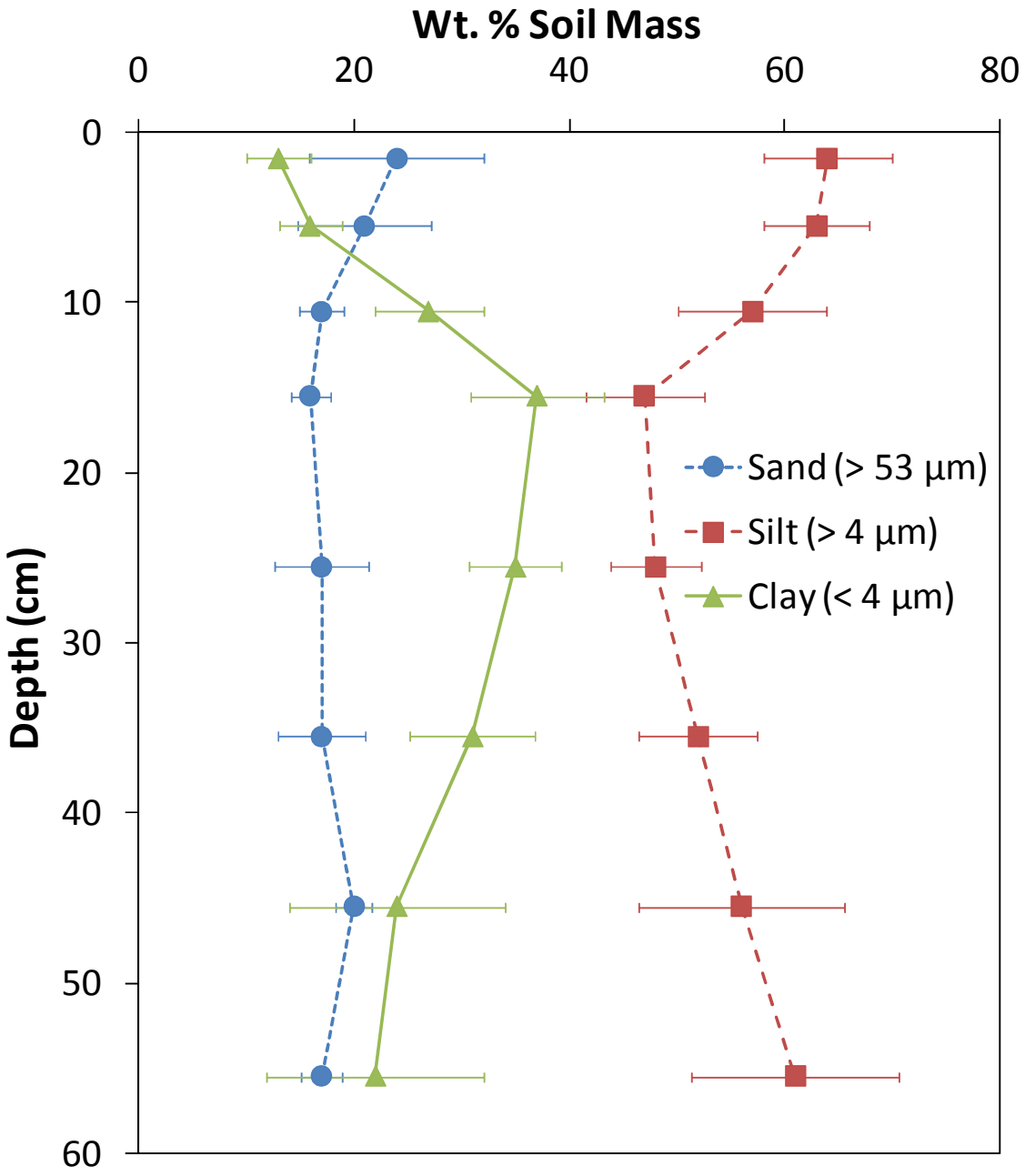

Figure A.5: **Depth distribution of grain size classes. Error bars are +/- 1 standard error (*n* = 4). See Figure 2 for sampling locations.**

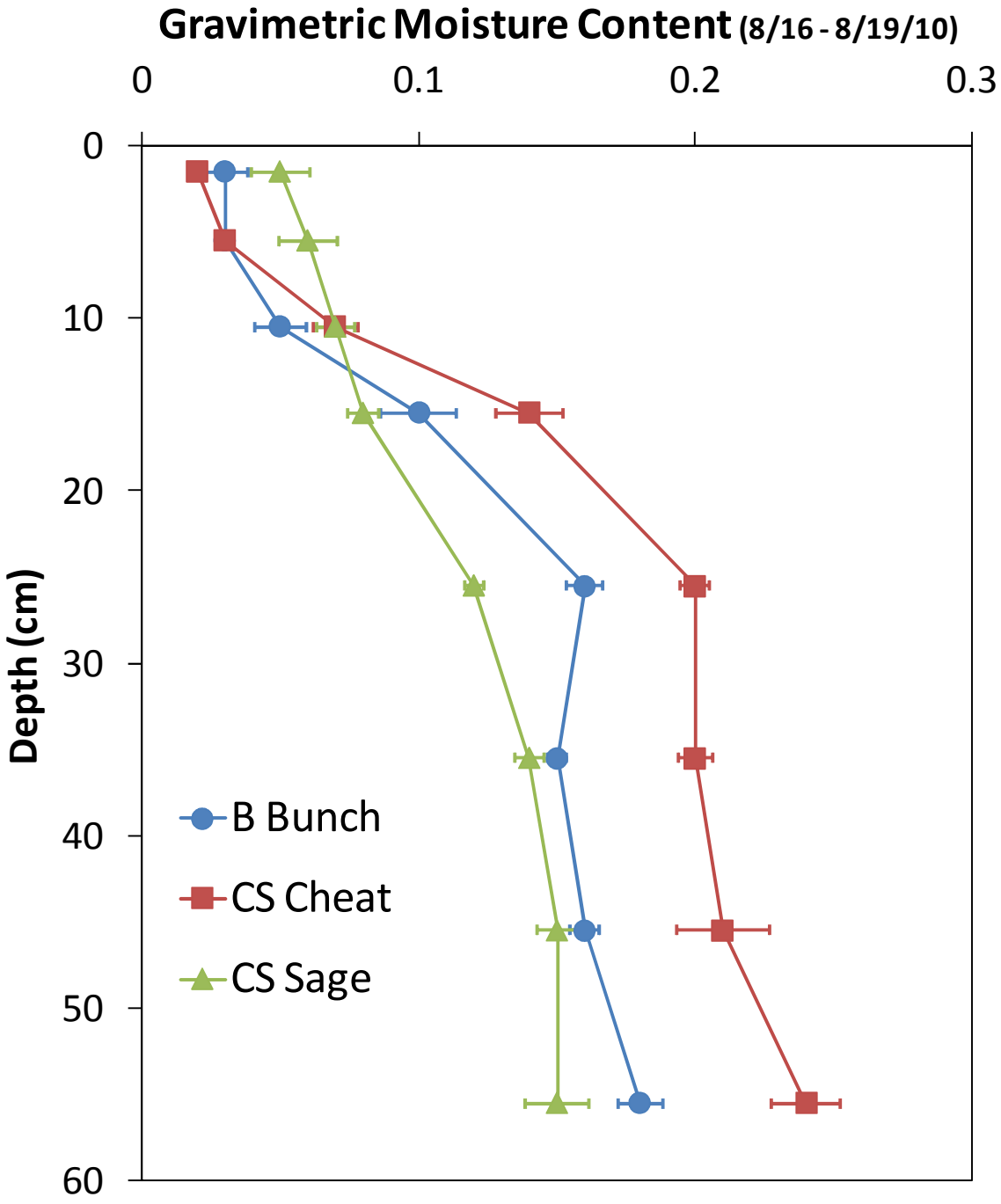

Figure A.6: Depth Distribution of gravimetric moisture content in August 2010. Error bars represent +/- 1 standard error (*n* = 10). See Figure 2 for sampling locations.

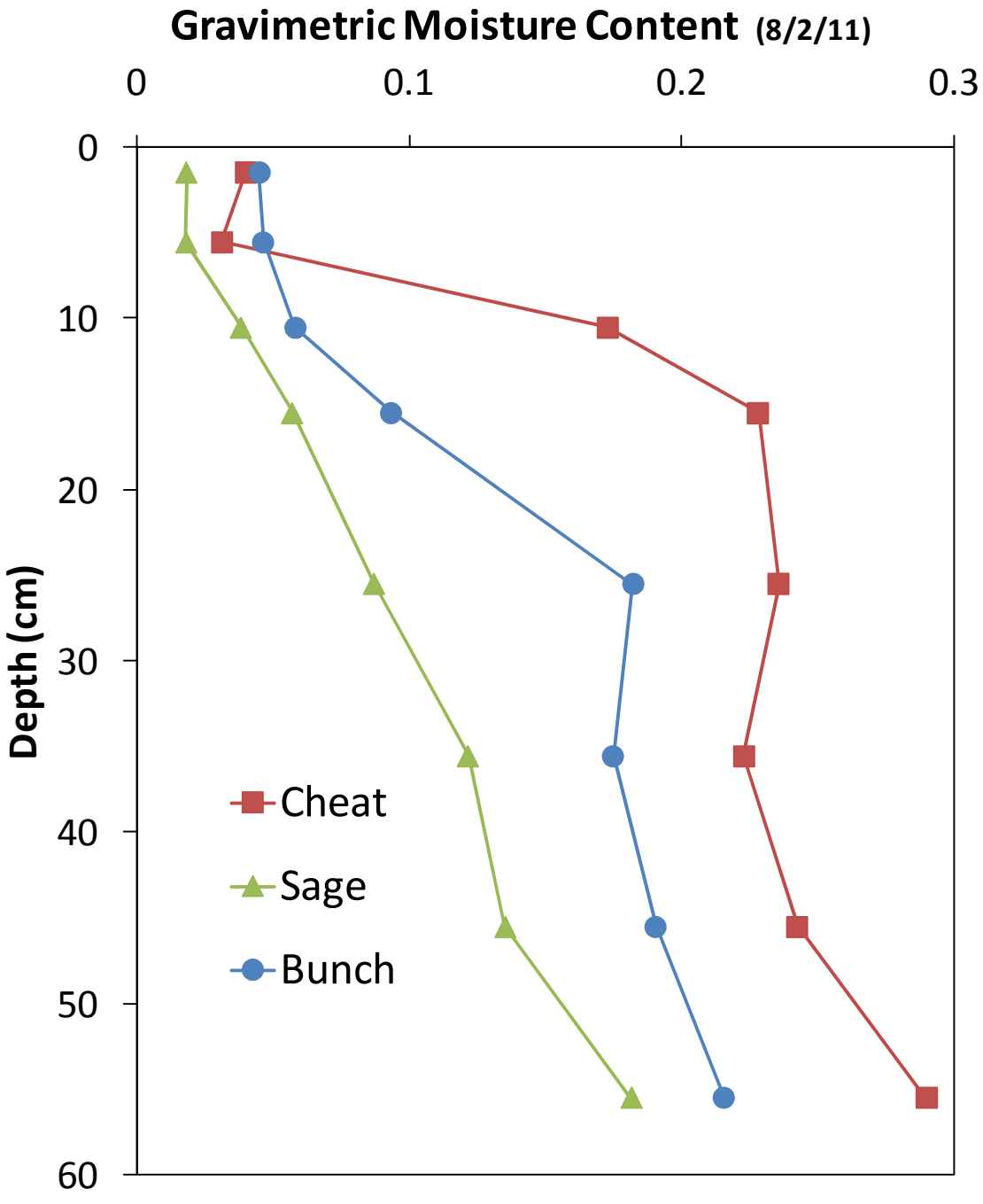

Figure A.7: Depth Distribution of gravimetric moisture content in August 2011. Lack of error bars is due to small sample sizes. See Figure 2 for sampling locations.

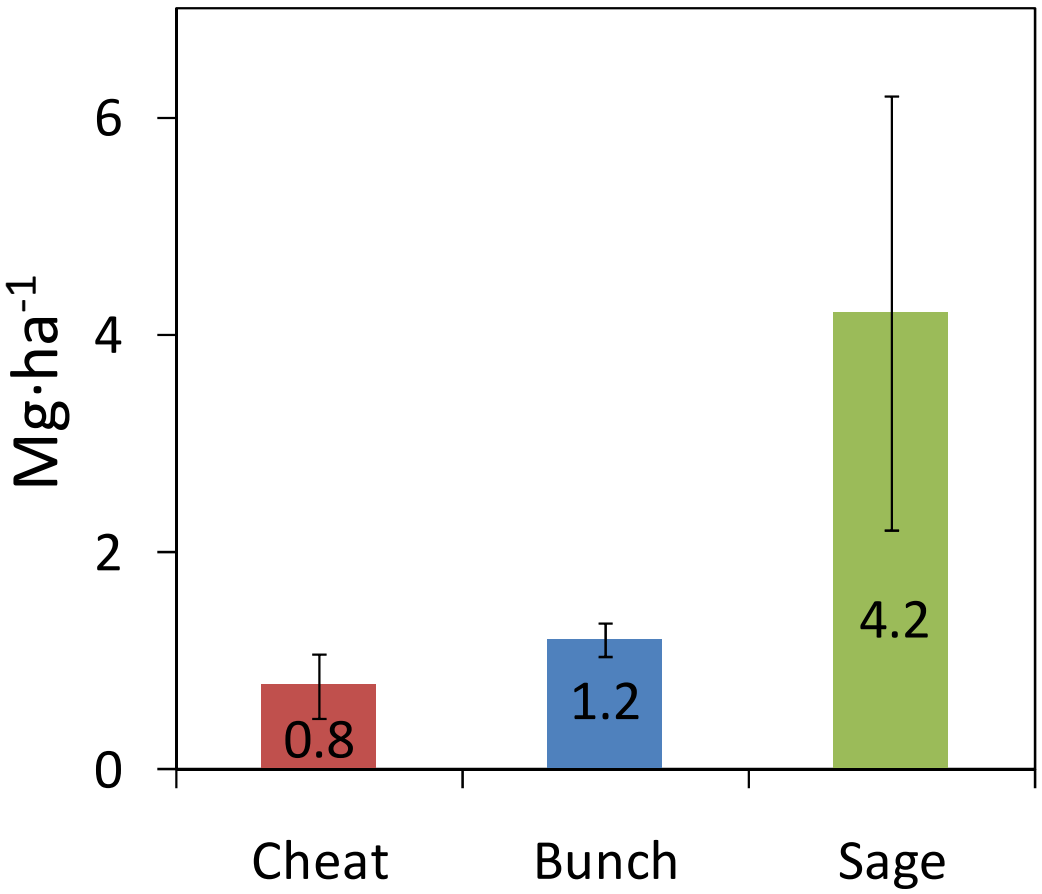

Figure A.8: Results for above-ground biomass. Error bars represent +/- 1 standard deviation (*n* = 3, 3, and 6 for cheat, bunch, and sage, respectively).

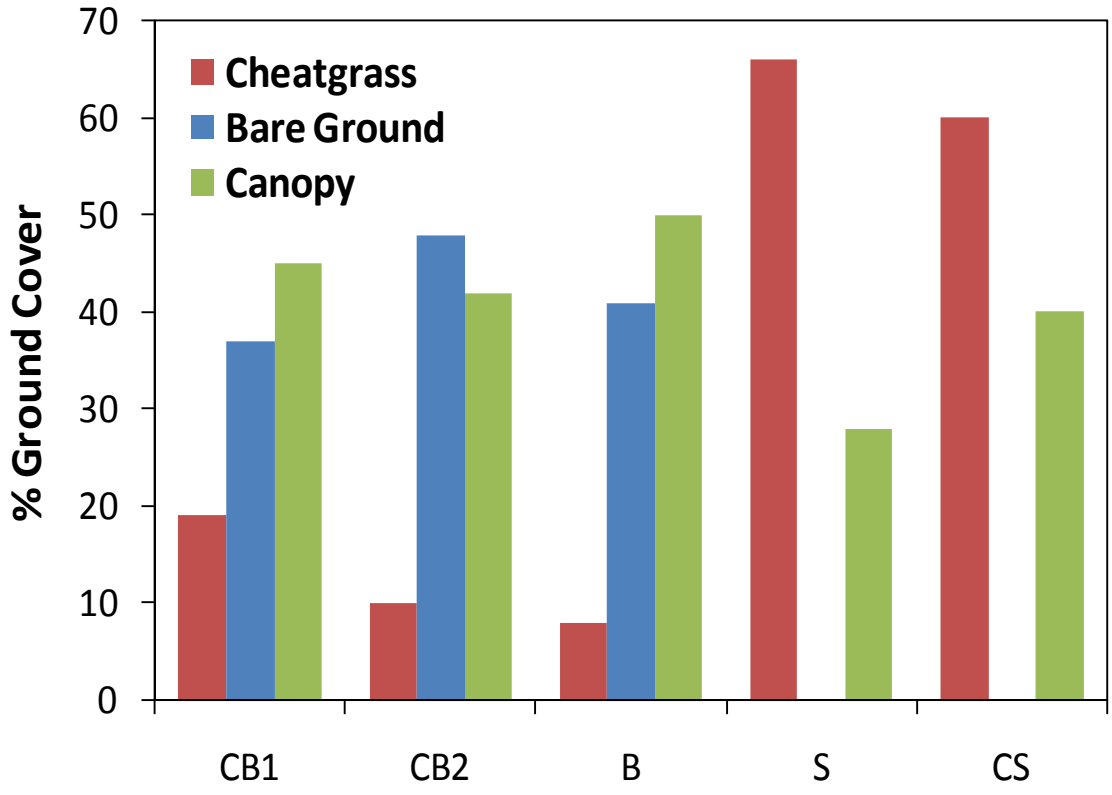

Figure A.9: Percent of ground cover for sampling transects. Ground cover calculated at 5 cm resolution. See Figure 2 for transect locations.

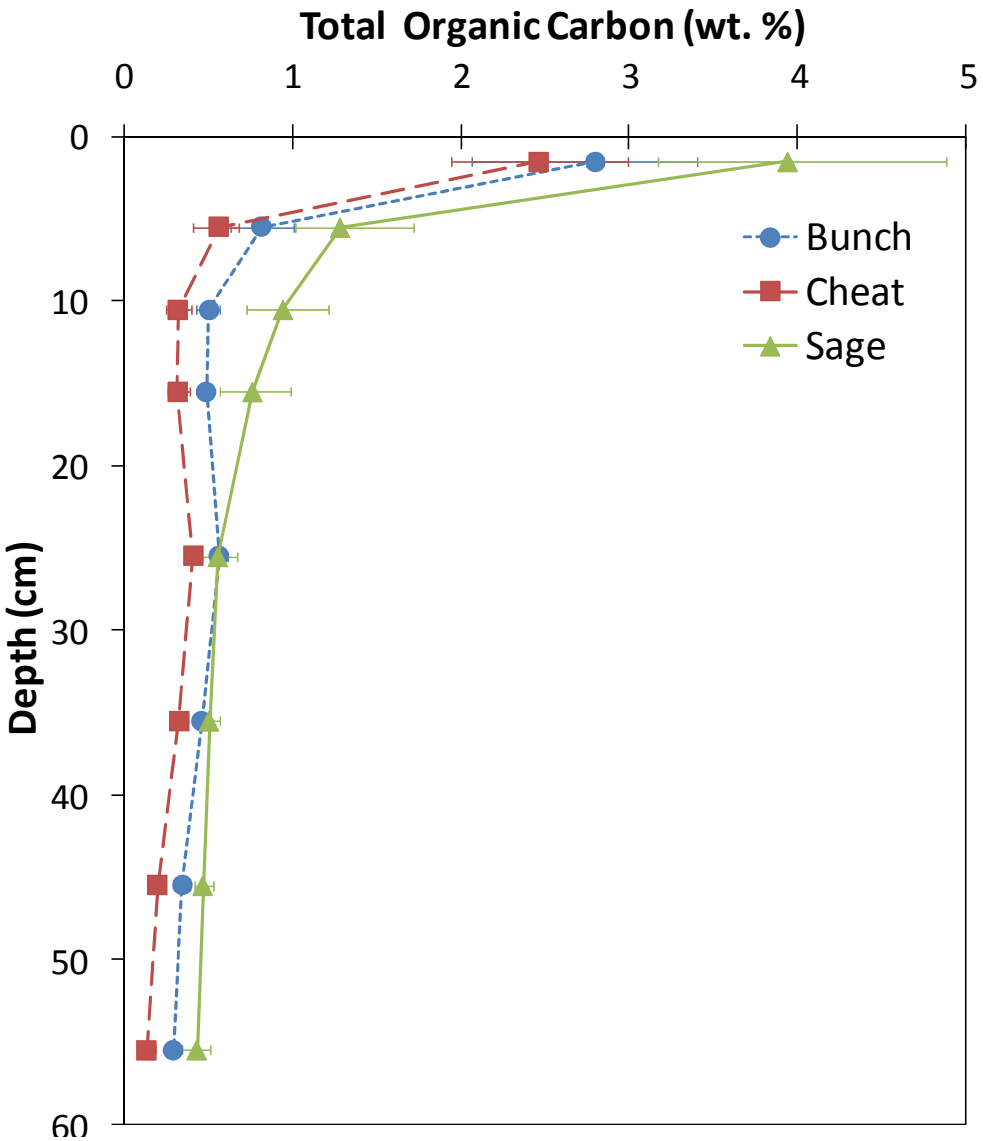

Figure A.10: Total Organic Carbon (TOC) wt. % for each plant community. Population sizes for cheatgrass, bunchgrass, and sagebrush were 38, 31, and 30, respectively, for each depth increment. Error bars represent 95% range in mean values calculated from 100 bootstrap simulations.

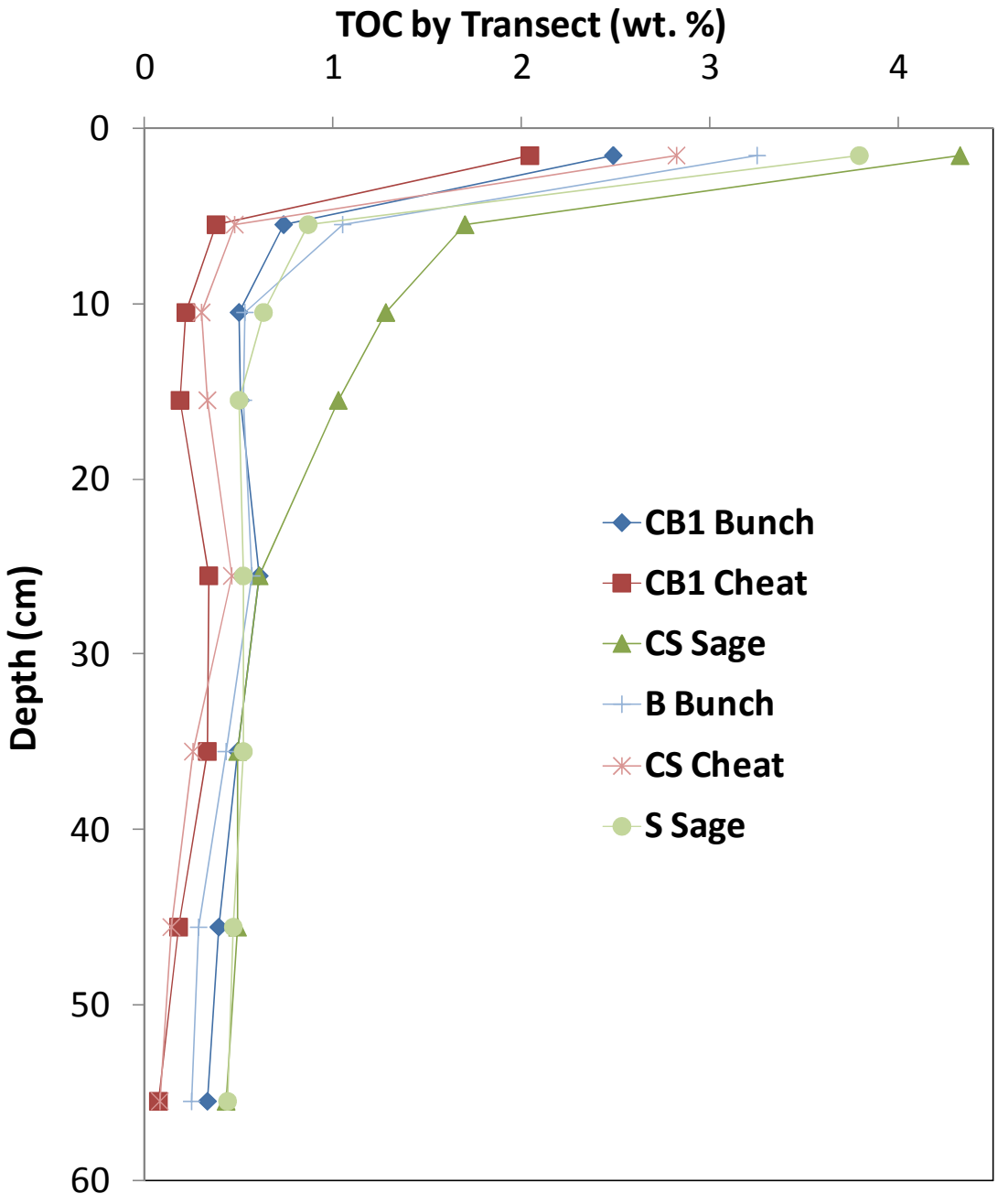

Figure A.11: Total Organic Carbon (TOC) wt. % for each plant community and for individual transects. See Figure 2 for transect locations.

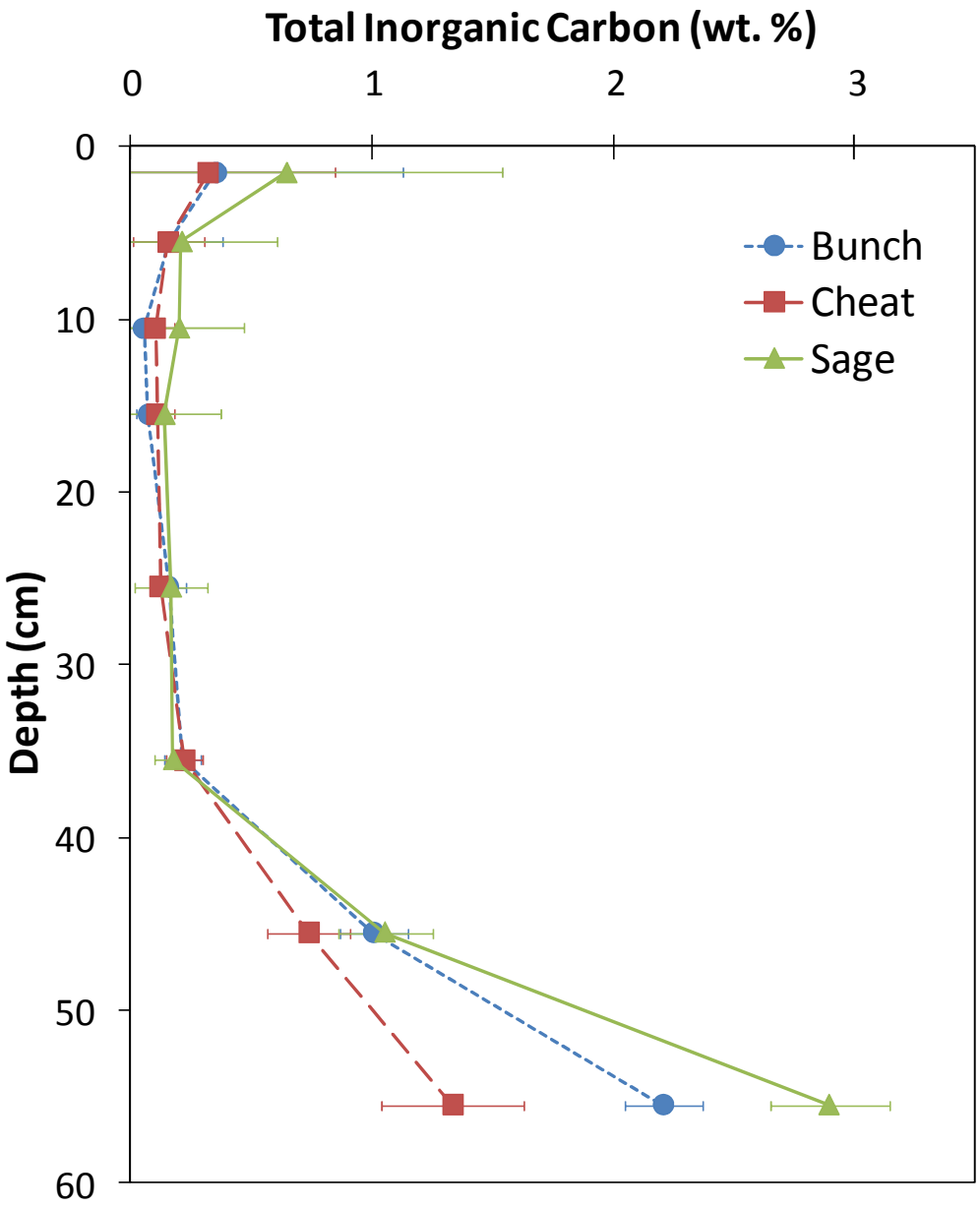

Figure A.12: Total Inorganic Carbon (TIC) wt. % for each plant community. Population sizes for cheatgrass, bunchgrass, and sagebrush were 38, 31, and 30, respectively, for each depth increment. Error bars represent 95% range in mean values calculated from 100 bootstrap simulations.

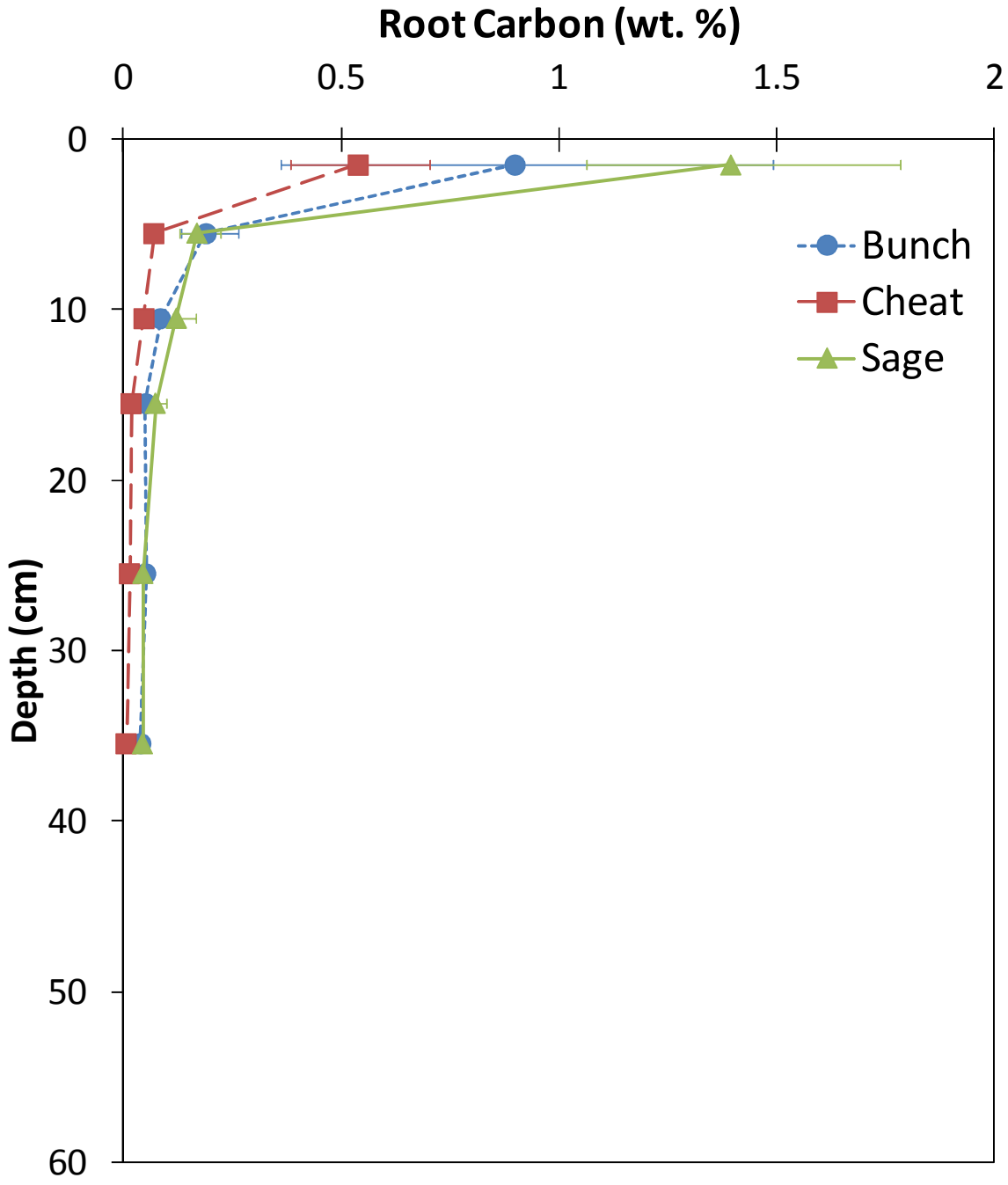

Figure A.13: Root carbon (wt. %) for each plant community. Error bars represent 95% range in mean values calculated from 100 bootstrap simulations. Where error bars are not visible, symbol sizes encompass the error range. R_b values can be calculated by multiplying the above concentrations of root C by a factor of 3.7.

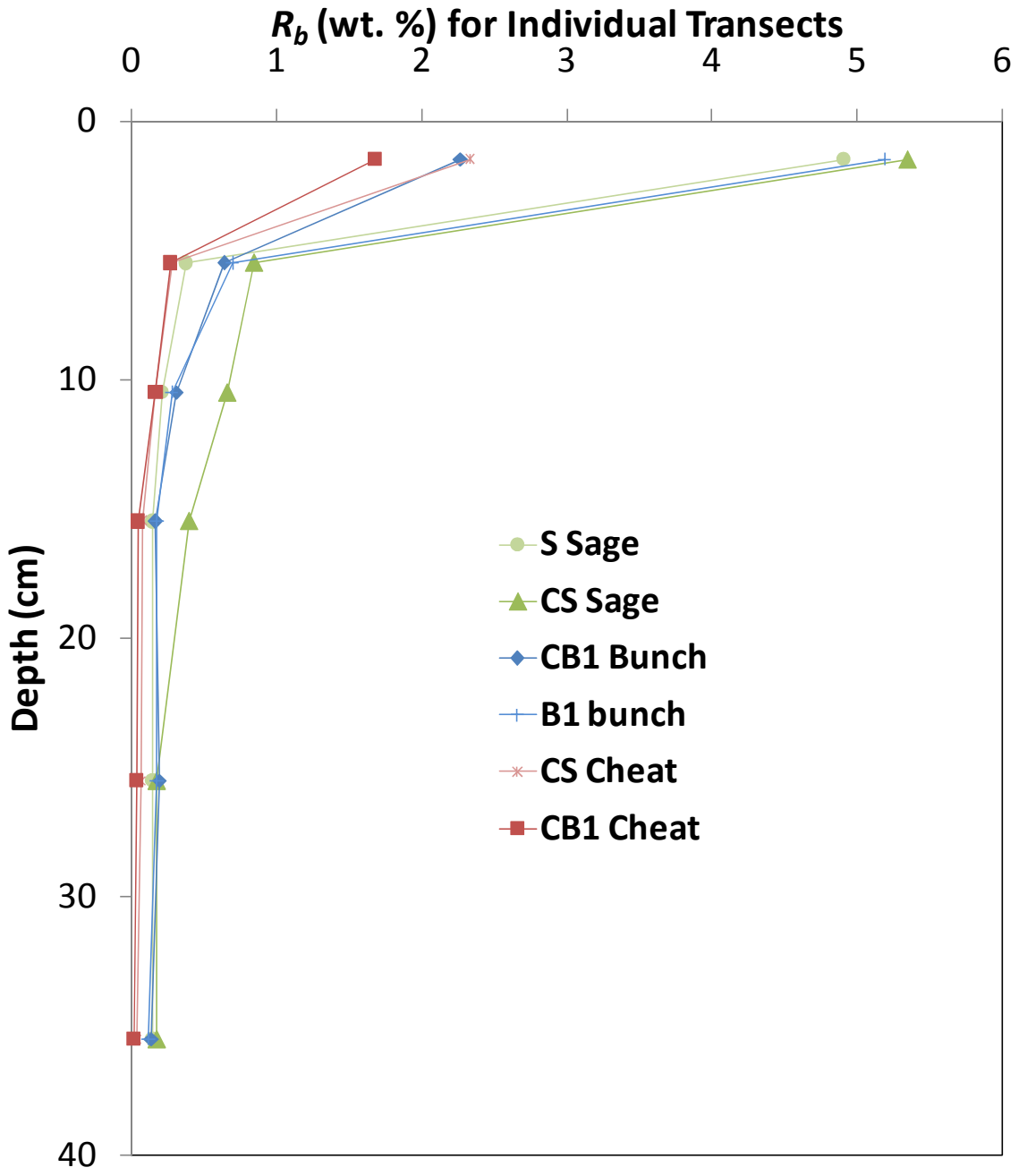

Figure A.14: Root Biomass wt. % (R_b) for each plant community and for individual transects. Root C values can be calculated by multiplying the above concentrations of R_b by a factor of 0.27. See Figure 2 for transect locations.

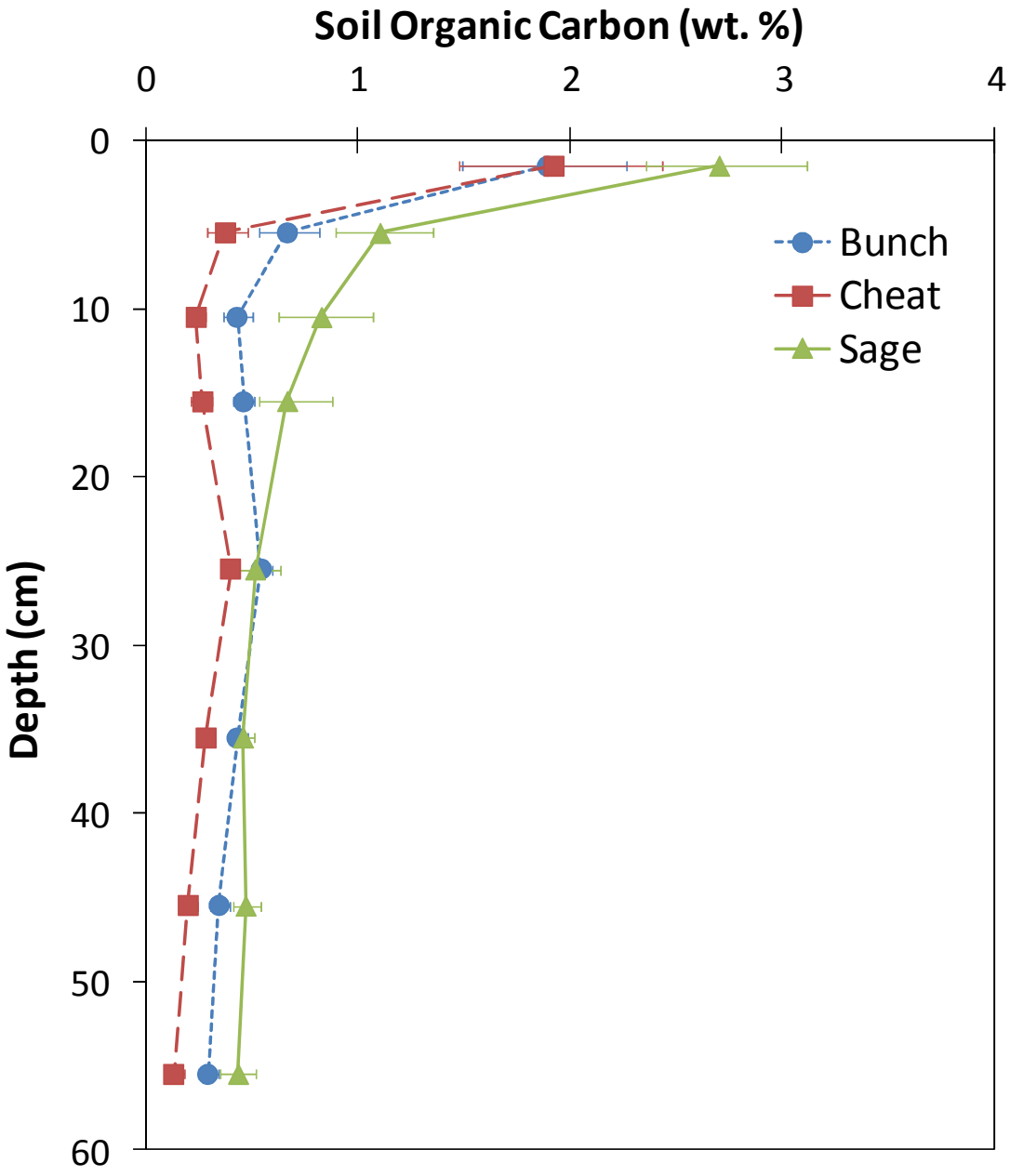

Figure A.15: Soil Organic Carbon wt. % (SOC) for each plant community. Error bars represent 95% range in mean values calculated from 100 bootstrap simulations. Where error bars are not visible, symbol sizes encompass the error range.

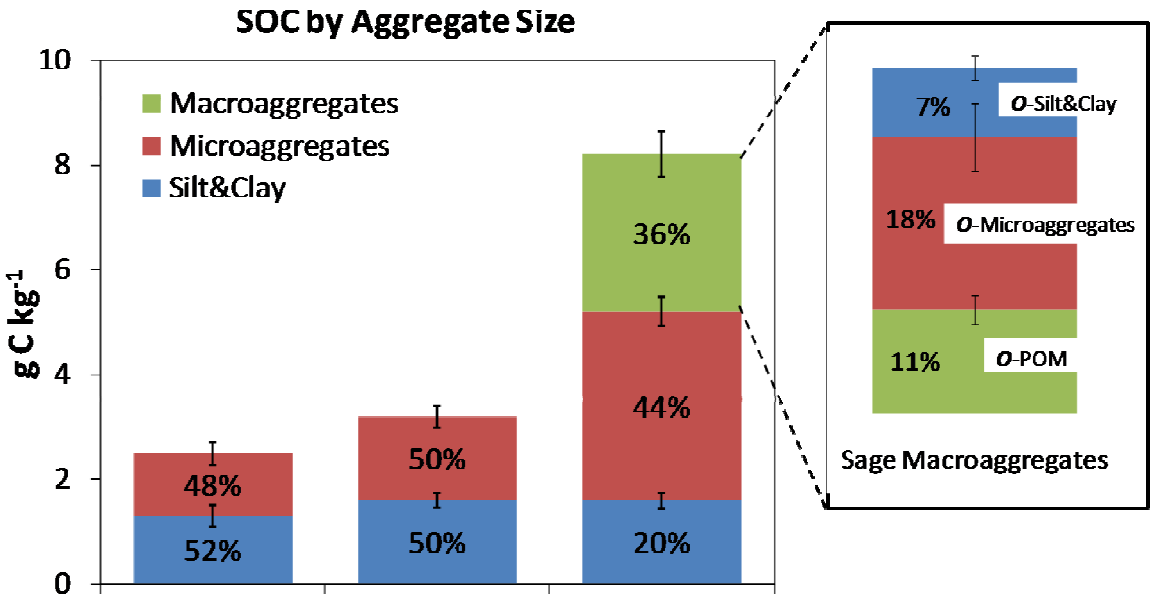

Figure A.16: Grams of SOC per kg soil. Data labels are weighted percent of total Soil Organic Carbon (SOC) by aggregate size for each community. Error bars represent +/- 1 standard error for *n* = 10 (5 from each transect, see Figure 2).

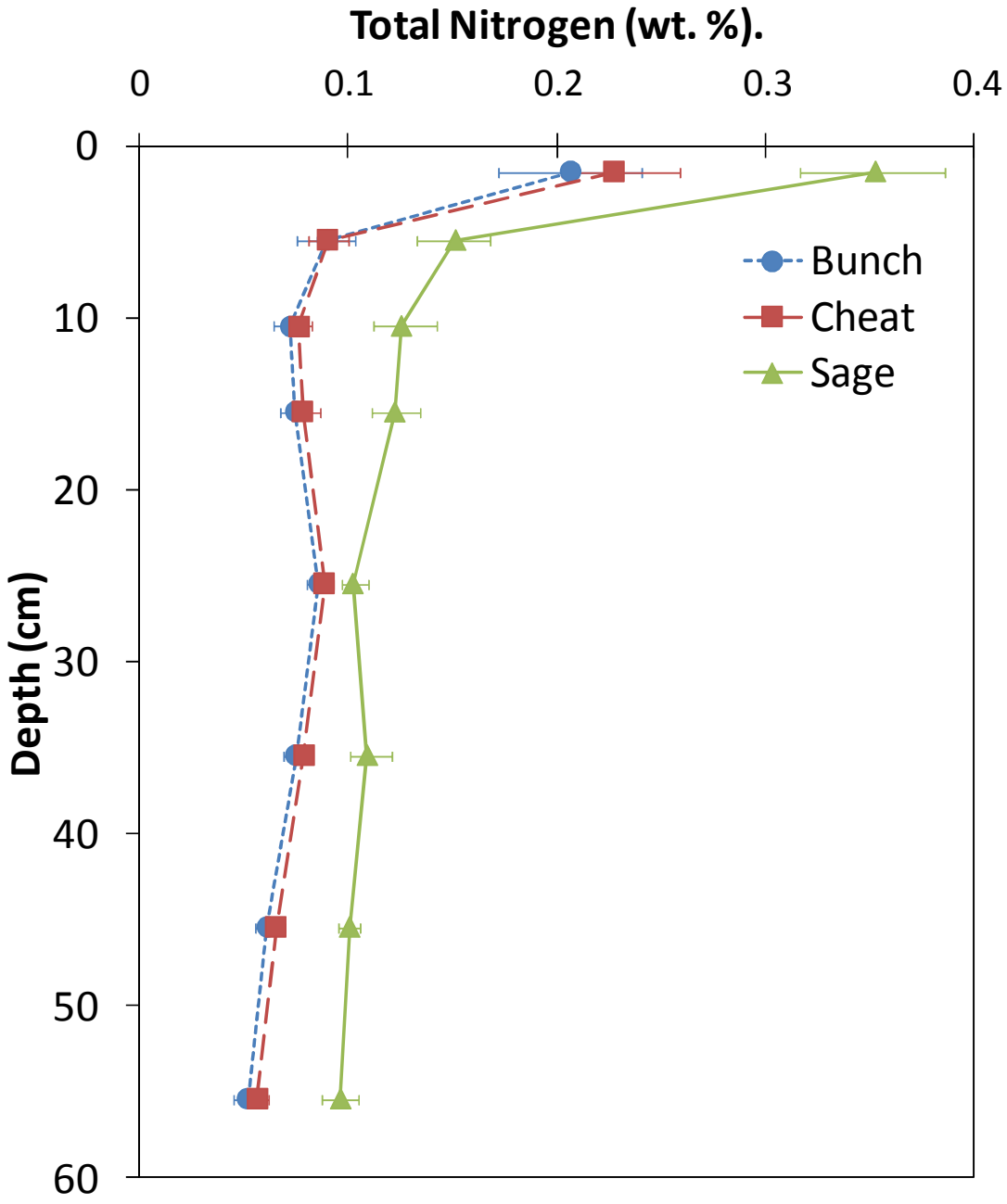

Figure A.17: Total Nitrogen (wt. %) for each plant community. Error bars represent 95% range in mean values calculated from 100 bootstrap simulations. Where error bars are not visible, symbol sizes encompass the error range.

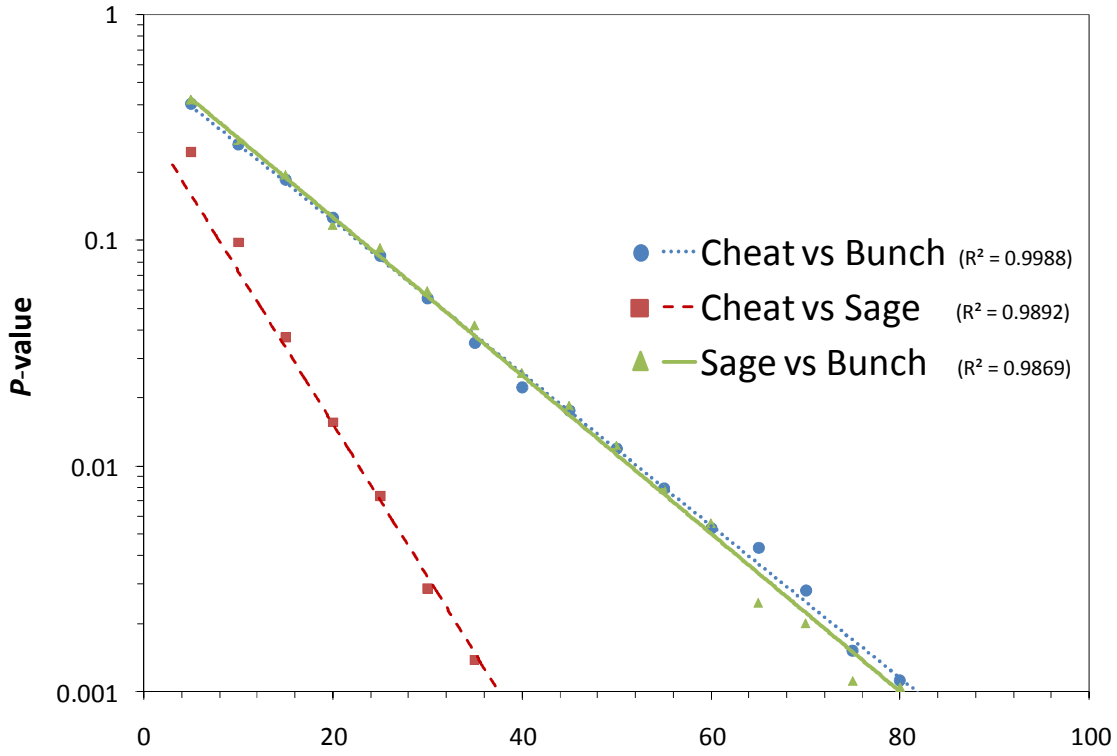

Figure A.18: Estimated number of soil cores needed to determine if two communities are significantly different using the K-S test ($p \leq 0.05$). Average *p*-value is reported for 1000 bootstrap simulations run for each sample size using the current data set.

* Number of Cores indicates the estimated number of soil cores from *each population* to reach a given *p*-value.

APPENDIX B

Tables

Table B.1: Previous Results for Studies Estimating Organic Carbon Pools

C pool	Study	# cores /community	*p* -value	*Sample depth*	Cheat		Bunch		Sage	
Aboveground					% Cover	MgC·ha^{-1}	% Cover	MgC·ha^{-1}	% Cover	MgC·ha^{-1}
	Hooker et al (2008)				80%	1.2 (0.1)	37%	1.3 (0.1)	38%	3.8 (0.7)
	Bradley et al (2006)[1] ‡				2(1) - 37(4)	0.22(0.02)-0.94 (0.26)	---	---	35(5) - 36(7)	3.4 (1.5) - 6.7 (2.9)
	Svejcar and Sheley (2001)[2] ‡				~100	0.12-.14	--	--	1-3	0.1-0.29 *
	This Study				~100	0.8 (0.3)	40-50	1.3 (0.15)	28-40	4.2 (2)
TOC										
	Hooker at al (2008)	20	0.21	0-100 cm		74.1 (4.2)		72.2 (3.5)		64.4 (4.5)
	Norton et al (2004) ‡	21		0-50 cm		18(12)-140(22)		--		36(15)-130 (13)
	Rau et al (2011)[3]	21		0-90 cm		--		--		43-49
	Chen and Stark (2000) ‡	5†	0.12	0-10 cm		--		42**		43**
	Gill et al (1999)	4	0.19	0-100 cm		80		89		102***
	Svejcar and Sheley (2001)[2] ‡	3		0-30 cm		12-17		--		10-16
	Bradley et al (2006)[1] ‡	40		0-10 cm		5.8 (0.3)-16.4 (0.5)		--		10.2(0.4)-12.4 (0.4)
	This Study	30		0-60 cm		26 (7)		35 (10)		48 (14)

* Data for sagebrush collected from sagebrush-steppe communities (bunchgrasses present within interspaces)

** Data collected within sage-steppe communities. Carbon content determined for soils beneath canopies of respective species.

*** Data for shadscale (*Atriplex confertifolia*) reported in place of sagebrush

† Core samples were composited from 9 separate cores collected within a plot (45 total)

‡ A value of 1.2 g·cm^{-3} was used to convert carbon concentrations to units of mass·area^{-1}

[1] Ranges correspond to increaseing levels of cheatgrass invasion and variable bunchgrass compositions

[2] Root mass & root C content averaged for 0 -10 and 10-30 cm depth increments as determined in May 1994. Root C was dded to SOC values determined in July 1994

[3] Data collected within sagebrush communities representing a continuum of cheatgrass invasion.

Table B.2: Results of the Lilliefors Test for Normally Distributed Data

	Cheatgrass						Bunchgrass						Sagebrush					
	TC		**TOC**		**R_b**		**TC**		**TOC**		**R_b**		**TC**		**TOC**		**R_b**	
Depth	*D* [1]	*Pr > D* [2]	*D*	*Pr > D*	*D*	*Pr > D*	*D*	*Pr > D*	*D*	*Pr > D*	*D*	*Pr > D*	*D*	*Pr > D*	*D*	*Pr > D*	*D*	*Pr > D*
0-3	0.139	0.06	0.001	0.2	0.001	0.22	0.321	0.001	0.001	0.339	0.001	0.321	0.118	0.346	0.5	0.098	0.001	0.215
3-8	0.15	0.03	0.072	0.136	0.001	0.211	0.16	0.04	0.027	0.167	0.001	0.271	0.206	0.002	0.022	0.173	0.011	0.184
8-13	0.125	0.135	0.07	0.137	0.002	0.203	0.094	0.5	0.5	0.099	0.002	0.238	0.218	0.001	0.002	0.211	0.001	0.247
13-18	0.166	0.01	0.146	0.123	0.001	0.22	0.084	0.5	0.456	0.108	0.364	0.132	0.256	0.001	0.001	0.235	0.001	0.254
23-28	0.088	0.5	0.5	0.074	0.001	0.214	0.233	0.001	0.315	0.118	0.303	0.137	0.321	0.001	0.001	0.276	0.128	0.141
33-38	0.275	0.001	0.409	0.102	0.001	0.231	0.187	0.007	0.398	0.112	0.301	0.138	0.186	0.011	0.111	0.146	0.112	0.146
43-48	0.322	0.001	0.095	0.137	--	--	0.109	0.448	0.5	0.084	--	--	0.131	0.5	0.5	0.102	--	--
53-58	0.262	0.001	0.005	0.206	--	--	0.106	0.5	0.171	0.135	--	--	0.145	0.477	0.043	0.216	--	--

[1] *D* is the maximum vertical deviation of the empirical cumulative distribution function from a normally distributed cumulative distribution function.

[2] *Pr > D* indicates the probability the two populations are from normal distributions. If less than 0.05, the null hypothesis (of normality) is typically rejected.

Table B.3: Percent Difference in Lab Duplicates for Specific C Pools

	Min	Max	Mean	Median
TC (*n* = 67)	0.33%	54%	8.2%	5.4%
TOC (*n* = 68)	0%	110%	11%	8%
$\mathbf{R_b}$ (*n* = 52)	0%	82%	19%	16%

Table B.4: Mass Percentage by Particle Size Class

Depth	% Sand	% Silt	% Clay	Textural Class
0-3	24 (8)	64 (6)	13 (3)	silt loam
3-8	21 (6)	63 (5)	16 (3)	silt loam
8-13	17 (2)	57 (7)	27 (5)	silt loam
13-18	16 (2)	47 (6)	37 (6)	silty clay loam
18-28	17 (4)	48 (4)	35 (4)	silty clay loam
28-38	17 (4)	52 (6)	31 (6)	silty clay loam
38-38	20 (2)	56 (10)	24 (10)	silt loam
48-58	17 (2)	61 (10)	22 (10)	silt loam

Values in parantheses indicate standard deviation (*n* = 4).

Table B.5: C Pool Sizes by Plant Community

	$Mg\ C \cdot ha^{-1}$		
C Pool	**Cheat**	**Bunch**	**Sage**
Aboveground	0.8 (0.3)a	1.2 (0.2)ab	4.2 (2)b
TC	61 (16)a	87 (14)ab	113 (22)b
TOC	29 (6)a	41 (7)ab	56 (12)b
TIC	32 (22)	46 (21)	57 (34)
Root C	3 (.8)a	6 (3)ab	8 (2.2)b
SOC	26 (5)a	35 (5)ab	48 (9)b

* Within the same row, values with different letters are significantly different ($p \leq 0.05$)

Table B.6: Results of the K-S Test for Significant Difference

	Cheat vs Sage				Cheat vs Bunch				Bunch vs Sage			
	TOC		**R_b**		**TOC**		**R_b**		**TOC**		**R_b**	
Depth	*D* [1]	*Pr > D* [2]	*D*	*Pr > D*	*D*	*Pr > D*	*D*	*Pr > D*	*D*	*Pr > D*	*D*	*Pr > D*
0-3	0.432	0.0025	0.468	0.0017	0.14	0.8705	0.183	0.7359	0.533	0.0002	0.509	0.002
3-8	0.477	0.0006	0.414	0.0072	0.292	0.0881	0.397	0.022	0.349	0.0362	0.165	0.835
8-13	0.599	< 0.0001	0.54	0.0001	0.441	0.0016	0.537	0.0005	0.434	0.0046	0.249	0.344
13-18	0.472	0.0007	0.61	< 0.0001	0.52	0.0001	0.579	0.0001	0.401	0.0101	0.239	0.394
23-28	0.263	0.1655	0.67	< 0.0001	0.517	0.0001	0.663	< 0.0001	0.306	0.0914	0.252	0.33
33-38	0.526	0.0001	0.83	< 0.0001	0.5	0.0002	0.794	< 0.0001	0.175	0.708	0.186	0.721
43-48	0.714	< 0.0001			0.521	0.0001			0.503	0.0025		
53-58	0.713	< 0.0001			0.637	< 0.0001			0.621	0.0003		

[1] *D* is the maximum vertical deviation of the empirical cumulative distribution functions for the two populations being compared.

[2] *Pr > D* indicates the probability the two populations are from different distributions. If less than 0.05, the null hypothesis (populations from the same distribution) is typically rejected.

Table B.7: Depth Distribution of TOC

	TOC ($Mg \cdot ha^{-1}$)		
Depth	**Cheat**	**Bunch**	**Sage**
0-3	8.9 (1.9)a	10.1 (2.4)ab	14.2 (3.5)b
3-8	3.4 (0.8)a	4.9 (1.1) ab	7.7 (1.9)b
8-13	1.9 (0.4)a	3 (0.4)b	5.7 (1.3)c
13-18	1.9 (0.4)a	2.9 (0.3)b	4.6 (1.3)c
18-28	4.9 (0.5)a	6.8 (0.6)b	6.7 (1.4)ab
28-38	3.9 (0.5)a	5.5 (0.5)b	6.1 (0.8)b
38-48	2.4 (0.5)a	4.2 (0.5)b	5.7 (0.8)c
48-58	1.6 (0.5)a	3.5 (0.6)b	5.2 (1)c
Total	29 (5.5)a	40.9 (6.4)ab	55.9 (12)b

* Within the same row, values with different letters are significantly different ($p \leq 0.05$)

Table B.8: Depth Distribution of Root C

	Root C ($Mg \cdot ha^{-1}$)		
Depth	**Cheat**	**Bunch**	**Sage**
0-3	1.9 (0.6)a	3.2 (2)ab	5 (1.3)b
3-8	0.4 (0.08)a	1.1 (0.4)b	1 (0.3)b
8-13	0.3 (0.06)a	0.51 (0.14)b	0.7 (0.2)b
13-18	0.1 (0.03)a	0.29 (0.06)b	0.4 (0.13)b
18-28	0.2 (0.04)a	0.63 (0.13)b	0.5 (0.12)b
28-38	0.1 (0.03)a	0.46 (0.11)b	0.5 (0.11)b
Total	2.8 (0.8)a	6.3 (2.9)ab	8.3 (2.2)a

* Within the same row, values with different letters are significantly different ($p \leq 0.05$). R_b values can be calculated by multiplying the above values by a factor of 3.7.

Table B.9: Depth Distribution of SOC

	SOC ($Mg \cdot ha^{-1}$)		
Depth	**Cheat**	**Bunch**	**Sage**
0-3	6.9 (1.8)	6.8 (1.8)	9.7 (1.6)
3-8	2.3 (0.5)a	4 (1.1)b	6.6 (1.6)b
8-13	1.4 (0.4)a	2.6 (0.4)b	5 (1.2)c
13-18	1.6 (0.3)a	2.8 (0.3)b	4 (1)b
18-28	4.8 (0.5)a	6.5 (0.6)b	6.2 (1.1)b
28-38	3.4 (0.5)a	5.2 (0.4)b	5.5 (0.5)b
38-48 *	2.4 (0.5)a	4.2 (0.5)b	5.7 (0.8)c
48-58 *	1.6 (0.5)a	3.5 (0.6)b	5.2 (0.1)c
Total	25.5 (5)a	34.7(5.7)ab	47.9 (8.8)b

* Root C was below level of detection. and SOC was assumed to equal TOC

** Within the same row, values with different letters are significantly different ($p \leq 0.05$). R_b values can be calculated by multiplying the above values by a factor o 3.7.

Table B.10: Mass Percentage of Soil and SOC Content of Aggregates

	Agggregate Size					
	> 250 µm		**53-250 µm**		**< 53 µm**	
Community	wt. % Soil	wt. % SOC	wt. % Soil	wt. % SOC	wt. % Soil	wt. % SOC
Bunch	6	0*	50	0.33	44	0.36
Cheat	7	0*	47	0.24	45	0.27
Sage	22	1.49	49	0.73	27	0.62

* Particles greater than 250 µm consisted entirely of rock and root fragments

Table B.11: C/N Ratio of Aggregate Sizes

	Aggregate Size		
	> 250 µm	**53-250 µm**	**< 53 µm**
Bunch		3.8 (0.5)	3.4 (0.3)
Cheat		3.1 (0.6)	2.6 (0.4)
Sage	8.7 (0.7)	6.4 (0.5)	5.2 (0.4)

Values in parantheses are one standard error (n= 10).

Table B.12: Percentage of TOC by Mass (Root C and SOC)

	Cheat		Bunch		Sage	
	Root C	SOC	Root C	SOC	Root C	SOC
0-3	22	78	32	68	35	65
3-8	13	87	23	77	13	87
8-13	15	85	17	83	13	87
13-18	6	94	10	90	10	90
18-28	3	97	9	91	8	92
28-38	2	98	8	92	9	91
38-48 *	0	100	0	100	0	100
48-58 *	0	100	0	100	0	100
Total	**10**	**90**	**15**	**85**	**14**	**86**

Values are percent mass of total organic carbon (TOC) for distinct C pools and for each plant community.

Human-started wildfires expand the fire niche across the United States

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The economic and ecological costs of wildfire in the United States have risen substantially in recent decades. Although climate change has likely enabled a portion of the increase in wildfire activity, the direct role of people in increasing wildfire activity has been largely overlooked. We evaluate over 1.5 million government records of wildfires that had to be extinguished or managed by state or federal agencies from 1992 to 2012, and examined geographic and seasonal extents of human-ignited wildfires relative to lightning-ignited wildfires. Humans have vastly expanded the spatial and seasonal "fire niche" in the coterminous United States, accounting for 84% of all wildfires and 44% of total area burned. During the 21-y time period, the human-caused fire season was three times longer than the lightning-caused fire season and added an average of 40,000 wildfires per year across the United States. Human-started wildfires disproportionally occurred where fuel moisture was higher than lightning-started fires, thereby helping expand the geographic and seasonal niche of wildfire. Human-started wildfires were dominant (>80% of ignitions) in over 5.1 million km^2, the vast majority of the United States, whereas lightning-started fires were dominant in only 0.7 million km^2, primarily in sparsely populated areas of the mountainous western United States. Ignitions caused by human activities are a substantial driver of overall fire risk to ecosystems and economies. Actions to raise awareness and increase management in regions prone to human-started wildfires should be a focus of United States policy to reduce fire risk and associated hazards.

anthropogenic wildfires | fire starts | ignitions | modern fire regimes | wildfire causes

The United States has experienced some of the largest wildfire years this decade, with over 36,000 km^2 burned in 2006, 2007, 2012, and 2015 (1). There is national and global concern over how fire regimes have changed in the past few decades and how they will change in the future (2–4). In the western United States, there is strong evidence that regional warming and drying, including that directly attributed to anthropogenic climate change, are linked to increased fire frequency and size and longer fire seasons (5–9). However, the role that humans play in starting these fires and the direct role of human-ignitions on recent increases in wildfire activity have been overlooked in public and scientific discourse because of the difficulty in ascribing a cause, either human- or lightning-started (10). Humans primarily alter fire regimes in three ways: changing the distribution and density of ignitions, shifting the seasonality of burning, or altering available fuels (2, 3). Geographic variability in regional and continental-scale fire activity in the United States is strongly tied to proxies for these human-caused changes, including population and road density, and different land-use and development patterns (10–15). Although changing climate and fuels also influence fire regimes across the United States (10, 16, 17), there can be no fire without an ignition source. Here, we explore the role that human-started wildfires play in modern United States fire regimes.

Ignitions are often presumed to be saturated (18, 19), and therefore have limited ability to predict fire activity. However, several studies suggest that humans play an important role in redistributing ignitions (20–22), particularly where lightning rarely occurs or where lightning is not concurrent with dry conditions (23). The human–fire connection in the modern era appears strongest at intermediate levels of development, as fires become less likely in the landscape beyond a certain population density, level of urbanization, or dependence on fossil fuels (11, 13, 24). Overall, humans expand the spatial and temporal "fire niche" by introducing ignitions into landscapes when fuels are sufficiently dry enough to ignite and carry fire, but when lightning is rare. Human ignitions are therefore a critical force acting to expand how the fire niche is realized across United States ecoregions.

National-scale analysis of human alteration of the fire niche is critical given that the annual expense of fighting wildfires has exceeded $2 billion in recent years, and the accrued direct and indirect impacts of wildfire on infrastructure and communities could be 30 times that amount (25). Policies that govern wildfire management and response are also directed at the national level, demanding analysis at a national scale (10, 22, 26). Although recent human influence on fire regimes has been studied at local (13) to regional scales (14), human influence nationally remains poorly understood (10). National policies can strongly influence fire regimes (27) and, with sufficient information on human ignitions, policy directives could target human behavior in ways that remediate increasing trends in wildfire risk.

Here, we ask how human ignitions have altered the spatial extents, seasonality, and temporal trends in wildfire across the coterminous United States. We analyze over 1.5 million records of both human- and lightning-started fires in the United States from

Significance

Fighting wildfires in the United States costs billions of dollars annually. Public dialog and ongoing research have focused on increasing wildfire risk because of climate warming, overlooking the direct role that people play in igniting wildfires and increasing fire activity. Our analysis of two decades of government agency wildfire records highlights the fundamental role of human ignitions. Human-started wildfires accounted for 84% of all wildfires, tripled the length of the fire season, dominated an area seven times greater than that affected by lightning fires, and were responsible for nearly half of all area burned. National and regional policy efforts to mitigate wildfire-related hazards would benefit from focusing on reducing the human expansion of the fire niche.

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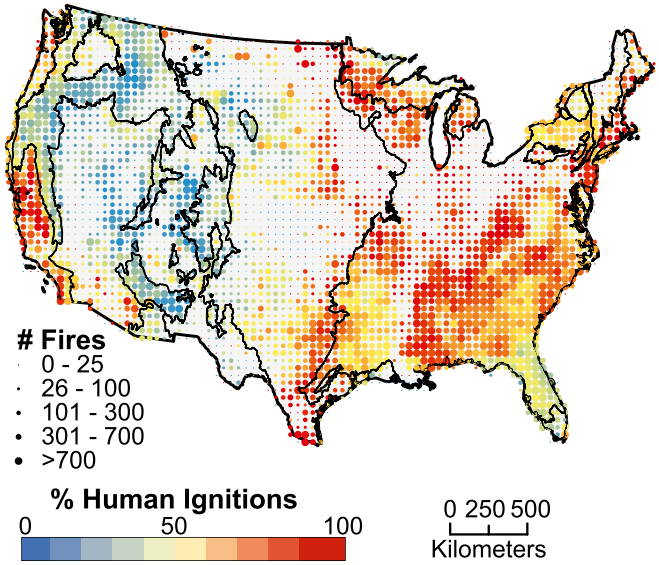

Fig. 1. The total number of wildfires (dot size) and the proportion started by humans (dot color: red indicating greater number of human started fires) within each 50 km × 50-km grid cell across the coterminous United States from 1992 to 2012. Black lines are ecoregion boundaries, as defined in the text.

1992 to 2012 (28). All of these wildfires necessitated an agency response to manage or suppress them, and therefore posed a threat to ecosystems or infrastructure; this record does not include intentionally set prescribed burns or managed agricultural fires. To our knowledge, this is the most comprehensive assessment of the role of human-started wildfires across the United States over the past two decades. We compare: (*i*) the spatial extents of human- vs. lightning-started wildfires, (*ii*) the seasonality of human vs. lightning wildfires, (*iii*) the climate niche for human- vs. lightning-started wildfires, and (*iv*) 21-y trends in large human vs. lightning wildfires. Our analysis documents the pronounced expansion of wildfire extent, seasonality of wildfires, and increasing numbers of large wildfires through time as a result of human-related ignitions across the United States.

Human-Related Ignitions Vastly Expanded the Extent of Wildfire

Human-started wildfires represented 84% of the 1.5 million wildfires included in this analysis (n = 245,446 lightning-started fires; n = 1,272,076 human-started wildfires). The eastern United States and western coastal areas were dominated by human-started wildfires, whereas lightning-started fires dominated the mountainous regions of the western United States (Fig. 1, Table 1 and Table S1). Here we define a fire regime as dominated by either human or lighting ignitions when one cause accounts for more than 80% of the number of fires in a given 50 × 50-km grid cell. Based on this definition, 5.1 million km^2, or 60% of the total land area of the coterminous United States, was dominated by human-started wildfires, whereas only 0.7 million km^2, or 8% of the area, was dominated by lightning-started fires. In addition to expanding the numbers of fires, humans also expanded the total area burned. Human-started wildfires burned a total of 160,274 km^2, or ∼44% of the total area burned from 1992 to 2012 (Table 1).

Human-Related Ignitions More Than Tripled the Length of the Wildfire Season

Human ignitions dramatically expanded the wildfire season in the United States, particularly during spring. The length of the human-started wildfire season [defined as the interquartile range (IQR) of human-ignited fires] was 154 d, more than triple that of the lightning wildfire season (IQR = 46 d) (Fig. 2 and Table 1). This national-scale expansion is driven by earlier (spring) human-started fires in eastern ecoregions coupled with later (late summer or fall) human-started fires in western ecoregions (Table S2). The median discovery date for human-started fires was over 2-mo (May 20th) earlier than lightning-started fires (July 25th). Summed across the 21-y record, the most common day for human-started fires by far was July 4th, US Independence Day, with 7,762 fires starting that day over the course of the record (Fig. 2), whereas, the most common day for lightning-started fires was July 22nd. Of all lightning-ignited fires, 78% occurred in the summer (June–August), 9% in the spring (March–May), and 12% in the fall (September–November). In contrast, human-ignited wildfires were more evenly distributed throughout the year, with 24% in summer, 38% in spring, 19% in fall, and 19% in winter. This pronounced expansion of the wildfire season was also evident spatially (Fig. 3), with human-ignited wildfires occurring predominantly in spring in the eastern United States and in the fall and winter in Texas and the Gulf states. See Table S1 for state-level analysis. When lightning-started fires were rare (<5% and >95% quantile; i.e., before May 13th or after September 16th), humans ignited 842,289 wildfires, effectively increasing the number of wildfires 35-fold compared with the 24,081 lightning-ignited wildfires during these spring, fall, and winter seasons.

Table 1. The number of wildfires, total burned area (ha), and fire season length (IQR, in days), by ecoregion (ordered by percent human-caused fires) and within the coterminous United States from 1992 to 2012

	No. of fires			Area burned (ha)			Length (IQR, days)		
Ecoregion	Human	Light	Human caused (%)	Human	Light	Human caused (%)	Human	Light	Human expansion (%)
MC	87,274	2,855	97	2,143,282	253,210	89	85	45	189
NF	61,673	2,574	96	302,561	82,721	79	51	79	N/A
ETF	815,499	44,859	95	3,827,045	829,293	82	167	66	253
MWCF	14,586	925	94	19,251	27,291	41	67	52	129
GP	134,944	17,586	88	3,992,557	2,564,955	61	148	47	315
SSH	7,504	2,167	78	340,873	254,418	57	55	41	134
TWF	4,832	1,917	72	357,150	350,477	50	98	52	188
NAD	55,422	52,044	52	2,394,677	8,880,691	21	92	40	230
NFM	76,735	94,017	45	1,895,622	5,731,733	25	75	36	208
TS	13,607	26,502	34	754,393	1,152,064	40	85	39	218
CONUS	1,272,076	245,446	84	16,027,412	20,126,852	44	154	46	335

CONUS, Coterminous United States; ETF, Eastern Temperate Forests; GP, Great Plains; MC, Mediterranean California; MWCF, Marine West Coast Forests; NAD, North American Desert; NF, Northern Forests; NFM, Northwest Forested Mountains; SSH, Southern Semiarid Highlands; TWF, Tropical Wet Forests; TS, Temperate Sierras.

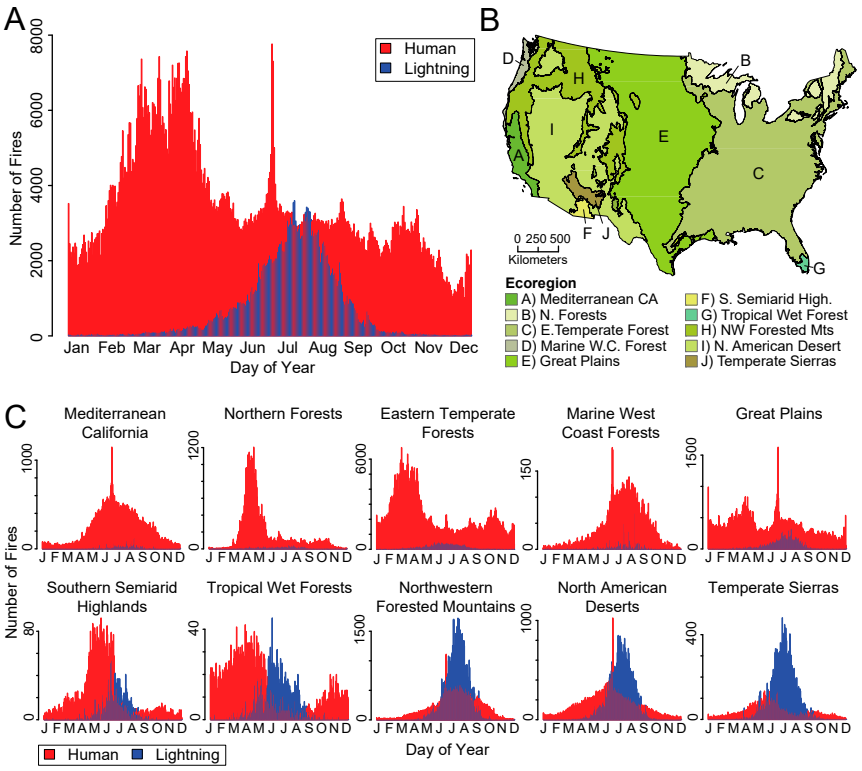

Fig. 2. Frequency distributions of human and lightning-caused wildfires by Julian day of year. (*A*) Frequency distribution of wildfires across the coterminous United States from 1992 to 2012 (n = 1.5 million); (*B*) map of United States ecoregions; (*C*) frequency distributions of wildfires by ecoregions, ordered by decreasing human dominance.

Human-Driven Expansion of the Fire Niche

Humans greatly expanded the natural fire niche (Fig. 4), which we calculated as the co-occurrence of the average monthly lightning density and 1,000-h dead fuel moisture. Regions and seasons of moderate to high lightning-started fire density (>0.4 fires per 1,000 km^2 per month) had a median lightning-strike density of 0.19 (IQR: 0.065–0.57) strikes per square kilometer per month and a median 1,000-h fuel moisture of 11.9% (IQR: 9.25–15.6%) (Fig. 4*A*). In contrast, regions and seasons of moderate to high human-started fire density (>0.4 fires per 1,000 km^2 per month) had a median lightning-strike density of only 0.11 (IQR: 0.025–0.39) strikes per square kilometer per month and a median 1,000-h fuel moisture of 17.8% (IQR: 15.95–19.25%) (Fig. 4*B*). The median fuel moisture and lightning conditions when human-started wildfires occurred were significantly different from those values for lightning-started fires ($P < 0.0001$). Areas and months of moderate to high human-caused fire density had approximately 40% fewer lightning strikes, and nearly 50% higher fuel moisture levels (based on median values) than for moderate to high lightning-caused fire density. Additional exploration of the fire niche for human-started and lightning-started fires relative to lightning density, fuel moisture, and net primary production (NPP), a proxy for fuels, is provided in Figs. S1 and S2.

Increasing Trends in Large Human-Started Wildfires

During the 21-y time period, there were significant increasing trends in large wildfires ignited by both lightning (n = 4,312; Theil-Sen estimated slope = 12.2; P = 0.001) and humans (n = 4,143; Theil-Sen estimated slope = 3.6; P = 0.004) (Fig. S3). There was a strong dichotomy in human vs. lightning trends seasonally (Fig. 5). Overall trends in lightning-caused fires were primarily driven by increasing numbers of large summer fires (Fig. 5*B*), whereas overall trends in human-caused fires were primarily driven by increasing numbers of large spring fires (Fig. 5*D*). Spatially, lightning-caused fires increased the most in the Northwest Forested Mountains ecoregion (Fig. S4*A*), whereas human-caused wildfires increased the most in the Great Plains ecoregion (Fig. S4*B*).

Discussion

Humans, the keystone fire species (29), play a primary role in spatially and temporally redistributing ignitions and resulting wildfires. We document that over 84% of the government-recorded

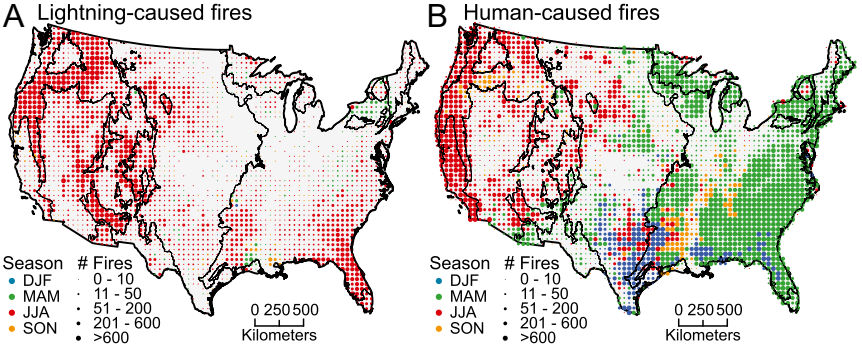

Fig. 3. Comparison of seasonality for (*A*) lightning- vs. (*B*) human-ignited wildfires. Human ignitions expand the seasonal fire niche considerably into spring and fall months. Colors show the season with the maximum ignitions caused by lightning and human within each 50 km × 50-km grid cell. Size of dot indicates the number of unique lightning and human fires between 1992 and 2012. Ecoregion boundaries are overlaid for visualization.

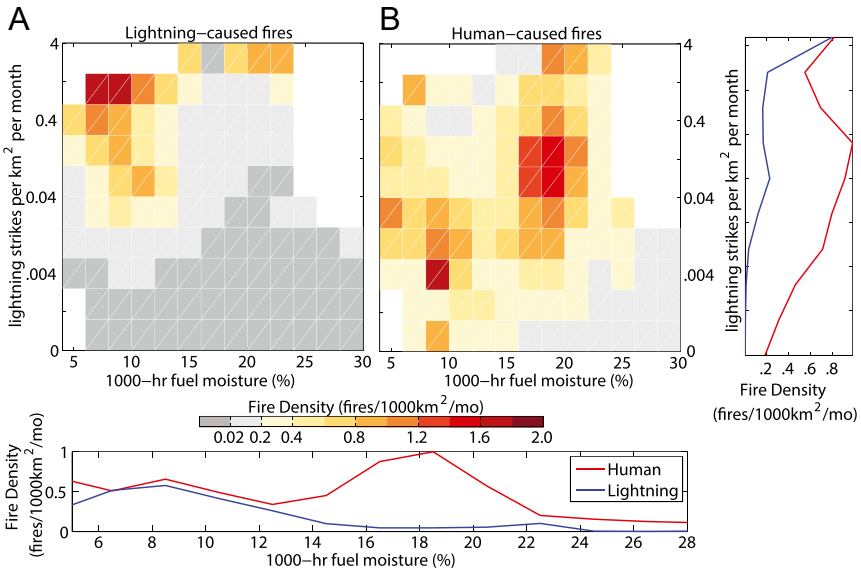

Fig. 4. Human vs. lightning fire niche relative to fuel moisture and lightning density, with greatest resulting wildfire density represented by dark red. (*A*) Lightning-started fires occur in areas with high lightning-strike density and dry fuels. (*B*) Human-started wildfires expand the fire niche to include areas with low lightning-strike density as well as areas with higher fuel moisture. Graphs on the bottom and far right show histograms of 1,000-h dead fuel moisture and lightning strikes, respectively, for human- and lightning-started fires.

wildfires were started by people from 1992 to 2012. Sixty percent of the total land area of the coterminous United States was dominated by human-started wildfires, whereas only 8% of the area was dominated by lightning fires. Humans tripled the length of the wildfire season, extending burning into the spring, fall, and winter months. During the spring, fall, and winter, people added more than 840,000 wildfires, a 35-fold increase over the number of lightning-started fires in those seasons. This expansion of the fire-niche was caused by human-related ignitions under higher fuel moisture conditions, compared with lightning-started fires. Moreover, during this 21-y record, large human-started wildfires increased significantly.

There was a strong national east–west dichotomy in the spatial distribution of human-started wildfires. Although human-started wildfires were pervasive across the United States (Fig. 1), the expansion of human-started wildfires relative to lightning-started fires was most dramatic in the eastern United States and central and southern California (Figs. 1 and 2*C*). Recent work for California confirms the important role of humans, with anthropogenic variables explaining half of the variability in fire probability over the past four decades (30). In contrast, lightning-started fires were found primarily in the intermountain west and Florida and occurred predominantly in the summer, reflecting national lightning strike patterns (31) (Fig. 2*C*). This finding supports other studies of human vs. lightning ignition sources that have found an important distinction between eastern and western United States fire patterns (10, 21) and drivers (32). Some explanations for this distinction include higher population and housing densities, lower proportions of public land, and more extensive land use and development in the eastern United States (33, 34), all of which could lead to more sources of anthropogenic ignitions. Synchrony between lightning activity and the seasonal nadir of fuel moisture in the western United States also likely contributes to these geographic differences. However, even with a projected increase in the number of lightning strikes as a result of anthropogenic climate change (50% by 2100) (35), humans would still remain the dominant ignition source across the majority of the United States land area. The majority of the wildfires requiring agency suppression in the east can be attributed to escaped fires from debris burning occurring in the spring months (or winter in Texas and the Gulf Coast) (Fig. 3). Between 1992 and 2012, wildfires caused by debris burning tended to be small (median

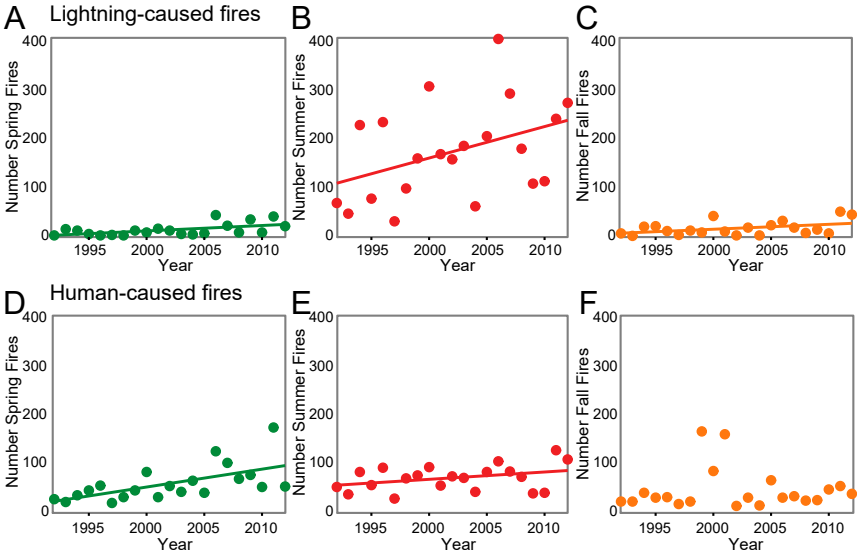

Fig. 5. Trends in the number of large wildfires verified by MTBS records from 1992 to 2012 for lightning-started fires (*A*–*C*) vs. human-started fires (*D*–*F*) in the spring (green: *A* and *D*), summer (red: *B* and *E*), and fall (orange: *C* and *F*). Where trend lines are shown, Theil-Sen estimated slopes are significantly different from zero ($P < 0.05$).

fire size 0.4 ha, IQR: 0.14–1.62 ha), but still an important source of risk to surrounding ecosystems. At finer scales, there are also notable patterns in human- vs. lightning-started wildfires (Fig. S5). Increased wildfires can follow road networks (36), the wildland–urban interface (13), and boundaries between agricultural and forested areas (37), highlighting just a few examples of how human activities and cultural drivers provide ignitions that substantially change the distribution of fire across the United States (38).

Our findings reinforce the strong imprint of people on fire regimes through changes in wildfire seasonality, which has been documented globally (39). In the past few decades, early onset of warmer and drier conditions has promoted greater fire activity across the western United States (6, 7, 40). However, our study highlights the equally important role of human ignitions in changing modern fire regimes by increasing the fire season length to encompass the entire year. The vast majority (78%) of lightning-started fires occurred during the summer months, whereas 76% of human-started fires occurred during the spring, fall, and winter months. Moreover, this trend varies substantially by ecoregion, reflecting again the principle dichotomy between the eastern and western United States (Fig. 3). Human-started fires extend the fire season earlier in the east, and later in the west (Fig. 3 and Table S2). Observations suggest that climate change has extended the duration of the fire weather season across most of the globe, including parts of the United States by a couple of weeks over the past three decades (5, 9), whereas we show that human ignitions in the United States increased the length of the fire season by more than three mo. There was also a notable mark of American culture on the distribution of wildfires, with the peak day of wildfires occurring on July 4th, concurrent with Independence Day fireworks displays (Fig. 2). Indeed, Americans start over twice as many wildfires on July 4th as any other summer day. A similar cultural mark has also been demonstrated globally with a marked decline in wildfires on Sunday compared with other weekdays (41).

Thus, at the national scale, human ignitions dramatically expand the spatial and seasonal niche of fire. The key components that define the fire niche are ignition sources, fuel mass, and desiccation. By exploring the fire niche along these axes, our results show that lightning fires are primarily constrained to areas with a lightning-strike density of greater than 100 strikes per grid cell per month (0.04 strikes/km^2 per month) and are concurrent with drier fuels (< 15% fuel moisture) (Fig. 4). Human ignitions expand fires into regions with higher fuel moisture (Fig. 4) and higher NPP (Figs. S1 and S2), suggesting that humans create sufficient ignition pressure for wetter fuels to burn. As a consequence, human ignitions have expanded the fire niche into areas with historically low lightning-strike density, such as Mediterranean California, or low concurrence of lightning and dry conditions, such as Eastern Temperate Forests (Fig. 1).

Over the past two decades, there was a significant increase across the United States for both human- and lightning-caused large fires (Fig. S3). The significant increase in large lightning fires is driven primarily by fires in summer months (Fig. 5) in the Northwest Forested Mountains ecoregion of the western United States (Fig. S4). This finding is consistent with other studies that have demonstrated an increase in large fires across the western United States (6, 7, 40), likely as a consequence of changes in climate and fuels rather than ignitions. In contrast, the significant trend in human-caused fires is primarily driven by an increase in large fires during spring months (Fig. 5) in the Great Plains ecoregion of the United States (Fig. S4). This increasing trend suggests that earlier springs as a result of climate change (42, 43) may be interacting with human ignition sources to increase the risk of large fires in the central United States.

The strong year-to-year variability in human ignitions (Fig. S3 and S4) may reflect the degree to which human choices can affect fire regimes. However, interannual climate variability also influences fuel moisture, NPP, and short-term weather conditions that enable the spread of human-ignited wildfires (44). There was a significant temporal correlation between large human- and lightning-started fires (R = 0.75). This pattern has been observed previously in the western United States (23) and suggests that large-scale climate drivers affect the frequency of both human- and lightning-caused fires. It is unknown how human actions will be affected by hotter and drier conditions, potentially increasing or decreasing ignitions from land use, recreation, and other sources. Increased public awareness and focused policy and management, particularly in years with elevated fire risk associated with climatic anomalies, are needed to reduce the number of human-caused ignitions.

In conclusion, we demonstrate the remarkable influence that humans have on modern United States wildfire regimes through changes in the spatial and seasonal distribution of ignitions. Although considerable fire research in the United States has rightly focused on increased fire activity (e.g., larger fires and more area burned) because of climate change, we demonstrate that the expanded fire niche as a result of human-related ignitions is equally profound. Moreover, the convergence of warming trends and expanded ignition pressure from people is increasing the number of large human-caused wildfires (Fig. 5). Currently, humans are extending the fire niche into conditions that are less conducive to fire activity, including regions and seasons with wetter fuels and higher biomass (Figs. 3 and 4). Land-use practices, such as clearing and logging, may also be creating an abundance of drier fuels, potentially leading to larger fires even under historically wetter conditions. Additionally, projected climate warming is expected to lower fuel moisture and create more frequent weather conditions conducive to fire ignition and spread (45), and earlier springs attributed to climate change are leading to accelerated phenology (42). Although plant physiological responses to rising CO_2 may reduce some drought stress (46), climate change will likely lead to faster desiccation of fuels and increased risk in areas where human ignitions are prevalent.

Uncertainty remains regarding how anthropogenic climate change will alter wildfire activity geographically and seasonally (47, 48), particularly in areas where human-caused fires dominate. Moreover, the current wildland–urban interface, where houses intermingle with natural areas, constitutes 9% of the United States total land area (33) but is projected to double by 2030, predominantly in the intermountain West (49). This expected development expansion will increase not only ignition pressure, but also the vulnerability of new infrastructure. Human-driven expansion of the spatial and temporal distribution of ignitions makes national- and regional-scale policy interventions and increased public awareness critical for reducing national wildfire risk.

Materials and Methods

For this analysis, we used the publically available US Forest Service Fire Program Analysis-Fire Occurrence Database (FPA-FOD) (28). This comprehensive dataset includes United States federal, state, and local records of wildfires (both on public and private lands) that were suppressed from 1992 to 2012, a total of ~1.6 million records. Previous studies have focused on the western United States (20), federal lands (22), or records from just one agency (21). Each entry includes at minimum the location, discovery date, and cause of the wildfire. We excluded 114,191 wildfires with an unknown cause and analyzed the spatial, seasonal, and temporal patterns of human- vs. lightning-started wildfires. In total, 1,517,522 wildfires were included in the analysis. Human-started wildfires were caused by a variety of sources, including the US Forest Service-designated categories of equipment use, smoking, campfire, railroad, arson, debris burning, children, fireworks, power line, structure, and miscellaneous fires (28). Spatially, we calculated the proportion of human- vs. lightning-caused wildfires within equal-area 50 × 50-km grid cells across the coterminous United States. This grid size corresponds roughly to the size of an average United States county. For each grid cell, we calculated the season (winter, spring, summer, or fall) when the majority of human-caused and lightning-caused wildfires were started. All spatial analyses were conducted in the Albers-Conical equal-area projection. To determine the seasonal distribution of wildfires, we plotted the distribution of human- and lightning-started fires by the day of year for the coterminous United States and for individual ecoregions. We used the level 1 ecological regions of North America, developed by the Commission for Environmental Cooperation (50). We calculated the length of the human- and lightning-caused fire seasons as the IQR of the Julian day of recorded fire ignition: that is, the difference between the first and third quartiles.

We determined how humans expanded the fire niche by comparing the lightning-strike density (i.e., natural ignition pressure) and fuel-moisture conditions under which actual human- and lightning-started fire events occurred. We obtained daily 1,000-h dead fuel moisture data from the surface meteorological data (51) on a 4-km grid from 1992 to 2012, and computed monthly averages across the 21-y study period. We obtained 4-km gridded monthly lightning-strike data from the Vaisala National Lightning Detection Network (https://www.ncdc.noaa.gov/data-access/severe-weather/lightning-products-and-services) and averaged the data over the 21-y study period. To account for fuel limitations, we also explored the fire niche as a function of fuel amount (approximated by NPP). We used MODIS mean annual NPP data (1-km resolution, from 2002 to 2015) (52) for this purpose. These three datasets were aggregated to the common 50 × 50-km grid cell. We calculated the number of human- and lightning-started fires by grid cell using the FPA-FOD dataset (28). We excluded any grid cells from subsequent analyses that did not report at least one lightning-caused or human-caused wildfire over the period of record. We tested whether fire niche expansion (as determined by fuel moisture and lightning-strike density) caused by human ignitions was significant based on Mann–Whitney tests between human- vs. lightning-started fires.

To assess trends in human- vs. lightning-caused wildfires through time, we used only large fires that were independently verified by the Monitoring Trends in Burn Severity (MTBS) project (53). We specifically focused on these large fires (>400 ha in the west, >200 ha in the east; n = 8,455) for comparability with previous research, which has examined temporal trends in the western United States and the link to climate warming (6, 7, 40), but has not investigated the relative contribution of human-started fires at a national scale. In addition to overall temporal trends, we tested for significant trends by ignition source versus season (spring, summer, fall) and versus ecoregion based on the level I ecological regions of North America (50). We explored a similar analysis using all available FPA-FOD data, but changes in reporting frequency through time for some states precluded a robust temporal analysis. We tested for trends in wildfire numbers through time using the nonparametric Theil-Sen estimator (54) and tested for trend significance using nonparametric Mann–Kendall tests (55).

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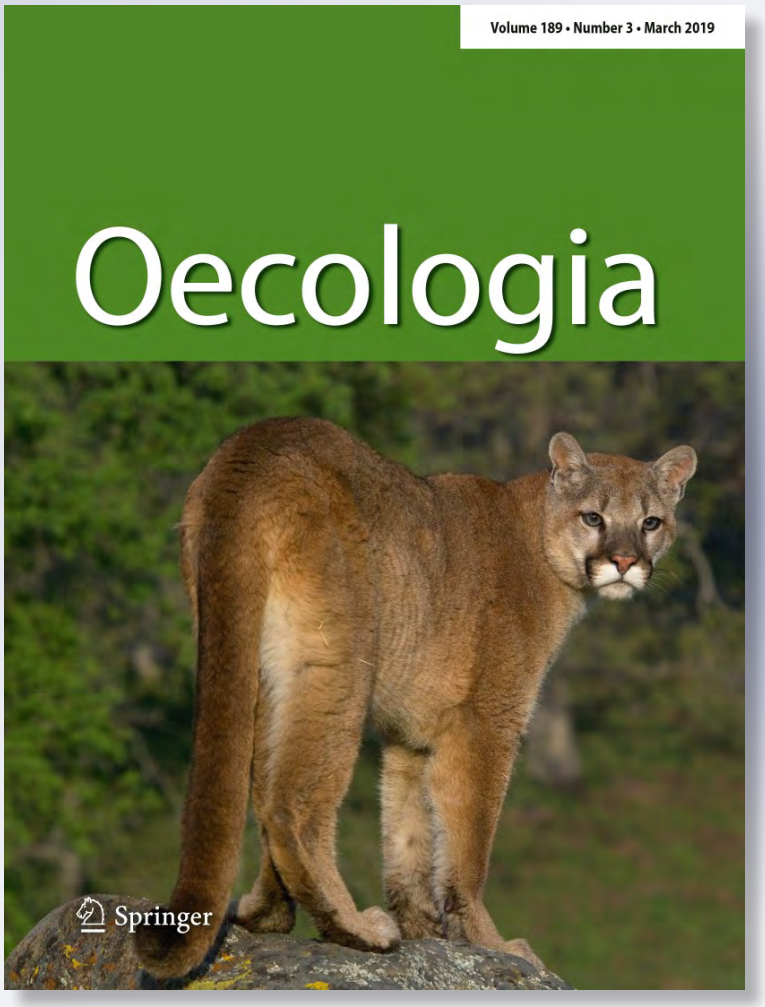

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HIGHLIGHTED STUDENT RESEARCH

Pumas as ecosystem engineers: ungulate carcasses support beetle assemblages in the Greater Yellowstone Ecosystem

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Abstract

Ecosystem engineers create physical changes in abiotic and biotic material, and through this process control the availability of resources for other species. Predators that abandon large portions of their prey may be ecosystem engineers that create habitat for carrion-dependent invertebrates that utilize carcasses during critical life-history periods. Between 04-May-2016 and 04-Oct-2016, we sampled beetle assemblages at 18 carcasses of prey killed by pumas and matching control sites in the southern Greater Yellowstone Ecosystem, USA, to measure the extent to which beetle families utilized these carcass "habitats". We used generalized linear-mixed models and linear-mixed effect models to examine changes in beetle abundance, species richness, and Simpson's Index of Diversity. We estimated kill rates and carrion production rates for individual pumas to better assess the impact of pumas on invertebrate communities. We collected 24,209 beetles representing 215 species. We identified eight beetle families that had significantly higher abundance at carcasses than control sites. Carcasses had a statistically large to very large effect (determined using Cohen's *d*) on beetle abundance, richness, and diversity for the initial 8 weeks of sampling. Our research revealed strong effects of an ecosystem engineer on beetle assemblages while highlighting the potential role of apex predators in creating and modifying physical habitats for carrion-dependent species. This suggests that there may be consequences for invertebrate communities where apex predators exist at reduced numbers or have been eradicated. The ecological role of invertebrates is often overlooked, yet they are essential taxa that provide critical ecological services upon which we depend.

Keywords Biodiversity · Carrion · Invertebrates · Pumas · Scavenging

Introduction

Ecosystem engineering is the ecological process by which an organism creates, modifies, or maintains habitat (Jones et al. 1994, 1997), and subsequently increases habitat heterogeneity and species richness (Jones et al. 1997; Wright et al. 2002). Arguably, all species engineer their ecosystems to some extent, and thus research has highlighted those engineers that have significant effects on their ecological systems (Wright and Jones 2006). For example, North American beavers (*Castor canadensis*) (Wright et al. 2002), Arctic foxes (*Vulpes lagopus*) (Gharajehdaghipour et al. 2016), African bush elephants (*Loxodonta africana*) (Pringle 2008), and termites (Infraorder Isoptera) (Jouquet et al. 2011) are among the species that have been identified as significant ecosystem engineers because of their effects on habitat. Many of these animals are also considered keystone species, defined as species that disproportionately affect their communities

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We offer a new predator as an ecosystem engineer. Our study design can reveal the positive role predators have in supporting insect communities. Our design can be applied to predators globally.

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given their biomass (Power et al. 1996; Soulé et al. 2005). Wright and Jones (2006), however, underscore the distinction between an ecosystem engineer and a keystone species; the former emphasizes ecological process, while the latter emphasizes the outcomes of processes and behaviors. Generally, predators are not often considered ecosystem engineers, but many are classified as keystone species because of the strong and wide-spread impact their predation behavior can have on community structure (e.g., trophic cascades; Winnie and Creel 2017) (Paine 1966; McLaren and Peterson 1994). Some predators, however, may be ecosystem engineers as well. In addition to directly and indirectly impacting prey species (e.g., through mortality and behavioral-mediated changes), predation may create habitat for invertebrate scavengers and decomposers that require carrion for critical life-history stages.

Carrion is the decaying flesh of dead animals and an ecological resource exploited by a diverse array of scavengers and decomposers that contributes to ecosystem structure, habitat heterogeneity, and biodiversity (DeVault et al. 2003; Wilson and Wolkovich 2011; Moleón et al. 2014; Moleón and Sánchez-Zapata 2015). Vertebrate scavengers facilitate energy transfer between trophic levels, increase linkages in food webs, and are essential vectors in spreading nutrients and other benefits of carrion across diverse terrestrial and aquatic ecosystems (DeVault et al. 2003; Wilson and Wolkovich 2011; Moleón and Sánchez-Zapata 2015). For numerous beetle species, however, carrion resources are not just food, but also key habitat where they complete crucial life-history events. For example, hide beetles (Family Dermestidae) and burying beetles (Family Silphidae) utilize carcasses as breeding and brooding habitat (Trumbo 1992; Hoermann et al. 2011). Carrion beetles (Family Silphidae) commune, seek mates, and reproduce on carcasses (Anderson and Peck 1985). Furthermore, the larvae of carrion beetles utilize carcasses as both sustenance and refuge until they have achieved their adult form.

Predators, such as gray wolves (*Canis lupus*) and pumas (*Puma concolor*), hunt prey larger than themselves and often abandon portions of their prey, which then become a substantial resource for diverse species (Wilmers et al. 2003; Selva et al. 2005; Elbroch et al. 2017b). Carrion provided by predators may function as important habitat for beetle scavengers and be more valuable than carrion provided by other processes such as disease, starvation, and old age. For example, predators provide carrion to their ecological communities throughout the entire year and across varied habitats, whereas carrion provided by other processes typically occurs in pulses during seasonal migrations as road kill, offal abandoned by human hunters in fall and early winter, or in late winter when some animals succumb to starvation (Wilmers et al. 2003; Selva and Fortuna 2007). Pulsed carrion produced in late fall through winter are likely less valuable to invertebrate scavengers because mammalian scavengers consume most winter carrion before beetles emerge on the landscape (Elbroch et al. 2017b; O'Malley et al. 2017). Carrion-dependent beetles, in particular, require fresh carcasses when they begin to flourish on the landscape between spring and summer, which is a period when natural deaths (e.g., disease, starvation, old age) are low. Therefore, predators are likely crucial for creating "habitat" for many beetle species, and pumas, which disproportionately provision ecological communities with large carcasses where they are present (Elbroch and Wittmer 2012; Elbroch et al. 2017b), may be top among them.

In this study, we sampled beetle assemblages at carcasses of prey killed by pumas and matching control sites in the southern Greater Yellowstone Ecosystem, USA, to document the array of beetle species that utilized these resources. We hypothesized that beetle abundance and species richness would be higher at carcasses than control sites. We also hypothesized that beetle diversity at carcasses would increase over the lifetime of carcasses, as early-colonizing, dominant species decreased (e.g., northern carrion beetles, *Thanatophilus lapponicus*; Ratcliffe 1996) and late-arriving species began to utilize carcasses. We predicted that carcasses would have a large effect on beetle biodiversity metrics, providing evidence that pumas are ecosystem engineers creating critical habitat for beetles, and perhaps other invertebrate scavengers and decomposers as well.

Methods

Study area

Our study spanned 2000 km^2 of the southern Greater Yellowstone Ecosystem, north of Jackson, *Wyoming* (43.51330, − 110.34419). Elevations in the study area ranged from 1800 m to > 3600 m. The area was characterized by short, cool summers and long winters. Plant communities at lower elevations included sagebrush (*Artemisia* spp.) and cottonwood (*Populus angustifolia*). The primary tree species at higher elevations were Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Our study area included a diverse community of large mammals. Carnivores in the study area included wolves (*Canis lupus*), black

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bears (*Ursus americanus*), grizzly bears (*U. arctos*), coyotes (*Canis latrans*), and red foxes (*Vulpes vulpes*). Ungulates included elk (*Cervus elaphus*), moose (*Alces alces*), mule deer (*Odocoileus hemionus*), bison (*Bison bison*), pronghorn antelope (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), and white-tailed deer (*Odocoileus virginianus*).

Puma capture and locating kills

This research was conducted as part of a larger, long-term study on pumas described elsewhere (Elbroch et al. 2017a, b). We captured pumas during winter months in the Bridger-Teton National Forest. We used trailing hounds to tree pumas, and then safely and humanely fit them with a GPS collar (Lotek Globalstar S or Iridium M, Newmarket, Ontario; Vectronics Globalstar GPS Plus, Berlin, Germany). Our capture protocols adhered to the guidelines outlined by the American Society of Mammalogists (Sikes and Gannon 2011) and were approved by two independent Institutional Animal Care and Use Committees (IACUC): the Jackson IACUC (Protocol 027-10EGDBS-060210) and National Park Service IACUC (IMR_GRTE_Elbroch_Cougar_2013-2015). We programed all of our GPS collars to acquire simultaneous location data every 2 h.

Beetle collection and abundances at carcasses and controls

We uploaded GPS data from collared pumas to Globalstar and Iridium satellites 1–6 times daily. We used ArcGIS 10.0 (ESRI, Redlands, CA) to display location data and to identify GPS clusters, which we defined as location with ≥ 2 GPS points within 150 m of each other, and where a puma spent ≥ 4 h (Elbroch et al. 2017b). We transferred puma location data to handheld GPS units, which we then used to guide us in the field to locate GPS clusters. If we located prey remains, we studied the area for signs of struggle, blood patterns, bite marks on the carcass itself, and the body parts consumed to determine whether the puma had killed the animal or was scavenging.

For this research, we conducted field investigations of kill sites as soon as possible after the puma had departed the area, as determined from GPS data, so as not to disturb the animal while it fed. If the prey was an ungulate with edible remains apparent, we initiated weekly beetle sampling. We set up three barrier pitfall traps around each carcass and replicated the set up at control sites established 20 m away within the same habitat type, and with similar vegetation (Hansen and New 2005). Our individual traps consisted of two, 32-ounce plastic cups filled with odorless soapy water that served as a killing and short-term preserving agent. We fixed a cup flush with the ground to both ends of each smooth, three-foot metal barrier. We positioned traps to surround carcasses, while also maintaining corridors through which some immigrating beetles could avoid traps and access carcasses.

We returned to each site once per week to collect adult beetle specimens, refill trap stations with soapy water, and fix damages caused by mammalian scavengers. We separated the specimens from unwanted material and rinsed them with clean water before we transferred them into dram vials with 90% isopropyl alcohol. We sent specimens to the Marsh Laboratory at Montana State University for species identification, and then counted them to determine relative abundance. We used a Pearson's Chi-squared test with a Bonferroni correction to test which beetle families had significantly more individuals at carcasses than control sites, limiting our tests to beetle families that had estimated counts greater than five. We also calculated effect size (Cohen's *d*) for summed abundance, richness, and diversity to better understand the strengths of the effects of carrion on beetle biodiversity metrics, if any, and ultimately determine whether pumas should be considered ecosystem engineers.

Quantifying and comparing beetle abundance, species richness, and diversity

We assigned each collection of beetles to 7-day time periods. We used generalized linear-mixed models with negative binomial distributions and a log link function to test for significant differences in beetle abundance and species richness between carcasses and their controls using the R package *MASS* (Venables and Ripley 2002). For our models, the fixed effects were group (i.e., carcasses and controls), time, group*time interaction, caching (a binomial variable representing whether the puma covered the carcass in debris or not), and prey species. We also included individual carcasses and controls as random effects. Then we used linear-mixed effect models to test for differences in Simpson's Index of Diversity using the R package *lmerTEST* (Kuznetsova et al. 2017). We calculated diversity using the Simpson's Index of Diversity (1-D) (Simpson 1949), which creates a metric ranging from 0 to 1, in which the larger the number the greater the diversity of the sample. We conducted a logit transformation on our diversity measurements using the 'logit' function in the R package *gtools* (Warnes et al. 2018). We calculated marginal means and Cohen's *d* for two different time periods: (1) our full collection period of 19 weeks, and (2) an 8-week time period, which was the point when biodiversity at carcasses stopped increasing and exhibited an

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asymptote, as determined with a piecewise regression analysis in the R package *segmented* (Vito and Muggeo 2003).

Quantifying puma resource provisioning

We replicated the methods of Elbroch and Wittmer (2012) to estimate age-specific prey weights and the amount of prey-resource abandoned per kill, allowing us to compare our provisioning data with their puma research in Patagonia. We used CyberTracker-certified researchers (Elbroch et al. 2011) to conduct site investigations as well as to determine the approximate age of prey. We assumed that 68% of an ungulate's weight (Wilmers et al. 2003) and 95% of a small vertebrate's weight (Ackerman et al. 1986) was edible material for pumas. We used the timestamps associated with the location data collected from the GPS collars to determine how many hours an individual puma spent at a carcass site. Lacking actual consumption rates, we used hourly consumption rates for captive pumas to estimate how much meat individual pumas consumed (Danvir and Lindzey 1981). Once we estimated the prey weight and amount of resource consumed by individual pumas, we calculated how much edible resource was provisioned by each puma at each kill site (n = 190) during our field season.

We calculated kill rates (prey animals/week) for individual pumas monitored continuously (i.e., every cluster was investigated in the field) for ≥ 4 weeks during the time period of this study (Elbroch et al. 2014). For pumas in which there was a gap in monitoring due to poor collar performance, and thus two or more sampling periods of continuous monitoring greater than 4 weeks in length, we calculated kill rates for each period separately, and reported their average. Then we used these kill rates and the mean amount of meat abandoned by individual pumas, determined as described above, to estimated weekly carrion production by individual pumas in our study.

Results

Puma carrion production and beetles

From 31-Mar-2016 to 03-Sept-2016, we investigated 501 GPS clusters for six pumas in the field, and found 190 kill sites, 261 bed sites, 21 carcasses scavenged rather than killed by pumas, and 29 sites with no evidence of specific behaviors. We sampled beetle communities at 18 fresh carcasses preyed on by pumas (Table 1), and initiated

Table 1 Eighteen carcasses sampled for beetle assemblages

Carcass number	Species	Sex	Age (subjective)	Estimated kill date	Estimated prey mass (kg)	Puma ID	Carcass utilized (%)	Estimated meat consumed (kg)	Edible resource abandoned (kg)
1	Elk*	F	Adult	31-Mar	236	F109	76–100	19.1	141.4
2	Elk*	U	Calf	03-Apr	148	F61	76–100	15.0	85.6
3	Elk*	F	Yearling	23-Apr	193	F109	76–100	6.8	124.4
4	Elk*	U	Calf	27-Apr	158	F109	76–100	10.9	96.5
5	Deer*	F	Adult	27-Apr	82	F61	51–75	27.3	28.5
6	Elk	F	Yearling	09-May	196	M85	26–50	31.4	101.9
7	Elk*	U	Calf	09-May	158	F109	76–100	10.9	96.5
8	Elk*	F	Yearling	10-May	196	F109	76–100	15.0	118.3
9	Elk*	U	Calf	10-May	158	F109	76–10	10.9	96.5
10	Deer*	F	Adult	02-Jun	82	F49	26–50	23.2	32.6
11	Elk*	F	Adult	07-Jun	236	F61	51–75	15.0	145.5
12	Deer*	U	Yearling	08-Jun	64	F72	76–100	19.1	24.4
13	Elk*	M	Yearling	19-Jun	178	F61	51–75	19.1	101.9
14	Deer	U	Yearling	04-Jul	65	F109	76–100	19.1	25.1
15	Sheep	F	Adult	16-Aug	60	F109	76–100	47.8	9.2
16	Deer	F	Adult	28-Aug	82	F61	76–100	19.1	36.7
17	Elk	F	Yearling	01-Sep	169	F49	26–50	23.2	91.7
18	Deer	M	Adult	03-Sep	90	F72	76–100	10.9	50.3

Carcass utilized (%) is the amount of carcass consumed by the individual puma and other vertebrate scavengers when beetle sampling began

*Carcasses used for mixed effect models

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Table 2 Puma kills, and the amount of edible resources abandoned

Puma ID	*n*	Mean prey mass (kg/SE)	Mean meat consumed (kg/SE)	Mean edible resource abandoned (kg/SE)	Kill rate (animals/wk)	Carrion production (kg/wk)
F47	32	52 (11)	13.2 (2.0)	22.4 (6.2)	1.3	29.1
F49	34	33 (6)	10.5 (1.1)	13.0 (3.3)	1.9	24.7
F61	27	62 (12)	15.1 (1.6)	27.9 (7.3)	1.2	33.5
F72	36	47 (10)	11.3 (1.6)	21.8 (5.9)	1.8	39.2
M85	31	72 (15)	9.9 (1.4)	39.5 (9.2)	1.1	43.5
F109	30	81 (16)	11.0 (1.6)	44.2 (10.2)	1.3	57.5

Here we report the number of kills documented by individual pumas (*n*), mean (± standard error) estimated prey mass, mean meat consumed per kill, and the mean amount of edible resource abandoned per kill. We also report each puma's kill rate in animals/week and the amount of carrion they produced per week, estimated simply by multiplying the kill rate by the mean meat they abandoned per kill

sampling of beetle scavengers on average 15 ± 11 |SD| days after an ungulate was killed. The carcasses were sampled weekly for an average duration of 12 ± 6 weeks. Pumas cached (i.e. covered the carcass in debris) 11 of 18 carcasses sampled for beetles. Individual pumas on average killed 1.4 ± 0.3 animals and produced 37.9 ± 11.7 kg of carrion each week over the course of this study (Table 2).

We collected 24,209 beetles, comprising 215 species and 33 families. Of our collection, 83.07% ($n = 20{,}111$) of our total specimens were found at carcasses. The northern carrion beetle was the most abundant species, comprising 60.6% of our total specimens; 98.27% ($n = 14{,}674$) were found at carcasses in comparison to control sites ($n = 254$). Our Chi-squared analysis identified eight beetle families that had significantly more individuals at carcasses in comparison to control sites (Table 3).

Linear-mixed effect analyses

We excluded six fresh carcasses from analyses: five sites were sampled late in the season when cold temperatures drastically reduced beetle presence at carcasses, and the sixth was usurped by coyotes after the second collection. We found that carcasses had a large to very large effect (Cohen's *d*) (Sawilowsky 2009) on abundance, species richness, and diversity of beetle assemblages during the first eight sampling weeks, and a medium effect over the full 19 weeks of sampling (Table 4). Beetle abundance and species richness were significantly higher at carcasses in comparison to control sites (Table 4, Fig. 1).

Our models revealed that "Group" and "Time" had a significant effect on beetle abundance, species richness, and diversity (Table 5). Beetle abundance and species richness did not differ between kills cached by pumas and those not cached (Table 5). Species richness did not differ between carcass species (elk and mule deer), but beetle abundance decreased significantly faster at deer carcasses than elk carcasses (Table 5).

Discussion

Our research revealed the large to very large effect (Cohen's *d*) of puma predation on the composition of beetle assemblages in the southern GYE, and thus provided strong evidence that pumas function as ecosystem engineers that have a significant effect on species richness and habitat heterogeneity (Wright et al. 2002; Pringle 2008; Jouquet et al. 2011; Gharajehdaghipour et al. 2016). These effects were most pronounced during the first 8 weeks of sampling, emphasizing that carrion is an important but ephemeral ecological resource in space and time (Barton et al. 2013). These effects were also more pronounced at larger carcasses of elk than deer, emphasizing the ecological importance of large carrion over small (Moleón and Sánchez-Zapata 2015). Similar to pumas in other geographic regions (Elbroch et al. 2014), individual pumas in our study killed 1.4 animals and produced 37.9 kg of carrion per week, providing a continuous supply of new carrion for vertebrate and invertebrate scavengers across the landscape and during critical life-history stages for beetles and other species that occur during the spring and summer.

We identified eight beetle families, comprising 113 species, which were disproportionately detected at carcasses as compared to control sites. Many of these families are known to utilize carcasses during their critical life-history stages, including courtship, mating, egg-laying, refugia, and for food for developing young (e.g., Family Dermestidae, Anderson and VanLaerhoven 1996; Family Carabidae, Lövei and Sunderland 1996; Family Cleridae, Majka 2006; Family

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Table 3 A summary of the beetle families and number of individuals trapped with Pearson's Chi-squared tests

Family	# of species	# of individual beetles		χ^2	*P* value
		Carcass	Control		
Silphidae	6	14,861	1114	11,830	< 0.001*
Carabidae	35	1480	1308	10.6	< 0.001*
Curculionidae	22	680	404	70.3	< 0.001*
Tenebrionidae	5	537	525	0.14	0.71
Staphylinidae	15	855	57	698	< 0.001*
Histeridae	7	573	78	376	< 0.001*
Scarabaeidae	20	352	176	58.7	< 0.001*
Elateridae	27	191	229	3.44	0.06
Dermestidae	5	298	22	238	< 0.001*
Cleridae	3	71	0	71.0	< 0.001*
Chrysomelidae	10	27	29	0.071	0.79
Byrrhidae	6	35	16	7.08	0.01
Lucanidae	1	27	16	2.81	0.09
Cicindelinae	3	16	23	1.26	0.26
Geotrupidae	1	14	20	1.06	0.30
Cerambycidae	10	23	11	4.24	0.04
Trachypachidae	1	27	21	0.75	0.39
Scolytinae	4	5	15	5.00	0.03
Cryptophagidae	4	8	10	0.22	0.64
Nitidulidae	5	6	3		
Hydrophilidae	2	6	1		
Cantharidae	2	4	3		
Coccinellidae	4	4	2		
Leiodidae	3	0	4		
Scydmaenidae	1	1	3		
Trogidae	1	4	0		
Buprestidae	3	2	2		
Melyridae	3	1	2		
Meloidae	2	0	2		
Anthicidae	1	0	2		
Micropeplidae	1	1	0		
Mordellidae	1	1	0		
Oedemeridae	1	1	0		

Eight beetle families were trapped significantly more at carcasses than control sites

*Bonferroni adjustment with significance at *P* value < 0.0026

Scarabaeidae, Midgley et al. 2012; Family Staphylinidae, Wang et al. 2017). We also detected significantly more beetles of the Family Curculionidae at carcasses, which was unexpected because they are primarily plant feeders.

Table 4 Effect size (Cohen's *d*) and mean (SD) beetle abundance, species richness, and Simpson's Index of Diversity at 12 carcasses and control sites for time periods 1–8 and time periods 1–19

	Mean (SD)		
	Carcass	Control	Effect size
Time periods 1–8			
Abundance	211 (304)	25 (20)	1.12 (0.67)
Richness	11.6 (4.9)	8.4 (4.1)	1.02 (1.12)
Diversity	0.55 (0.25)	0.80 (0.12)	− 1.43 (0.71)
Time periods 1–19			
Abundance	99 (216)	21 (23)	0.59 (0.26)
Richness	8.7 (4.8)	6.9 (3.8)	0.49 (0.62)
Diversity	0.68 (0.23)	0.78 (0.14)	− 0.74 (0.22)

Nevertheless, they might have colonized ungulate carcasses because the stomachs of ungulate prey were full of partially digested vegetation. Furthermore, we detected several beetle families known to utilize carrion, but were too rare to be statistically significant at carcasses. For example, we collected four individuals of the small Family Trogidae, all of which are known to utilize carcasses a few months after death (Vaurie 1955). Similarly, we collected three species from the genus *Omosita* (Family: Nitidulidae), which are often found in the later stages of carrion decomposition (DiZinno et al. 2002).

Generally, arthropod assemblages rapidly occupy carcasses, attain maximum abundance and richness quickly, and then decline (i.e., they exhibit a unimodal distribution; Schoenly and Reid 1987). We observed that beetle assemblages at carcasses typically peaked in abundance and richness during our first collection week, which was on average 15 ± 11 |SD| days after the prey was killed. The initial peak in beetle abundance and richness may be due to several factors. First, we commenced sampling only after the puma abandoned the site. Therefore, we likely started sampling during the active decay stage and missed the period of initial mass beetle immigration to the carcass. Additionally, if the first stage (i.e., the fresh stage) does not emit a significant number of volatile compounds that signal the location of the carcass (Kalinová et al. 2009), or those compounds are hindered by caching or other puma behaviors, species richness may have increased slowly during this stage. Further, vertebrate scavengers typically dominated large carcasses in the first week following predation (Elbroch et al. 2017a, b), and their competitive dominance may have impeded access

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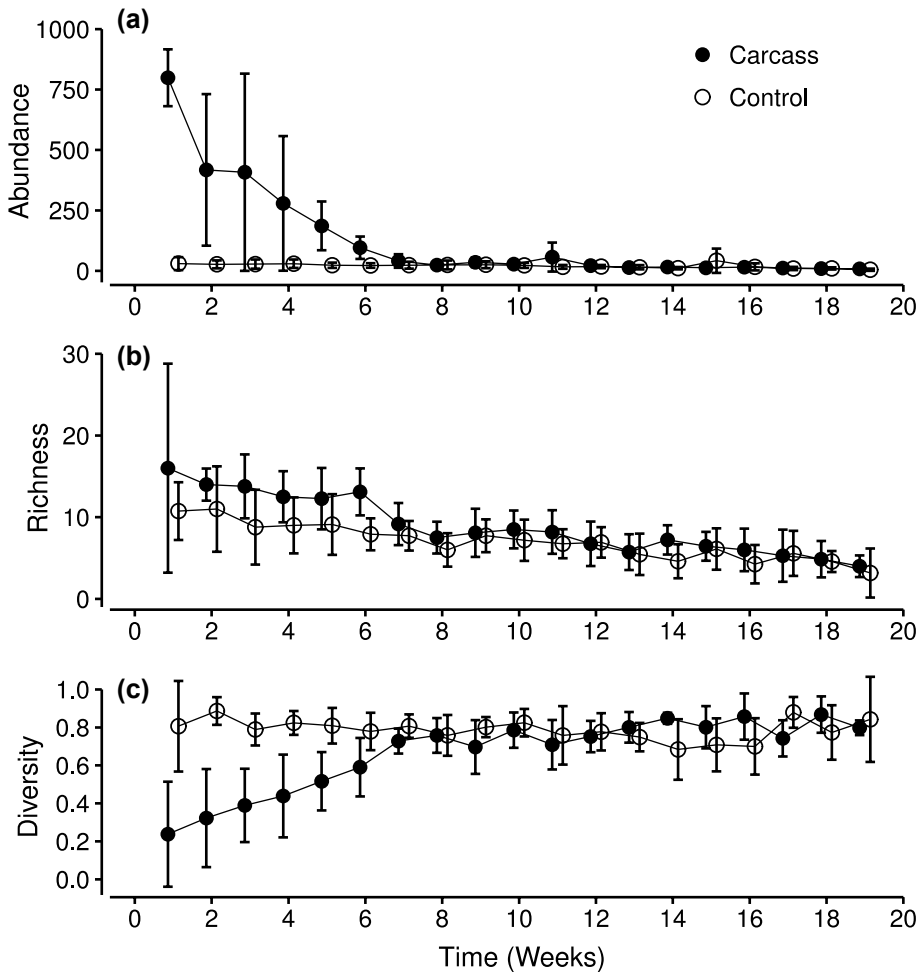

Fig. 1 Changes (mean ± 95% CI) in beetle (**a**) abundance (**b**) species richness (**c**) and Simpson's Index of Diversity for 12 fresh carcasses (filled circles) and controls (open circle)

to carrion for beetles, diminishing the typical unimodal pattern of beetle abundance and richness during the first week of decomposition (Pechal et al. 2014).

The northern carrion beetle's quick arrival in large numbers, competitive dominance, and short residency at carcasses impacted numerous biodiversity metrics, including high peaks in beetle abundance and low peaks in diversity in early collections. The large abundance of northern carrion beetles in overall sampling created such an unevenness that beetle diversity skewed as a consequence (evenness assesses inequity in the distribution of species richness; Wilsey and Potvin 2000). Thus, the Simpson's Index of Diversity was typically higher at control sites even though beetle abundance and species richness was higher at carcasses. Adult northern carrion beetles exhibit exceptional sensory abilities that allow them to detect and colonize carcasses early in the fresh stage. They then monopolize space on carcasses, their large bodies providing them greater food reserves and physical dominance over competitors (Ratcliffe 1996; Hocking and O'Regan 2015). Adult northern carrion beetles are also known to dominate fresh meat in cold-adapted environments (Anderson and Peck 1985; Ratcliffe 1996).

Our findings demonstrate the large effect that an apex carnivore had on beetle assemblages in the southern GYE. Coleopteran species at carrion have been well documented globally (Anderson and Peck 1985; Anderson and VanLaerhoven 1996), but research pertaining to the importance of predator-produced carrion has primarily focused on vertebrate scavengers (e.g., Selva et al. 2005; Allen et al. 2015; Inger et al. 2016; Elbroch et al. 2017b). Invertebrates are an often-overlooked yet essential taxa that provide numerous critical ecological services upon which we depend (e.g., Prather et al. 2012; Barton and Evans 2017). If ecologists can determine how predators create and modify physical and chemical resources essential to the persistence and diversity of the various invertebrate scavengers and decomposers, we may be able to predict their engineering effects on invertebrate distributions at larger scales (Wright and Jones 2004),

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Table 5 Estimates of fixed effects for 12 carcasses and controls from time periods 1–19

	Fixed effects	Estimate (SE)	*Z* value		*P* value
Abundance	Carcass	6.26 (0.16)	40.12		< 0.01
	Control	− 2.75 (0.22)	− 12.45		< 0.01
	Carcass ~ time	− 0.24 (0.01)	− 16.99		< 0.01
	Control ~ time	0.20 (0.02)	9.70		< 0.01
	Not cached	6.43 (0.22)	29.08		< 0.01
	Cached	− 0.41 (0.33)	− 1.25		0.21
	Not cached ~ time	− 0.25 (0.02)	− 12.12		< 0.01
	Cached ~ time	0.012 (0.03)	0.39		0.70
	Deer	6.47 (0.31)	20.87		< 0.01
	Elk	− 0.15 (0.36)	− 0.41		0.69
	Deer ~ time	− 0.34 (0.04)	− 9.68		< 0.01
	Elk ~ time	0.10 (0.04)	2.65		< 0.01
Richness	Carcass	2.80 (0.07)	37.68		< 0.01
	Control	− 0.39 (0.11)	− 3.58		< 0.01
	Carcass ~ time	− 0.07 (0.01)	− 9.52		< 0.01
	Control ~ time	0.018 (0.01)	1.72		0.09
	Not cached	2.89 (0.09)	32.20		< 0.01
	Cached	− 0.20 (0.14)	− 1.46		0.14
	Not cached ~ time	− 0.07 (0.009)	− 7.42		< 0.01
	Cached ~ time	− 0.005 (0.01)	− 0.38		0.70
	Deer	2.78 (0.14)	20.5		< 0.01
	Elk	0.10 (0.16)	0.67		0.50
	Deer ~ time	− 0.10 (0.02)	− 5.91		< 0.01
	Elk ~ time	0.03 (0.02)	1.64		0.10
	Fixed effects	Estimate (SE)	*t* value	*df*	*P* value
Diversity	Carcass	− 0.80 (0.36)	− 2.19	114	0.03
	Control	2.38 (0.51)	4.62	115	< 0.01
	Carcass ~ time	0.20 (0.03)	6.67	330	< 0.01
	Control ~ time	− 0.18 (0.04)	− 4.15	330	< 0.01

Carcass, Not Cached, and Deer are treated as baseline intercepts and baseline slopes. Estimates for abundance and richness are log transformed, and diversity estimates are logit transformed. Subsequent estimates are differences from baseline. *P* values < 0.05 are considered significant

as well as gain additional insights into the cascading effects of predator removal on other species (Prugh et al. 2009; Ripple et al. 2014).

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Author contribution statement JMB and LME conceived and designed the experiment. JMB and LME conducted the field work. JMB and MEAL conceived and performed statistical analyses. LS and AK conducted laboratory work on the beetle dataset. JMB and LME wrote the manuscript, with constructive feedback and additions from all authors. HBQ, MMG, and RJS provided institutional support for the work and graduate student training.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures performed in this study involving animals were in accordance with the ethical standards of the American Society of Mammals and were approved by two independent Institutional Animal Care and Use Committees (IACUC): the Jackson IACUC (Protocol 027-10EGDBS-060210) and National Park Service IACUC (IMR_GRTE_Elbroch_Cougar_2013-2015).

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THE COUGAR IN THE SANTA ANA MOUNTAIN RANGE, CALIFORNIA

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Final Report

ORANGE COUNTY COOPERATIVE MOUNTAIN LION STUDY

June 1 1993

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INTRODUCTION

This report summarizes cougar (mountain lion, Felis concolor) research in Orange County from April 1 1988 through February 1 1993. This research was pursued under interagency agreements FG7510 and FG0217 between the California Department of Fish and Game and the University of California at Berkeley, and Agreements D87-232 and FG0233 between the County of Orange and the California Department of Fish and Game. The following headings encompass the 18 objectives explicitly set forth in the contracts. The language following each heading is taken directly from the objectives contained in the contracts. The 10 chapters in this report follow these same headings.

1. Home ranges and habitat use. Document home range sizes for male and female cougars. Document habitat use in the Santa Ana and Santa Margarita mountain ranges.

2. Population density and structure. Determine the density of cougars, and the sex and age class structure of the cougar population.

3. Distribution and travel corridors. Document cougar use of existing County Parks, including habitat use within these Parks, and travel corridors between Parks. Investigate reports of cougar sightings in the San Joaquin Hills and Laguna Greenbelt areas. Evaluate and document the actual and potential movement corridors necessary to insure the integrity of the cougar population.

4. Population dynamics. Document reproductive activity, litter sizes, and recruitment into the population.

5. Utility of track surveys. Evaluate the validity of track survey information.

6. Activity patterns. Document daily and seasonal activity patterns for male and female cougars. Document movements of individual cougars.

7. Prey relationships. Document cougar prey relationships based on field surveys including deer herd composition surveys and examination of cougar-killed prey carcasses.

8. Impact of urban growth. Determine the actual and potential impacts of expanding urban development on cougar habitat. Provide information applicable to proposed highway projects.

9. Cougar-human encounters. Document factors which may help explain the recent increase in cougar-human encounters. Document the reaction of collared cougars to humans and to artificial food sources including garbage. Determine if such reactions vary with changes in cougar density, age of cougar, or the reproductive status of the cougar. Test the feasibility of conditioning cougars to avoid humans by removing artificial food sources and other practical methods. Monitor trends in cougar use of areas on the fringes of development.

10. Public education. Prepare a slide presentation for use in park Visitor Centers, to include: study results, natural history and social behavior of cougars, information on conservation of cougars, and warnings of the potential dangers inherent in having cougars as part of the wilderness.

This report follows this 10-point outline. We are also providing to the County and the Department data files of cougar locations for use in planning and management activities.

Acknowledgments

We gratefully acknowledge the financial support of the California Department of Fish and Game, and of the County of Orange, California. The Department of Fish and Game also supplied capture specialists, vehicles, telemetry equipment, training in animal handling, and air services. Terry Mansfield. Eric Loft, and Bill Clark of the Department were especially important in insuring continued support for this project. We also thank CDFG employees in Region 5: Rich Anthes, Esther Burkett, Jim Davis, John Fallon, Greg Gerstenberg, Cheryl Heffley, Larry Henson, Lisa Kramer, Art Lawrence, Marty Matorini, John Massey, Larry Sitton, Ralph Sugg, Jeff Veal, Ken Walton, Jan Yost, and Al Zamudio. The County of Orange assisted with access to public and private lands and supported the project in many other ways, most notably in allowing Donna Krucki flexibility in her work schedule at Caspers Wilderness Park so that she could assist us in field work. We especially thank County employees Stan Bengtson, Bruce Buchman, Donna Krucki, Al Macias, Gary Madeiros, Tim Miller, Tim Neely, Cathy Nowak, and Chuck Thornberg.

Paul Beier, Allan Brody, Jeff Brent, David Choate, Pete de Simone, Karen Drewe, Donna Krucki, W. Douglas Padley, Tracy Tennant, and Duggins Wroe carried out most of the field work. Dug Wroe's capture skills and Dave Choate's careful field work were critical to our success. Jeff Hornacek, Jack Williams, and Bob Chipman generously loaned their airplanes and services as pilots.

Special thanks go to Doug Padley and Joel Weintraub. Padley monitored radio-tagged cougars for the County of Orange in 1986-87 and for US Marine Corps Base Camp Pendleton in 1987-1989; his data are included in this report. He also worked as a volunteer on this study, and shared data from his 1990-1991 work on mule deer. Joel Weintraub of California State University at Fullerton performed the determination of prey remains in cougar scats.

For gracious access to land holdings, we thank Boy Scouts of America, California State Parks, Ford Aerospace, Hon Development Company, Irvine Company, Metropolitan Water District, National Audubon Society, Orange County, Rancho Mission Viejo, Rancho Santa Margarita, Riverside County, San Diego County, San Diego State University, The Nature Conservancy, TRW Corporation, US Forest Service, US Marine Corps Base Camp Pendleton, and US Naval Weapons Station Fallbrook. Camp Pendleton was especially helpful in arranging access, loaning equipment, sharing data, and in many other ways. Rancho Mission Viejo generously provided several kinds of support, including living space for volunteer field workers.

We offer heartfelt thanks to many others who helped in ways too numerous to mention, among them Jon Atwood, Greg Ballmer, Cameron Barrows, Celia Beier, Michelle Beier, Gary Bell, Pete Bloom, David Bontrager, Dave Boyer, Dave Bramlet, Phil Brylski, Slader Buck, Ray Chandos, Charlotte Clarke, Steve Coontz, Pete de Simone, Sandy de Simone, Paul Edelman, Mike Evans, Merrillee Fellows, Scott Ferguson, Em Fermin, Phil Feyerabend, Dave Fjelline, Robert Frazer, Amy Greyson, Maribeth Gustafson, Loren Hays, Jean Jenks, David Kossack, Sharon Lockhart, Steve Loe, Karlin Marsh, Sherrie Meddick, Lori Merkle, Claudia Meuller, Sara Miller, Pat Mock, Donna O'Neill, Richard O'Neill, Richard Orisio, Marie Patterson, Spence Porter, Fred Roberts, Gordon Ruser, Larry Salata, Joel Shows, Connie Spenger, Maryann van Drielen, Lee Waian, Ken Weaver, Susan Wroe, and Cliff Wylie. We apologize to these people for so brief a mention and to the many others whose names we failed to list.

BACKGROUND, STUDY AREA, METHODS

Background

The cougar (Felis concolor) is also known by the names mountain lion, puma, and panther. Cougars have the broadest distribution of any terrestrial mammal native to the New World, ranging from southern Yukon to southern South America (Lindzey 1987:657). Once native to all of the contiguous United States, cougars now occupy less than half of this historic range, mainly west of the 100th Meridian (Anderson 1983). The main cause of this range contraction was persecution of cougars, which began with European colonization and ended as each state ended its bounty system during 1958-1970. Cougars were present as recently as 1950-1976 in several states where the species is now extinct, including Arkansas, Louisiana, Oklahoma, Tennessee, and West Virginia (Currier 1978, Anderson 1983:80-83). Since the end of the bounty system, cougars have increased in most western states (Smith 1989). However, there are local declines in some areas due to habitat loss and fragmentation. These same processes may prevent cougars from recolonizing the eastern United States. There is no statistically sound and precise estimate of total numbers of cougars for any entire state. The cougar's elusive habits and low density make any such estimate prohibitively expensive. The California population was estimated at 4100-5700 animals in 1984 (Mansfield 1986), a number far larger than for any other U.S. state or Canadian province (Smith 1989).

Hornocker (1969, 1970) carried out the first intensive study on the ecology of cougars, following individually marked animals over time and observing population processes in a well-defined study area. Virtually all our knowledge of cougar ecology has been obtained since 1970. The best summaries of the scientific literature on cougars are provided by Anderson (1983) and Lindzey (1987); Anderson et al. (1992) reference most of the more recent literature. Excluding a half-dozen studies of trends in cougar numbers and depredation incidents, only 3 intensive studies of cougar ecology were carried out in California prior to the present study. Sitton and Wallen (1976) radio-tagged 14 cougars and ear-tagged 2 cubs in a 2-year study in southern Monterey County. Hopkins (1981, 1989) radio-tagged and studied cougars in the Mount Hamilton area (Santa Clara County and adjacent areas) during 1978-1988. Neal et al. (1986) reported on home range use and density in the North Kings River area (west central Sierra Nevada) during 1983-1985.

Until 1986, cougar studies in southern California were limited to track surveys. In that year the National Audubon Society began plans for a radio-telemetry study centered on Starr Ranch Sanctuary. In November 1986, CDFG radio-tagged 2 adult female cougars near Caspers Park and took the lead in planning a larger study. CDFG and County of Orange agreed to jointly fund the study, and in February 1988, the University of California signed a contract to carry out the project; field work began in April 1988. Meanwhile, Camp Pendleton had begun a study using radio-tagged cougars in summer 1987. The two studies were closely coordinated. In late 1989 the Camp Pendleton study terminated and we took over monitoring of those animals. This report treats data from both study sites as a single data set.

The results of the present study appear in several documents in addition to this report:

- Much of the Camp Pendleton data were summarized in Padley's (1990) Master's thesis.
- Padley (in press) reports on social interactions among female cougars in a paper submitted to Journal of Mammalogy.
- Beier (1993) simulated the population dynamics of this cougar population and demonstrated the critical importance of

preserving corridors for wildlife movement. This paper appears as Appendix 1 in this report.

- Beier (1991, 1992) presented the historical record of cougar attacks on humans in the United States and Canada. These papers are included as Appendix 2 and Appendix 3.
- Beier and Loe (1992), in a paper partially related to this study, suggested how to evaluate impacts to wildlife movements. This paper is included as Appendix 3.
- Beier (1993b) described a version of the software used in these simulations, modified for use as a teaching tool.
- Beier reports on "Dispersal movements of cougars in fragmented habitat" in a paper to be submitted for publication this summer.

Additional papers, presently being prepared for publication, will present other results to the scientific community.

Study Area

The Santa Ana Mountain Range was our study area. It included about 2070 square km (800 mi^2) of contiguous wildlands used by cougars; these wildlands include the Santa Margarita Mountains, the Santa Rosa Plateau, the Chino Hills, and the nearby San Joaquin Hills (Figure 1). The study area thus straddled 5 counties and abutted 17 incorporated cities. About 61% of cougar habitat in the study area is in some sort of protected status (Table 1). The largest of these parcels (Trabuco Ranger District, Camp Pendleton, Starr Ranch, and Caspers Park) form a large central habitat area. Many of the smaller protected parcels are at risk of being fragmented from the central habitat area (Table 1), and the central habitat area itself is at risk of being isolated from the adjacent population in the Palomar Range (Figure 1).

The 1988 contract defined the original study area as "Rancho Mission Viejo, Rancho Santa Margarita, Coto de Caza, Starr Ranch Sanctuary, Ronald Caspers Wilderness Park, O'Neill Regional Park, and Wagon Wheel Canyon Regional Park." This area is only about 260 km^2 (100 mi^2, or about 12% of the area used by the cougar population), and we soon realized that meaningful biological results demanded expanding to the entire range. In spring 1989 the study area expanded to include Irvine Company holdings east of I-5 and the Cleveland National Forest. From September 1987 through August 1989, US Marine Corps Base Camp Pendleton funded a companion study of cougars on Camp Pendleton and Fallbrook Naval Weapons Station (Padley 1990). From the beginning, the sister studies co-operated closely, and after September 1989 we formally included these lands in our study. In early 1990 we expanded into the San Joaquin Hills, Chino Hills, and the Santa Rosa Plateau. This final study area included all large wildlands west of Interstate 15 north of State Route 76 and south of State Route 60. These man-made boundaries delimit a biologically meaningful study area because these urban features circumscribe the real confines of a single cougar population. Our study thus encompassed an entire cougar population for its final 2½ years.

The area included a diversity of vegetation communities including:

- **chaparral**, dominated by chamise (Adenostema fasciculatum), ceanothus (Ceanothus spp.), scrub oak (Quercus dumosa), and mountain mahogany (Cercocarpus betuloides). Sumac (Rhus and Malosma spp) and toyon (Heteromeles arbuitifolia) were also common at lower elevations, as was manzanita (Arctostaphylos spp.) at higher elevations.
- **oak woodlands**, dominated by coast live oak (Q. agrifolia) and engelmann oak (Q. engelmannii).

Table 1. Area (hectares) of protected lands contained in cougar habitat in the Santa Ana Mountain Range.

Ownership and Parcel Name	Areas forming a large contiguous block	Areas surrounded by unprotected land
Federal:		
Cleveland National Forest	53,604[a]	
Cleveland National Forest (6 parcels)		626
Camp Pendleton	49,292[b]	
Fallbrook Naval Weapons Station	3,099	
Bureau of Land Management (7 parcels)		550
Bureau of Land Management (1 parcel)	364	
State:		
Chino Hills State Park		5,059
San Diego State University Field Station		1,805[c]
Department of Fish & Game Coal Canyon Preserve	385	
Orange County Parks:		
Caspers	3,085	
Limestone Canyon		2,169[d]
O'Neill		805
Whiting Ranch		632
Irvine		193
Wagon Wheel		178
Santiago Oaks		142
Private Reserves:		
Santa Rosa Plateau Preserve		2,803[e]
National Audubon Society Starr Ranch	1,578	
Rancho Mission Viejo Conservancy		486
Total	111,407	15,448

[a] excludes private inholdings.
[b] includes land leased to San Onofre Beach State Park; excludes 1700 ha in urban uses and airfield; includes some bombing ranges that may not be suitable habitat.
[c] includes 510 ha of BLM land administered by the field station.
[d] expected to be transferred to County from private ownership.
[e] administered by The Nature Conservancy (TNC); includes lands owned by TNC, State of California, and Riverside County.

- **riparian areas**, dominated by coast live oak, sycamore (Platanus racemosa), willow (Salix spp.), mule fat (Baccharis pilularis), and alder (Alnus rhombifolia)
- **coastal sage scrub**, dominated by buckwheat (Eriogonum fasciculatum), true sages (Salvia spp.), and (near the coast) California sagebrush (Artemisia californica),
- **conifer forests**, including bigcone doug-fir (Pseudotsuga macrocarpa), coulter pine (Pinus coulteri), and Tecate cypress (Cupressus forbesii), were found mainly at higher elevations, especially on north-facing slopes.
- **grasslands**, a mixture of native perennials (Stipa spp) and exotic annuals.
- **orchards**, predominantly of oranges or avocados

The topography was rugged, with elevations ranging from sea level to about 1690 m. Very few drainages had perennial surface flow throughout their length, but seeps and other water sources were well-distributed throughout the area. Most water sources remained reliable throughout the drought years that characterized the first half of the study.

Methods

We relied heavily on data obtained from radio-tagged cougars. A total of 32 cougars were captured and radio-tagged during this study. Animals were tagged and died at different times, so that the number monitored at any point in time varied from 4 to 16 (Table 2). To avoid burdening young animals with the stress of pursuit and the weight of a radio-tag, we did not pursue or capture animals under about 10 months of age.

Cougars were captured by using hounds or snares, and immobilized with ketamine hydrochloride and xylazine hydrochloride in a concentrated 5:1 mixture (Jessup and Clark 1986). Immobilized cougars were examined and assigned an age based on tooth wear, pelage, and body mass (Ashman et al. 1983). Some animals were ear-tattooed with a distinctive letter or number code. External body measurements were taken and body mass was measured on a spring scale for most animals. Antibacterial dressing was applied to any wounds, and ophthalmic salve was applied to prevent drug-induced corneal dehydration. Each cougar was assigned a letter-number code, with the letter indicating sex (M, F), and the number indicating the order in which the animal was captured (starting with 1 for the first animal of each sex). Blood was drawn from most cougars and sent to CDFG's Wildlife Investigations Lab (WIL) (Rancho Cordova CA) and/or to National Cancer Institute (NCI) (Frederick MD). WIL tested the blood for pathogens and other characteristics. NCI received tissue from 11 animals (Males 6, 10, 12, 13; Females 2, 5, 15-19) for use in their study of cougar population genetics across the Americas. Johimbine was administered to most cougars to speed recovery from the drugs, and each animal was observed until it was able to walk.

Each captured cougar was fitted with a radio-transmitter collar, weighing about 650g (model 500, Telonics, Inc., Mesa, AZ). Mortality sensors in each collar caused the pulse rate to increase after 6 hours of inactivity. Animals were recaptured to replace the transmitter about 30 months after transmitter deployment.

We regularly determined locations of radio-tagged cougars. Locations were determined from the air about once every 10 days. Ground locations were obtained more frequently, usually every 1-4 days, using standard triangulation techniques (Mech 1983), usually with a single observer.

On over 180 occasions during this study, a focal animal was located by triangulation every 15 minutes for periods of up to 24 hours. Seventy four (74) of the early sessions were for full diel (24-hour) periods, usually noon to noon. Because cougars were rarely active during daylight, 108 of the later session were nocturnal, starting 1 hour before sunset and continuing until 1 hour after sunrise. In selecting the focal animal for a session, we gave strong preference to dispersing juveniles exploring new terrain, to cats at the wildland-urban interface, and to cougars that might yield information on unknown travel routes.

Other field methods included spotlight surveys to determine deer herd composition, track surveys for cougar presence, search of historical records for cougar attacks, building a population simulation model, post-mortem examinations to determine cause of death, and collection and analysis of scats to determine prey. These methods are discussed in the relevant sections of this report.

Table 2. Dates of birth, capture, and death for 32 cougars radio-tagged in the Santa Ana and Santa Margarita Mountain Ranges during 1986-1992. ID# begins with "F" for females or "M" for males. Animals designated "alive" were living as of Feb 1 1993.

ID #	Birth Year	Date of capture	Date of death	Notes:
F1	1981	Oct 31 1986	Jul 1 1989	no litters 1986-89, killed by cougar
F2	1982	Nov 5 1986	Mar 12 1991	litter Jul 1989 (sons M3 & M4), broke femur in vehicle accident Dec 1989, had unusual kinked tail; died of intestinal disease
F3	1983	Sep 16 1987	Dec 28 1989	litters in Nov 1987 (3 cubs, all died by Feb 1989) and Jul 1989 (3 cubs); died of intestinal disease
F4	1979	Jan 8 1988	Jul 20 1990	litter Jul 1989 (2 cubs died within 3 mos); died of "old age"
F5	1984	May 17 1989	alive	no litters 1989-1992; very thin, blue eyes, stump tail
F6	1984	May 20 1989	May 23 1992	litter Aug 1990 (sons M11 & M12), killed by cougar
F7	1986	May 27 1989	--	lost radio contact Aug 15 1992
F8	1986	May 29 1989	Aug 14 1989	killed in vehicle accident on S.R. 91
F9	1983	Oct 17 1987	Mar 1 1992	radio failed Jul 1988, killed on I-15 south of Temecula
F10	1982	Feb 11 1987	Oct 1991?	disappeared Oct 1991 (death suspected); litters Jul 1989 (son M7) and Jun 1991 (2-3 cubs).
F11	1985	Aug 14 1988	Jan 25 1993	litter Jul 1989 (daughter F14), shot (goat depredation)
F12	1983	Aug 15 1988	Dec 21 1990	litter May 1989 (sons M8 & M10), killed on I-5
F13	1981	Mar 25 1990	Oct 10 1990	may have had a yearling cub at capture; killed on S.R. 74
F14	1989	Dec 21 1990	--	collar slipped off
F15	1987	Feb 21 1991	Jun 13 1992	bred several times with M9, but no litters 1991-92; broke hip in vehicle accident Jun 4 1992, died several days later
F16	1989	Jul 28 1991	Sep 19 1991	died 5 weeks after vehicle accident
F17	1989	Jul 28 1991	Jan 7 1992	died of unknown causes (no acute trauma)
F18	1986	Jul 28 1991	alive	litter Dec 1989 (daughters F16 & F17)
F19	1987	Aug 8 1991	alive	no litters during 1991-92
M1	1980	Jan 13 1988	Feb 6 1988	breeding male (several consorts); shot (sheep depredation)
M2	1987	Oct 10 1989	Mar 4 1992	breeding male (many consorts); shot (goat depredation)
M3	1989	Jun 5 1990	Feb 16 1991	entered residential area as a disperser (Feb 8 1991), died of disease
M4	1989	Jun 5 1990	Nov 10 1990	died in vehicle accident or killed by cougar (fed upon by F2 & M3)
M5	1989	Aug 3 1990	Sep 22 1991	captured as disperser in a residential area, broke hip and knee in vehicle accident Apr 23 1991, injuries were major factor in death
M6	1989	Aug 27 1990	alive	captured as disperser; crossed S.R. 91 at Coal Canyon 22 times
M7	1989	Oct 23 1990	alive	successfully dispersed; no breeding documented
M8	1989	Oct 29 1990	May 3 1991	dispersed from Pendleton to Chino Hills, killed on S.R. 60
M9	1986	Feb 17 1991	alive	breeding male (many consorts)
M10	1989	Feb 25 1991	Sep 15 1992	dispersed from Pendleton to S.R. 91, broke femur May 7 1991 in vehicle accident, killed on impact in second accident
M11	1990	May 4 1991	Feb 29 1992	light injury in vehicle accident Feb 4 1992, shot in City of Oceanside
M12	1990	Aug 15 1991	Apr 1 1992	dispersed via Pechanga Corridor into Palomar Range; died of unknown causes
M13	1988	Oct 25 1991	alive	captured as disperser; no breeding documented

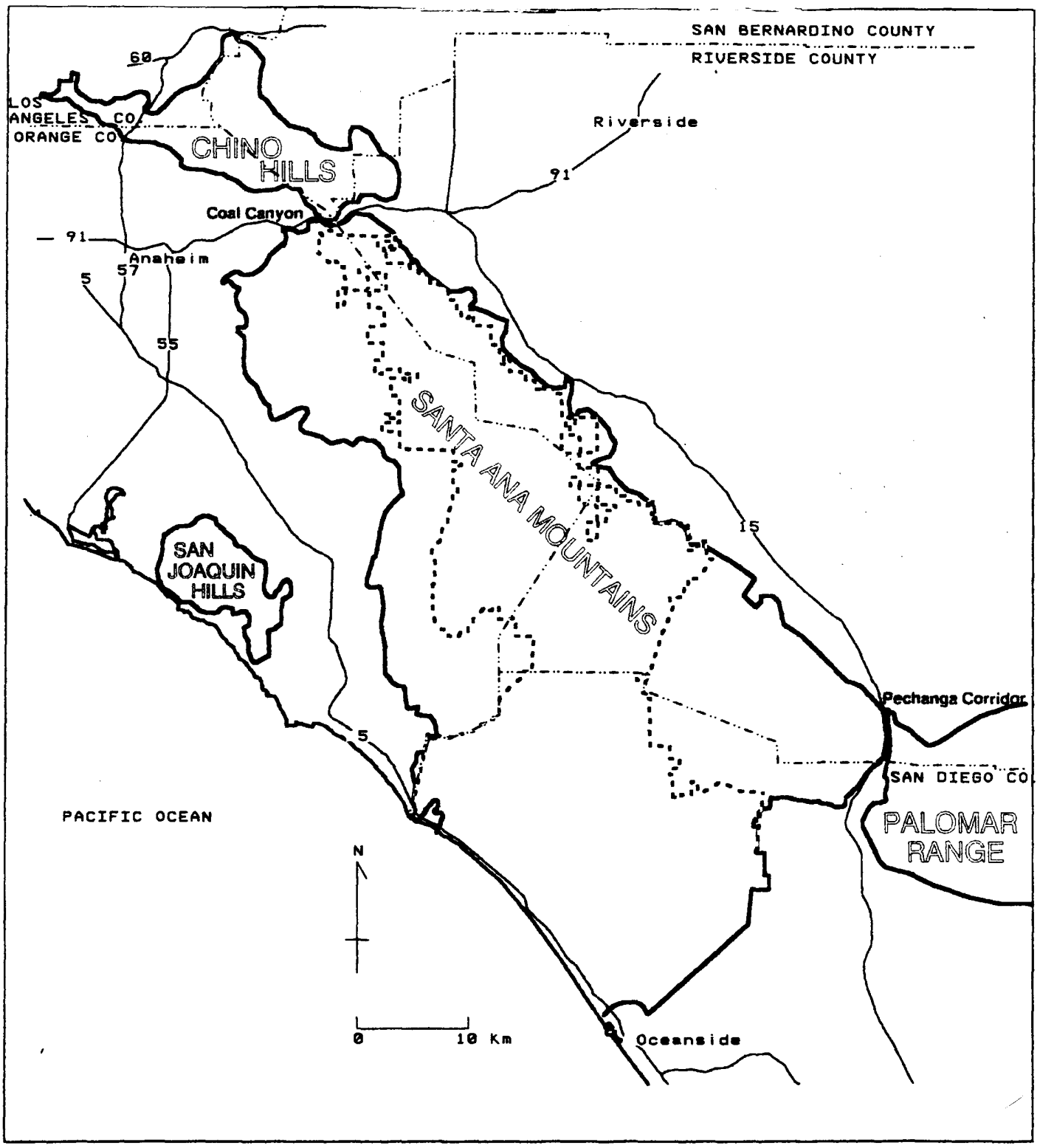

Figure 1: The heavy solid lines enclose 3 areas: 800 mi^2 (2070 km^2) of cougar habitat in the Santa Ana Mountain Range (including the Santa Margarita Mountains and the Chino Hills); 29 mi^2 (75 km^2) of suitable habitat in the San Joaquin Hills (subpopulation recently extinct); and (east of Interstate Highway 15) a portion of the habitat of the adjacent population in the Palomar Range. The heavy dashed line encloses 430 mi^2 of protected areas forming a large contiguous block of habitat (Cleveland National Forest, Camp Pendleton, Fallbrook Naval Weapons Station, Caspers Park, Starr Ranch Sanctuary).

CHAPTER 1. HOME RANGES AND HABITAT USE

Home ranges

The minimum convex polygon (MCP) method was used to calculate seasonal and cumulative home range size for each adult cougar. Home range sizes were calculated separately for the wet season (November-April) and the dry season (May-October). Home ranges were not calculated for: (1) animals monitored for fewer than 160 days out of each season's 182 days, (2) animals with less than 45 locations in a season (unless the home range size was larger than average), or (3) mothers with young (0-8-weeks-old) cubs during that season. In addition, F5 was excluded in several seasons because she exhibited 2 distinct home range areas separated by a large intervening area with little use (see below). Occasionally an animal would make an excursion far outside its normal home range, and these outlying points were excluded from MCP home ranges.

Home ranges of adult females averaged about 113 km^2 (6-month season) and 218 km^2 (cumulative) (Table 3). Male home ranges were about 4 times the size of female ranges, averaging about 485 km^2 (6-month season) and 767 km^2 (cumulative). Home range size did not differ between wet and dry seasons ($P > 0.50$ for females or males). The smallest female seasonal home range was 56 km^2 (F1 in the wet season of 1986-87), and the largest was 195 km^2 (F19 in the 1992 dry season). Seasonal ranges of males varied from a low of 356 km^2 (M2, 1990 dry season) to a high of 635 km^2 (M9, 1991 dry season).

Table 3. Seasonal and cumulative home range areas (km^2) for adult cougars in the Santa Ana Mountain Range, as computed by the minimum convex polygon method. Wet Season = November-April; dry season = May-October; n = number of seasons monitored. We excluded F5's locations for 1989-90, when she wandered widely. See Table 1 for duration of cumulative ranges. Number of locations includes no more than 1 location per day. Areas were computed only when there were at least 45 locations spanning 100 days within a season.

Cougar	Wet Season		Dry Season		Cumulative	
	mean area	n	mean area	n	area	no. of locations
F1	108	3	123	2	252	433
F2	77	4	76	3	268	718
F3	65	2	91	1	112	590
F4	77	2	124	2	208	537
F5	76	2	94	2	127	151
F6	164	2	154	2	272	267
F9	108	1		0	144	213
F10	121	2	135	3	297	380
F11	115	4	87	4	191	357
F12	96	2	97	1	162	304
F15	151	1		0	349	131
F19	145	1	195	1	230	130
Female Mean	**109**		**118**		**218**	
M2	494	3	367	2	705	290
M9	552	1	527	2	829	129
Male Mean	**523**	**4**	**447**	**4**	**767**	**210**

Our sample included only 2 adult males (M2 and M9) with known histories of consorting with females. Most other radio-tagged males died before establishing a stable adult home range. Three of the young males (M6, M7, and M13) exhibited stable home ranges during

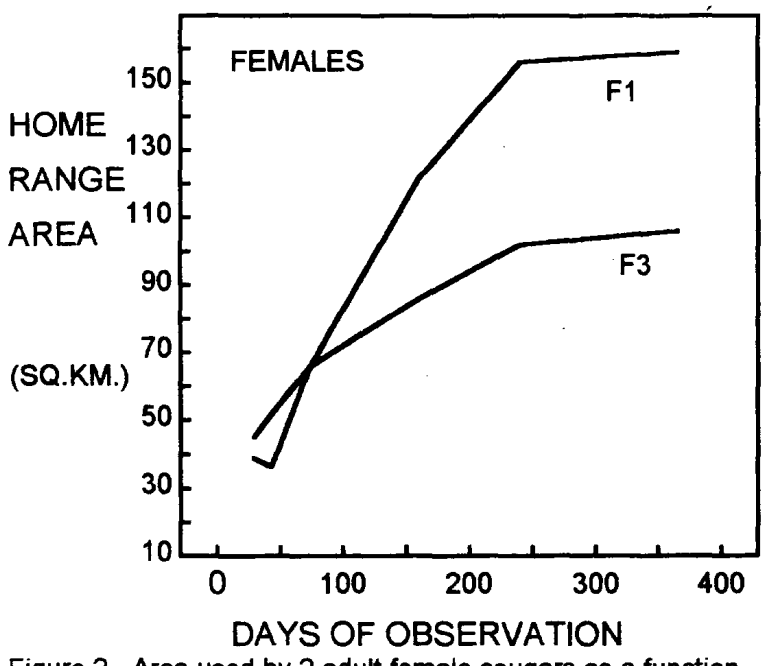

Figure 2. Area used by 2 adult female cougars as a function of length of the observation period.

the last months of the study, and these home ranges will probably form the nucleus of their eventual adult home ranges if they continue to survive. However, their home ranges remained markedly smaller than those of M2 and M9 through the end of the study. The home ranges and movements of these and other dispersing juveniles are discussed in detail in Chapter 6.

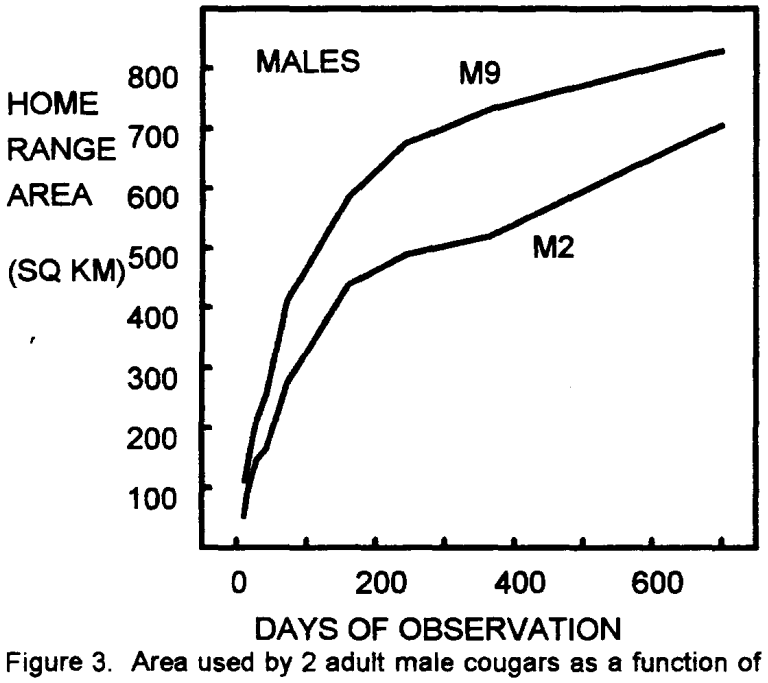

Figure 3. Area used by 2 adult male cougars as a function of length of the observation period.

One adult female, F5, exhibited an unusually large home range during 1989 dry season and the 1990 wet season. During these months she alternated between 2 widely separated home range areas (Figure 4). F5 was unusual in several other respects that may or may not have any bearing on her home range pattern: (1) During 2.5 years of monitoring we could not confirm that she consorted with a male or had any cubs, (2) F5 was markedly thinner than other adult females (although not emaciated), and (3) F5 was the only adult in our study with blue (rather than yellow) eyes. The latter 2 traits were evident both during the initial capture and during recapture to replace her radio-collar 26 months later.

The size of each adult cougar's home range increased with the length of the observation period, but it eventually reached an asymptote (plateau) at about 200-250 days for females, at which point there was only about a 10% increase in area for an additional 200-400 days of observation (Figure 2). For males, home range size continued to increase with increasingly long observation periods (Figure 3), This means that it took about 7 months for an adult cougar to use most of its home range, and that only a fraction of its range was used in any given week or month. An adult female cougar typically used less than a third of her home range in any given month (Figure 2).

This finding has implications for using tracks or other sign to detect cougar presence. For example, such sign is often used to determine whether the site of a proposed project is being used by cougars. No sign for a 200-day sampling period would be strong evidence that the site is not a normal part of any cougar's home range. However, shorter efforts could well fail to detect the presence of a resident cougar.

Overlap among home ranges

Home ranges of adult females overlapped extensively when viewed on an annual basis (Figures 4 & 5). This pattern of wide overlap among adult females has been reported in 14 of 16 studies addressing this issue (references in Anderson 1992:Table 35).

Home ranges of adult males overlapped each other minimally (Map 4). However, home ranges of transient males were overlapped almost entirely by the ranges of adult males. Of 14 previous studies addressing the issue of overlap among males, 8 reported little or no overlap and 6 studies reported considerable overlap among adjacent males (summary in Anderson 1992:Table 35). Because many studies did not distinguish subadult males from territorial adults, some reports of male-male overlap could reflect tolerance of subadult males by adults. Alternatively, the studies reporting non-overlap were based on only 2-4 males (versus 4-7 males in studies noting overlap); they may have failed to detect overlap simply due to under-sampling.

Adult female cougars regularly encountered each other, and on many occasions pairs of adults remained close together (0-300m apart) for 1-3 days. Such pairings were observed on about 20 occasions, and included 8 different females. Observations of such associations among adults have been reported very rarely in previous studies; W. D. Padley (J. Mammalogy, In Review) summarizes most of the data on female-female interactions collected in this study effort.

Habitat use

Radio-tagged cougars in the Santa Ana Mountain Range used all available habitats, although some types were apparently preferred and others avoided. In a future report, we will overlay cougar locations on vegetation maps and give a more formal analysis of habitat use and preference. We have obtained digitized habitat data for Riverside County (west of I-15) and for Camp Pendleton, but Orange County and San Diego County did not have vegetation data ready for release in time for us to analyze the data and include them in this report. We anticipate receiving the San Diego data in June 1993 and the Orange County data in Fall 1993.

In the interim, we offer the following qualitative assessments based on our field experience with respect to 5 factors that influence habitat suitability, namely: vegetation, topography, fire, human use, and habitat size and connectivity. We caution that future conclusions from quantitative analyses of vegetation data may differ from these tentative conclusions.

Vegetation. Cougars clearly used all native vegetation types, but used large grasslands (e.g. Horno Canyon near San Juan Capistrano, large areas in the Chino Hills and Santa Rosa Plateau) much less than would be expected on the basis of relative availability of that habitat type. Horno Canyon, for instance, was used by only 2 cougars, both subadult males, and only on a few occasions. Smaller grassland areas (e.g., much of the Cañada Gobernadora and Cañada Chiquita flood plains) were more readily used than large grasslands. When cougars crossed grasslands during overnight monitoring sessions, they usually moved quickly across them to the nearest woody vegetation. The cougar's reliance on stealth and ambush probably accounts for this tendency to avoid open areas. Row-crop agricultural areas were strongly avoided, and orchards were moderately avoided, by cougars.

There have been 3 previous quantitative assessments of cougar preference for various vegetation types (Laing and Lindzey

1991, Logan and Irwin 1985, and Belden et al. 1988). These studies also reported avoidance of agricultural areas, habitats lacking woody vegetation, and habitats that provided little horizontal (hiding) cover.

Topography. Cougars used all types of terrain, including the steepest slopes and rock outcrops, and all aspects. During all night monitoring we documented that cougars hunted, traveled, and rested in a variety of topographic situations. We suspect there might also be some avoidance of flat areas, as reported by Logan and Irwin (1985) and Laing and Lindzey (1991), but this would be difficult to document in our study because almost all flat areas had been cleared for housing, row crops, or livestock pastures.

During long distance movements, cougars seemed to prefer the scour zones in the bottoms of larger canyons. Dirt roads often paralleled these zones, and typically a cougar alternated between walking in the road and in the wash. Ridgetops were also favored travel routes, especially when a dirt road or hiking trail created an easy path through chaparral or other brushy vegetation. Although the preference for canyon bottoms and ridgetops for travel was pronounced, it was far from absolute; on many occasions cougars traveled midslope along a contour line, along the fall line of a steep slope, or diagonal to the fall line. Even when traveling predominantly along a ridge or wash, cougars made frequent detours into other topographic situations.

Fire. Radio-tagged cougars experienced several large fires during the study. The animals always successfully avoided the flames. When a fire occurred within a cougar's home range, the cat usually re-entered the burned area (or at least the unburned patches within that area) within 2 weeks after the fire. For example, on October 18-20 1989, a 9000-acre fire burned portions of Camp Pendleton, Rancho Mission Viejo, and Cleveland National Forest. The burned area includes large portions of Talega, San Mateo, and La Paz Canyons, which are very important parts of F3's and F4's home ranges. In the first week following the fire, both cats avoided the burn area, but started re-using it within 2 weeks and made extensive use of the burn within 6 weeks. A similar patterns of short-term avoidance of burn areas was exhibited by F11 on Camp Pendleton on 2 occasions.

Human use. Radio-tagged cougars traveled through some rural areas with low housing density, e.g., Williams Canyon, Santiago Canyon just west of Modjeska, the cluster of dwellings on Starr Ranch. Cougars categorically avoided denser areas such as the communities of Modjeska, Silverado, and Trabuco Canyon, although they would skirt these areas within 100 meters of the peripheral homes.

It is difficult to specify the housing density at which cougars will cease to use an area. Cougars clearly tolerate 1 dwelling per 40 acres, if the area is adjacent to unpopulated areas. Our best estimate is that the transition from habitat to nonhabitat occurs at about 1 dwelling per 20 acres. Under ideal conditions (no tall fences, no free-roaming dogs, low-speed roads, minimal loss of native vegetation, no goats or sheep to provoke depredation incidents, tolerant landowners) we suspect that cougars might tolerate housing densities as high as 1 dwelling unit per 10 acres.

Habitat Size and Connectivity. Because cougars have large home ranges and do not reach high population density, habitat must be either contiguous with or connected to at least several hundred square miles of suitable habitat. Because the undeveloped portion of the Santa Ana Mountain Range is only about 2070 km^2 (800 mi^2), connectivity is critically important, and loss of connectivity is the main factor threatening to cause many wildlands to cease being cougar habitat. For example, the

San Joaquin Hills, which was ideal habitat with respect to the first 4 criteria, has not been cougar habitat since it was isolated from larger areas of habitat. It is simply too small to support a cougar population in isolation. This subject is discussed at greater length in Chapters 3 and 4, and in Beier (1993).

In summary, cougars in the Santa Ana Mountain Range were habitat generalists. Although some habitat types were used more than others, cougars were neither obligate users of any particular vegetation type, nor did they show a categorical aversion to any native vegetation type that included woody cover. In general, all land in the Santa Ana Mountain Range (including the Santa Margarita Mountain Range, the Santa Rosa Plateau, and the Chino Hills) was cougar habitat if it met all 5 of the following criteria:

1. The vegetation was predominantly native.
2. There was some woody vegetation.
3. The area had ample prey, especially mule deer.
4. There was a low density of buildings and human dwellings.
5. The area was contiguous or connected to the main block of cougar habitat (see Figure 1).

CHAPTER 2. POPULATION DENSITY AND STRUCTURE

Thirty-two cougars were radio-tagged during this study (Table 2). The number of radio-tagged animals increased in the first 3 years as our effort and the size of the study area increased, and then decreased in the final 1.5 years as we discontinued capture efforts. These changes do not reflect changes in cougar numbers. In all likelihood, the number of adult cougars has not changed markedly during the 5 years of the study. Although the long-term prognosis is for cougar numbers to decrease as habitat is lost and fragmented, we could not detect significant change in this 5 year period.

The sample of radio-tagged cougars was largest in August-September 1991; at that time the population consisted of a minimum of 7 adult females, 3 adult males (counting M6 as an adult who had not yet established a full-size territory), 3 subadult males, 2 female cubs, and 2 male cubs, for a total of 10 adult and 7 juvenile cougars.

Because a relatively large fraction of the population was radio-tagged in September 1991, we estimated cougar numbers in the Santa Ana Mountains for that month. In these estimates, cougars are classed as cub (from birth until dispersing out of its mother's home range at 18-24 months of age), subadult (from age of dispersal until a stable home range is established), or adult (over 24 months of age and exhibiting a stable home range). "Juvenile" refers collectively to cubs and subadults. We estimate that there are about 2070 km^2 (800 mi^2) of suitable cougar habitat (Figure 1).

The true population size in September 1991 was larger than the sample of radio-tagged animals. We made no attempt to capture or radio-collar cubs younger than 10 months of age, and we know that at least 2 such cubs (offspring of F10) were alive at that time. M13 (a subadult collared October 1991) and another young male shot on a depredation permit in January 1992 (see below) were also present in September 1991 (unless they immigrated from the Palomar Range). Tracks indicate that at least 3 other uncollared cougars (females or subadults) were present in easily-surveyed areas in late 1991. Furthermore, much of the Cleveland National Forest is not conducive to capture efforts or track surveys, so probably several more uncollared animals were not detected. Finally, the regular appearance of dispersing subadult males that were not the offspring of radio-tagged females indicates that there were additional adult females.

Nonetheless, 3 lines of evidence suggest that a large fraction of the population (at least those over about 20 months of age) in the Santa Ana Mountain Range was radio-tagged in Fall 1991:

(1) **Depredation incidents**. During 1991, Orange County Animal Control, CDFG wardens, or citizens relayed to our study team about 12 reports of domestic goats or sheep being killed by cougars. Eight cases were promptly investigated (in other cases, the report was received too long after the fact to be useful). In 7 of these 8 cases, a radio-tagged cougar was almost certainly the offending animal, based on its proximity to the fresh carcass. Although 1 cougar (M12) was the offender in 4 of the cases, the other cases involved 1 uncollared and 3 different radio-tagged cougars.

Although 7/8 of these livestock depredations involved radio-tagged cougars, it would be inappropriate to conclude that 7/8 of the entire population was radio-tagged. The depredations all occurred in the western foothills of the range (Santiago Canyon, Williams Canyon, Live Oak Canyon, La Paz Canyon, and San Onofre Canyon). The study team was most active in these foothills throughout the study, and may in fact have

collared about 80% of the cougars using these foothills. However, in other parts of the range, a smaller proportion of the cougars was radio-tagged.

(2) **Highway accidents**. Highway Patrol officers, Camp Pendleton wardens, police, local Animal Control agencies, and citizens regularly relayed to us reports of cougars being hit by automobiles. During August 1990 through January 1992, we received 9 such reports (we exclude an incredible and unverifiable report from Dana Point). Seven of these 9 accidents involved radio-tagged cougars (see last Quarterly Report). The other 2 accidents involved an animal killed on I-15 near Temecula (October 1990) and a probably valid report of a non-fatal accident on Basilone Road (Camp Pendleton, August 1990).

Again, the collisions occurred in well-roaded areas which were also the areas where we were most able to detect and radio-tag cougars, so we caution that we probably had not radio-tagged 78% (7/9) of the population. Nonetheless every cougar faced some risk of a vehicle collision (each radio-tagged cougar crossed paved roads on several to many occasions) and clearly these data show that a large fraction of the population was radio-tagged.

(3) **Inadvertent recaptures** in Roblar and lower De Luz Creeks. After F10 and her cubs disappeared in late October 1991, we put 5 snares in her home range and checked them for 33 days. Although we did not catch F10, 3 other radio-tagged animals (M9, F15, and F18) tripped these snares during that time. The snare sites were in peripheral and rarely-used portions of the home ranges of F18 and F15. Most significantly, no uncollared cougar visited any of the 5 snare sites during this time. Although a 30-day effort does not rule out use of these canyons by uncollared animals (Chapter 1: home range size), clearly there were far more radio-tagged than uncollared cougars in the vicinity of Roblar and lower De Luz Canyons.

This evidence strongly indicates that in September 1991 we had captured at least half, but certainly not all, of the adult population. To estimate the total number of adult cougars, we examined maps of cougar home ranges for adults of each sex during 1991 and 1989.

Home ranges of adult females did not vary over the years either in size or in amount of overlap (Chapter 1). Home range overlap is well illustrated in the Camp Pendleton area in 1991 (Figure 5) and in several areas in 1989 (Figure 4). If we extrapolate this amount of overlap throughout the range, we estimate that we had collared about half of the adult females. Thus, there may have been about 14 adult females in the entire Santa Ana Mountain Range in September 1991.

The range may well be capable of supporting more than 14 adult females. There was a failure in reproduction in much of the southern half of the range during 1988 and it is possible that the number of adults in 1991 may not yet have rebounded to normal levels. This would be supported by the fact that 2 adult females used the Caspers Park area as the core of their home ranges in 1989 (Figure 4), whereas no adult female did so during 1991-92 (Figure 5, and road-tracking data: any adult female would have been detected in almost daily track searches by our crew or by trained Park rangers). Because Caspers Park is excellent cougar habitat, it will doubtless be occupied again. As recruits fill in vacancies created by recent adult mortality, it seems reasonable to expect that the mountain range can probably support 3-4 additional adult females.

A similar map of adult male home ranges as of October 1991 (Figure 6) includes 2 young males (M6 and M7) who exhibited stable

home ranges for several months. Although the 1991 home ranges of M6 and M7 were significantly smaller than those of M2 and M9, they were far larger and more stable than the ranges of dispersing males, and probably were early adult territories. Based on the minimal overlap among these ranges and the lack of suitable habitat not occupied by these males, probably no more than 1 adult territorial male was not radio-tagged in September 1991. Male territory sizes are probably somewhat plastic, and a larger number of males could probably coexist by using smaller territories and tolerating more overlap. However, it seems that a reasonable estimate for the maximum number of adult territorial males is 7 or 8.

In summary, we estimate that the Santa Ana Mountain Range contained 10-14 adult females in September 1991, and that it may be able to support an average of 10-19 adult females in the long run. We also estimate that the Range contained 4-5 adult (or near-adult) males in September 1991, and that it may be able to support as many as 7-8 adult males in the long run. Juvenile mortality is very high and variable, as is reproduction, so we offer only a very rough estimate of 10-20 juvenile cougars in the Range.

Schoenfelder and Kimple (1979) used road transects to estimate cougar numbers in the Santa Ana Mountain Range in 1977 and 1978. They defined any medium or large size track traveling alone as "adult" (this would include both subadults and adults as defined herein). They estimated 12-18 adult-size cougars within the 400 square miles of the Santa Ana Mountain Range they surveyed. Assuming that about 25% of these animals were subadults, and extrapolating to the current total of 2070 km^2 (800 mi^2) of habitat, their estimate would be 18-27 adults. Our estimate of 14-19 adults (in September 1991) and 14-27 adults (potential long term carrying capacity) is similar to theirs. Given the poor accuracy and precision of track surveys (Van Dyke et al. 1986, Van Sickle and Lindzey 1992, Kendall et al. 1992), this agreement is probably due largely to chance.

Sex Ratio. The ratio of adult females to males in September 1991 was 1.75:1 for radio-tagged animals (counting M6 and M7 as adults; the ratio would be 2.3:1 if M7 is classed as subadult). Using estimated population size for Fall 1991, the adult sex ratio was between 2.5:1 (10/4) and 2.8:1 (14/5). In the long-term the expected sex ratio would be about 2:1 (15/7.5). Most other studies have also reported a sex ratio of approximately 2:1 (Seidensticker et al. 1973, Currier et al. 1977, Ashman et al. 1983, Murphy 1983, Hemker et al. 1984, Logan et al. 1986, Neal et al. 1987, Hopkins 1989). A few studies have reported other adult sex ratios, but all vary between 1:1 and 3:1 (Hornocker 1970, Seidensticker et al. 1973, Currier et al. 1977, Shaw 1977, Hopkins 1981, Quigley et al. 1989).

Carrying capacity. Dividing the long-term number of adults by the total 2070 km^2 of habitat, we estimate carrying capacity as 0.7 adult females and 0.35 adult males per 100 km^2 (or about 2 adult females and 1 adult male per 100 mi^2 of habitat). Previous studies have provided widely varying estimates of density many of which are roughly the same as our estimates (Hornocker 1970, Seidensticker et al. 1973, Sitton and Wallen 1976, Currier et al. 1977, Shaw 1977, Hemker et al. 1984, Logan et al. 1986, Neal et al. 1987, Hopkins 1989). It is difficult to determine how well previously reported densities correspond to our estimate because some studies lump non-breeding subadults with adults and because some study sites were chosen because of atypically high cougar densities.

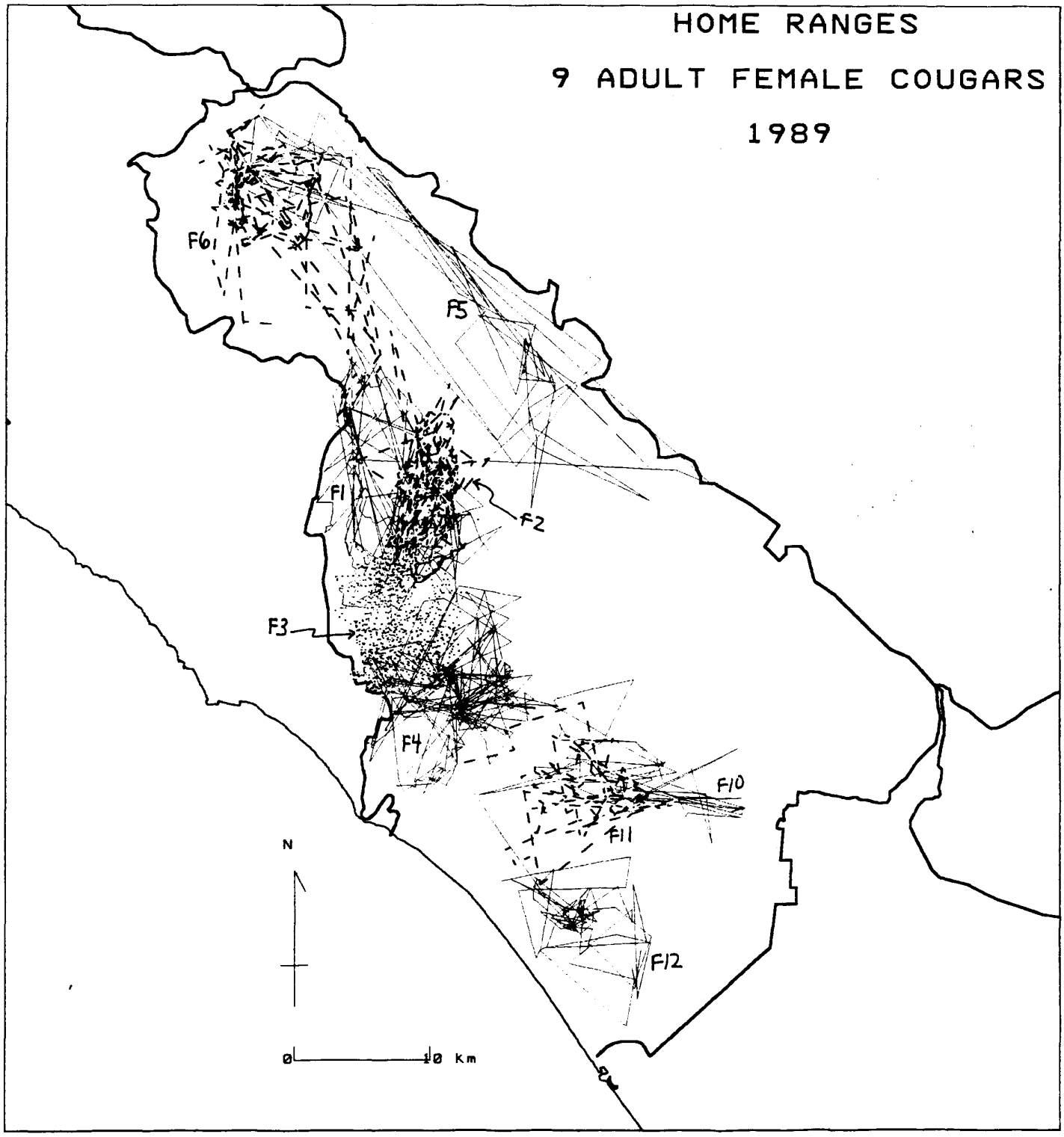

Figure 4. Home ranges of the 9 adult female cougars radio-tagged in July 1989. For each home range all locations for 1989 are connected in chronological order. The heavy solid line encloses 800 mi^2 of cougar habitat in the Santa Ana Mountain Range.

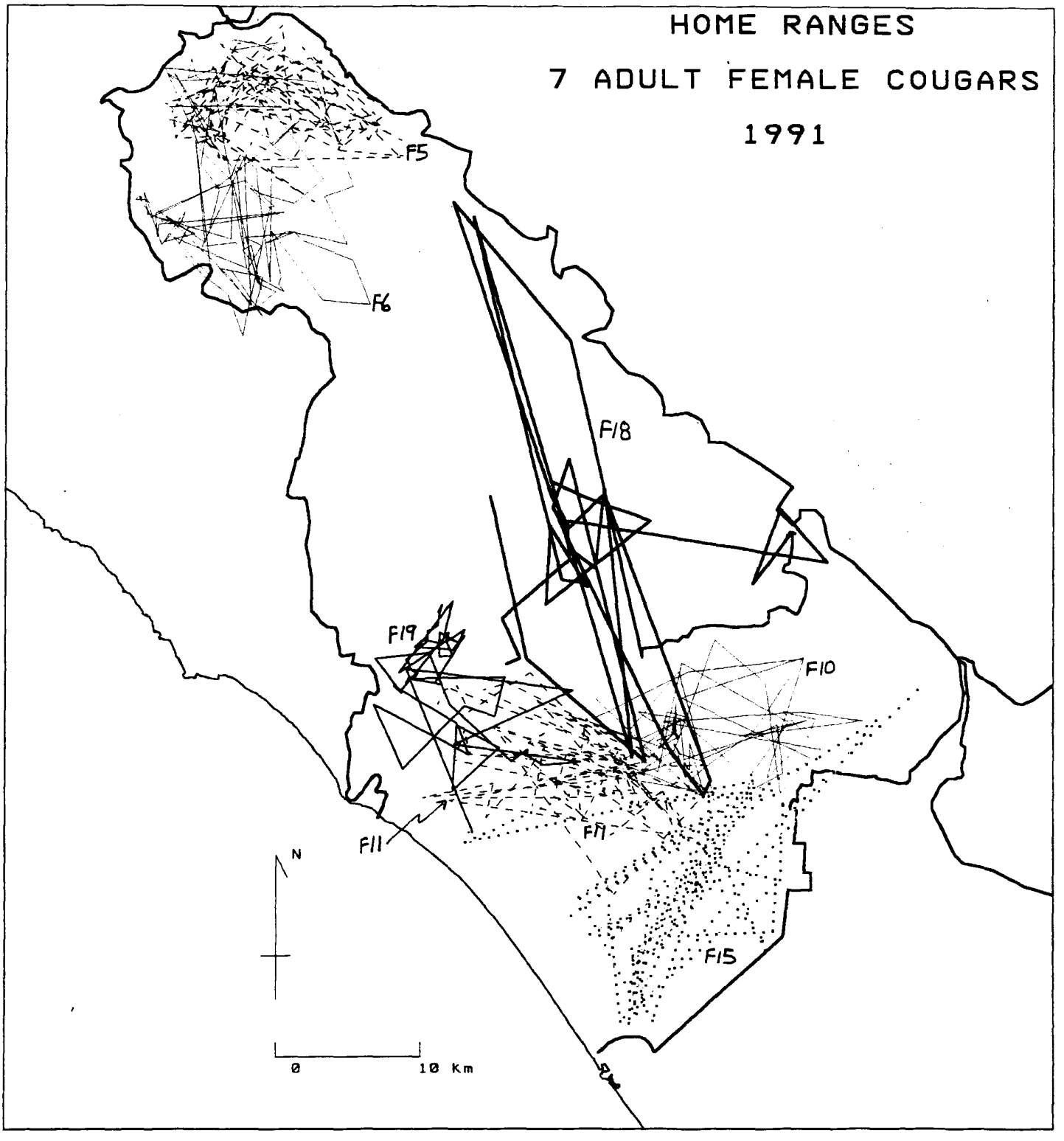

Figure 5. Home ranges of the 7 adult female cougars radio-tagged in September 1991. For each home range all locations for 1991 are connected in chronological order. The heavy solid line encloses 800 mi^2 of cougar habitat in the Santa Ana Mountain Range.

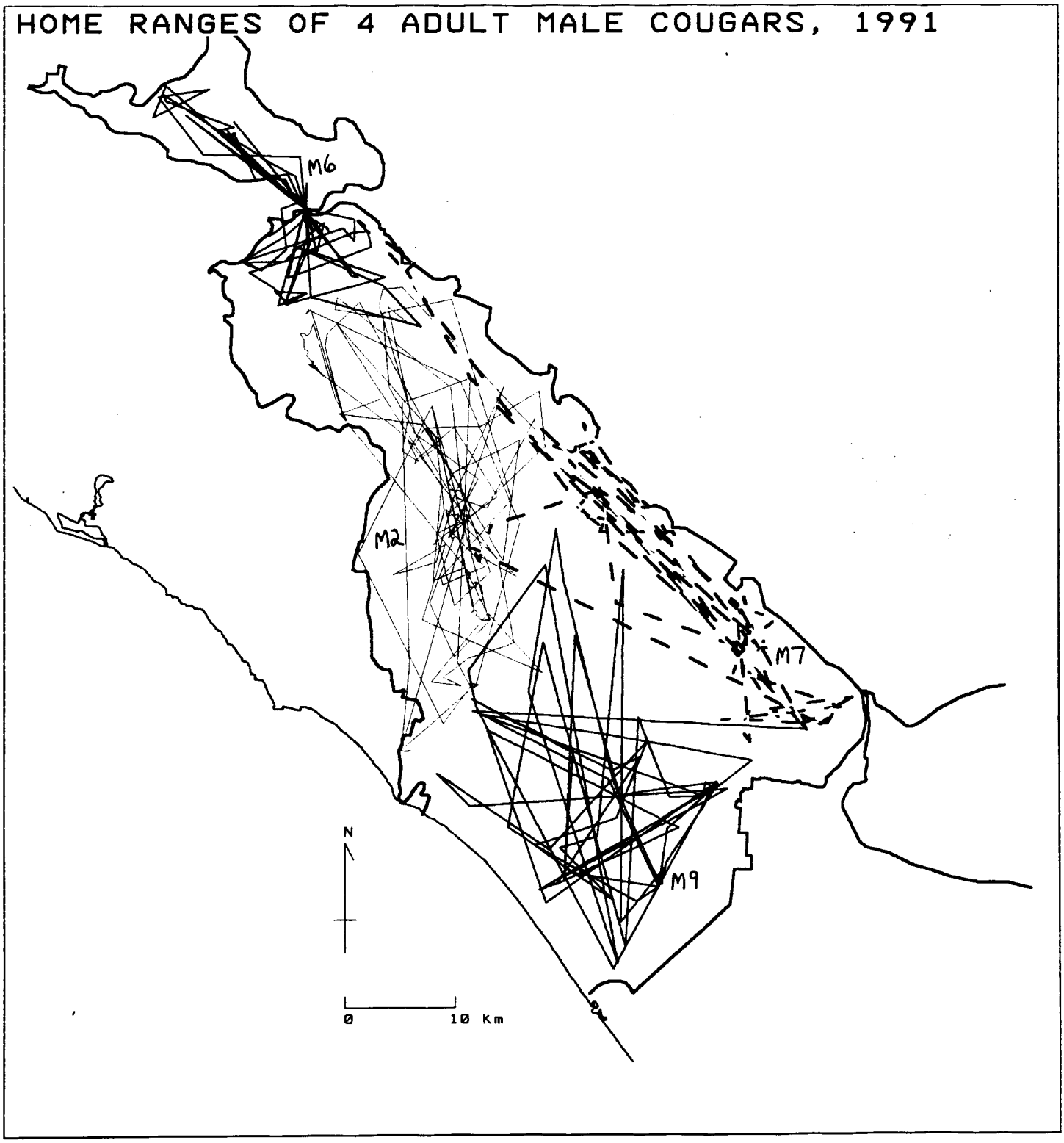

Figure 6: Home ranges of the 2 adult male cougars (M2 and M9) radio-tagged in December 1991 and 2 near-adults (M6 and M7). M6 and M7 continued to expand on these home ranges throughout 1992. For each home range all locations for 1991 are connected in chronological order, except for M6 (whose range excludes dispersal movements and includes only Oct 91-Jan 92 locations). The heavy solid line encloses 800 mi^2 of cougar habitat in the Santa Ana Mountain Range.

CHAPTER 3. DISTRIBUTION AND TRAVEL CORRIDORS

Cougar Habitat in the Santa Ana Mountain Range

Using the 5 criteria listed at the end of Chapter 1, there was about 2070 km^2 (800 mi^2) of cougar habitat in the Santa Ana Mountain Range during 1988-1992. We obtain the same estimate by computing the area within a polygon enclosing all cougar locations. The largest uncertainty in this estimate concerns over 50 km^2 of land in and around the Santa Rosa Plateau that had a mix of orchards, low-density housing, and semi-open pasture. These areas were included in our estimate on the basis of documented cougar use (usually brief visits). However, much of this area was clearly marginal habitat, and will become unusable if human use intensifies.

Cougar Use of County Parks East of I-5

All major regional parks east of I-5 were cougar habitat. Caspers Wilderness Park, Limestone Canyon Regional Park, Whiting Ranch Regional Park, Wagon Wheel Regional Park, Weir Canyon Regional Park (proposed), Irvine Regional Park (including the Villa Park impoundment) and O'Neill Regional Park (including the Arroyo Trabuco) were all used regularly by radio-tagged adult cougars. Each of these 7 parks was an important part of the home range of at least 1 radio-tagged adult cougar.

In addition, Peters Canyon Reservoir Regional Park and Santiago Oaks Regional Park were both used by subadult radio-tagged cougars, although we never documented use by any adult cougar. Only one cougar (M5) used Peters Canyon Reservoir. He first encountered and used the reservoir during his dispersal explorations, but most of his use of the area was after he broke his hip and knee in a vehicle accident. Both M5 and M10 used Santiago Oaks Regional Park (both after their vehicle accidents). Although both parks offered excellent habitat in terms of good native vegetation, ample woody cover, and ample prey, each was marginal with respect to housing density and connectivity (see Chapter 1: habitat use). Both parks were immediately adjacent to and nearly surrounded by high density housing tracts, and both had only a narrow connection to the central block of habitat. Indeed the only non-urban terrain adjacent to Peters Canyon Reservoir was an open grassy area nearly 400 m wide, with only 2 thin stringers of shrubs leading toward larger suitable habitat.

Peters Canyon Reservoir will become unusable by cats if the Eastern Tollroad or East Orange Project is built. Even without these projects, it will remain marginal and rarely-used habitat.

In contrast, good riparian vegetation connects Santiago Oaks Regional Park to Irvine and Weir Canyon Parks. Santiago Oaks Regional Park will probably continue to receive occasional use by cougars, especially by dispersing juveniles and injured animals. However, if the proposed Eastern Tollroad (and the tract homes that follow it) isolates Irvine and Weir Canyon Regional Parks from the central habitat area to the east, it will remove cougars from all 3 of these Regional Parks.

We never documented any cougar use of Carbon Canyon Regional Park in the Chino Hills. Nonetheless it did meet all 5 criteria for cougar habitat, and we believe that it was occasionally used by cougars during 1988-1992. It certainly will be potential cougar habitat as long as cougars remain in the Chino Hills.

All regional parks, except Caspers Wilderness Park, will become unusable by cougars if urbanization isolates them from the central habitat block. Loss of the Limestone Canyon-Whiting Ranch Parks complex would be a severe blow to the cougar population, and such isolation is certain to occur without careful management of urban growth along Santiago Canyon Road. The proposed Eastern Tollroad and the housing tracts that will follow it will (unless carefully planned) similarly prevent cougars from using Irvine Regional Park and the proposed Weir Canyon Regional Park. Ongoing and future urbanization, especially that associated with the proposed Foothill Tollroad, threaten to isolate O'Neill and Wagon Wheel Regional Parks. These issues are discussed at greater length under "corridors" below.

Cougar Use of the San Joaquin Hills

West of Interstate 5 there is only 1 area - the San Joaquin Hills - that meets 4 of the 5 criteria for cougar habitat. The San Joaquin Hills offer ample native vegetation, woody cover, and prey (including mule deer). About 75 km^2 (29 mi^2) of the area had low (essentially zero) housing density in 1990-91. The area included 5 relatively pristine canyons: Muddy Canyon, Moro Canyon, Emerald Canyon, Bommer Canyon, Shady Canyon, and Wood Canyon. Good habitat also existed in portions of Laguna Canyon and about half of Los Trancos Canyon. The only missing habitat element lacking was connectivity, with about 5 km (3 mi) of urban sprawl isolating these hills from the main block of cougar habitat. Although this area became isolated only about a decade ago and probably supported a few cougars for several years afterward, our population model (Chapter 4) demonstrates that an area of this size cannot sustain a breeding population of cougars.

Nonetheless, there were persistent reports of cougars being sighted in the San Joaquin Hills. On several occasions (October 8 1989, 2 dates in winter 1990, and September 21, September 30, and October 3 1992) we were able to initiate track surveys within hours of such reports. On each occasion we searched the site of the report and adjacent washes, ridges, trails, and dirt roads for tracks. Although tracks of many species were evident, no cougar tracks were seen.

On the chance that 1-2 cougars might still be hanging on in the San Joaquin Hills, we undertook intensive track surveys in the San Joaquin Hills from May 21 through May 26 1990 (6 consecutive days). Dusty road conditions were optimal for tracking on all survey routes. On each survey, we covered a Basic Survey Route consisting of 2 tributaries of Laguna Canyon and the full lengths of Moro, Shady, Emerald, and Wood Canyons. Portions of Bommer, Los Trancos, and Muddy Canyons were covered on some of the survey dates. A detailed route map was included in this study's Quarterly Report dated August 1 1990. To design the Basic Survey Route we first identified the roads that traversed the best cougar habitat, selecting those that crossed the area from one developed edge to the other. In addition to the Basic Survey Route, on each day we also covered some road segments on secondary canyons or ridges. On average, each secondary segment was covered twice during the survey period.

Our rationale in repeatedly checking the same long roads daily for a week was based on the habits of radio-tagged cougars. Although a cougar may remain in one place for 3-4 days while feeding on a deer, over the course of a week there are several nights during which the cat hunts, traveling several km per night. The only exception is a mother with newborn cubs who may remain within 2 km of the den for the first few weeks postpartum. In all other circumstances, we would expect a

cougar to cross dirt roads on several occasions during a week-long period.

The track survey was usually carried out by a 2-person team. One person drove the vehicle at 5-8 mph while the second sat on the hood and searched the ground for tracks. On 2 survey dates, the route was covered by a single observer. On these days the observer attempted to compensate by driving very slowly and frequently stopping to investigate on foot.

No cougar tracks were detected on any of the surveys. We did find tracks of prey species, including deer, cottontail rabbits, coyotes, raccoon, fox, opossum, and bobcat. Emerald Canyon had markedly more deer tracks than the other canyons surveyed.

Because our coverage of the area was so thorough and the tracking conditions so good, we conclude that cougars no longer live in the San Joaquin Hills.

Wildlife corridors

A wildlife corridor is a piece of habitat, usually longer than wide, with vegetation and topography that facilitate the movements of wild plants and animals from 1 large patch of suitable habitat to another (Harris and Gallagher 1989). Forman and Godron (1986:364-426), Adams and Dove (1989), and Harris and Gallagher (1989) provide comprehensive reviews of the literature on corridors.

Over most of the cougar's range in North America, cougars have access to a vast interconnected landscape and there is no pressing need for corridors. In the Santa Ana Mountain Range, however, urbanization has nearly isolated the cougar population from the only adjacent population (in the Palomar Range) and urban growth will fragment most or all of the population into non-viable sub-units unless linkages are maintained among habitat patches. Without careful planning, the 5059-ha (12,500-acre) Chino Hills State Park and all but one of Orange County's Regional Parks will soon become isolated and unusable as cougar habitat. Even cougars in the central block of habitat, including Caspers Wilderness Park, are at great risk if the Santa Ana Mountain Range becomes isolated from the Palomar Range (Chapter 4, Beier 1993). Our dispersal data (Chapter 6, Beier 1993, manuscript in preparation) clearly demonstrates that dispersing cougars will find and use suitable corridors if available.

Factors influencing corridor suitability for cougars

Although this section deals solely with factors influencing corridor suitability for cougars, any corridor design should consider the needs of more than a single species. Beier and Loe (1992; included as Appendix 4 in this report) and Harrison (1992) should be consulted for an overview of such issues. In evaluating a potential corridor, it is important to keep in mind that a corridor facilitates travel for the entire distance between 2 significant habitat areas, not simply for the length of a highway underpass or other constriction. In rapidly urbanizing southern California, no corridor will be effective unless it encompasses the entire corridor length and explicitly connects to 2 or more larger habitat areas.

Applied to wildlife corridors, the term "design" is not used in its traditional sense of drawing a plan on a blank slate. Instead corridor design involves preservation of an existing travel route, minimizing impacts to an existing route, or leaving a route in an area that formerly allowed unobstructed movement. We cannot usually design corridors that force animals to travel in locations that are convenient for development plans. Therefore, if a project may impact a corridor, the project

proponent should be required to monitor animal use of the corridor area both pre- and post-project (Beier and Loe 1992).

For cougars, the major factors influencing success of a movement corridor are:

- **location**: a cougar cannot use the corridor unless its normal travel pattern causes it to encounter the corridor entrance. Conversely, a corridor along a natural travel route is likely to be used even if habitat conditions within the corridor are suboptimal. Foster and Humphrey (1992:17) noted: "Most importantly, [corridors] must be located where animals naturally [travel]. Thus prior knowledge of traditional travel landscape-determined travel routes of the target animals is essential. [Corridors and] underpasses installed away from such crossing points are ineffective." Thus cougars are much more likely to cross State Route 91 via the suboptimal crossing at Coal Canyon than via the superior undercrossing 1.6 km east, simply because Coal Canyon is a well-used cougar travel route. In our intensive monitoring sessions, we have identified the routes by which cougars traveled among various parks and protected areas. In planning future urban growth, these routes provide ideal corridor sites. In the absence of data from radio-tagged animals, canyons with scour zones, or ridgelines free of artificial light, are likely locations for cougar travel routes.
- **cover**: Some native woody vegetation should be present to provide visual cover. Cougars will move up to 400 m across open terrain within a wildland matrix, but would not move across this length of open terrain with dense housing on either side.
- **lighting**: cougars travel mostly at night and avoid brightly-lit areas. Lights are especially detrimental in a bridged undercrossing. In several monitoring sessions, radio-tagged dispersers exploring new terrain apparently oriented toward dark areas and away from city lights. Thus lighting would probably also be effective in deterring an animal from entering a "cul-de-sac corridor" that looks inviting at its entrance but which leads to urban areas instead of good habitat (e.g., Temecula Creek).
- **roads:** Roads can render a corridor useless or cause animal injury and mortality. Where heavily-used roads cross a corridor, a bridged undercrossing is preferable to a culvert, and fencing can guide animals away from a high-speed road and toward the underpass. In Florida, an 8' x 24' precast segmental box culvert with 2.5% grades was a cost effective design with high probability of use by large wildlife, including cougars (Florida Department of Transportation 1992). Foster and Humphrey (1992:25) recommend that animals should have an unobstructed view of the habitat or horizon on the opposite side of a crossing structure, and that medians be open rather than covered. However, if the median is narrow, an opening may admit more noise and debris than light, and should probably be covered (Reed et al. 1975). The Florida study found that a 10-12-ft high chain-link fence topped with 3 strands of barbed wire was effective in inducing cougars to stay off highway right-of-way and use underpasses. We believe that a chain-link fence 8 feet high topped with 1-2 outrigger strands of barbed wire would also be effective and cheaper. A cougar could, but probably would not, climb or jump such a fence. Humphrey (1992) provides an excellent annotated bibliography on the limited literature relating to wildlife undercrossings and highway fencing. We believe that overpasses would also be readily used by cougars if the roadbed is recessed into the terrain, if the overcrossing is free of artificial light, and if there is appropriate visual screening so that the animal does not expose itself to view. On rural roads,

vehicle speeds can be kept low through appropriate design elements (e.g., curves, grades, narrow road width, speed limits). Rural access roads should be 1.5 lanes wide with pullouts to encourage slow driving; wildlife undercrossings would not be necessary on such roads.

- **disturbances**: Unrestrained domestic dogs can harass cougars (and other wildlife) and render a potential corridor unusable. Dogs may be less of a problem adjacent to tract homes (where pets are usually restrained at night) than adjacent to a rural community, where dogs often roam free. Daytime use of a corridor by equestrians and hikers is fully compatible with use for cougar movement. Rural housing impacts can be minimized by having housing pads set back from stream courses or ridgetops, and by requiring large (10-40 acre) minimum parcel sizes.
- **frequency of use**: A corridor between the Santa Ana Mountains and the Palomar Range need be used only by a handful of immigrants per decade, with each animal making a single passage. In contrast, because the Chino Hills is smaller than an adult male home range, it requires a linkage that will allow a male to repeatedly use the corridor to breed with the resident females. The Regional Parks, being smaller than an adult female home range, require high-quality, preferably multiple linkages, to allow resident females to use them as part of their home range.
- **width**: It is impossible to specify a general minimum width, because the width needed depends on all of the above factors, and also on the length of the corridor. Width can also vary along a corridor. For instance, a width of 10 feet may be acceptable for a road undercrossing but not for the entire length of a corridor. As a rule of thumb, if other conditions (woody cover, no lighting, freedom from dogs, canyon bottom location, etc.) are met, we suggest that a corridor designed for use by cougars should be at least 100 m (300 ft) wide if the total distance to be spanned is 800 m (½ mi) or less. To the extent that other elements are deficient, and as the corridor length increases, corridor width should also be increased.

As mentioned above, knowledge of the traditional movement patterns of the target animal is the most important factor in corridor design. By intensive monitoring of individual focal animals, we learned the actual routes by which cougars traveled from the protected core area (Table 1, Figure 1) to most regional parks and smaller protected parcels. We describe these routes in the remaining sections of this chapter. Although most these routes now traverse pristine open space, they will become corridors (at best) as continued urban growth removes the adjacent habitat.

The most critical link: the Pechanga Corridor from the Palomar Range to the Santa Ana Mountain Range

Due to past urban growth, the cougar population in the Santa Ana Mountain Range is isolated from all other cougar populations except that in the Palomar Range to the southeast (Figure 1). Aerial photographs suggest that the amount of habitat and the size of the cougar population are much larger in the Palomar Range. A corridor to allow immigration from the Palomar Range is necessary to insure survival of our cougar population (Chapter 4, Beier 1993). Any viable corridor must link the Palomar District of Cleveland National Forest and the adjacent Pechanga Indian Reservation (the westernmost protected area in the Palomar Range) to San Diego State University's Margarita Field Station (the easternmost protected area in our mountain range) (Figure 7). If successful, The Nature Conservancy's Santa Margarita River Project will allow movement westward from the

SDSU parcel to Camp Pendleton and the Trabuco Ranger District.

We have named this linkage the "Pechanga Corridor" because Pechanga Creek is the main watercourse leading between the 2 areas. The 2 main threats to this linkage are I-15 and urban growth in and south of the City of Temecula. Although I-15 is the biggest hurdle today, within a few short years urbanization, if not controlled, will present an even more impenetrable barrier. This report's focus on I-15 should not obscure the fact that an effective corridor must be much longer than a highway underpass. In the following discussion, bear in mind that only west-bound immigration will reduce extinction risk. Because the cougar population in the Palomar Range is much larger, it does not need immigrants from the Santa Ana Mountain Range.

During our study several cougars attempted to cross I-15 to move between the 2 mountain ranges (Figure 8). Between October 1 1990 and December 31 1992, 3 cougars were killed on I-15 just north of the Border Patrol Station and a fourth cougar was killed on I-15 just north of Flynn Nursery at the north edge of the village of Rainbow. The dispersing M12 crossed I-15 about 500 m south of the Santa Margarita River. The dispersing M5 was initially captured and radio-tagged after being treed by domestic dogs in the city of Temecula; his tracks indicated that he had come from the confluence of Pechanga and Temecula Creeks, about 700 m upstream from the Santa Margarita Bridge. He probably had reached this confluence from the Santa Margarita River. From the west, M7 approached I-15 at the Santa Margarita River on several occasions, and may have made short forays east of I-15. During our study no cougars were road-killed elsewhere along I-15, nor did we have evidence that any cougars approached I-15 outside of this same area.

These patterns clearly show that the natural travel route for cougars leads them to cross I-15 at the crest just north of the Border Patrol Station. This is certainly **the** crossing point for any cougar traveling in the critically important westward direction, because urban sprawl strongly discourages west-bound cougars from approaching I-15 north or south of this area.

Beier (1993) was pessimistic about the present utility of this corridor. But the number of attempted crossings since that paper went to press suggests that dispersing cougars occasionally have crossed from east to west across I-15, and in sufficient numbers to benefit the cougar population. During 1990-92, night-time traffic on I-15 was light and the five road-kills may have been matched by a similar number of successful (but less detectable) crossings. As few as 1 or 2 successful west-bound dispersals during that 2-year period would significantly benefit the cougar population in the Santa Ana Mountain Range (Beier 1993). Nonetheless, we have not documented a single successful west-bound crossing of I-15.

Unfortunately, as traffic volumes increase in concert with urban growth, cougars will soon be unable to make at-grade crossings of I-15. Of equal concern, there is no safe underpass within 1 km of the ridgetop crossing area. Cougar habitat abuts I-15 only for about 6 km starting at and south of the Santa Margarita River bridge. There were 3 bridges and about 10 culverts on I-15 between Temecula and Mission Road (Fallbrook). None of the culverts offered a suitable undercrossing. All culverts were corrugated metal pipes 3 or 3½ feet in diameter (except 1 that was 6 feet in diameter), at least 150 feet in length, and steeply sloped with no light visible from the other end.

Of the 3 bridges, only the bridge over the Santa Margarita River is currently a feasible undercrossing for regular use by cougars. The bridge at Rainbow Creek is unusable because a trailer park lies squarely under and alongside this bridge, and to the east the creek meanders through an open area with large container-stock nurseries. The bridge for a 2-lane paved road 650 m south of Rainbow Creek does not lie along a natural travel corridor for cougars, especially for a west-bound animal, due to the village of Rainbow with its housing and large nurseries. The Santa Margarita Bridge is an excellent undercrossing structure, and the River itself would readily lead a west-bound cougar into the central habitat block. However, urban sprawl in Temecula makes it difficult for a cougar to encounter the underpass from the west. Pechanga Creek (the best watercourse leading west toward the bridge) has been highly devegetated, lined with concrete on parts of its north bank, subject to light pollution from adjacent housing tracts on the north bank, and has a large golf course resort on the south side.

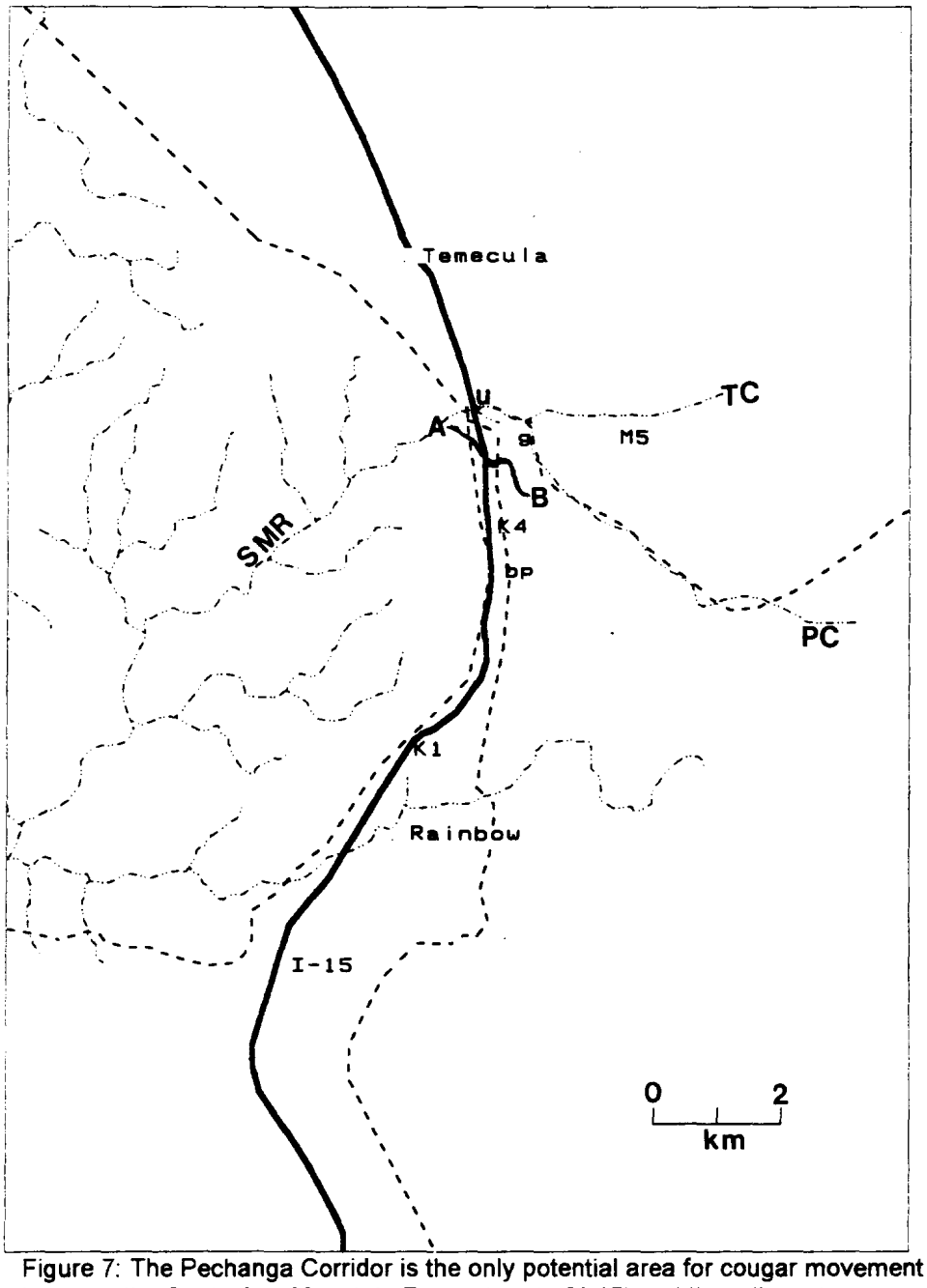

Figure 7: The Pechanga Corridor is the only potential area for cougar movement between the Santa Ana Mountain Range (west of I-15) and the adjacent population in the Palomar Range (east of I-15). Thick dashed line = wildland/urban edge. Note that Temecula Creek, **TC**, is a cul-de-sac corridor (it dead-ends in unsuitable habitat). During August 1990-December 1992, 3 cougars were road-killed at point **K4** (just north of the Border Patrol station, **bp**), 1 cougar was killed at **K1**, 1 cougar (M5) was treed by domestic dogs near the Temecula cul-de-sac at **M5**, and M12 crossed eastward along line **A-B**, passing near the golf course, **g**. The 3 options for allowing safe west-bound animal movement are restoration of Pechanga Creek (**PC**), using fencing to divert animals to the suitable underpass at **u**, or an overpass at **K4**. **SMR** = Santa Margarita River.

Without preventive action, this corridor will be lost. There are 3 options for

insuring the future integrity of this linkage, and a 4th option requiring continued human intervention:

1. Restore Pechanga Creek. Pechanga Creek leads directly to the only suitable undercrossing. Restoring the creek would be costly but would protect a corridor of regional significance. If this option were taken, restoration measures should include:

- Physically prevent vehicles from driving in the creek bottom
- Enhance native vegetation in Pechanga Creek. Revegetate a strip of land (at least 35m wide) along the Creek-Golf Course edge.
- Direct lighting from creekside homes away from the creek. Prevent free-roaming dogs in the creek. Unleashed dogs keep out not only cougars but also deer and other species whose presence would make the creek attractive to cougars. In 1990 we found no deer tracks, pellets, or other deer sign in the Creek, probably due to high use of the Creek by dogs.
- Discourage cougars from moving upstream along Temecula Creek from its confluence with Pechanga Creek. In 1990-92, Temecula Creek had a denser riparian forest and greater water flow, and probably would appear more inviting to a dispersing animal than Pechanga Creek. However, 800 m above the confluence it "dead-ends" in tract homes. Cougars can probably be deterred from entering the cul-de-sac by installing bright lights and removing a small amount of riparian vegetation near the Wolf Valley bridge.
- Prevent further urbanization along and south of Pechanga Creek.
- Fence I-15 south of the Margarita Bridge to prevent animals from being killed there.

2. Divert animals from the ridge route toward the River undercrossing. The natural travel route for west-bound cougars follows the ridge to an at-grade freeway crossing just north of the Border Patrol station. As traffic volumes increase, animal mortality will increase and eventually this route will become infeasible. To prevent road-kills and preserve a crossing, several measures would be needed:

- Fence I-15 from the village of Rainbow to the Santa Margarita River; the fence should be at least 8 ft high with a barbed-wire outrigger. Hopefully at least some west-bound animals encountering this fence would make the "right" decision to turn north rather than south.
- Keep the area along the fence as wild as possible. A west-bound cougar deflected by the fence would have to follow the fence north for 1500m, including 700m of golf course, before reaching the Santa Margarita River. The golf course along most of this area is relatively wild, and was traversed by M12 in January 1992. However, it would help to redesign the open area around the driving range area; its large fences intersect the animal travel route.
- Prevent urbanization along the wooded ridge that leads from the east to the current crossing area.

3. Build an overpass at the natural crossing area. A freeway overcrossing at the natural travel area just north of the border patrol station would maintain the linkage. Because I-15 is dug into bedrock for about 1.5 km north and south of this crossing area, it would be nearly impossible to retro-fit an underpass here. The overpass would in effect create a tunnel for vehicular traffic on I-15. If wide (say 100 ft), covered with natural substrate and vegetation, and with sidewalls to block vehicle light and noise, such an overcrossing would probably facilitate cougar movements at least as well as any other option.

Dirt roads (closed to motor vehicles at night) leading to either end of the overpass would further enhance the corridor, because cougars and other animals often to use such roads to travel through woody vegetation. Such roads would also allow the overcrossing to be used by hikers and equestrians. This option should also include freeway fencing and preventing urbanization along the ridge east of the crossing point. This option is novel but may be appropriate given this region's accelerating urbanization.

4. Import animals into the Santa Ana Mountain Range. When a cougar enters a residential area without posing a threat to human property or safety, the current policy of California Department of Fish and Game (CDFG) is that the animal is captured and moved to the nearest appropriate habitat. Such incidents occur regularly in southern California. Several administrators have suggested to us that this policy could be modified to favor translocating such non-problem animals into the Santa Ana Mountain Range. Although clearly more artificial and less aesthetically pleasing than maintaining natural connectivity and letting cougars immigrate on their own, such an approach may be feasible. However, it would clearly be an unprecedented experiment, and would require a commitment (by CDFG) and funding (most appropriately from the planning agencies and developers that cause loss of existing linkages) in perpetuity. If such an option is pursued, it should include:

- importing only animals of dispersal age (12-28 months of age).
- importing only animals from a similar habitat type in southern California.
- monitoring the results. This would be a large experiment. Transplanted animals would suffer high mortality, and could disrupt the social structure or resident cougars; such impacts would depend on the existing demographics of the population. If the translocation option is chosen, many resident cougars and all transplanted animals should be radio-tagged and monitored. The monitoring effort should continue for at least 20 years, with annual support similar to that expended in our study.

Chino Hills State Park to Trabuco Ranger District

A wildlife corridor for cougars between the Santa Ana Mountain Range and the Chino Hills will allow cougars to use an area (the Chino Hills) that cannot support a population of cougars if it were to become isolated (Beier 1993). Quite simply, if there is no corridor, then there will be no cougars in the Chino Hills. To be effective, such a corridor must not simply be a freeway underpass, but must reach from Trabuco Ranger District and the adjacent Tecate Cypress Reserve in upper Coal Canyon (the northernmost protected parcels in the Santa Ana Mountain Range) to Chino Hills State Park (the southernmost protected parcel in the Chino Hills).

We approached our evaluation of potential movement corridors from the perspective of a cougar attempting to travel north from the Santa Ana Mountain Range into the Chino Hills (Figure 8). State Route 91 (Riverside Freeway) and associated urban growth form a narrow band separating the Chino Hills on the north from the Santa Ana Mountain Range to the south. Cougars can approach the south side of Highway 91 along the entire 5.5 km from Gypsum Canyon to the Green River Road exit. Unlike I-15 near Temecula, the Riverside Freeway's 8 lanes are too busy at night to allow safe at-grade crossings by wildlife. There were 11 culverts and 3 vehicle underpasses in this 5.5-km section. Seven of the culverts were < 3 ft in width and height and were located such that it would be nearly impossible for a cougar to find the entrance. Two others (a 4-ft diameter cylinder and a 5-ft wide box) were similarly

inaccessible. On May 7 1991 M10 was struck by a vehicle on the Riverside Freeway within 50 feet of the 5x5-foot box culvert, which was inconspicuous from as close as 20 feet away. Only 2 culverts (B Canyon and Coal Canyon) were large (10 ft wide and 8-12 ft high) and located at canyon mouths where cougars could reasonably be expected to encounter the entrance; these are considered in greater detail below.

Of the 3 underpasses, the Mindermann or Green River underpass (a 1-lane paved access road for the old Minderman Ranch) did not lie along a canyon or ridge and would not be encountered by a traveling cougar. The Gypsum Canyon Road underpass was at an excellent location with respect to topography and cougar travel patterns, but the 500-m long underpass was occupied by the Gypsum Canyon Road interchange, where heavy traffic precluded cougar use. In August 1989 (even before the interchange was opened to Bridge traffic), F8 was road-killed at this interchange. Only 1 vehicle underpass (Coal Canyon) was located along a natural travel route and was undisturbed enough to allow cougar passage. Because this underpass lies immediately adjacent to the Coal Canyon culvert, the 2 are considered together below.

The 2 potential culverts and 1 vehicle underpass thus yield only 2 potential crossings of SR-91:

1. Coal Canyon. The Coal Canyon Road vehicle underpass and the twin box culverts alongside it offer by far the best route to cross SR-91. The main factor is that it lies at the mouth of Coal Canyon, a major wildlife travel route. We have abundant evidence that Coal Canyon is a major travel route. Coal Canyon was used by 6 radio-tagged cougars (F5, F6, F17, M6, M8, and M10), three of which either crossed or attempted to cross the freeway there. The dispersing juvenile M10 moved from Camp Pendleton, entered upper Coal Canyon for the first time on May 8 1991, moved rapidly down the Coal Canyon to the freeway on May 9, and was struck on the freeway May 10. In April 1991, M8 entered the Chino Hills, almost certainly via this corridor, and was later road-killed at the north end of the Chino Hills. Most dramatically, M6 traveled this corridor at least 22 times during June 1 1991 - December 31 1992 (Figure 8). Finally, 1-2 uncollared cougars (probably 1 juvenile female based on track size) used the culvert to cross the freeway in 1991.

On 18 of his 22 crossings, M6 used the box culvert under SR-91. On the other 4 crossings we found no tracks in the excellent substrate in the B Canyon or Coal Canyon culverts, so we conclude he used the (paved) vehicle underpass. M6's preference for a culvert is not typical of cougars confronted with roads. Other radio-tagged cougars preferred to cross 2-lane paved roads at grade rather than use a culvert directly in front of them, and all cougars used bridged undercrossings without hesitation. Certainly with enhancement of woody vegetation in the underpass, the vehicle underpass would be the preferred route for all animals.

2. B Canyon. The B Canyon culvert lies about 400 m east of the clubhouse for the Green River Golf Courses. Its canyon is well-wooded and has a spring in its headlands. A cougar in B Canyon could follow it to the culvert, which is physically ideal for animal movement. The problem then becomes getting into B Canyon, which now receives little cougar use. Even M6's, whose home range straddles SR-91 (Figure 8, Figure 23), has never used the B Canyon crossing and has never been located in B Canyon. Only 2 radio-tagged cougars (M10, F5) were documented using B Canyon; both of them entered via the lowermost main tributary of Coal Canyon (Cut-Across Canyon in Figure 8). Thus B Canyon, already rarely used, would receive extremely little use if the main access via Cut-Across Canyon is removed

by urban growth. Dispersing cougars are so proficient at finding travel routes that a rare disperser probably would use B Canyon to enter the Chino Hills even if Coal Canyon is destroyed. However, the Chino Hills is such a small area of habitat that it needs more than 1 immigrant every few years; it needs regular visitation by an adult male (Beier 1993). In short, the Chino Hills need visitation such as was demonstrated by M6's use of Coal Canyon Corridor in 1991 and 1992 (Figure 8, Figure 23). B Canyon does not allow this level of use today, and it is inconceivable that it would do so if access to B Canyon from Cut-Across Canyon were lost.

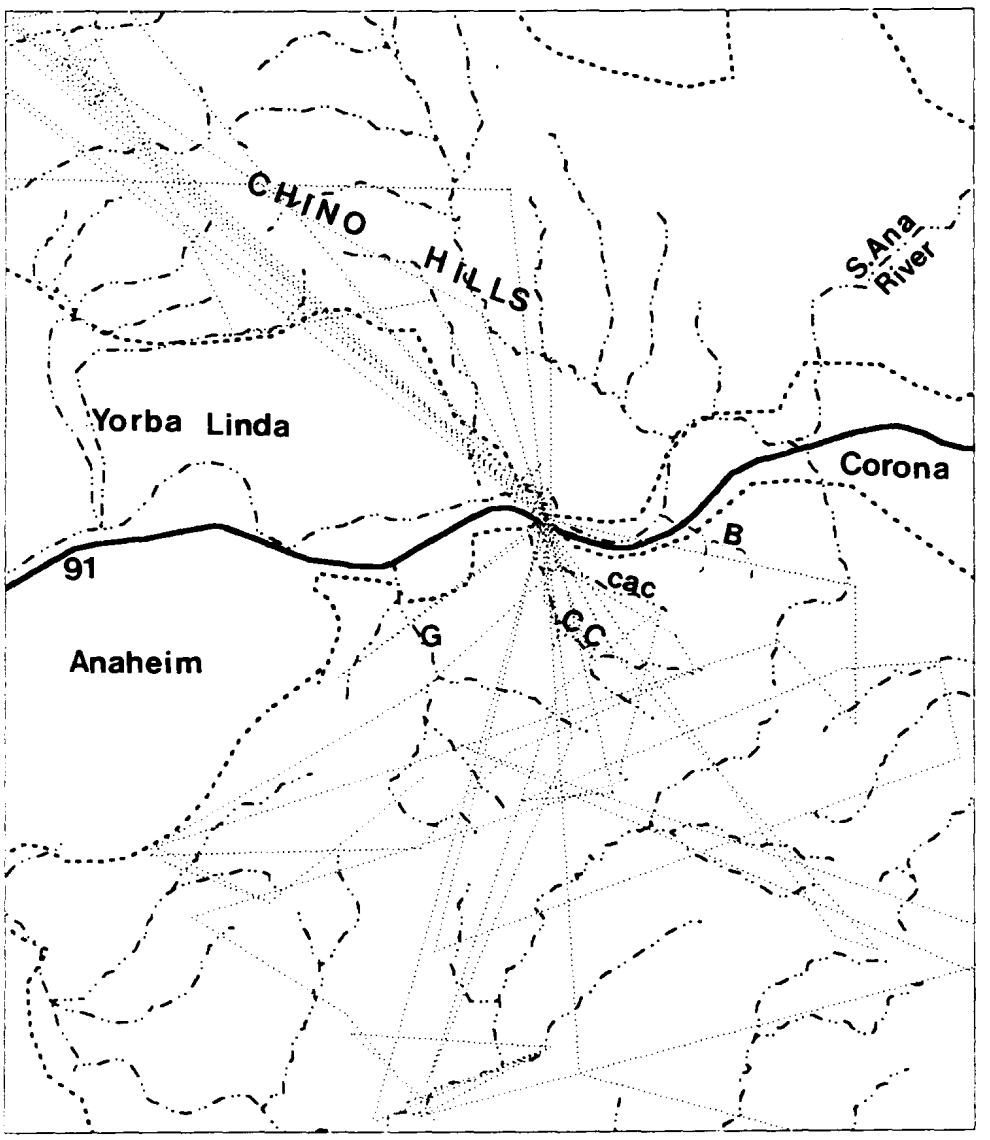

Figure 8. The corridor at Coal Canyon (**CC**), is the only route capable of allowing the frequent movements needed to maintain cougars in the Chino Hills. B Canyon (**B**) provides a suitable undercrossing but is not a major travel route. Cougars access B Canyon via Cut-Across Canyon (**cac**). A proposed housing tract would block both Coal and Cut-Across Canyons. **G** = Gypsum Canyon. Dotted lines indicate M6's travels during May-Dec 1991, including 12 of his 22 passages through the Coal Canyon Corridor.

On March 3 1992, the Anaheim City Council voted to allow construction of up to 1500 homes in Coal Canyon. The Council did so despite the conclusion in the City's EIR that the project would "result in the loss of potential for a cougar population to occur in the Chino Hills." By guaranteeing the loss of cougars from the Chino Hills, the project would also reduce the amount of habitat available to the cougar population in the Santa Ana Mountain Range by about 8%. adding to the risk of extinction for the larger population (Figure 11).

No construction has begun on the Coal Canyon project, in part because the City stipulated that no building permit can be issued nor any homes sold in Coal Canyon until additional lanes are added to SR-91. Thus there is still an opportunity to plan urban growth in a way that preserves the Coal Canyon Corridor. The following steps are

necessary for corridor preservation:

- minimize urban growth in Coal Canyon (including the parcel in Yorba Linda just north of SR-91) and along the Green River Golf Course.
- Increase the amount of woody vegetation near the underpass. Ideally take the creek out of the culvert and into the underpass, removing the pavement and adding vegetation to the underpass.
- fence SR-91 to funnel animals toward the underpass and culvert and keep them off the freeway.
- keep night-time vehicle traffic at the Coal Canyon Road interchange at its present level, (i.e., virtually no vehicle use at night). Remove the existing lighting in the underpass.
- If possible, increase shrub and tree cover at the edges of the golf courses, and on the large grassy field just northeast of Scully Hill.

Because many of these steps could be implemented when new lanes are added to the Riverside Freeway, Paul Beier conveyed these recommendations to CalTrans on February 6 1992; Beier stressed that the growth-inducing impacts of the freeway were the most critical issue to address and quoted the City of Anaheim's conditions of approval to the effect that 9,500 homes could not be built or sold in Gypsum and Coal Canyons until CalTrans widened SR-91. CEQA requires an EIR for any project with growth-inducing impacts, and an appropriate mitigation for this induced growth would be for CalTrans to work with the Cities of Anaheim and Yorba Linda to develop a cross-jurisdictional plan to preserve the wildlife movement corridor. In late February 1992 CalTrans issued a statement that no EIR was needed for the project.

The third entity with planning authority over the Coal Canyon Corridor is the City of Yorba Linda. During 1992, Yorba Linda approved language in its General Plan stating that the Yorba Linda will protect the corridor if the City of Anaheim will co-operate in the effort.

O'Neill-Arroyo Trabuco-Wagon Wheel Regional Parks to the Protected Core Area

At least 10 radio-tagged cougars (F1, F2, F13, M2, M3, M4, M8, M10, M12, M13) used the Arroyo Trabuco and Wagon Wheel Parks during this study. Animals moved to these Parks from the central habitat block by using both northern and eastern routes (Figure 9). The 2 northern routes are based on overnight monitoring sessions on F1 and M12, and the 2 eastern routes are based on overnight monitoring on M8, M1, F2, and M2, and a long series of tracks by an uncollared cougar. Although the Arroyo Trabuco appears a logical corridor on a map, cougars avoided the Arroyo Trabuco for about 2 km of its length, starting at the developed portions of O'Neill Park and continuing well north of Live Oak Canyon Road.

These routes will remain viable only if protected along their entire length between these smaller parks on one end and either National Forest Land (to the north) or Caspers Park (to the east) on the other ends. Maps describing these routes were given to the County of Orange and the Transportation Corridor Agencies (TCA) in 1991. Both the County and the TCA responded with good-faith efforts to minimize impacts to these routes.

Excellent regulations for protecting wildlife movement along the northern routes were included in the recent Foothill-Trabuco Specific Plan. If these regulations are strictly enforced. these northern routes should remain usable by cougars and other wildlife.

. Significant planning has also been made to protect the eastern corridors, although problems remain. To mitigate impacts to wildlife movement, the County of Orange modified the southern edge of the proposed Las Flores Planned Community and added plans for a bridge to Antonio Parkway just south of Oso Parkway. These measures will effectively mitigate the impact of these 2 projects on wildlife movement. To mitigate impacts further east, the TCA added several bridges, and shifted part of the alignment of the Foothill Tollroad. As of late 1991, however, the TCA had not resolved the problem of how to build the interchange with Crown Valley Parkway without blocking one of the routes. Most importantly, the underpasses provided by TCA do not in themselves protect the entire length of these travel routes. In the long term, Tollroad-induced urban growth will cut off these corridors unless effective restrictions are put on future land use.

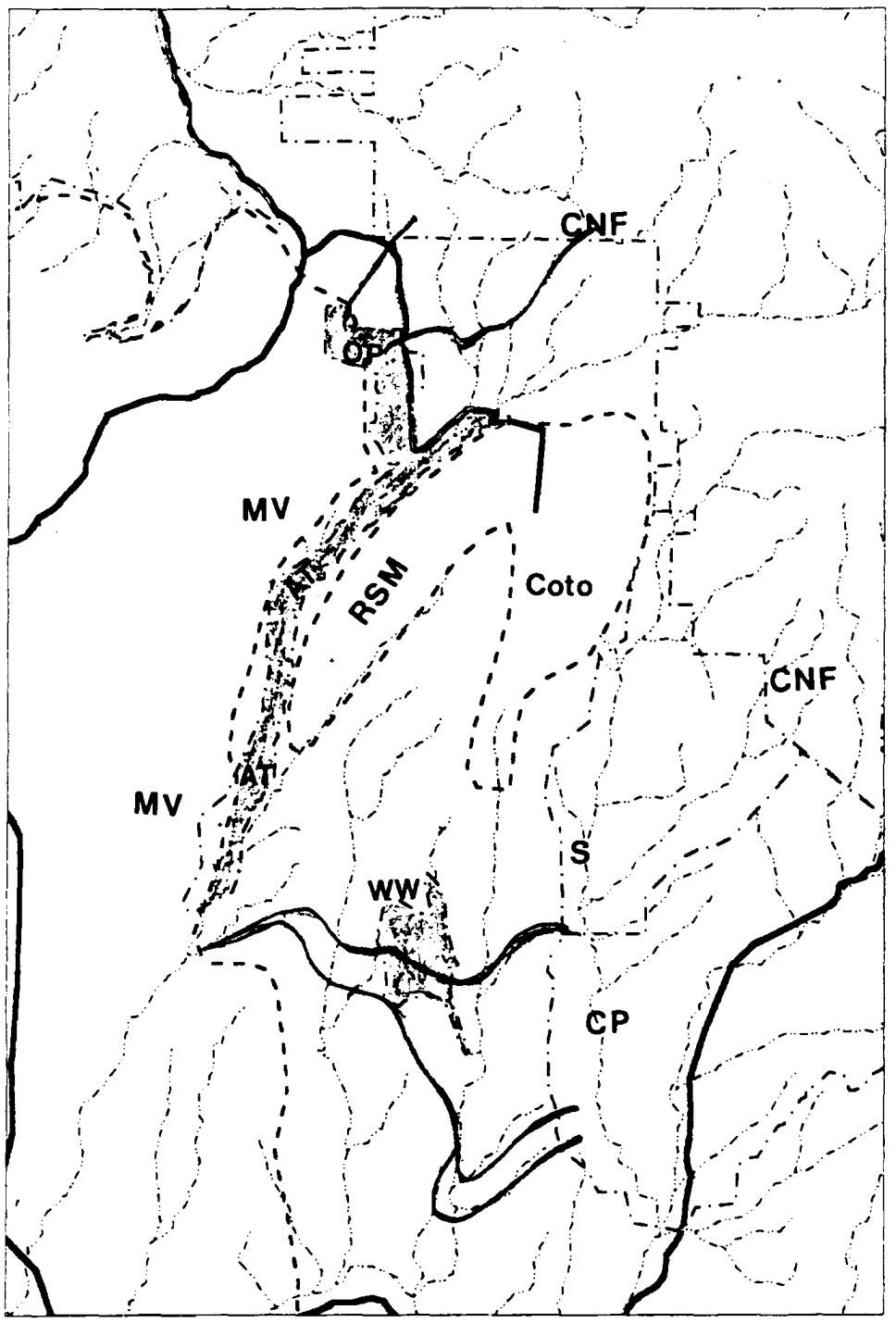

Figure 9. Linkages between O'Neill Park (**OP**), Arroyo Trabuco (**AT**), Wagon Wheel Park (**WW**) and the central habitat block (Cleveland National Forest - **CNF**, Caspers Park - **CP**, and Starr Ranch - **S**). Dashed lines indicate approximate edge of habitat, thick lines indicate paved roads, thin lines indicate approximate cougar travel routes. **MV** = City of Mission Viejo; **RSM** = Rancho Santa Margarita; **Coto** = Coto de Caza. Note that the Arroyo Trabuco is a narrow corridor of habitat lined with tract homes.

Weir Canyon-Santiago Oaks-Irvine Regional Parks to Trabuco Ranger District

Eight radio-tagged cougars (M5, M6, M10, M11, M12, F6, F5, F8) used the proposed Weir Canyon Regional Park. Most of these animals also used at least the Villa Park impoundment within Irvine Park, but we believe that only 2 (M5, M10) used Santiago Oaks Park. During 1988-1992,

there were no significant barriers to animal movements in the 6 km (4 mi) between these contiguous 3 parks and the Trabuco Ranger District (the nearest parcel in the protected core area).

However, the combined impact of the proposed 8000-home Mountain Park project, the proposed 13,000-home East Orange project, the proposed Eastern Tollroad, and future (Tollroad-induced) urban growth threatens to sever the connection between these 3 parks and National Forest land. In the draft EIR released in late 1991, the TCA committed itself to only 1 wildlife undercrossing, to be provided by a bridge over Santiago Creek. Unfortunately, this bridge does not correspond with the travel routes of radio-tagged cougars and it is unlikely that it would be used by them. It will become impossible for cougars to use the Santiago Creek undercrossing after the 13,000-home East Orange project is built upstream. TCA listed (but did not promise bridges at) 5 additional potential crossing points, 4 of which would be useless as wildlife crossings due to topography, approved housing projects, or planned interchanges. TCA's potential bridge at "WC4" is at an excellent crossing area, but is located in an area that is already being considered for the new county landfill and for tract homes. In January 1992, we suggested including measures to protect the approaches to WC4 or building a bridge to accommodate a different cougar travel route in the uppermost part of Blind Canyon. Our new route was used by several radio-tagged cougars, is in a steeper (less developable) area, and would require less habitat to be preserved between Weir and Fremont Canyons than the routes leading to TCA's potential bridge sites. As of spring 1992, TCA had elected not to incorporate these suggestions.

Limestone-Whiting Regional Parks to Trabuco Ranger District

Nine radio-tagged cougars (F6, F17, M2, M5, M6, M8, M10, M11, M12) used these contiguous wilderness parks. The parks offered excellent cougar habitat and at 6920 combined acres, they approached the size of Caspers Park (7620 acres). Unlike Caspers Park, however, these parks did not abut the Cleveland National Forest, but were surrounded by private property. If urban growth on the private land is not controlled, these parks will become isolated from the National Forest. Because 6920 acres is smaller than a single cougar home range, this area will be lost to cougars unless high quality connections are maintained to the main block of wildlands to the east. A marginal corridor that allows only occasional cougar use would greatly reduce or eliminate the ability of this land to help maintain a cougar population in the Santa Ana Mountain Range.

Based on data from radio-tagged cougars, topography, and the location of existing roads and housing, there are presently 2, and possibly 3, such linkages that can be maintained in the long term. These linkages are described in detail and shown in 3 maps in our Quarterly Report of October 1 1992. The northern corridor ("South Silverado") and the southern corridor ("Equestrian") have each been used by radio-tagged cougars on several occasions. The large size and importance of these wildlands warrants maintaining both of these corridors. Reliance on a single corridor may prove disastrous if we miscalculate what is needed to protect it, or if a single defiant landowner ignored protective regulations. Furthermore, even if a single corridor is adequate for cougars, many other species need corridors and some of these species may not be served by the limited number of habitat types, soil conditions, etc., that can be contained in a single corridor.

We have no data to indicate that the "Pancho Canyon Corridor" was used by cougars, and in July 1992 we noted active grading in the mouth of Pancho Canyon continuing north nearly to the mouth of Williams Canyon. We mention it mainly to consider all feasible options. With appropriate screening from the new project, the topography and habitat suggest that this could be a functional corridor. Although it is also relatively long, the eastern portion (Harding Canyon) may already be protected if strict zoning prohibits building there to protect water quality in Modjeska Reservoir.

A critically important step in protecting each of these corridors is to construct a wildlife undercrossing under Santiago Canyon Road where each corridor's major drainage crosses the road, along with fencing to keep animals off the road and to funnel them toward the undercrossing. Santiago Canyon Road is a busy, high-speed road, and use will increase greatly if the proposed 13,000-home East Orange Project and the proposed Eastern Tollroad are built. The County is already planning to rebuild the Road to accommodate projected traffic, and the road rebuilding can be used as an opportunity to construct bridges beneath which cougars and other animals can walk.

Our data for radio-tagged cougars along the South Silverado Corridor indicate that they crossed Santiago Canyon Road at grade just a few feet north of a 5-ft box culvert there. Fencing could be used to guide animals to the existing culvert. However, a better solution (when the road is rebuilt) would be to build a bridge to allow a larger undercrossing.

At the Santiago Equestrian Center, a larger undercrossing could be built during the rebuilding of Santiago Canyon Road by moving the road about 200m north for about 300m on either side of the stables. This would get the Road out of Aliso Creek and allow the road to bridge the 2 tributaries of upper Aliso Creek which meet just below the Stables. As configured in 1991, the equestrian center apparently was not a barrier to cougars. If the corridor is to be maintained, there should be no increase in night-time human use or lighting at the stables, and no additional clearing of vegetation near the stables. It is especially important to avoid any significant loss of habitat on the ridge immediately west of the stables; animals must cross this ridge to reach the Parks. Constructing one or more unlit trails (for hikers or equestrians) over this ridge would not degrade its utility as a wildlife corridor, and may make it more acceptable for some species, including cougars

In addition to the 3 corridors mentioned above, we have documented that cougars cross Santiago Canyon Road at 2 other locations further west. Because both of these areas lie in or adjacent to the approved East Orange Project, they will remain functional only if the project is not built. One well-used crossing point was the first small canyon east of the hillcrest fire station. The sparse vegetation made this a surprising location for cougar movement, but both M5 and M10 were struck crossing Santiago Canyon Road at this canyon, and 2 uncollared cougars were killed there in 1989. The second area was about 200m southeast of the junction of Hicks Haul Road and Santiago Canyon Road.

Rancho Mission Viejo Conservancy to Camp Pendleton

The Rancho Mission Viejo Conservancy was used by 13 radio-tagged cougars (M2, M6, M8, M9, M10, M11, M12, M13, F3, F4, F13, F17, and F19) and is excellent cougar habitat. F3 chose a canyon in this parcel for her parturition site in 1989. The alignment for the Foothill Tollroad lies near the eastern edge of the Conservancy, and threatens to isolate it from Camp Pendleton (the nearest

large protected parcel). Cougars now access the Conservancy across an unobstructed landscape. With the tollway and tollway-induced urban growth there will be at most 2 routes, namely Gabino-Blind Canyon and upper Christianitos Creek. The TCA has promised bridges at both sites. TCA's late 1991 map of the alignment omitted the *upper* Christianitos bridge, because TCA thought our suggestion was for a bridge where the Tollroad crosses *lower* Christianitos Creek. However, TCA responded to this misunderstanding by verbally promising the upper bridge. Assuming that the bridges are built, long term protection of these corridors requires protecting an unbroken route to Camp Pendleton.

CHAPTER 4. POPULATION DYNAMICS

Reproductive activity and litter sizes

Prior to expansion of the study area (May 1989), 3 full-time biologists and several volunteers intensively monitored 7 radio-tagged females in the vicinity of Caspers Wilderness Park, Rancho Mission Viejo, and Camp Pendleton, locating most cougars daily and looking carefully for sign of cubs or adult males. The evidence overwhelmingly indicates that there was no reproductive activity in this area for over 12 months due to lack of a breeding male in this portion of the mountain range (our Quarterly Reports; Padley 1990). Despite intense searches, there was no evidence (e.g., tracks, scrapes) of a breeding male. Only 1 female had cubs at heel (F3's litter born November 1987) and none of the 7 females gave birth during 1988. In early 1989, 2 young males (who we believe we later radio-tagged as M2 and M9) established adjacent territories that overlapped these 7 females. We immediately detected the tracks of these males and heard the northern male (presumably M2) copulating with 4 females in April 1989 . Exactly 83-104 days (1 gestation period) after we first noted sign of these adult males, 6 of the 7 females bore cubs. Such a reproductive failure, although it was temporary, demonstrates that the population was demographically unstable. Such demographic instability is to be expected in small, isolated populations of cougars (Beier 1993).

Of 9 known parturition dates for radio-tagged cougars, 5 litters were born in July, and 1 litter in each of May, June, August, and November (Table 1). A 10th litter probably occurred in December, based on the estimated ages at capture of F18's cubs. These data show a birth peak in late spring through summer, with no litters being born during the months of January-April. In previous North American studies (summarized by Anderson 1983, 1992), about 60% of births occured during April-August; the others were scattered among all other months. The more pronounced peak noted in this study (about 80% of births during May-August) was largely due to 2 new breeding males entering the study area in early 1989, causing a burst of 5 litters in July that ended a year of reproductive failure in the southern part of the range.

For 9 litters, the mean known litter size was 2.4 cubs per litter. However, in most cases we did not attempt to document litter sizes until several weeks or months after the suspected parturition date. Because some mortality likely occurred during the first weeks after birth, the mean litter size at birth was certainly higher than 2.4. Across the cougar's range, litter sizes average about 2.7 cubs per litter (summarized by Anderson 1983:34).

For 3 cougars, we can estimate the gestation period based on dates of copulation (as evidenced by vocalizations) and parturition. F3 and F4 were bred by the same male in the same canyon during April 4-7 1989, and their neonates (eyes closed, poor mobility) were seen and photographed on July 13 1989. Both F3 and F4 had arrived and stayed at their respective den sites on July 7 or 8. We believe that the parturition date for each cat was during July 7-9, and thus the gestation periods were between 91 days (if they conceived on April 7 and gave birth July 7) and 96 days (conceived April 4, born July 9). F2 was bred during April 21-23 1989; although her neonates were not observed, her greatly constricted movements indicate that she established her den site during July 25-August 3. Assuming that her cubs were born within 24 hours of establishing the site, her gestation period was 93-104 days.

We can also estimate gestation period for F10. Although we did not get close enough to hear copulatory vocalizations, F10 apparently consorted with M9 during April 8-10 1991 (16 days after her son M7 dispersed). She moved to her den site during July 2-10 1991, indicating a gestation period of 83-93 days. Using the midpoints of these ranges as

our best estimate, we observed 4 gestation periods that averaged 93 days and ranged from 88 to 96 days. To our knowledge, our data are the first to estimate gestation period for wild cougars. The mean gestation period for 42 litters born to captive cougars averaged 92 days and ranged from 84-98 days (Anderson 1983).

We inspected the exact den sites of F3 and F4 within a week of parturition, and revisited these sites a week after the cubs were moved. In addition, we knew the den sites of F12 and F2 to within 100m and investigated these sites after the cubs had been moved. Several traits were common to all 4 sites. Each site was in a small tributary canyon with very dense brush on the canyon sides and in the canyon bottom, lacked a well-developed scour zone in the canyon bottom, had no detectable animal trails, and had very few trees (except for some Rhus or Malosma plants with shrubby growth form). Each canyon was away from regular cougar travel routes, and the vegetation made it very difficult for a person to crawl to the birth site. The micro-sites were in drainage bottoms and in the upper ¼ of the drainage. No site was associated with a cave or rock outcrop.

At the 2 den sites where neonates were observed, there was no physical modification of the soil or vegetation at the site; the cubs were simply in a location that looked much like any other nearby spot in the dense shrubs. Even after 40 days of use, the only sign of use was some compression of the leaf litter. In particular there were no scats, no urine odors, and no noticeable trampling or breaking of live vegetation. Because these sites lacked distinctive topographic features (e.g., a cave) and any "nest" or other modification, we use the term "den site" simply to designate the place where cubs spend their first few weeks. These observations suggest that den sites are selected mainly because they are unlikely to be visited by other predators, and that mother cougars avoid enlarging passageways or leaving scents that might increase the likelihood of such visits. Movement patterns of the adult females suggest that the den site was used for about 6 weeks.

In addition to the 10 known litters, tracks indicated that F4 probably had a yearling at heel when she was initially captured in January 1988. Tracks of this cub were no longer evident after May 1988, indicating either death or dispersal occurred at about that time. Similarly, tracks suggested that a small-footed cat may have accompanied F13 just prior to her initial capture in March 1990. However, the tracks may also have been F13 doubling back on her route, and there was no subsequent evidence of a cub accompanying her.

In all cases of known parturition, the adult female greatly constricted her movements for the next 5-7 weeks. During the first 2 weeks, her daytime locations were almost always at the parturition site. About 7 weeks after birth, cub tracks could often be seen near their mother's tracks. Thus birth of a litter was easy to detect at our level of monitoring. Twelve females were monitored for over 12 months with sufficient intensity to detect successful cub-rearing if it occurred. To our surprise, 4 of these 12 females never gave birth during these years of monitoring, or if they did give birth, their cubs died within days of birth. We followed 3 of these females with sufficient intensity that we are quite certain that they had no litters that survived more than 2 weeks during the time they were monitored. The 4th female (F5) ranged widely and used many remote areas, and was not monitored as intensively. Although F5 may have had litters that we did not detect, it is very unlikely that any such litter survived more than a month. The non-reproducers were:

- **F1**: no successful litter during October 1986-July 1 1989. F1 was bred May 2-4 1989 (copulatory vocalizations heard), but at her death in early July 1989 she was not pregnant nor lactating.
- **F5**: no successful litter during May 1989-January 1993. F5 was located very close

to M2 on 2 occasions, and with M6 on 2 occasions (we were unable to get close enough to hear copulatory vocalizations). F5 was very thin, which may have contributed to her lack of reproduction. During the first year of monitoring, May 1989-May 1990, she exhibited a home range over twice as large as any other adult female. Perhaps the lack of home range stability during that first year inhibited her from reproducing (Seidensticker et al. 1973), but this would not explain her last 2.5 years of non-productivity. F5 was also unusual in having blue eyes, unlike the normal yellow eye of adults.

- **F15**: no successful litter during February 1991-June 1992. F15 definitely bred (copulatory screams heard all night long) with M9 on July 29-30 1991. She also apparently consorted (we did not get close enough to hear vocalizations) with M9 April 4-8 1991, August 31 1991, January 9 1992, and January 27-February 4 1992. At her death following a vehicle accident in June 1992, F15 was not pregnant or lactating.
- **F19**: no successful litter during August 1991-December 1992. She possibly consorted with M9 in early October 1992, but apparently there was no other breeding activity.

Four other adult females (F7, F8, F9, F13) were not confirmed to have any offspring during the time they were radio-tagged. However, each of these animals was monitored for less than 7 months, and it would be inappropriate to draw any conclusions from the lack of breeding evidence for these cats.

We had expected that virtually all females would bear cubs in any year in which they had no surviving cubs from the previous year, and we were surprised to learn that 4 of 12 adult females failed to reproduce. To our knowledge, no previous research has reported a similar lack of births in adult females followed through time. Robinette et. al. (1961) necropsied 199 female cougars and reported the pregnancy rates and the proportion whose tracks were accompanied by cub tracks. Although our inspection of their data show that nearly 40% of those females apparently were neither pregnant nor accompanied by young, Robinette et al. (1961) did not mention this apparent lack of fecundity. Certainly not all dependent cubs would be detected by a track search near the female, some immature females were probably included in their sample (Robinette et al. 1961:216), and they were unable to detect pregnancy during the first 2.5 weeks after conception (p.216); these factors probably caused them to avoid speculating on infertility rates. Perhaps this result was so unexpected that they were reluctant to mention it. We do not know if this is typical of parturition rates of cougars in other populations, nor if it is typical of our population in the long run.

Beier's (1993) population model presumed that all adult females would either have young at heel or have a new litter each year. This assumption is violated by the presence of females that do not bear young for several years. Therefore the predictions of Beier's model are probably unrealistically optimistic, and true extinction risk is probably somewhat higher than predicted.

Juvenile survivorship

Each cougar was considered a juvenile from birth until establishing a stable home range independent of its mother. Nineteen cubs were monitored for periods ranging from 1 to 22 months each, for a total of 288 juvenile-months of monitoring (Table 4). We calculated survival rates from these data using 1-month time intervals and the product limit (or Kaplan-Meier) procedure with staggered entry (Pollock et al. 1989). The product of 12 monthly rates

yielded an estimate of annual survival rate, and the average of these running products yielded a single point estimate.

The annual survival rate for juveniles was 0.52. Thus a cub in the Santa Ana Mountain Range had a 52% chance of living for another 12 months. Assuming that on average 30 months (2.5 years) elapsed between birth and adulthood (defined by a stable, independent home range), then about 20% ($0.524^{2.5}$) of cubs born could expect to reach adulthood. There were insufficient data to determine if juvenile survivorship varied for first-year versus second-year animals, or by sex.

The actual juvenile survival rate was certainly somewhat lower than 52%, because we always estimated each litter at the minimum known number. We intruded on new families to count neonates in only 2 cases (both in July 1989, when F3 had 3 cubs and F4 had twins). In other cases we waited several weeks to count cub tracks accompanying females. By this time some cubs probably died, and when cubs were small it was often difficult to detect how many distinct sets of cub tracks were present. Although the most common litter size in cougars is 3 cubs, our analyses included only the number of cubs that we actually verified by handling or on the basis of clearly unique tracks. Thus our computations presumed that F10 had 1 cub (M7) in July 1989 and 2 cubs in June 1991, that F2 had 2 cubs (M3, M4), that F6 had 2 cubs (M11, M12), that F12 had 2 cubs (M8, M10), and that F18 had 2 cubs (F16, F17). A reanalysis presuming that each litter had 3 cubs and that the "added" cubs died by age 12 months yielded an estimate of 0.45. The true juvenile survival rate for our population probably lay between 45% and 52%.

Our juvenile survival rates were lower than other published estimates, perhaps because high vehicle mortality in our population was only partially compensated by reductions in other types of mortality (e.g., shooting). However, we suspect that our rate of 52%

Table 4. Survivorship and causes of death for juvenile cougars in the Santa Ana Mountain Range 1987-1992. In addition, 3 surviving cougars (M7, M6, M13) were used in the survival rate estimates.

Animal ID	Birth Month	Death Month	Cause of death
son of F3[a]	Nov 1987	Aug 1988	vehicle accident
son of F3[a]	Nov 1987	Feb 1989	injured by cougar, died during capture attempt
daughter of F3[a]	Nov 1987	Feb 1989	killed and eaten by cougar
M3	July 1989	Jan 1991	disease
M4	Jul 1989	Nov 1990	killed by cougar? eaten by brother and mother
3 offspring of F3	Jul 1989	Dec 1989	died after being orphaned
2 offspring of F10	Jul 1991	Oct 1991	died after mom disappeared; 1 may have been captured illegally
2 daughters of F4	Jul 1989	Sep 1989	not known, "disappeared"
M8	Jul 1989	May 1991	vehicle accident
M10	Jul 1989	Sep 1992	vehicle accident
M5	early 1989	Sep 1991	vehicle accident
M11	Aug 1990	Feb 1992	unknown, not caused by vehicle, cougar, or acute physical trauma
M12	Aug 1990	Apr 1992	shot
F16	Dec 1989	Sep 1991	vehicle accident
F17	Dec 1989	Jan 1992	unknown, not caused by vehicle, cougar, or acute physical trauma

[a] not included in survival rate computation, due to small sample size in 1987-88; including these animals would have lowered the survival rate estimate.

may be typical of, or only moderately less than, that of other populations. Three of the 4 previously published rates provided unrealistically high estimates of true survival rates. Comparing mean litter sizes near birth and at 12 months (not the same litters followed through time) Ashman et al. (1983), suggested a value of 78%. Similar data in Robinette et al. (1961:213, inferring age from weight) suggested a survival rate of about 73%. However this method considers only litters in which at least 1 cub survived to 12 months of age. Whenever all cubs in a litter died within 12 months, the method would not detect a litter, thus ignoring a large number of cub deaths (Robinette et al 1961:213). Hemker et al. (1986) followed marked animals over time, reporting a survival rate of 72% for cubs between 3 and 10 months of age and 92% for cubs from 10 months to dispersal at 16-19 months, in an area of extremely low cougar density (gross density of 0.5 cougars per 100 km^2). Hemker et al. (1986:330) cautioned that their estimates did not reflect overall juvenile survivorship because they excluded the 2 periods of highest mortality, namely the early neonatal period (age 0-3 months) and the post-dispersal period. Their estimates also may reflect density-dependent enhancement of survival rates at low density. Using methods similar to ours, Anderson et al. (1992) computed the survival rate for yearling cougars as 0.642, an estimate much closer to ours than the previous reports; they did not attempt to monitor or estimate density for juveniles less than 1 year old.

In many cases, we could infer cause of death of juveniles (Table 4). Vehicle accidents and being orphaned were the leading causes of death for juvenile cougars (5 cases each). Cougar-inflicted injuries were implicated in 3 deaths. These cases are discussed in greater detail in later sections of this chapter. In most other cases, the cause of death could not be determined.

Adult survivorship

Adult survivorship was computed from data on 20 adults monitored for periods of time varying from 2 to 58 months, or a total of 497 cougar-months. There were insufficient data to compute survival rates separately for males and females, and our sample was mostly females. We analyzed these data using 1-month time intervals and the product limit procedure with staggered entry (Pollock et al. 1989). The product of 12 monthly rates yielded an estimate of annual survival rate, and the average of these running products yielded a single point estimate.

The annual survival rate for adults was 75%. This means that on average an adult had a 75% chance of being alive in 12 months. F7 and F10 were dropped from the computations in the month we lost their signal. If these animals in fact died at the time of disappearance (which is probably true for F10 at least), then the adult survival rate was 72%. As with juveniles, vehicle accidents were the leading cause of death (Table 5), killing 5 adults (F8, F9, F12, F13, F15). Two adult cougars (F1, F6) were killed by other cougars. Two (F2, F3) died of intestinal illnesses (probably not the same disease). Three adults (M1, M2, F11) were shot on depredation permits after eating goats or sheep. Two cougars (F7, F10) disappeared abruptly; there is some evidence that F10 may have been poached. Each cause of death is considered in greater detail in the following sections.

Our estimated adult survival rate of 75% is higher than the approximately 68% inferred from hunting returns of marked animals by Ashman et al. (1983) and from existing age structure by Robinette et al. 1977:123). Our estimate is nearly identical to the 74% observed in Utah by Lindzey et al. (1988), and somewhat lower than the approximately 80-92% observed in Colorado

Table 5. Causes of death for radio-tagged cougars and their offspring in the Santa Ana Mountains, 1988-1993.

Cause of Death	Juveniles	Adults	Total	Per Cent
Vehicle accidents	5	5	10	32%
Orphaned	5	0	5	16%
Probable intestinal disease	1	2	3	10%
Probable other disease	2	1[a]	3	10%
Intraspecific strife	3[b]	2	5	16%
Illegally killed	0	1(?)[c]	1(?)	3%
Depredation permit	0	3	3	10%
Shot legally by police	1	0	1	3%
Total	17	14	31	100%

[a] "old age" and capture stress contributed to F4's death
[b] includes a severely-injured juvenile that died during capture attempt
[c] Just after F10's disappearance, we received a report of a poaching in that vicinity. In addition, F7 abruptly disappeared 3 months after transmitter deployment.

by Anderson et al. (1992:53). The latter estimates, like ours, were derived using the Kaplan-Meier procedure on data from radio-tagged cougars in non-hunted populations (although several cougars in the Colorado study were killed by hunters off the study area).

Mortality factors

Collisions with motor vehicles caused 32% of the 27 documented cougar deaths in all age classes (Table 5). Vehicle accidents were not a mortality factor in any other study in the western states, but caused 49% of cougar deaths in Florida (Maehr et al. 1991). In most previous studies, hunting and predator-control activities caused most deaths (Shaw 1977, Shaw 1980, Hornocker 1970, Anderson et al. 1992, Murphy 1983), although natural deaths predominated in studies by Sweanor (1990) and Lindzey et al. (1988).

Disease

Three cougars (F3, M3, F2) apparently died of intestinal diseases, although no pathogen or other cause was identified. Disease was a likely factor in 3 other cougar deaths (F4, F17, M12).

Cougar **F3** died on December 27 1989; we retrieved her carcass within 24 hours. Pale mucous membranes and submucosal bleeding in the small bowel suggested that she died due to loss of circulating blood. The patchy distribution of the bleeding suggested that the bleeding was caused by a bacterial infection in the bowel. The bleeding could also have been caused by trauma to the abdomen, but there was no evidence to suggest trauma from collision with a vehicle, ingested poison, a gunshot wound, or being kicked by a large hoofed animal. The cougar had low fat reserves and an empty stomach, but was in fair condition and certainly not emaciated. She weighed 86 pounds at death.

M3 died on February 16 or 17 1991. A previous severe injury to his palate (sometime during June-October 1990) had healed remarkably well and had not prevented him from growing to normal size and weight. He had just started dispersing from his mother's home range on January 27 1991, when on the night of February 8 was treed by a domestic dog in a residential area adjacent to cougar habitat. Animal Control officers injected M3 with 6cc of ketamine via tranquilizer dart. M3 fell out of the small tree, striking his head on a planter box. On release that night in his mother's home range, his physical condition appeared good and his movements appeared normal for an animal recovering from ketamine.

By morning he had walked 200m up canyon but he remained at that site for the next week until he died. He apparently had not eaten during that week. Tracks indicated that he had walked 20m to a small pool of water at least once during February 12-18. The carcass weight was 79 pounds with moderate subcutaneous fat; he had obviously lost some weight during the previous week. We recovered his carcass on February 19, by which time no cause of death could be determined. There was no apparent skull or neck injury at death. We suspect intestinal disease simply because his mother died of intestinal disease after encountering his carcass.

F2 (M3's mother) had been in another part of her home range during the time M3 was dying. After necropsy we left M3's carcass in a trench near some dwellings on Starr Ranch. On the night of February 21-22, F2 arrived at M3's carcass, apparently encountering it by chance, and was seen walking away from his carcass at dawn on February 22. At that time, a strip of muscle had been torn from the carcass, presumably by F2, but left at the site, uneaten. F2 had covered the carcass with grass and leaves in the manner of a cougar covering a fresh prey carcass, but she did not return to feed on it. F2 bedded within 250m of the carcass for the next 3 days, and then moved about 600m further from the site to a confluence of 2 streams. She killed and ate a raccoon at that confluence on March 4. On March 10 we walked in on her after she had been daybedding at this confluence for 2 weeks. We observed that she was weak and losing weight and we conferred with veterinarians at the San Diego Zoo, who agreed to evaluate her. However, she died a few hours before we arrived to capture her on the morning of March 12. She weighed 73 pounds, a loss of 17 pounds since we last handled her on December 13 1990. Amy Shima, DVM (San Diego Zoo) reported that her death was apparently related to dehydration and diarrhea, but no pathogen could be identified.

F4 died on July 20 1990, at 12-14 years of age, which approaches the maximum lifespan for cougars. She had the most severe tick infestation we observed on a cougar during the study. Her upper left canine tooth and both upper carnassial (shearing) teeth were missing, the other canines were short and blunt, and her incisors were worn to the gumline. Her 70-pound weight did not look thin on her light frame and her pelage and body fat reserves were normal. Four days prior to her death she had moved about 3 km west of her previous home range into open grassland habitat where she bedded near a spring in a small arroyo, killing and eating at least 2 coyotes there. We recaptured her to replace her collar at that site on July 18, and the capture operation went smoothly with no sign of abnormal recovery. She fed on a coyote carcass the night after the capture but died 2 days later. In this case a combination of "old age," capture stress, and extreme heat probably all contributed to F4's death.

Two other carcasses (**F17, M12**) clearly had not suffered acute physical trauma (gunshot, vehicle accident, cougar-inflicted injuries, etc.) and it appeared each cougar had crawled into a typical wooded daybed site before death. Neither animal appeared emaciated. It seems likely that disease played the dominant role in these deaths.

M12 died under an oak tree in dense chaparral. His carcass was too decomposed to allow examination of soft tissues or tests for pathogens. The intact skin on the right side of his body showed no sign of trauma; his skull and leg bones had no injuries. The 2nd cheek tooth on the right mandible was missing, and the adult tooth, fully formed, lay below the bone, as if ready to erupt. However, part of the new tooth lay below the 3rd (fully erupted adult) cheek tooth, and the gap between the erupted teeth appeared too small for the new tooth. Thickening of the mandible alongside the

unerupted tooth suggested that the delayed eruption was causing some bone disease. Otherwise all the adult teeth were in good condition and formed a functional shearing apparatus.

F17's carcass was in good condition for an exam, due to cool temperatures at her death. She appeared in excellent condition with no sign of external injury and a thick layer of subcutaneous fat. The only remarkable internal finding was the presence of blood in her lungs and bronchi. The intestinal tract lacked any evidence of recent feeding; there was a small amount of tarry black stool in the colon.

Intraspecific strife

Three cougar deaths were unambiguously due to fights with other cougars; 2 of these 3 carcasses were also cannibalized. In a 4th case, a cougar was fed upon by other cougars, but death may have been due to other causes. A cougar-inflicted injury and capture trauma contributed to a fifth death. In all, about 16% of deaths were related to intraspecific strife. In addition to these cases, F13 had multiple wounds on the right side of her face and on her left shoulder at her initial capture; these injuries had almost certainly been inflicted by another cougar; the injuries had completely healed by her death 6 months later.

This level of intraspecific aggression is not unusual in cougars. Our observation that 16% of mortalities were cougar-related falls about midway between a rate of 3-5% in populations that have high man-caused mortality (hunting and predator control) (Anderson 1983:58, and Anderson et al. 1992:51) and a rate of 31% in a population with very low man-caused mortality (Sweanor 1990:36).

Two uncollared cubs of F3. During intensive monitoring on the night on February 8 1989, F3 traveled a short distance and spent almost the entire night in 1 location before moving to a more secluded location at dawn. We expected to find that she had been feeding on deer, but at the site where she had spent the night we found the very fresh and partially consumed carcass of F3's yearling daughter (not radio-tagged). She was in very good physical condition prior to death (abdominal fat 26mm). There was extensive subcutaneous bleeding and muscle trauma on her forelimbs and face, indicative of a prolonged fight using her forelimbs for defense, and her neck was broken between the skull and top vertebra. We set snares on her carcass and captured a yearling cougar, almost certainly her sibling, the following night. The male cub had severe, infected wounds from cougar bites to his hind quarters, and died during the capture operation. Fat reserves and overall size in relation to age indicated that the male yearling was also in good physical condition before the attack. Steady night-time rainfall obliterated tracks in the vicinity of the kill, and we could not determine the identity of the cougar that killed the female cub and injured the male. Perhaps the 2 cubs injured each other in a fight, but we speculate that an uncollared male was responsible. Five months later, F1 was killed (but not eaten) by a cougar less than 250m from the same location.

F1. F1 was killed by an uncollared cougar on July 3 or 4 1989. Her carcass was lying among some cattails adjacent to a creek near the confluence with the small dry tributary in which the 2 yearling offspring of F3 died in February 1989. Her position indicated that she had crawled there on her own; the only wounds were two conspicuous canine punctures, one entering her skull downward above her right eye (crushing the supraorbital arch) and the other entering upward near the posterior margin of the right mandible. Tooth size, distance, and position indicate that this bite was delivered by another cougar; the attacker did not feed on her. Her stomach contained a freshly consumed

opossum, and she had minimal abdominal fat (approx. 5 mm). No tracks (not even those of F1) were found in the immediate vicinity of the cougar carcass. However, tracks of an uncollared male had been seen on several occasions within a 2-km radius for several days both before and after her death.

M4. During intensive monitoring on the night of November 11 1990, F2 and her 15-month-old cubs (M3 and M4) stayed in 1 location all night long. We presumed they were feeding on a deer, but at the site where they had spent the night we discovered that they had almost totally consumed M4. Their feeding activity had kept M4's collar from entering mortality mode. The amount of consumption and the locations of the 3 animals on the preceding days indicate that F2 and M3 also fed on him the nights of November 9 (when M4 probably died) and November 10. The trio had been together for several days both before and after M4's death.

Because of the near-total consumption, we could not determine cause of death. M4 could have been mortally injured crossing the Ortega Highway on the night of November 9-10, when the trio crossed the highway. If so, the injured M4 walked 1.3 km (0.8 mi) up Horsetail Canyon from the Ortega (a 220-foot elevation gain). Because Horsetail Canyon offers excellent cover much closer to the road, it is not likely that M3 and F2 dragged his carcass that distance, nor was a drag mark evident on November 12.

M4 could have died of disease, but we have no evidence for this. The final possibility is that he was killed by his brother, his mother, or another cougar. It is extremely unlikely that F2 killed her son after investing 18 months of pregnancy, lactation, teaching, and feeding on him. Fratricide is also maladaptive (on average siblings share 50% of the same genetic material) but siblings do not have the same energetic investment in each other as a mother has in them, and siblings are competitors for their mother's hunting skills. And the fact that M3 enjoyed superior growth during the interval between previous captures (June 5-October 1) suggests that such competition may be intense and that M3 may have been more aggressive, dominating his brother at shared carcasses. If M4 was killed by a cougar other than M3, the most likely suspect would be M2 (the resident male in the area, and the presumed sire of M4). On November 9, M2 was 1.5 km WSW of where M4 died, with only 1 major ridge separating them. However, on the next 2 nights, M2 moved successively further west, and there is no evidence to suggest that he traveled east toward M4 or that he fed on M4. If M2 killed M4, he apparently was not injured in the fight (on Nov 12, we treed and examined him through binoculars, looking for sign of a recent fight).

F6. F6 was killed by another cougar on about May 23 1992. She had been dragged about 70m from the kill site to a location where her carcass was largely consumed. There were several canine punctures in her skull, and the top of the skull had been broken and the brain consumed. There were no tracks at the site clear enough to indicate the sex-age class of the cougar that killed her.

An unusual injury

Between captures on June 5 and October 1 1990, juvenile M3 suffered a severe, non-fatal, and apparently natural injury. His palette had been broken along the midline and the left premaxillary was pressed about 10mm upward into the skull, so that the 3 left incisors no longer occluded with the lowers. There was very little wear on the left incisors, suggesting that the injury occurred early during the interval, but the scar tissue still appeared fresh on October 1. At his death in February 1991, the injury had healed remarkably well but there was persistent malocclusion of the incisors and

canines on his left side. Despite this injury, M3 was otherwise quite healthy on October 1, with ample fat reserves and minimal ectoparasites. His sibling M4 was larger framed than M3 on both June 5 and October 1. Although the animals were of similar weight on June 5, M3 had a thicker layer of subcutaneous fat, despite his injury which must have made feeding painful for several weeks. No other injuries were evident. His skull is now in the Museum of Vertebrate Zoology at the University of California at Berkeley.

Highway mortality and injuries

Nineteen cougars (12 radio-tagged and 7 uncollared) were involved in 20 collisions with automobiles during 1988-1992 (M10 was in 2 accidents). This list (Table 6) probably includes all or almost all accidents during September 1990-January 1993, but almost certainly excludes some accidents involving non-radioed cougars during April 1988-August 1990, especially if they occurred in San Diego or Riverside Counties.

The roads with the most accidents were Santiago Canyon Road (4), Ortega Highway (4), Interstate 15 (4), and State Route 91 (2). All 4 accidents on Santiago Canyon Road were on the 2-km grade leading west from Irvine Lake up to the fire station at the crest of the road. All 3 accidents on the Ortega were in Caspers Park or just west of the Park. Three of the 5 accidents on I-15 were just north of the border patrol station midway between Temecula and Rainbow; the fifth was about 3 km (2 mi.) further south. The cluster of locations on I-15 coincide with the point where M12 successfully crossed I-15, and clearly indicate a threatened point along the critically important corridor linking our cougar population to the only adjacent population.

There was 1 accident on each of the following roads: Pomona Freeway, Interstate-5 (at Las Flores Creek), Clinton Keith Road, Basilone Road, Van De Grift Road, and Fallbrook Naval Weapons Station Road. Eight of the 12 accidents involving radio-tagged cougars were promptly reported to law

Table 6. Fate of 18 cougars involved in automobile accidents. There were no reports of human injury in any accident.

Fate	Cougar
Died near accident site	F8, M8, F12, M10[a], F9, F15, UF1[b], UC1[b], UC2[b], UC3[b], UF2[b], UM1[b], UX[b]
Euthanized at accident site[c]	F13
Did not recover, but survived 30 days	F16
Did not recover, but survived 6 months	M5
Apparently recovered	"FX"[d]
Fully recovered	F2, M10[a], M11

[a] M10 fully recovered from his first accident in May 1991, but was killed in a second accident in September 1992.

[b] "U" = uncollared. UF1 was an adult female killed on Santiago Canyon Road in fall 1988; cub UC1 was killed at the same site 1 week later. UC2 was a 9-month old cub of F3 killed on the Ortega Highway in Aug 1988. In Dec 1992, the small cub UC3 was killed on the Ortega Highway and juvenile female UF2 and adult male UM1 were killed on I-15 at the border patrol station, where UX was killed in October 1990.

[c] shot because she appeared unable to walk away from the accident site. The recoveries of F2, M10, and "FX" suggest that this may not have been necessary. There were no major injuries to bones or internal organs.

[d] We never identified the radio-tagged cougar struck on Fallbrook Naval Weapons Station (Dec 23 1991); when we arrived the next day all collared cougars were at least 1.5 km away and showed no abnormal movements in the days that followed.

enforcement agencies; the non-reported accidents involved F2, F8, F15, and M8.

Eleven of 16 accidents (69%) were at locations where wooded canyons intersected roads; we never precisely identified the location of the other 4 sites. The one clear exception to this pattern of crossing at major drainages is provided by the 3 accidents on I-15 which occurred along a wooded ridge. This site is somewhat surprising because there is an excellent canyon-bottom crossing site 1.5 km north (the Santa Margarita River). This illustrates that crossing points might not always occur where one might guess by looking at aerial photographs.

We documented the nature of some of the injuries sustained. M5 broke his left hip and his right femur just above the knee. F8 died of massive internal injuries. F12 was completely destroyed by the impact. F13 had no apparent skeletal injuries, or any gross internal injuries. M8 broke his pelvis near the midline and again through the right acetabulum (hip socket) and separated his right shoulder, but had no broken limb bones. F2 broke her left femur. M10 broke his left femur in his first accident, recovered, and then died of massive internal injuries in his second accident. M11 broke no major bones and was apparently only lightly injured.

Of 5 animals that survived for more than 10 days after their accident, 3 apparently recovered, and 2 eventually died as a result of the injuries. Of the 3 recovered animals, M11 was apparently not severely injured, and F2 and M10 suffered broken femurs. F2 managed to raise her 2 cubs (4½ months old at the time of the accident) and lived for 14 months before dying of an intestinal disease. M10 was photographed in the freeway median with blood trickling from his face 15 minutes after the accident, but he then moved back off the freeway and soon recovered. He lived another 16 months and was of normal weight at death. Figure 10 contrasts the movement patterns of the "recovered" animals to the pattern for the cats that eventually died of their injuries ("temporary survivors"). Each of the 4 animals traveled 200-650m from the apparent accident site to their location the next morning. The recovered cats differed most markedly from the temporary survivors in the average distance moved during the first 10 days: recovering cats averaged over 400m between daily locations versus 0m and 149m for the 2 temporary survivors.

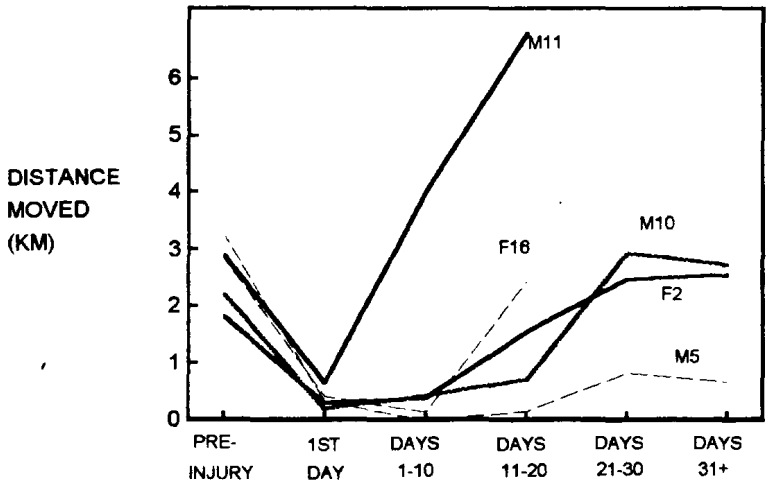

Figure 10: Distance moved by 5 cougars injured in vehicle collisions. Each point (except "1st day") is the average of at least 6 straight-line distances between consecutive locations obtained at least 1 day apart. Dashed lines indicate cougars that eventually died as a result of their injuries; solid lines indicate animals that apparently recovered fully. F16's last point = days 11-30. M11 was shot 20 days after his accident.

The individual accidents are described below:

F2: Ortega Highway at Cold Springs confluence, December 18 1989. F2 broke her left femur and remained close to flowing water in San Juan Creek during December 18-27. She recovered sufficiently well to kill a deer on December 29, although her tracks clearly showed that she was avoiding her left hind foot at that time. During visual observation on January 6, 1990 this leg was still unable to take the cougar's full weight, but she did

not avoid using it. During diel monitoring on January 6-7 and again on January 14-15, F2 traveled at normal speeds. During recapture on June 5 1990, she showed no evidence of the injury. She successfully raised 2 male cubs (4 months old at the time of the accident) to dispersal age. F2 died in March 1991.

F8: Riverside Freeway at Gypsum Canyon, 3:00 AM August 14 1989. F8 walked 800 m south of the freeway before dying. She died of massive internal injuries, but appeared in otherwise excellent condition with large fat reserves. Her carcass was delivered to Irvine Park so that the mounted skin, skull, and other material could be used in the new Visitor Center in Irvine Park.

"FX" (F9?): Fallbrook Naval Weapons Station Road, 4:00 PM December 23 1991. Camp Pendleton wardens, responding to a report of an accident involving a cougar, observed a radio-tagged cougar on the south side of the road, bleeding slightly from the face. After about 10 minutes, she moved through a 4-strand barbed wire fence into the nearest cover, where she remained out of sight for at least 20 minutes. Then as wardens advanced toward her, she flushed and crossed back through the fence, across the road, and through the fence on the north side, and into a clump of shrubs 20m north of the road. The wardens watched her there for several minutes until she got up and walked over a slight grassy rise (20 ft elevation) and out of sight to the north. We investigated the scene on foot the following morning, and with hounds on December 25, but found no evidence of a cougar in the area. Evidently the animal's injuries were less severe than any we have previously documented, because she apparently moved away from the scene fairly rapidly.

We had located all of the cougars with functional radio-transmitters on the morning of the accident and again on the morning after the accident. The only feasible victim with a functioning transmitter was F15. However, F15 had been 3.5 km from the site 6 hours before the accident, and by December 24, she was about 6 km from the accident site, and on succeeding days she moved distances typical of an uninjured animal. Most likely the injured animal was F9 (whose collar had failed in August 1988 and was later killed on I-15). The accident site was within F9's home range.

F9: I-15 south of Temecula, 8:30 PM March 1 1992. The accident site was near the Flynn Nursery at the north end of the village of Rainbow, at the southern edge of the last potential corridor linking the Santa Ana Mountain Range with the Palomar Range. F9 weighed 92 pounds, was not pregnant, had a scant 5mm of subcutaneous abdominal fat, but appeared in otherwise good condition. F9's transmitter had failed in July 1988.

F12: Interstate 5 at Las Flores Creek, 2:00 AM December 21 1990. F12 was demolished by multiple impacts. She weighed 103 pounds (the heaviest female weight we have recorded in this population), was 5-6 years old, and had been in excellent physical condition.

F13: Ortega Highway, 7:00 PM October 10 1990. F13 was killed about 1 km north of the Caspers Gate while crossing from east to west. This crossing point was used by several cougars, and lies about 300m north of a 12-foot wide culvert unused by cougars. She was in excellent condition and suffered no major injury in the accident, but was euthanized by a law officer at the scene because she appeared unable to walk. Her carefully skinned hide was also delivered to Orange County Harbors Beaches and Parks.

F15: Van De Grift Road, June 6 1992. Starting June 6, F15 stayed in a very small area in a dense riparian thicket in the Santa Margarita River, where she died on June 15, having moved no more than 100m during June

9-15. Her left pelvis had been shattered at the hip socket, with several bone fragments (up to 2 inches long) separated from the rest of the bone, and no visible growth of scar tissue. The femur was not damaged.

F16: Clinton Keith Road, 06:30 AM August 15 1991. The yearling F16 was struck near the crest of the road west of Murietta. She remained in a wooded canyon with flowing water at the accident site during August 16-27. She left the accident area by August 31 1991 and traveled considerable distances around Mesa de Burro, Mesa de Colorado, and upper De Luz Creek during August 31- September 16. Her movements seemed to reflect recovery from the accident, but she died about September 19. F16 had been accompanied by her mother 24 hours before the accident, but never after the injury. F16's sister (F17) dispersed from her mother a few days later and perhaps the accident occurred during agonistic interactions accompanying family breakup. The accident injuries combined with the stress of being newly independent were the primary factors in her death.

M5: Santiago Canyon Road, 6:00 AM April 23 1991. Shortly after the accident M5 moved about 400 m from the accident site into a well-wooded canyon. He moved very little for 3 weeks after this collision. A small seep about 250m away was M5's nearest source of water but a lack of tracks suggests that he went a full week without water. Tracks show that he did drink from the seep between April 30 and May 5; the seep dried up between May 7 and May 11. He also appeared not to have eaten for the first 7 days. A thorough search on April 30 turned up 1 dried scat from his last meal before the collision. An opossum that died at the seep about April 28 rotted there untouched by M5. A fresh scat indicated that M5 killed and ate an opossum on about May 10. On May 17, M5 moved 3.5 km (2.2 miles) to Peters Canyon Reservoir, which had ample water, dense woody cover, and abundant small prey; for the next 3 weeks he remained in the small dense willow forest surrounding this lake.

For the remaining 5 months of his life, M5 moved very short distances per day, repeatedly covering the same short travel routes in areas of very level terrain. M5's preference for level terrain brought him into areas of intense human use (described in greater detail in Chapter 9), including Irvine Regional Park, Santiago Oaks Regional Park, and Santiago Creek downstream from these parks. In 6 post-accident months of travel in such areas, there were only 2 reported sightings of M5, and this underweight animal never acted in a way that threatened humans or their pets. His only documented kills after the accident were opossums. On about September 22 1991, M5 died in the willow forest behind Villa Park Dam. All of his daytime locations (n = 10) during the preceding 3 weeks had been within 400m of the death site and within the level impoundment area. There was no sign of fresh injury on his carcass. He was markedly underweight for a 3-year-old male (82 pounds), but his skull and skeleton were of normal size for his age.

His skeletal remains revealed 2 severe leg injuries from his accident. His right femur was broken about 2 cm above the knee, and had rotated backwards about 90°, and laterally (outward) about 20°. Massive scar tissue had created a solid replacement bone, and the wear pattern on the femur and tibia indicated that the knee joint functioned normally in this new position. The more severe injury was to M5's left hip. The ball joint on his left femur was completely sheared off at its base, and was no longer part of the joint. New articular surfaces had formed on the fracture surface at the top end of the femur and on the dorsal ridge of the acetabulum (socket). The articular surface on the femur was about 1 cm^2 and rubbed against a worn area at least 6 times this large along the entire upper half of the socket ridge. Thus this replacement hip joint must have been weak and

sloppy. Large rough tuberosities had grown around the acetabulum and on the medial surface of the upper 6 cm of the femur. It is remarkable that he survived 5 months with injuries this severe.

M8: Pomona Freeway, about May 1 1990. M8 had a separated right shoulder and internal injuries, but no broken bones. His carcass was found about 3 days after the accident in weeds alongside the road.

M10: Riverside Freeway at Coal Canyon, 9:00 PM May 7 1991. M10 was hit broadside, breaking his left femur and both car headlights, and knocking off the car's front license plate. He was photographed in the freeway median with blood trickling from his face 15 minutes after the accident, but when police arrived he moved south of the freeway. He spent the next 7 days in a small canyon along the freeway. Then on the 8th and 9th nights he moved 0.7 and 2.0 km, respectively. We monitored his movements overnight on May 22-23 and again on May 23-24; he exhibited almost normal movement patterns, and killed and ate a skunk at 0030 on May 24. For the next 15 months, his movement patterns suggested no impairment of his locomotor abilities, and he weighed a normal 137 pounds at his death in September 1992. However, his elongate temporary home ranges were located along the urban-wildland interface, suggesting that he remained a subordinate male, probably because his injuries prevented him from attempting to defend a territory.

M10: Santiago Canyon Road, about 10:00 PM September 15 1992. At death, M10 weighed 137 pounds, had ample fat reserves, and appeared to have been in good condition. His spleen had ruptured and there was extensive bleeding in the abdominal cavity.

Illegal take and harassment

We encountered little evidence of illegal take and harassment of cougars. Chasing cougars with hounds (the dominant method of capture) is a high-profile activity and is difficult to hide in most of the study area. Access is strictly controlled on Camp Pendleton and is limited by topography and lack of roads on most National Forest land in the study area. The owners of private wildlands in Orange County actively discourage trespassers, who would be very conspicuous in these large holdings. However, on the Santa Rosa Plateau and north and west of the Plateau there are many small and medium-sized private ownerships, many non-resident landowners, ample roads, and relatively good access to National Forest land. This area offers the greatest potential for cougar harassment, and 3 such incidents were related to us during 1988-1992. Doubtless other cases were not brought to our attention. In none of these incidents do we have proof that local cougars were harassed or killed. The 3 incidents were:

1. In March 1992 we learned that CDFG wardens had seized a cougar skin several months earlier at an estate residence on upper De Luz Creek. The warden indicated that there was substantial evidence that the homeowner had captured the animal locally, had raised it in a cage on his property for 4 years, and had then had it killed and mounted because of the difficulties of continuing to maintain it in captivity. The evidence (statements that homeowner allegedly made to several other persons) was not strong enough to prove in court that the animal was trapped locally.

2. In spring 1992 we were called by an Orange County resident who had been hiking in the National Forest near the Santa Rosa Plateau the previous day. Near dusk he was approached by some tired dogs wearing radio-collars and tags with a phone number. When no one came

looking for the dogs for about an hour, the reporting party took the dogs home and called the owner, who came to pick up the dogs the next day. When the dog owner came by, he stated that he had been using his dogs "to chase mountain lions."

3. F10 disappeared in mid-October 1991. Our last ground fix on her and her family was October 11 1991, when tracks indicated that F10 and 2 or 3 cubs (born July 1991) were alive in Roblar Canyon. Since then, we were unable to locate her or any sign of her cubs, despite many telemetry flights, intense track searches, and a 5-week trapping effort. In the latter effort, we put 5 snares in the core of her home range and checked them daily during November 19-22 and November 25-December 24 1991. It is unlikely that she and her cubs could have avoided these areas for 5 weeks, and they probably died. On January 31 1992, a person telephoned us to report that a female cougar had been poached by 2 orchard workers in a western tributary ("Conquistador Canyon") of lower Sandia Canyon on October 19 1991. The caller claimed that he had confronted the 2 men as they were dragging out a live male cub wired to a makeshift noose-pole. He says he took the cub from the 2 men and announced his intention to release the cub. The 2 men responded that they had just killed the mother and that release would probably be fatal to the cub. The caller claimed that he kept the cub and that the cub was then (January 1992) nearly 40 pounds in weight and being kept by his "brother in Ohio." The man called us because the cub was becoming difficult to keep and he wanted some sort of permit that would enable him to legally transfer the animal to a better facility. We advised him to contact CDFG for how to dispose of the cub, and promptly relayed the report to CDFG wardens. We cannot confirm that the incident took place, and have no firm evidence that F10 and her cubs were involved if it did take place. However, Conquistador Canyon had been part of F10's home range.

The only evidence of illegal harassment in Orange County comes from 3 observations on Irvine Ranch property north of Santiago Canyon Road; the most recent occurrences were March 27 1991 and April 13 1992 (we failed to record the date of the first incident). On each occasion tracks of several hounds, 2-3 men, and 1-2 cougars strongly suggested that long chases had taken place within the previous 24 hours. These apparent chases occurred in Gypsum, Weir, Blind and Fremont Canyons. In none of the cases was there any evidence that a cougar had been killed. After the second incident we asked the cattle lessee on that property if he was aware of the activity; he claimed he had been out at night trying to break his dogs from chasing deer.

A final observation may or may not be related to illegal harassment. On July 17 1991, we recaptured F5 to replace the transmitter deployed in May 1989. In the interim she had lost all but the basal 31cm of her tail. Scar tissue had formed over some small wounds (apparently canine punctures) on her tail and left hip, but not on the surface of the stump, so the tail loss appeared more recent than the other injuries. Based on his experience with hounds, field assistant Duggins Wroe believes the tail and other injuries were inflicted by dogs. However, the injuries could also be cougar-inflicted.

Depredation

All depredation losses involved cougars being shot for eating goats or sheep. Although there were 4 large cattle operations in the study area, to our knowledge there were no requests for depredation permits due to loss of calves or cows. We were aware of only 1 large sheep operation in the study area, namely the sheep-grazing lease on Camp Pendleton. Since 1989, Camp Pendleton has required the sheep lessee to bear the cost of depredation losses without

recourse to depredation permits. Most goats in the Santa Ana Mountain Range were kept as pets or for fuel control near rural homes; most owners had 1-3 goats. We were aware of only 3 ownerships with more than 5 goats, 2 of which attempted to generate some revenue from them.

Depredation losses are summarized below.

Sheep: In February 1988, M1 and an uncollared adult female cougar were shot on Camp Pendleton.

Goats: On January 28 1992, an uncollared male cougar (2 years old, excellent condition, 135 lbs) was shot near Bolero Peak in Santiago Canyon. His carcass was donated to Irvine Regional Park which will mount the skin for display in their visitor center. At about 9 PM March 4 1992, M2 (4-5 years old, excellent condition, 155 lbs) was shot by the same goat rancher. On January 26 1993, F11 (about 8 years old, excellent condition, blunt and worn teeth normal for age, 80 lbs) was shot about 3 km east of Redondo Mesa, and about 5 km (3 mi) outside the home range she had used during the previous 5 years of monitoring. On February 4 1993, 2 uncollared male cougars were shot by the same livestock owner that killed F11. The CDFG official reported that the first male was about 1-2 years old, in good condition, and weighed 88 lbs, and that the second male was 5-6 years old and weighed 114 lbs. If the latter age estimate was accurate, then the older male was markedly underweight.

Synthesis: a population model

Population dynamics involves only 4 basic processes, namely birth, death, immigration, and emigration. This study has provided some information on each of these processes. However, to move from observed data to an understanding of population dynamics is much more complex, because these processes vary with age and sex of the animal, population density relative to carrying capacity, area of habitat available, and availability of movement corridors. Forecasting how the cougar population will grow or decline in the future requires a mathematical method of integrating these data and projecting them over time.

To do this, we developed a simulation model to forecast the likelihood that a cougar population can persist, under various estimates for the important biological parameters (birth and death rates, carrying capacity, etc.) and various projections about management decisions (amount of habitat protected, preservation of habitat corridors). This model is described in detail by Beier (1993, included as Appendix 1 in this report); this paper should be considered one of the most important parts of this Final Report. In brief, the model demonstrates that if thousands of square miles of suitable habitat containing cougars were divided into isolated chunks, each less than 500 square miles in size, cougars would inevitably become extinct over the entire area because of this fragmentation. However, if the habitat areas are instead connected by movement corridors, the cougar population will likely survive.

All models are defective to some unknown degree, and extinction is a serious consequence. Therefore, in evaluating the results of this sort of model, an "acceptable" level of risk is generally at most 1-2% (Shaffer 1987). Model predictions are also sensitive to errors in our estimates for carrying capacity, birth rates, or survival rates (Beier 1993). As mentioned elsewhere, the model used a birth rate estimate that may be higher than the true rate ("Reproductive Activity" earlier in this chapter), and true carrying capacity may also be somewhat lower than the estimate used in the model (last section in Chapter 7). Both of

these errors would cause the results shown in Figure 11 to underestimate the extinction risk.

With respect to the cougar population in the Santa Ana Mountain Range, the model makes several clear predictions (Figure 11):

- The 2070 km2 of habitat remaining is precariously close to the smallest isolated area that can support a cougar population.
- Without a corridor for immigration from the Palomar Range, every additional parcel of habitat lost to urban growth increases the risk of extinction.
- If only the central habitat block (Figure 1, Table 1) is preserved, the extinction risk is 33% in the short term, and a virtual certainty in the long term.
- With a high-quality corridor to Palomar and good connections among existing protected lands, the extinction risk can remain low even while adding thousands of new homes and losing many acres of wildlands to urbanization.
- Loss of the Coal Canyon Corridor would cause the extinction of cougars from the Chino Hills. Because the Chino Hills is 8% of the total habitat area in the Mountain Range, this also would increase the risk to the larger population and push the population to the steeply rising part of the extinction risk curve (Figure 11).
- Without corridor protection, cougars will be lost from Limestone Canyon-Whiting Ranch Regional Park and all smaller protected parcels in the Mountain Range.

Perhaps the most surprising result of the model is the finding that a corridor that allows even rare immigration (1-4 juvenile immigrants per decade) dramatically reduces extinction risk. The model results are made much more meaningful by 2 additional findings in this study:

1. Our data on dispersal of juvenile cougars (Chapter 6) show that cougars will find and use corridors. In particular, dispersing cougars used all 3 major corridors (Coal Canyon, Pechanga Creek, Arroyo Trabuco) in the study area.

2. By closely following radio-tagged cougars, especially on intensive monitoring sessions, we have mapped the actual routes by which animals move between protected habitat parcels. Although many of these routes are now pristine open space, they will become corridors (at best) as urban growth removes the adjacent habitat. These maps have been provided to the County and other appropriate agencies in previous reports.

Finally, the model and related data underscore the need for regional planning. The Santa Ana Mountain Range straddles 5

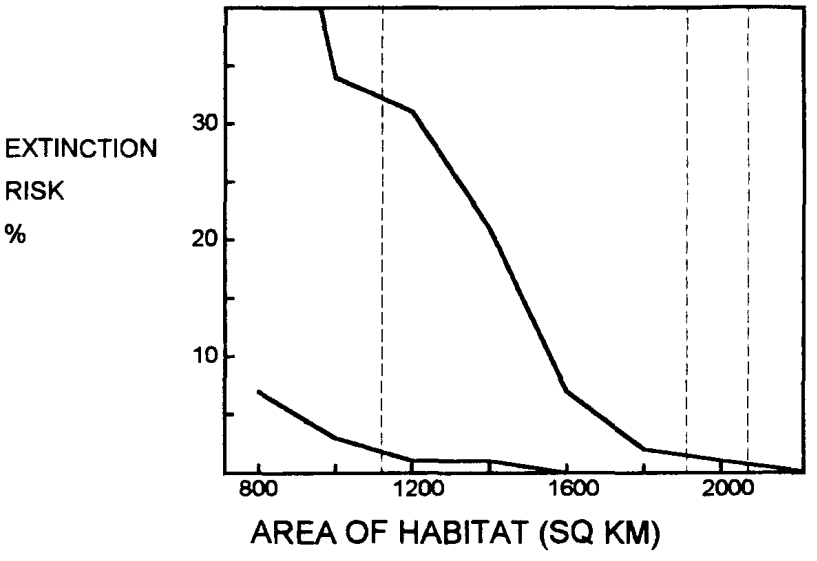

Figure 11. Extinction risk (percent of simulated populations that went extinct within 100 years) for the cougar population in the Santa Ana Mountain Range. The upper line gives the risk if the Pechanga Corridor is lost to urban growth, and the lower line the risk if that Corridor can be maintained. From *right* to *left*, the dashed vertical lines indicate total habitat available in 1992, total habitat available if the Coal Canyon corridor is lost, and total area of the protected and interconnected habitat block (Table 1, Figure 1).

counties and abuts 17 incorporated cities. Two freeway-building agencies and the world's largest water district also make critical land-use decisions. Because the cougar population needs large habitat areas and viable connections between protected habitat parcels, no single agency takes account of the cumulative impacts of land-use decisions on viability of this cougar population. For instance, the short wildlife corridor at Coal Canyon lies within the jurisdiction of Yorba Linda, Anaheim, and CalTrans, and the latter 2 entities refused to engage in a multi-jurisdictional attempt to preserve the corridor. Without dramatic changes in land-use plans at a regional scale, there is little hope for survival of this cougar population.

CHAPTER 5. UTILITY OF TRACK SURVEYS

Track surveys for cougars can be used for 3 purposes: (1) to detect simple presence of cougars, (2) to detect increases or decreases in population size, or (3) to estimate the total number of animals in a population. The first type of survey is relatively inexpensive and potentially useful, and is discussed in the first part of this chapter. The second type of survey is very expensive and has low power to detect change in numbers. It is nonetheless feasible and is discussed at the end of this chapter. The third type of track survey (to estimate numbers) would be extremely expensive, probably requires surveying more road mileage than exists in our study area, would produce estimates of low precision and unknown accuracy, and will not be discussed further.

Surveys to detect cougar presence

There are frequent reports of cougar sightings within County Parks. Under most circumstances it is unlikely that County Parks would want to use a track survey to validate or discredit a report, because valuable manpower would be spent without gaining any new information. However, in certain circumstances (e.g., a report of a cougar engaged in unusual or bold behavior) a track survey to detect cougar presence might be appropriate. Track surveys for presence are also useful to detect whether cougars are still using an area that has been impacted by urban growth.

Most cougar sightings are bogus and do not need validating

In our experience during 1988-1992, at least 75% and perhaps as many as 95% of the routine sightings were cases where the observer has misidentified a bobcat, coyote, domestic dog, domestic cat, raccoon, or deer. The following 3 examples illustrate that even people with extensive experience with animals mistakenly identify other animals as cougars, even under ideal viewing conditions.

1. In 1988 we received occasional reports of cougar sightings from security personnel at the TRW facility on Rancho Mission Viejo. These reports seemed credible because the guard station had a fine view, because 2 radio-tagged cougars used the areas within their view, and because each guard spent 40 hours a week in the station. At about 8:00 on December 25 1988, as one of the study team drove up to the guard station, 2 guards excitedly stated that they had been watching a cougar in the canyon below, using binoculars, from a distance of about 250 yards, for about 5 minutes. They pointed to a shrub behind which the animal had just walked. A minute later a coyote walked out from behind the shrub.

2. Rancho Carillo is a community completely surrounded by designated wilderness areas, inhabited by about 70 families who have chosen a remote lifestyle. They live in the middle of cougar habitat, and we tended to believe many of their reports of cougar sightings. In July 1989, a resident of Rancho Carillo reported that for 2 days a cougar had been resting near a woodpile and trailer about 200 feet from his house. He had watched the animal several times, during the daytime, using a spotting scope, and several of his neighbors had also seen it. When 2 members of the study team went to investigate on the morning of July 28 1989, the informant and several other observers said they had just seen the cougar bed down behind the trailer. The informant stood by his spotting scope while we went to investigate. As we approached the trailer, a house cat ran out from under the trailer and the observers shouted: "There goes the lion."

3. At 12:45 PM on February 5 1990, Orange County Animal Control called to report that an adult cougar and a spotted cub were in a clump of pampas grass at 24252 Cataluna Circle in the City of Mission Viejo. An animal control officer had been called to the scene by a local resident, saw the cats himself, watched the cats enter the pampas grass at noon, and had watched the clump of grass continuously since that time, calling for assistance with his hand-held radio. The officer was certain that he was watching so closely that the cats could not have escaped. When we arrived we crawled into the pampas grass to flush the animals into the open where the assembled Animal Control Officers and CDFG wardens could attempt to shoot the cougars with tranquilizer darts. We flushed a 10-pound yellow house cat.

Finally, the power of suggestion can greatly increase the number of reported sightings. We usually received fewer than 6 reported sightings per month during 1988-1992. However, as a result of publicity surrounding the court hearings on the Laura Small case, we received about 6 reported sighting per week. We could investigate only a fraction of these reports; none of them could be verified by the presence of cougar tracks or other sign.

Given the unreliability of sightings, we make the following conclusion:
If
(a) the report did not allege that the cat acted aggressively toward people, and
(b) the Park is already known to be cougar habitat,
then,
it is a waste of time to investigate the report, **because**
(a) the report is probably in error, and
(b) even if the report is confirmed, no new information will be gained from the effort. If the park was known to be cougar habitat before the sighting, a confirmed sighting would not change this fact in any way.

When a track survey for presence may be warranted

If a reported sighting of a cougar includes an account of unusual behavior (e.g., the cat deliberately approached the park visitor at close range) or if the sighting occurs in an area thought to be outside cougar habitat (e.g., any park west of I-5), Harbors Beaches and Parks (HBP) may wish to validate these reports. There may be reasons why HBP may prefer not to investigate; for instance, HBP may feel that chasing phantasms is diverting resources from important work or they may decide to refer the report to CDFG. Our purpose here is merely to point out that if HBP wishes to validate a report of unusual cougar activity, a prompt track survey can be a useful approach.

Track surveys for presence can also be used to monitor the success of wildlife movement corridors impacted or created by human activities. In approving projects with narrow habitat strips for animal movement, planners often decline to require wider corridors because it is impossible to know in advance that the narrow corridor won't work. However, we would soon gain such knowledge if we monitored animal use of such habitat strips (Beier and Loe 1992:438). If track surveys are used to detect cougar use of a site, it may be necessary to rake the ground or import dirt to increase the detectability of tracks, and sites should be checked at dawn (before nocturnal tracks are degraded). Because cougar home ranges are so large, track monitoring should take place at least twice a week for several months, with equal sampling intensity before and after project impacts. Further suggestions for such monitoring are given by Beier and Loe (1992:438).

Using tracks to verify a reported sighting

In the course of investigating many reported sightings, our staff and the personnel at several county parks have developed a simple procedure for using tracks in an attempt to verify a reported sighting. If the followup investigation is carried out within an hour of the sighting, there will usually be some useful evidence. Fresh dog or bobcat tracks at the very point where the sighting occurred would disprove the sighting. Fresh cougar tracks in the vicinity would verify the report. In some cases the sighted animal will still be present if the investigator arrives promptly. However, we caution that in some cases no useful evidence will be found; such lack of evidence should be used neither to accept nor to reject the sighting. We first presented the following procedure at a seminar for HBP Rangers at Santiago Oaks Regional Park on September 5 1991.

1. Have the informant describe the animal in their own words. Prompt the informant by asking questions such as "What colors did you see on its coat?" and "Describe the tail." Do not ask leading questions such as "Was it brown all over?" or "Did it have a real long tail?"

A cougar has a black tip on its tail, but no black elsewhere. If they describe "some black" on the sides or belly, it was probably a bobcat. A cougar's tail appears nearly as long as its body (although it's not really that long), and is usually held so that it nearly touches the ground.

2. If the informant described a cougar, visit the site promptly to look for tracks. Hikers, bikers, equestrians, and winds can obliterate tracks within minutes. When you go to the site, bring a track identification guide (Figure 12). If possible, have the informant take you to the exact location where they saw the animal.

3. While holding a track identification guide (Figure 12) in your hand, check for tracks everywhere within about 400 m (¼ mile) of the sighting area. If the cougar walked in a dirt trail it will almost always leave tracks. If the cougar was not reported to have walked in a trail, check nearby portions of the trail anyway.

4. If you find cougar tracks in an unusual location (e.g., west of I-5, in a city park) or in connection with reported aggressive behavior, document the fact with photographs. Use a camera that can focus on a track a few inches from the lens. Take under-exposed photos in addition to normally exposed photographs; overexposed photos do not reveal the details needed for a positive identification. Try to get strong side-lighting so that the edges of the tracks cast big shadows. In low light,

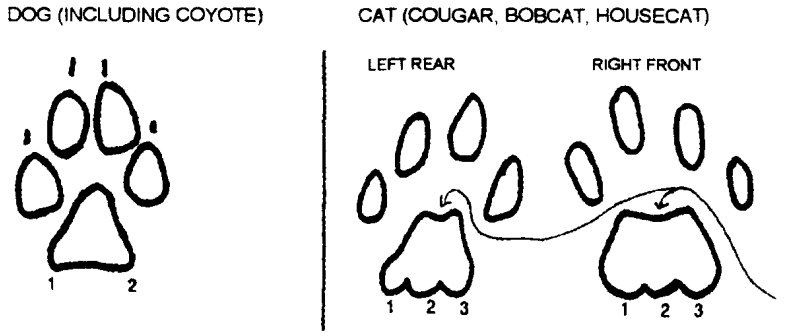

Figure 12. A field guide to distinguish cougar tracks from dog tracks. Size is worthless as a criterion: some dog tracks are larger than cougar tracks. If you can see claw marks, it is a dog track; however, tracks without claw marks can also be dog tracks. **The critical field marks relate to track *shape***: A dog track has a roughly triangular 'heel' pad with 2 lobes at rear, and near-perfect symmetry (you can rarely tell right from left). The 'heel' pad of a cat track has 3 lobes at the rear margin and a dimple in front (arrows). A cat track is also asymmetric: you can tell right from left. If the heel pad of a cat track is over 37 mm (1.5") wide, it is a cougar track; if narrower, it is a bobcat or housecat.

use a lantern, auto headlights, or a detachable flash to create strong side lighting.

Surveys to monitor population trend

By resurveying dirt roads and trails on an annual or multi-annual schedule, it would be possible to detect long-term changes in population size. In the case of the Santa Ana Mountain Range, such information could be used to detect whether cougar numbers are declining, so that remedial measures could be taken. We do not feel that such monitoring would be useful, however, because simulation modeling (Chapter 4 and Beier 1993), present population size (Chapter 2), the near-isolation and accelerating fragmentation of the population (Chapter 3), and highway mortality (Chapter 4) all clearly indicate that our cougar population faces a bleak future unless careful land-use planning is implemented rapidly. Data from an expensive long-term track survey would add little to the urgency that already exists, and could be used to delay effective action.

Such a survey also has limited ability to detect change in numbers. As Kendall et al. (1992:428) cautioned, a well-designed track survey for trend "will not detect small, annual population fluctuations but may reveal long-term trends or impending disaster.... We emphasize that, at best, such data will reliably detect only substantial, potentially threatening declines, and then only with large sample sizes [and] relatively abundant sign." Similarly Van Dyke et al. (1986) and Van Sickle and Lindzey (1992) found weak correlations between track density and cougar numbers (r^2 = 0.38 and 0.73, respectively) and the latter cautioned that the technique can detect "only relatively large changes in cougar population size."

Despite these reservations, a trend survey using tracks is technically feasible and managers may decide to implement such a survey. Based on our experience and our survey of the literature, we offer the following survey procedures, designed to detect a 20% decline in cougar numbers with a statistical power of 0.8 (80% chance of detecting a real decline) and significance level of 0.1 (10% risk of falsely suggesting a decline, one-tailed test). We chose a procedure that uses presence-absence data on each mile surveyed, rather than track density because the 2 types of data provide highly correlated results (Kendall et al. 1992), because our procedure avoids subjective judgments of whether or not a new track occurrence represents a different animal, and because our procedure (by allowing the observer to stop observing in each 1-mile segment after a track is detected) is much less expensive. This is not a highly sensitive procedure, but further sensitivity would require considerably greater effort. Indeed the limited length of dirt roads in the mountain range may preclude design of a more sensitive survey.

If such surveys are to be carried out, the following simple procedures are recommended:

1. Train observers to recognize cougar tracks. On a map, allocate dirt roads in the Santa Ana Mountain Range into Routes, each 30 miles long. This is the maximum distance that can be covered by a single observer in a single session. Some Routes can consist of a few short roads totaling 30 miles, with minimal transit time between the road segments. For statistical purposes, each Route must be run 3 times per year, and there must be at least 900 total miles (30 Routes) surveyed. Foot trails can also be used. Arrange the routes so as to achieve an even coverage of the entire mountain range. The 900-1000 miles needed probably approaches the total mileage of dirt roads and trails in the mountain range. Try to select routes that will not be paved in the future.

2. To reduce vehicle and manpower costs and increase detection of tracks, use a single observer driving a motorcycle on dirt

road Routes. Alternatively, it is equally effective (but with added costs and safety concerns) to use a team of 1 driver and 1 observer in a car or truck, the latter riding on the hood of the vehicle.

3. When driving each Route, start at dawn (before winds and vehicle traffic obliterate nocturnal tracks), maximize the time spent driving into the sun (this increases track detection), and stop before the sun is high. On roads with no vehicle traffic and calm daytime winds, late afternoon is also an acceptable time to survey.

4. Drive at about 5-8 mph, scanning the ground in front and alongside the vehicle carefully for tracks. When cougar tracks are suspected, stop and look closely. For each mile as measured on the odometer, record whether or not cougar tracks were detected. Do not attempt to determine how many different cougars made tracks. Thus if a cougar track is detected at 0.1 miles, you can stop looking for the rest of the mile and resume looking at the next whole mile. Use the same data form for each of the 3 surveys during a single year; if a track was detected on a given mile during 1 the times that Route was previously surveyed in a given year, you can omit checking on that mile.

5. Repeat the routes 3 times per year. The 3 repetitions should be run at the same times each survey year. We suggest running them about June 1, August 1, and October 1, because dusty road and trail conditions maximize track detection and the interval is sufficient to insure that you will never count the same track twice. The 2-month interval also increases the chance of detecting a mother with cubs whose restricted movements might not be detected if all 3 surveys fell in the early neonatal period. There is no particular advantage to longer (e.g., 3-4 month) intervals, and such spacing would risk encountering rain, floods, or washed-out roads.

6. The index of cougar density is simply the fraction of the 900-1000 miles sampled that had cougar tracks at least once during the year. Compute the standard error following Kendall et al. (1992).

7. Repeat the entire procedure every 2 or 3 years, looking for changes in the index since the last survey.

CHAPTER 6. ACTIVITY PATTERNS

Daily activity patterns

We carried out 180 intensive monitoring sessions, during which we determined location of the focal animal every 15 minutes. Most of the early sessions were for 24-hour periods (usually noon-to-noon). Because these early sessions showed that cougars were overwhelmingly nocturnal in their movements, later sessions started 1 hour before sunset and ended 1 hour after sunrise. Data from these sessions were analyzed by computing the straight-line distance moved between 1 location and the next location (15 minutes later). In each 15 minute interval, the cougar's behavior was categorized as traveling (distance > 0) or as static (distance = 0). Consecutive intervals of traveling or stasis were termed "travel bouts" or "periods of stasis," respectively. By simple addition, we computed the total elapsed time (always a multiple of 15 minutes) and distance traveled in each bout ot travel or stasis. Travel speed was computed as the distance traveled divided by the duration of a travel bout. Percent of time moving was computed separately for daylight and dark hours.

For the entire monitoring session, total distance was computed as the grand total of all 15-minute distances, and net distance was computed as the straight-line distance between the first and last location of the session. All times were converted to Pacific Standard Time before averaging across sessions.

On the day following most sessions, we walked the animal's route, often assisted by hounds, looking for prey remains, scats, or other evidence that would allow us to identify the behaviors associated with several distinct movement patterns. In this chapter, we summarize data from the first 78 sessions of monitoring (almost all of them for a full 24 hours). We are preparing a manuscript for scientific publication using all 180 sessions, but these analyses were not completed in time for this report.

There were 4 distinctive movement patterns. Our followup showed these patterns were associated with 4 different behaviors. Each of these 4 patterns is discussed in greater detail in the following sections:

1. walking all night (which we refer to as "hunting" although in fact we do not know what motivated the cougar to move steadily all night long),
2. feeding on a previously killed deer,
3. killing a deer during the session and then feeding on it, and
4. killing and eating smaller prey.

We observed the hunting pattern on half (49%) of the sessions; on these days the cougar walked steadily and our followup suggests that it did not kill anything as large as an opossum. This was a surprising result, and suggests that cougars frequently went several days without eating. The patterns and our followup show that cougars killed an opossum-sized animal about once very 6 days (13% of sessions), killed a deer about once every 10 days (10% of sessions), and fed on a previously killed deer carcass on 23% of the sessions. The latter 2 frequencies suggest that cougars fed on a single deer for about 3½ nights (including the night of the kill). Thus days of non-feeding alternate with days of only-feeding creating an overall pattern of "feast or famine."

Three other behavior types were observed. (1) The focal animal was primarily involved in social interactions (breeding, or prolonged vocalizations between adult females) in 5% of the sessions. These movements usually followed a pattern similar to feeding on a previously-killed deer. (2) In 6 sessions the focal animal was an adult female with young (< 6-week-old) cubs; these sessions showed the "hunting" pattern for the first half of the night, and the mother usually spent the rest of the

night with her cubs. Thus the movements plotted against time resembled the pattern when a deer was killed near midnight (Figure 13: curve B). However, the starting and ending location was always the site where the cubs were hiding. (3) Dispersing juveniles generally displayed a "hunting" pattern, but were doubtless exploring at the same time; data from these animals were excluded from the results presented here.

Table 7. Summary statistics for cougar movement patterns while presumably hunting. Data are from 33 monitoring sessions, in which the focal animal was located every 15 minutes.

Trait measured - units	Average	Modal class[a]	Range
percent of night time traveling - %	51	41-50	25-83
percent of daylight time traveling - %	13	0-10	0-42
total distance traveled in 24 hours - km	9.0	8.0-8.9	2.1-19.4
traveling speed - meters/hr	920	500-750	120-3400
number of travel bouts per 24 hours - n	9	8	4-14
number of travel bouts per night	7.4	7	3-14
number of travel bouts in daylight	1.6	1	0-6
duration of travel bout - hours	0.91	0.25&0.75[b]	0.25-6.75
duration of periods of stasis (night time) - hours	0.78	0.25	0.25-3.75
distance traveled in 1 travel bout - m	975	50-250	50-9800

[a] In some cases the mode (the most frequently occurring value or class) is a better indicator of "typical" behavior than the average.
[b] bimodal

Hunting

This pattern consisted of walking most of the night, with no period of stasis longer than 3.75 hours. Because the cougar moved steadily and almost certainly did not kill any prey as large as an opossum, we have labeled this pattern "hunting" although the cougar may have been moving for some other reasons.

Data from 33 sessions showing this pattern are summarized in Table 7. A "hunting" cougar spent about half the night traveling, and did virtually no traveling during daylight hours. On only 2 of the 33 sessions did the cougar travel over 3 km during the daytime. Hunting cougars usually traveled at a leisurely pace of about 900m/hr. Travel occurred in about 9 short bouts per day, each typically less than 1 hour in duration and less than 1 km in distance moved. Night-time travel bouts alternated with shorter periods of stasis. The overall pattern thus consisted of short, slow-speed travel bouts, during which the animal probably searched for prey or moved to a new site, alternating with shorter periods of stasis, during which the cougar probably stalked prey or waited in ambush. During some periods of stasis, the cougar may have fed on small prey, drank water, or rested. Daytime sedentary periods typically lasted all day; during these periods the cougar probably simply rested.

The overall pattern exhibited by a "hunting" cougar is illustrated and contrasted to other patterns in Figure 13 (line A).

Killing and/or feeding on prey

In contrast to the steady alternating between travel and stasis, a very different pattern was evident when cougars made a kill or fed on a previously-killed deer. In the sessions when the focal cougar fed on a previously-killed a deer, the cougar traveled very little, with virtually no activity between 8AM and 2PM, and very little movement at night (Figure 13: line C). The peak activity periods were at dusk and dawn, reflecting movements between the carcass and a daytime rest site.

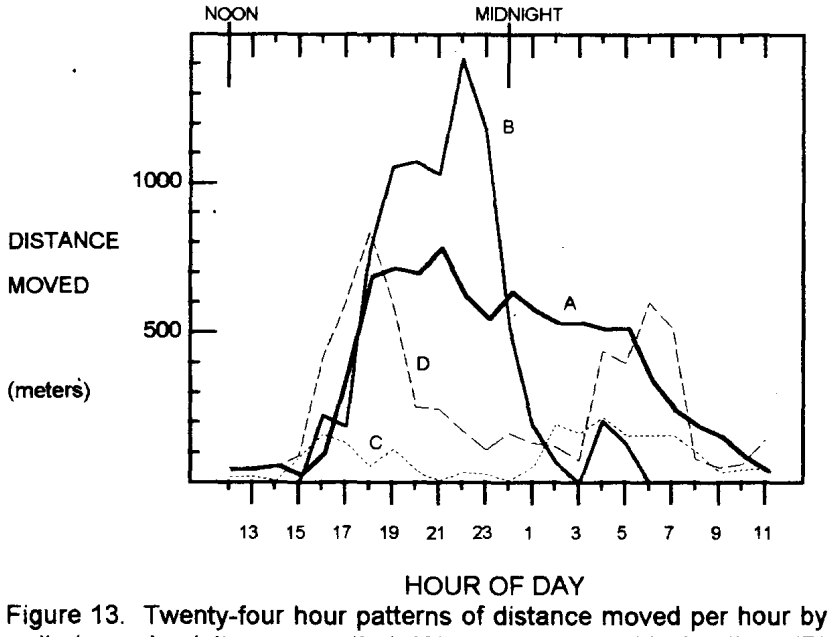

Figure 13. Twenty-four hour patterns of distance moved per hour by radio-tagged adult cougars that (A) were presumably hunting, (B) killed a deer near midnight, (C) fed on a previously-killed deer, or (D) killed and ate an opossum.

When the cougar killed a deer during a monitoring session, the "hunting" pattern was evident up to the time of the kill, after which the cougar moved very little for the rest of the night (Figure 13:line B). After some deer kills, there was a travel peak near dawn; in some cases this reflected a quick movement to water and a quick return to the carcass, and in other cases the cougar moved to a daybed site at some distance from the carcass.

Cougars killed medium-sized prey (mostly opossums) on 13% of the sessions. In these sessions, the movement pattern resembled the "hunting" pattern up to the time of the kill, and returned to that pattern after about 6 hours (at which time the prey was fully consumed) (Figure 13: line D). In most cases the medium-sized prey was killed about 3-4 hours after sunset.

Seasonal changes in distance moved per day

We used "net daily distance" moved per day as an index of activity. "Net daily distance" is simply the straight-line distance between 1 animal's locations on 2 consecutive days. We calculated about 2800 such distances, and then averaged them for each cougar in each month, deleting any case based on fewer than 3 distances. To evaluate seasonal changes in cougar activity, we plotted average net daily distances against month (Figure 14).

Males traveled much longer net distances per day (average = 5.7 km) than females (average = 3.2 km). The variation

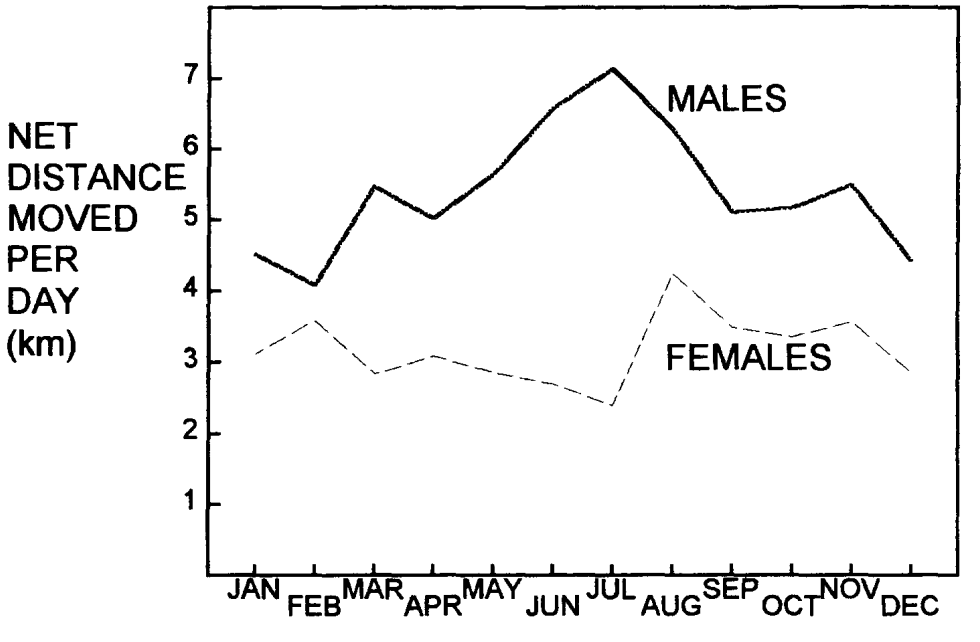

Figure 14. Seasonal pattern in average net distance moved in 24 hours by adult cougars. Males moved much longer distances. Within sex, there was no significant differences among months.

among months was not statistically significant (ANOVA, $P > 0.50$ for both males and females).

Dispersal movements of juveniles

Dispersal is the movement of an animal away from its place of birth to establish a new home range elsewhere. For cougars, the process of dispersal usually begins at 12-24 months of age, and continues for several months, during which the animal searches for suitable habitat that has minimum risk of conflict with other resident adults of the same sex. Adult males are especially intolerant of a young male taking up residence within the adult's range. As a result, juvenile male cougars usually travel into a different mountain range to find an area without an adult male. In Nevada, 75% of the yearling males and 20% of the yearling females moved out of the mountain range in which they were born (Ashman et al. 1983).

Juvenile dispersal in cougars is important in maintaining small populations and for recolonizing habitat where chance local extinction has occurred (Hemker et al. 1984, Beier 1993). Seidensticker et al. (1973) concluded that recruitment into the adult population occurred mainly via immigration of juveniles from adjacent populations, with the population's own offspring emigrating to other areas. Dispersal may also help maintain gene flow among populations (Greenwood 1980). Data on dispersal can be important in maintaining appropriate habitat for dispersal movements and for conserving genetic variation. Despite its importance, dispersal is "amongst the least understood factors of population biology" (Gadgil 1971:253).

In the Santa Ana Mountain range, dispersal is increasingly impeded by urban growth which has created many impenetrable barriers to animal movement. Pitted against these barriers is an innate tendency to disperse, evolved over millions of years. Our study was the first to examine how cougars attempted to disperse in confined and fragmented habitat.

Urban expansion has also created several narrow corridors, and we were most interested in whether dispersing cougars would find and use them. The 3 main corridors of interest were:

1. The Pechanga Corridor (Figure 7) provided the only possible link to the adjacent cougar population in the Palomar Range (Chapter 3).

2. The Coal Canyon Corridor (Figure 8) provided the only cougar travel corridor to the Chino Hills (Chapter 3).

3. The Arroyo Trabuco (Figure 9) was a redundant corridor in the sense that a cougar can travel between the large wildlands north and south of the Arroyo by a longer route to the east. Nonetheless it was of interest because it was a very long (about 6 km, or 3.8 mi.) and narrow (300-600m , or 0.2-0.4 mi.) strip, hemmed in by dense tract homes on either side, but with excellent cougar habitat within the Arroyo (Figure 9).

We followed the dispersal movements of 8 male cougars and 1 female cougar (Table 7). The juveniles were 9-18 months old at the time of capture, and were monitored until death or a stable adult home range was established. We had radio-tagged the mothers of 7 of these 9 animals, and thus we know their predispersal history in some detail. The other 2 animals (both males) were tagged as dispersers; their predispersal home ranges and ages at dispersal were not known. We found:

1. Mean dispersal age for 6 male cougars was 18.3 months (range 13-21); their ages were accurately known because the dam was radiotagged before birth (Table 1). The males captured as dispersers (M5, M6) were about 19 months of age based on weight and tooth wear (Ashman et al 1983:19-27). At

Table 8. Dates of birth and dispersal, and maximum dispersal distances for 1 female and 8 male juvenile cougars (Felis concolor) in southern California.

ID	birth date	capture date	dispersal start date[a]	dispersal end date[a]	N1[b]	N2[c]
F17	Dec 1989[e]	28 Jul 1991	3-10 Sep 1991	died 6-9 Jan 1992	39	5
M3	5 Aug 1989[f]	5 Jun 1990	26-29 Jan 1991	died 15-18 Feb 1991	14	0
M5	Jan 1989[g]	3 Aug 1990	pre 3 Aug 1990	died 18-24 Sep 1991	163	3
M6	Jan 1989[g]	27 Aug 1990	pre 27 Aug 1990	16 Dec 1991	117	2
M7	15 Jul 1989[f]	23 Oct 1990	28 Mar-4 Apr 1991	continues		1
M8	15 May 1989[f]	29 Oct 1990	4-7 Dec 1990	died 1-5 May 1991	73	8
M10	15 May 1989[f]	25 Feb 1991	22 Mar-3Apr 1991	died 15 Sep 1992		8
M11	9 Aug 1989[f]	4 May 1991	16-22 Jan 1992	died 29 Feb 1992	20	1
M12	9 Aug 1989[f]	15 Aug 1991	25-28 Sep 1991	died 24 Mar-10 Apr 1992	37	3

[a] Starting date range is last date within mother's home range until first date off natal range, or (M5, M6) date captured as a disperser. For death date, range is last date known alive until date found dead. For M6, end date = date on which 60% of the animal's stable home range had been visited (Minimum convex polygon).
[b] number of days with locations between start and end (or death) dates.
[c] number of sessions of intensive (overnight) monitoring between start and end (or death) dates.
[e] F17's mother was also radio-tagged 28 Jul 91, so maternal home range is known, but birthdate is estimate.
[f] ± 4 days; mother was radio-tagged before birth of the juvenile.
[g] Estimate (captured as a disperser, mother not radio-tagged)
[h] In addition, travel path out of the mountain range on about 20 Jan 1992 was traced from tracks and scent.

dispersal, the female was probably about 19 months old based on weight (although tooth wear suggested an age of about 13 months). Littermates (2 pairs) did not disperse at the same time. M12 was the youngest disperser at 13 months of age, 4 months before his brother M11. M8 dispersed at 18 months, and his brother M10 was the oldest disperser at 21 months.

2. Dispersal was often initiated by the mother leaving the cub at one edge of her home range while she moved to the opposite edge of her home range for about 2 weeks. In some cases, the mother moved off of her home range temporarily. The cub usually stayed in a very small area where its mother had abandoned it. After about 2 weeks, the cub abruptly and rapidly moved out of its mother's home range, usually in the direction away from its mother. Dispersal began in January (2), March (2), September (2), and December (1); M6 and M5 were captured as dispersers in August after starting dispersing some days or weeks earlier.

3. Dispersal took several weeks to months, during which a succession of temporary home ranges were occupied; following Hornocker (1970), we refer to these as "transient" ranges. The move from 1 transient range to the next was usually very rapid. Some juveniles returned to their natal ranges several weeks after dispersal and stayed 7-20 days before departing again; no juvenile returned more than once. For males, a transient home range was occupied from 2 weeks-8 months, and was much smaller than (1% to 30%) the size of an area an adult male would use in the same time span. Transient home ranges were usually near the urban-wildland interface, and often elongate along that edge.

4. All dispersers explored extensively throughout the Santa Ana Mountain Range. Cubs born and raised at the southern edge of the range (M8, M10) dispersed northward and cubs born at the north edge (M11, M12)

dispersed south, apparent trying to move to a new mountain range.

5. Seven of the 9 dispersers died before establishing a stable home range, usually (4 of 7) as a result of vehicle collisions. In addition to the 4 fatal accidents, dispersers were involved in 2 nonfatal vehicle collisions.

6. Dispersers explored the urban-wildland interface very thoroughly with remarkably little human interaction. All dispersers came within 100 m of urban areas and heavily used parklands for periods of time ranging from several hours to several weeks (following sections, and Chapter 9). Dispersers often crossed and used terrain avoided by adult cougars (e.g., M12's exploration of the grasslands west of San Juan landfill, M11's exploration of the San Luis Rey River, M5's exploration of Temecula Creek, F17's foray to the Anaheim Hills). Such exploration of marginal and edge habitat is very important because it is how juveniles find and use corridors (next point) and how they learn to avoid these areas by adulthood. None of the 9 dispersers behaved aggressively toward humans, although some livestock were taken in rural areas and 3 dispersers entered urban areas, apparently by mistake. We received only 5 reports (involving 3 cats: M3, M5, M11) of a disperser being seen by humans; no case involved cougar aggression.

7. Dispersers found and used movement corridors. Three of the 9 dispersers found and tried to use the Coal Canyon Corridor (2 succeeded and 1 was hit by a vehicle); 1 of them (M6) used the Coal Canyon Corridor (Chapter 3) at least 22 times. In addition an uncollared juvenile cougar also found and used the Coal Canyon Corridor. Three dispersers also found the Pechanga Corridor, 2 of them used it, 1 successfully (M12) and 1 unsuccessfully (M5). In addition, there were 5 vehicle mortalities in this corridor during October 1990-December 1992. At least 2, and probably 3 of the dispersers found, used, and explored the Arroyo Trabuco (M8, M10, and probably M12). Three dispersers each used 2 of the 3 corridors. Only 3 of the 9 dispersers *failed* to find and use at least 1 of the 3 corridors.

The last finding has very important implications for land-use planning, because it clearly demonstrates that efforts to retain and enhance existing linkages will not be in vain. In the following sections, we briefly summarize the dispersal history of all 9 dispersers. We are preparing a manuscript on cougar dispersal for publication in a scientific journal.

Dispersal of M8

After F12 and M8 had spent several days together in the northern part of her home range, F12 abandoned M8 on November 27 1990, moving to the southern edge of her home range. M8 stayed in a small area for several days, then moved off to the north sometime during December 4-7. On December 8 we documented M8's first independent kill of a mule deer (a male fawn). He fed on it for 3 nights. During December 17 1990-January 4 1991, M8 stayed mostly in the small (0.3 km^2) estuary of San Mateo Creek between the Pacific Ocean and I-5, known locally as Trestles Beach (Figure 15: Tr and HR1). M8 stayed in the estuary's thick willow forest and marsh, and there were no reported sightings from the many surfers and beachgoers during his stay.

We believe that no other radio-tagged cougar used Trestles Beach during our study, although the habitat just east of I-5 was regularly used by several cougars. M8 made only short local movements during intensive monitoring December 17-18. On December 23 we documented that he had killed and eaten at least 2 opossum and 2 raccoons in the area. M8 made 2 brief excursions (December 27 and December 31) east of I-5 during his stay at Trestles, crossing I-5 under the San Mateo Creek bridge and moving up to 3 km inland. On his second excursion M8 daybedded near adult male M2 and presumably the 2 cougars encountered each other. M8 returned to Trestles Beach the next day and M2 remained in the vicinity during January 1-5. On about January 4, M8 left Trestles Beach and returned to the center of his mother's home range.

Meanwhile his mother had been killed on I-5 on December 20 1990. On January 15 1991, M8 left his natal area for good, soon moving further north than before. He killed 2 mule deer in Gabino Canyon during January 17-19, consuming only 1 of the carcasses before moving north again.

On January 20-21, we observed M8's movements over terrain that he was exploring for the first time. One hour after sunset on

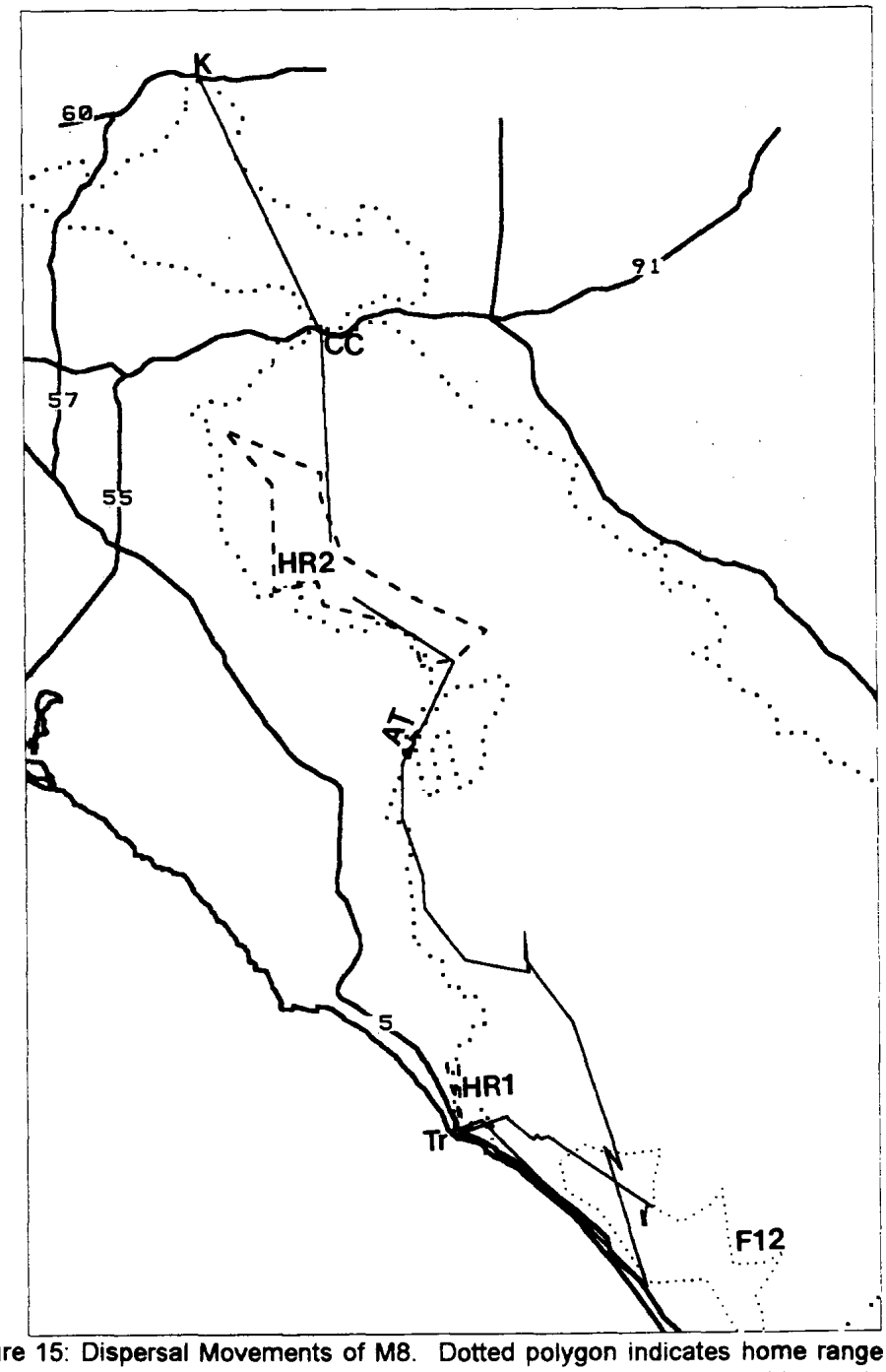

Figure 15: Dispersal Movements of M8. Dotted polygon indicates home range of his mother (**F12**). Heavy dotted line indicates limits of cougar habitat. His initial dispersal movements brought him to a small transient home range (**HR1**) in and near Trestles Beach (**Tr**). After a brief visit back to his natal range, he moved rapidly north, intensively exploring the Arroyo Trabuco Corridor (**AT**) and then using a new transient home range (**HR2**) along Loma Ridge during Feb-Mar 1991. In April he moved into the Chino Hills via the Coal Canyon Corridor (**CC**) and about April 30 was killed (**K**) on SR-60.

January 20, M8 left his daybed in Trampas Canyon and slowly explored or hunted in the upper basin of that canyon for 1½ hours. At 2000, he reached the basin's south rim, and quickly moved west along the rim, then north along the west rim for 800 m before turning west and heading down an unnamed canyon toward the San Juan Capistrano Landfill in Prima Deshecha Canyon. About halfway down, the canyon opened out into a broad grassy slope with no woody vegetation. At this point M8 moved north, quickly crossing 2 small, west-flowing, sparsely-shrubbed drainages; from the intervening ridges he doubtless saw the lights of San Juan Capistrano spread out to his west. The 3rd west-flowing canyon was much larger and contained good woody cover; he stopped there for about 40 minutes. At 2300 he resumed his rapid walk, heading down this wooded canyon all the way to La Pata Avenue. He reached La Pata Avenue (the paved access road for the landfill, which receives no night-time traffic) about 700 m south of the Ortega Highway, walked quickly north 350m along La Pata, turned NE through the nursery at the SE corner of La Pata and Ortega Highway, and crossed the Ortega into San Juan Creek just after midnight. M8 stayed in San Juan Creek for 4 hours, moving very little. At 0415 he walked up San Juan Creek about 400 m, returned downstream to the mouth of Cañada Chiquita and then quickly moved north on the west slope of Cañada Chiquita, staying east of the ridgeline. At 0545 he stopped and daybedded in a wooded canyon west of the Sea Tree nursery, northwest of the Santa Margarita sewage plant.

Although at least 6 radio-tagged cougars used Trampas Canyon, only dispersing animals (M8, M12) used the canyons west of Trampas Canyon. Their rapid pace suggested that they were not comfortable in the area's open grassland.

On the following night (January 21-22), M8 moved another 8 km, discovering and entering the Arroyo Trabuco corridor. He daybedded near the San Francisco Solano site, between the cities of Mission Viejo and Rancho Santa Margarita. During overnight monitoring on the nights of January 22-23 and January 23-24, he spent both nights in local movements (within about 800 m of the San Francisco Solano site), suggesting that he was hunting in the area and exploring small side canyons. Each morning at dawn the ridgetops came alive with earth movers and M8 daybedded near the Arroyo bottom.

On the night of Sunday January 26-27 we monitored the movements of M8. F2 had entered the Arroyo from the south the previous night and was daybedded < 1 km south of M8. We hoped to learn how F2 would react to a juvenile male in her home range. Trespassers traveling by foot, pickup truck, and dirt bike passed near both cats until dusk. Shortly after sunset, both cats started moving slowly towards each other, passing with 250 m (width of the Arroyo bottom at that point) without pause. We presume the cats were aware of each other, but we were not close enough to hear vocalizations. After this non-encounter, F2 continued north and M8 continued south at about 1km/hour. At 2000, a low-flying helicopter shone a spotlight at the radio-tracker (50m from the cougar) and M8 stopped moving for about 30 minutes. At 2130, M8 passed through the Oso Bridge construction site, an area of bare compacted ground with bulldozers, huge steel I-beams and construction debris on the ground, huge steel scaffolds, and a half-complete road bed above. A trespassing vehicle that had earlier broken its radiator was parked under the bridge, and a steamy windshield suggested that its driver was spending the night there.

M8 continued south to the mouth of Corridor Canyon (the large brushy canyon at the south edge of the site of the proposed Las Flores Planned Community). He promptly turned east into Corridor Canyon and walked

halfway up the canyon; his unhesitating move into this canyon suggests that he probably used this route when he first entered the Arroyo on the night of January 21-22. After stopping for less than an hour halfway up the canyon, at 2330 he backtracked to and up the Arroyo. He stopped just north of the Oso Bridge site and spent 5 hours exploring 3 small grassy canyons on the Mission Viejo side of the Arroyo. On several occasions he reached the ridgetop, from which he could see the lights of Mission Viejo < 1 km to the west, but he apparently never walked west of the ridgeline. Two of the 3 side canyons he explored had no woody vegetation, and only about 3 inches of new green herbaceous growth. He spent 2 full hours in the smallest of the 3 canyons, in which a dozen Russian thistles were the largest plants. We presume he was hunting for gophers, voles, and ground squirrels there; a few badger holes were also present. At 0500, M8 returned to the Arroyo and moved north, bedding near his starting location.

On the night of January 28-29, M8 left the Arroyo and resumed his northward travel. He was in Joplin Canyon on January 29, just NE of Cooks' Corner on January 31-February 1, across Santiago Canyon Road in Round Canyon on February 3, and in the Villa Park impoundment (willow forest) on February 8. He had traveled 56 km (35 mi) north of the north edge of his mother's home range.

During February 9-April 10 1991, M8 used an elongate home range pressed against the western edge of cougar habitat, mostly along Loma Ridge and its associated canyons, with occasional forays into Santiago Canyon above Modjeska (Figure 15: HR2). During April 8-10, he moved abruptly north, crossing the Riverside Freeway into the Chino Hills. We were unable to locate him with intense aerial telemetry searches south of the Freeway on April 12, April 15, April 26, and April 30, but on May 3 1991, a motorist stalled in traffic found M8's carcass on the north edge of the Chino Hills, in weeds along State Route 60 between Phillips Ranch Road and Diamond Bar Boulevard in Pomona (Figure 15). He had been struck by a westbound vehicle 3-5 days earlier as he tried to cross to the north side of the freeway. He had no doubt spent his last 3 weeks in the Chino Hills. Lack of tracks in any culvert under SR-91 indicates that he reached the Chino Hills via the Coal Canyon vehicle underpass.

In all his dispersal movements, M8 consistently moved north, hugging the western edge of cougar habitat and occasionally attempting to explore further west, only to find that there was no habitat to the west. This pattern was evident in his use of Trestles Beach, his travel through the grasslands west of Trampas Canyon, his exploration of the west ridge of the Arroyo Trabuco, his temporary home range along Loma Ridge, and his eventual death on SR-60.

Dispersal of M10

M10 (sibling of M8) began dispersal during March 22-April 4 1991, 3 months after his mother's death. He first moved about 16 km (10 mi) north of his mother's home range and stayed near a sheep grazing operation in San Mateo Creek during April 4-16, eating several sheep (Figure 16: HR1), then moved 51 km (32 mi., straight-line distance) north in 16-20 days, reaching upper Coal Canyon by May 6. His northward path was east of that taken by his brother.

On the night on May 6-7, we followed M10's movements down Coal Canyon. He started moving well before sunset and moved 3 km down the canyon at a brisk pace, following the main ridge between Gypsum and Coal Canyon. He approached the Riverside Freeway at 2100, stopping at the debris catchment before the main wash enters the culvert under the Freeway. From the catch basin, M10 had a

clear view of the Freeway and the twin box culverts but not of the vehicle underpass < 100m to his east. After pausing there for 10 minutes, M10 moved west 200 m to a small hill overlooking the freeway.

After 30 minutes, M10 moved west a short distance crossing one tiny canyon and stopping in the second small, parallel dry wash flowing toward the freeway. He spent the rest of the night at the lip where the wash dropped over a cut bank, from where he could see the freeway (200m away) and the darkness of the Chino Hills beyond the freeway. By dawn he could see that the dark area was suitable habitat. Just after the next sunset, at 2100 on May 7 1991, M10 was struck by an eastbound vehicle on the Riverside Freeway, breaking his left femur. He was photographed sitting in the median strip, but soon ran back into the tiny canyon from which he had come.

After a rapid recovery (Chapter 4: highway injuries) in a small post-accident home range (Figure 16: HR2), in mid-June M10 moved south, encountering and traveling the Arroyo Trabuco corridor from north to south, and continuing through Cañada Chiquita and Christianitos Canyon to Horno Creek (Camp Pendleton) at the north edge of his natal home range. He thus moved at

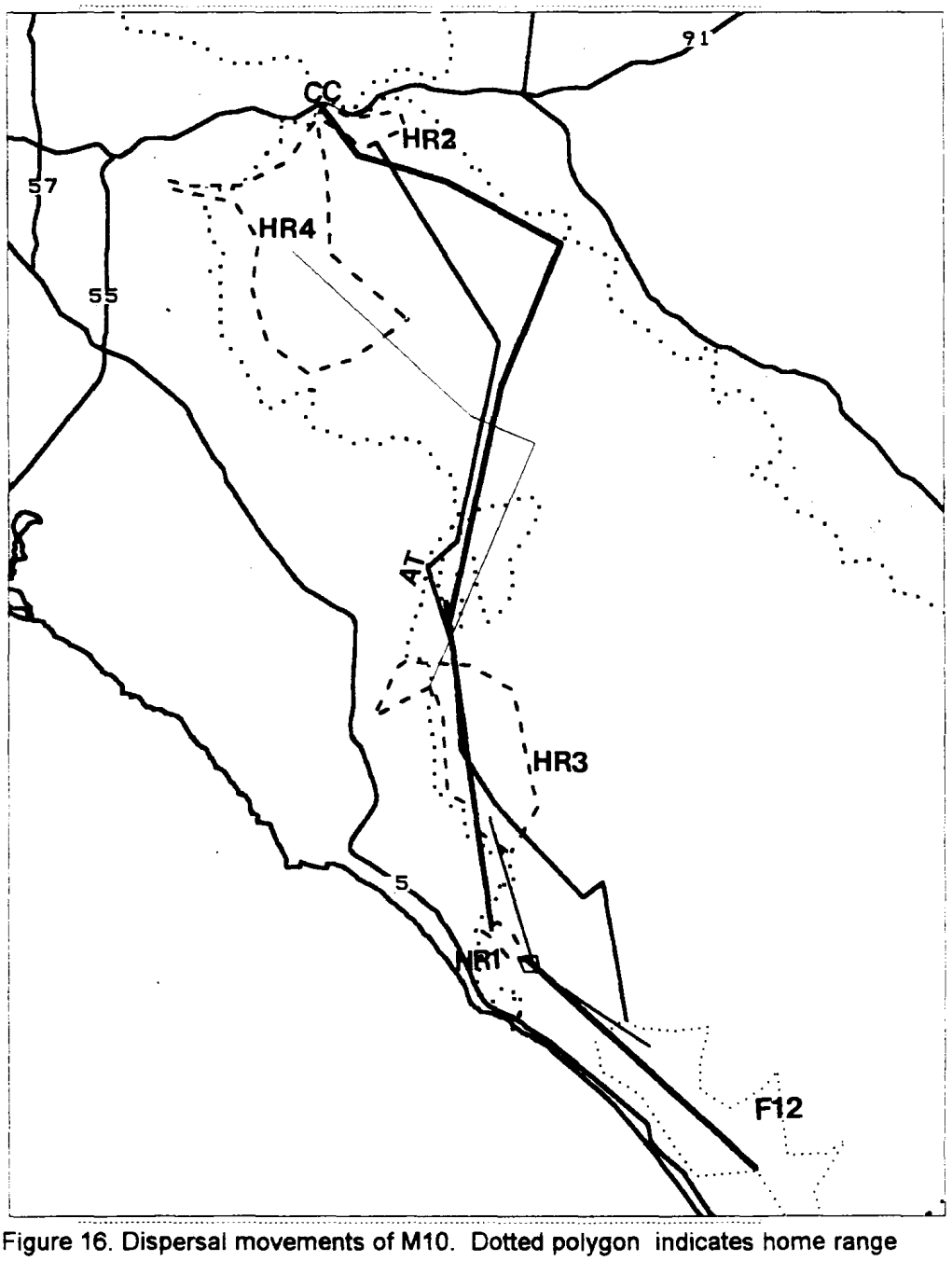

Figure 16. Dispersal movements of M10. Dotted polygon indicates home range of his mother (**F12**). Dashed polygons indicate his transient home ranges; heavy dotted line indicates limits of cougar habitat. The sequence of M10's travels are indicated by progressively thinner lines. After a brief stay in **HR1** (April 4-16 1991), M10 rapidly moved north to Coal Canyon, where he was struck on SR-91 (**CC**) on May 7. After a brief stay in a small post-accident home range (**HR2**), and despite a broken femur, M10 rapidly moved south, using the Arroyo Trabuco Corridor (**AT**) and returning to his natal home range (**F12**). 10 days later he moved north to **HR3**, which he used for 5½ months before moving to **HR4**, which he occupied for 8 months until he died in a second accident.

least 64 km (40 mi) in 14-19 days. He spent 10 days in his natal home range, and then established a transient home range (Figure 16: HR3) that included the area from upper Christianitos Canyon to Cañada Chiquita. After 5½ months in this area, he abandoned it in late January 1992, traveling north for 10 days and establishing another transient home range (Figure 16: HR4) along Loma Ridge and lower Santiago Creek. He remained in that home range until his death in a second vehicle accident on Santiago Canyon Road in September 1992.

Dispersal of M3

In fall 1990 M3 and his brother M4 spent increasingly long periods of time apart from their mother (F2), but they always traveled together within her home range. The longest such period away from their mother lasted for 10 days in early October 1990. Sometime during June-September 1990, M3 received a severe injury to his palate (Chapter 4). M4 died in early November 1990 and was fed upon (and possibly killed by) M3 and F2 (Chapter 4).

M3's dispersal was atypical in that he seemed reluctant to move off his mother's home range, making 2 brief excursions to the east before finally dispersing to the west. During November 26-29, M3 and F2 consumed a deer in the central part of their home range, but 2 days later F2 moved to the western edge of her home range where she spent 2 days near adult male M2 in the Arroyo Trabuco at the west edge of her range, an area she had not visited for over a year. M3 remained where F2 had left him in Bell Canyon.

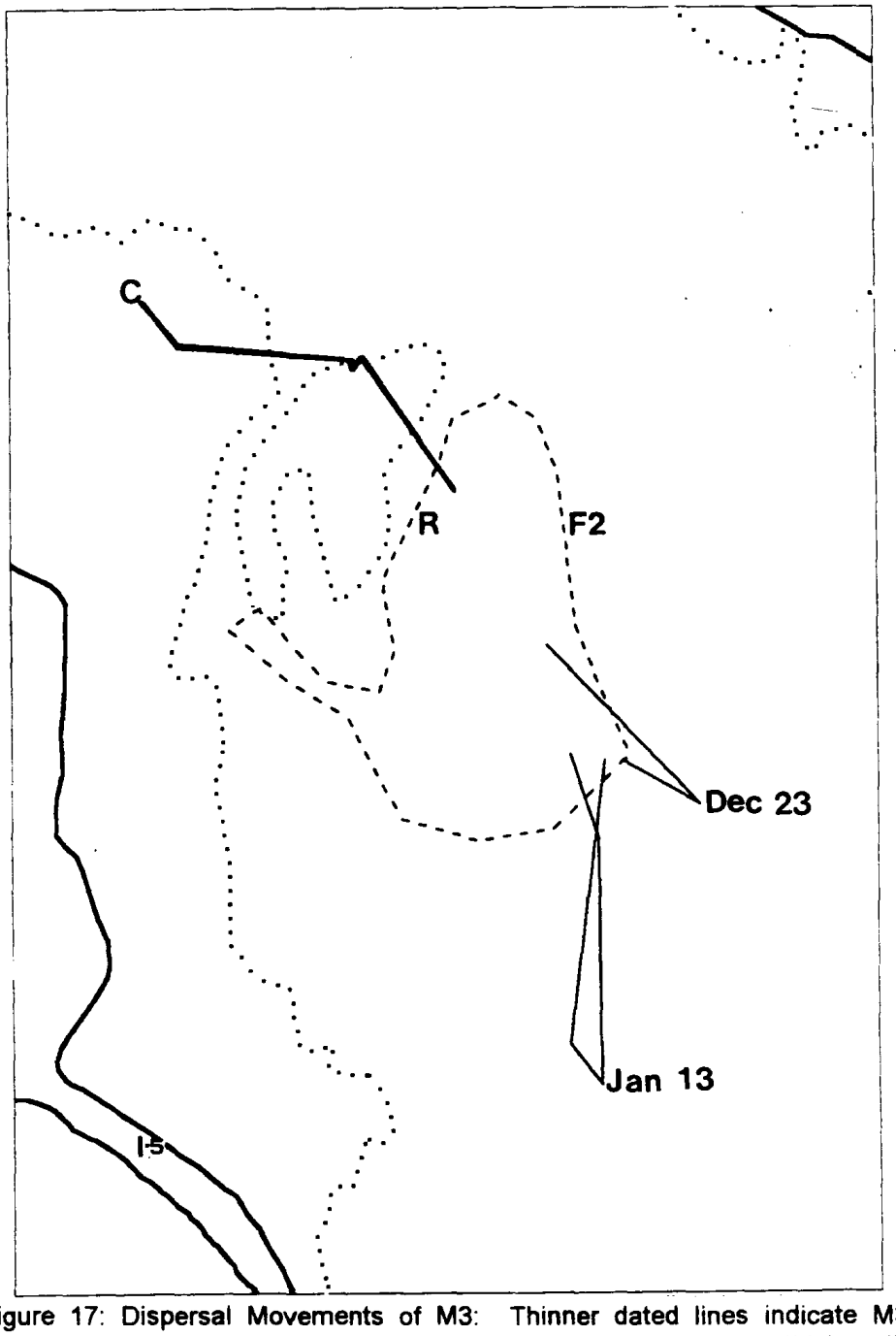

Figure 17: Dispersal Movements of M3: Thinner dated lines indicate M3's predispersal explorations outside his mother's home range; thicker line segments show his short dispersal into Irvine. He was captured in a residential area on 8 Feb 1991(C) and was released at R, where he died 1 week later. The dashed polygon indicates the home range of his mother (F2).

On December 4, F2 returned to her son's location for 1 day and then moved 2.4 km off the southwest edge of her normal home range. There she killed a deer (December 10) and fed on it for 3 days. She then moved back to Arroyo Trabuco. Meanwhile M3 slowly moved eastward within and then beyond her home range (Figure 17: Dec 23). Up to this point, the dispersal pattern and timing was typical except that F2 had abandoned M3 near the center, instead of the edge, of her home range.

However after less than a week away from home, M3 returned to the eastern part of his mother's home range on December 28-29. F2, after a month in the southwest parts of her home range, moved east and encountered M3 in her home range on January 7. M3 immediately moved east again, a bit farther this time (Figure 17: Jan 14). However, by January 16 he again returned to the eastern and northern portions of F2's range. F2 remained far to the west and did not encounter her son.

On January 30 1991, M3 moved off again, this time to the northwest (Figure 17). He moved into the north end of the Arroyo Trabuco where he killed and ate a coyote. During February 4-7, M3 continued dispersing northwest, moving along the wildland-urban edge and through areas interspersed with orchards. As he moved from the Oso Lake area into Serrano Creek, a motorist saw him run north across El Toro Road at the sign marking the future crossing of the Foothill Transportation Corridor (6:00 AM, February 5). On February 8 he had moved into avocado orchards further northwest, and was located about 1 km west of Siphon Reservoir, just east of the intersection of Jeffrey Road and Irvine Boulevard. Early on the night of February 8, M3 moved 1 km west, penetrating 2 blocks into a residential area adjacent to the orchards. There he was treed by a German shepherd dog in a yard at 50 Hunter St. in Irvine shortly after dark. At 2100, Animal Control officers tranquilized M3 and released him back into his mother's home range. He remained near the release site and died there 1 week later (Chapter 4: Disease).

Dispersal of M7

M7 left the home range of his mother (F10) in April 1-4 1991, moving slowly northeast while F10 moved to the southern part of her home range. He initially moved northeast from his mother's range to the Mesa de Burro area. This area immediately became the nucleus of a transient home range (Figure 18: HR1).

After 4 weeks he began to enlarge his transient home range. In May he expanded to include the peaks and canyons west of Lake Elsinore (16 km north), and in July to include the upper Santa Margarita River area several km south. On several occasions, M7 was very close to the I-15 bridge and he doubtless encountered this entrance to the Pechanga Corridor. However, we have no evidence that he ever crossed I-15. In mid-September 1991, M7 made a 65-km excursion to the northern edge of the range, reaching Hagador and Main Street Canyons near Corona, and quickly returned to his transient range (Figure 18: thinner line segments).

In late January 1992, after almost 10 months in this transient range, M7 abandoned it for a new home range (Figure 18: HR2). The south edge of his new home range abutted the north edge of his old range, and he had passed through much of this new range in his September foray. As with most transient ranges, both M7's ranges were elongate and had 1 long edge along the wildland edge (Figure 18). In his movements within each home range, M7 often stayed in 1 canyon for 3-8 days and then moved to another canyon. This was very different from the pattern of adults M2, M9, and M6, who rarely stayed in 1 locality for more than 3 days. As of January 1993, M7

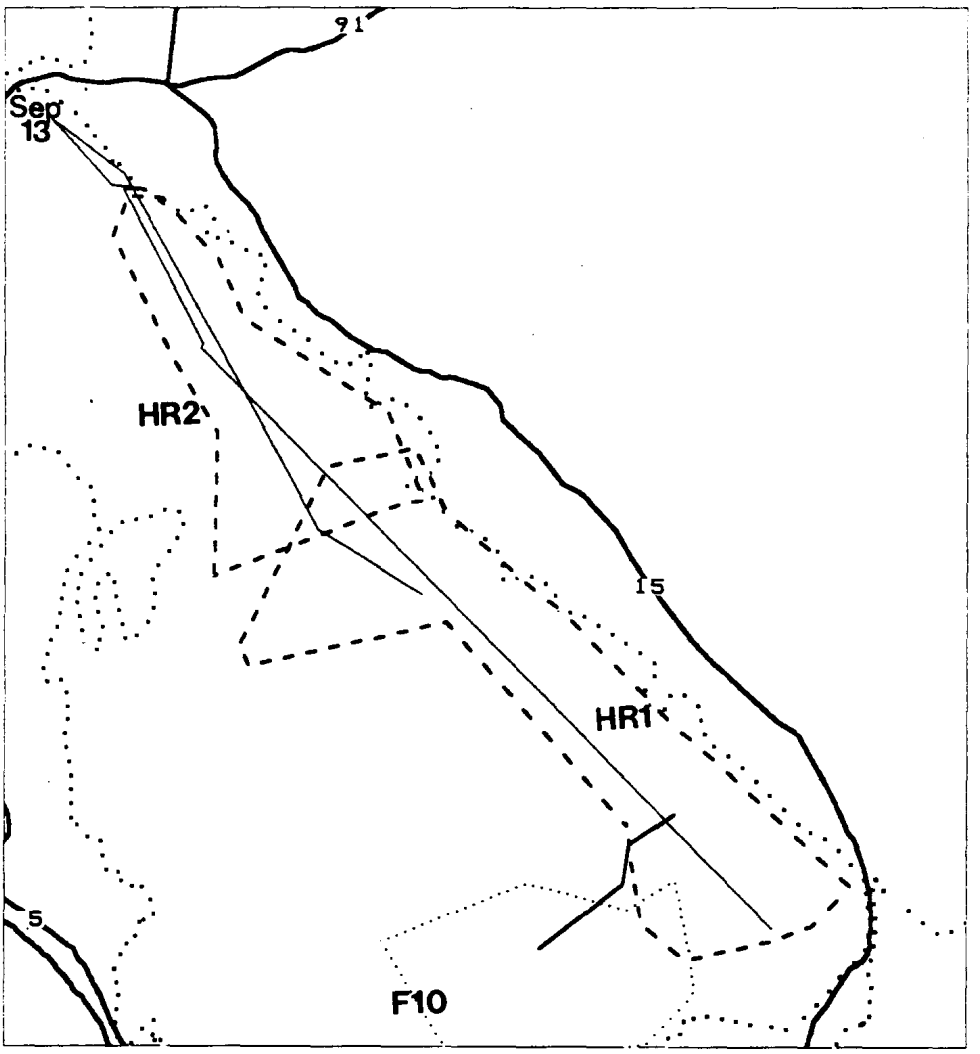

Figure 18: Dispersal Movements of M7. M7 moved a short distance (heavy line) from his mother's home range (**F10**) to a transient home range (**HR1**) which he occupied for 10 months. Thinner line segments indicate a long excursion from HR1 during September 1991. In January 1992 he abandoned HR1 for a second home range (**HR2**) that will probably become the nucleus of his adult home range if he survives. Heavy dotted line indicates limits of cougar habitat.

still occupied this second home range. This area was not overlapped by M6, M2, or M9, and if he lives we suspect it will form the nucleus of his adult home range. However, his movement patterns, and the relatively small size of this home range, suggest that it was not yet a true adult territory.

Dispersal of M12

M12, his brother M11, and their mother F6 had spent 2 weeks traveling together, when F6 and M11 abandoned M12 in a small brushy canyon on September 3 1991. M12 stayed in and near this canyon for 17 days, while his family ranged widely without him, mostly to his north. Tracks indicate that he used nearby dirt roads regularly. Finally, during September 20-22, he started dispersal movements to the south (Figure 19: thickest line segments).

During overnight monitoring on October 1-2 1991, M12 was moving steadily south through previously unvisited terrain when he encountered the noisy and well-lit California Silica Products factory and its adjacent open quarries. His first several attempts to pass by led to parts of the quarry or factory, and it took him 2 hours to select a route that skirted the east edge of the facility. Once past the plant, he rested on a ridge top for 2 hours and then moved west toward Trampas Lake but turned back before reaching the lake. Although M10 was also at the lake, the 2 cats did not meet each other; M12 may have detected M10's scent. M12 returned to his previous resting place, spent another hour there, and then continued southward, crossing into the Christianitos Creek watershed, and walking another 2 km south along the ridge just west of Christianitos Road.

On this initial move south, M12 travelled over 40 km (25 mi), reaching

Margarita Peak on October 17. He then moved rapidly back north and established a transient home range immediately south of this mother's home range (Figure 19: HR1). He spent almost 3 months in this transient range, killing at least 5 domestic goats in at least 3 incidents. In December 1991, he took a second exploration to the south.

This excursion (Figure 19: medium-width line segments) began during December 6-13, when M12 moved to La Paz Canyon, quickly finding the only domestic goats in south Orange County. He killed several goats in a single night before moving west to Trampas Lake. At the start of overnight monitoring on December 23-24, M12 and M13 were both at Trampas Lake (the 2 animals apparently did not encounter each other). About 2 hours after sunset, M12 started moving rapidly west. At 2000 he entered the San Juan landfill in Cañada Prima Deshecha, and spent about 2½ hours exploring heavily-grazed grasslands near the dump. This was the only time we documented a cougar exploring Prima Deshecha and the landfill area. But an even more unusual exploration followed. M12 skirted north of the landfill and moved further west, exploring the big grassy ridge that separates the cities of San Juan Capistrano and Capistrano Beach. M12 walked over 6 km through this 2-km-wide peninsula of marginal habitat fringed by homes. This area is so open and treeless, and so fringed by urban uses, that we had never obtained gate keys to these parcels; our limited access made it impossible to determine his exact travel path. At 0400, he reached an oak grove alongside I-5 between the exits for Camino Las Ramblas and San Juan Creek Road, and he daybedded there on December 24 (Figure 19: W). Tens of thousands of motorists passed within 200m of the cougar on the clogged freeway that Christmas Eve. There were no reported cougar

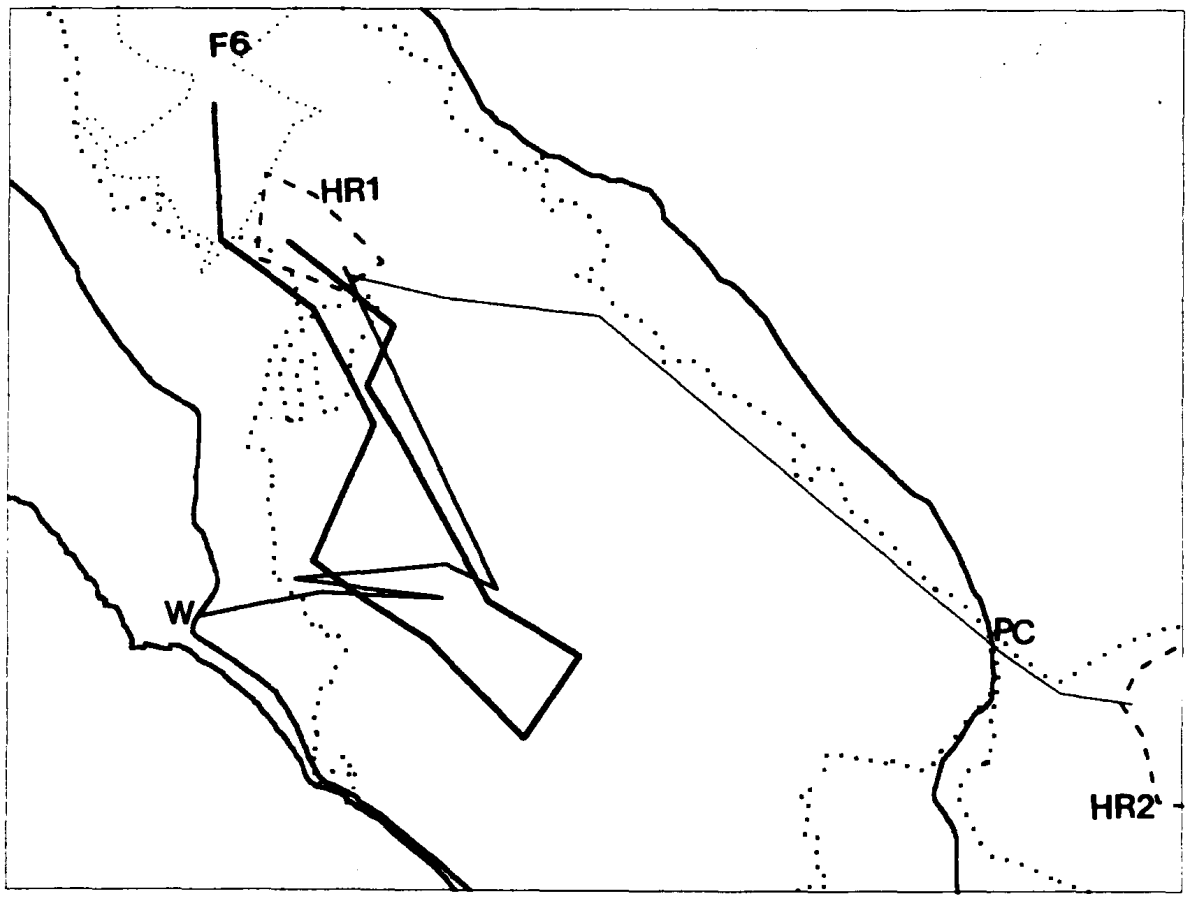

Figure 19: Dispersal Movements of M12. Dashed polygons indicate his transient home ranges; heavy dotted line indicates limits of cougar habitat. The sequence of M12's travels are indicated by progressively thinner lines. His first transient home range (**HR1**) abutted that of his mother (**F6**). On the foray to the west (**W**) (Dec 23-24 1991), M12 moved from Trampas Canyon through open terrain to within 100m of I-5 in San Juan Capistrano; he returned to **HR1** within 48 hours. M12 took less than 8 days to travel from HR1 to **HR2** in the Palomar Range, using the Pechanga Corridor (**PC**) to cross I-15 (see Figure 7 for detail).

sightings. Within 48 hours M12 returned 29 km (18 mi) back to his transient home range. Although this foray did not lead anywhere, it attests to the remarkable ability of dispersing cougars to explore habitat peninsulas and corridors without detection by humans.

On January 13 1992, M12 left his transient home range for the last time (Figure 19: thin line segments). Eight days and 59 km (37 mi) later, he became the first cougar in our study to move into or out of the Santa Ana Mountain Range, crossing I-15 via the Pechanga Corridor into the Palomar Range. We first located him east of I-15 on January 22; he was then in upper Pechanga Creek on the Pechanga Indian Reservation. On the morning of January 23 his tracks leading up to I-15 were fresh enough to be tracked visually and scent-trailed by hounds. M12's eastbound tracks left the Santa Margarita River about 400 m before the I-15 bridge. Although he could not have directly viewed the lights of Temecula from the river channel at that point, he could see the glow of city lights in the sky, and perhaps he gained elevation to better see what lay ahead. He climbed until he reached a dirt road about 50 vertical m above and parallel to the river, and he continued to walk east. As he got closer to the freeway, he left the road and moved southeast and then south, until he was roughly parallel to the freeway. His path took him away from the city lights. Perhaps using darkness as a cue to judge where appropriate habitat might be, he moved away from the bridge that offered the only good crossing under the freeway. Cliffs to his right gradually pinched him closer to the freeway, and where the cliffs met the road, he turned and crossed I-15 at grade about 800 m south of the bridge. On the east side he walked down the embankment 50 m to a paved golf course service road. At this point we lost his scent, suggesting that he traveled south along this road for at least 300m. There were no tracks in the dusty road and sandy stream bed to the north of the crossing point, in Pechanga Creek at several points along the golf course, nor in Pechanga Creek 400 m upstream from the uppermost housing tract. Thus he must have traveled southeast across a series of low wooded ridges for 2-4 km before dropping further east into upper Pechanga Creek where he spent the next few days.

M12 then established a large transient home range north and east of Mount Palomar from January 20 until he died there in late March 1992, apparently of natural causes (Chapter 4).

Dispersal of M11

M11 began to disperse in early January 1992. His pattern of separation was similar to M12's: He and his mother had spent several days together within F6's home range. Then F6 moved about 16 km away toward the northern part of her range (Gypsum Canyon) and left M11 in Round Canyon on Loma Ridge. M11 stayed there, moving little, for about 7 days, and then suddenly began moving south (Figure 20: thick line segments). Within 5 days he had moved 40 km (25 mi). Like many dispersers, he spent several days along Trampas Ridge near San Juan Capistrano.

From the Trampas Lake area, M11 continued south into Camp Pendleton, where he was struck by a vehicle on Basilone Road on the evening of February 4 1992. His injuries apparently were minimal, as he spent only about 48 hours within 1 km of the accident site, and then resumed his exploration of Camp Pendleton (Figure 20: dashed polygon). His period of post-accident recovery was far shorter than that of other accident victims (Chapter 4).

In late February, apparently fully recovered, M11 continued southeast and became the first radio-tagged cougar to move across the open grassland at the south edge of Camp Pendleton to reach the San Luis Rey River (Figure 20: thin line segments). This remarkable movement again illustrates the ability of cougars to move across marginal habitat in their dispersal explorations. However, the San Luis Rey River is too impacted by urbanization to function as a corridor. M11 moved down the River, crossing under I-5 into the City of Oceanside. At 0230 on February 29, M11 was sighted near the River in central Oceanside, about 3 blocks from the Pacific Ocean. At 0600, after about 3½ hours of pursuit through 8-12 residential blocks south of the river, M11 was shot at least 9 times by police officers near the intersection of 6th and Pacific Streets. Although we do not have data showing exactly how M11 reached the San Luis Rey River from Camp Pendleton, the most probable

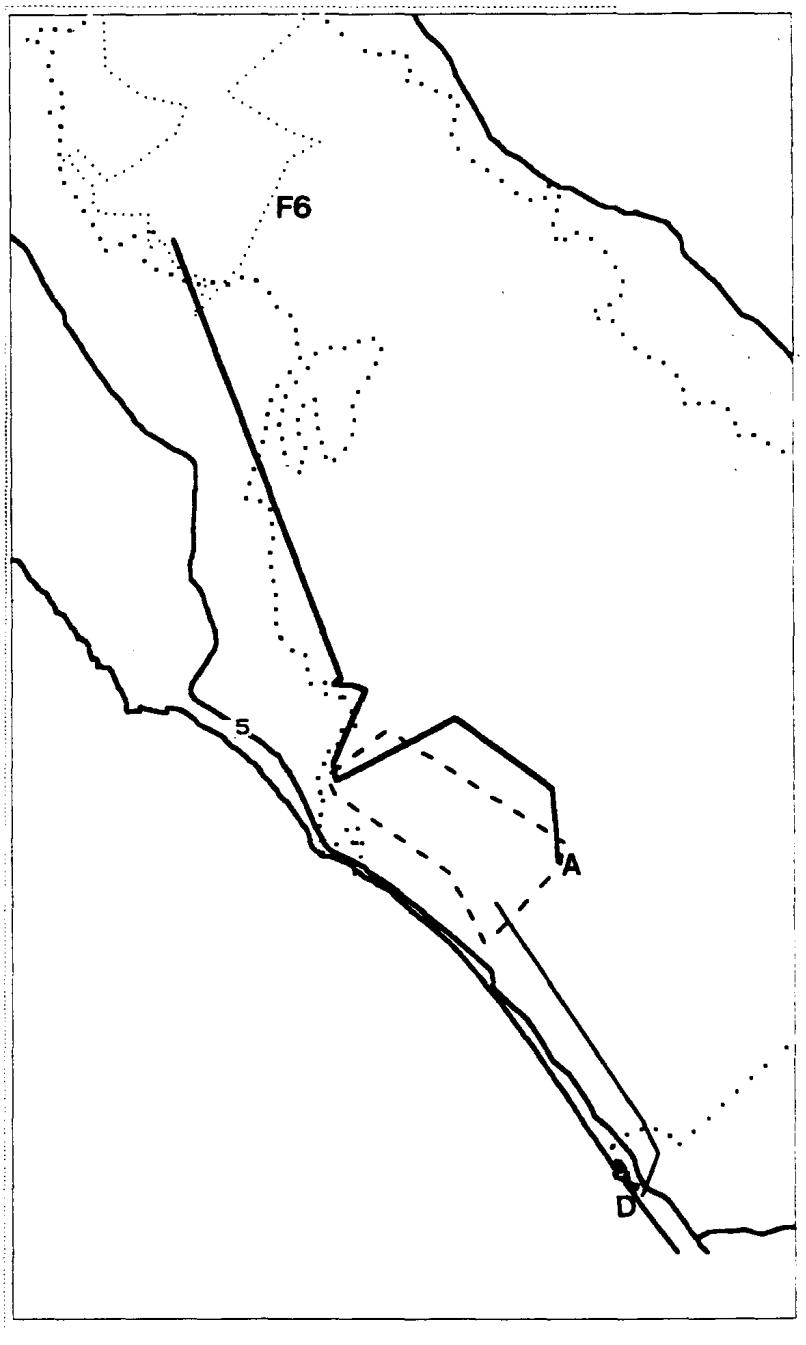

Figure 20: Dispersal Movements of M11. Dotted polygon indicates home range of his mother (**F6**). The thick line segments indicate his movements from Jan 16 1992 until his automobile accident (**A**) on Feb 4. The dashed polygon indicates his post-accident home range (3 weeks). The thin line segments indicate his travels into the San Luis Rey River. He died in Oceanside (**D**) on Feb 26 1992. Heavy dotted line indicates limits of cougar habitat.

routes were Tuley Canyon or Pilgrim Creek.

Dispersal of F17

During August 22-25 1991, F17's mother (F18) moved 16 km northeast of her home range, abandoning F17 in San Mateo Canyon in the center of their home range. After waiting there alone for 2 weeks, F17 started dispersing northwest about September 3. F18 returned during September 3-10.

For the next 123 days, F17 ranged widely over the northern 2 thirds of the mountain range, staying north and west of her mother's home range (Figure 21). During that time she never occupied a transient home range. She traveled a minimum distance of 342 km (214 miles), ricocheting off the east, west, and northern edges of suitable habitat several times (Figure 21).

During September 25-27, F17 spent 3 days in the area where Main Street Canyon leaves the steep mountainous terrain and opens into the alluvial plain, now bearing avocado orchards, on the outskirts of Corona. Curiously, M7 (on a foray from his first transient home range) also spent 2-3 days in the same location on September 17-18 (10 days earlier). During overnight monitoring there September 26, F17 walked near 2 rural houses to enter an abandoned avocado orchard where she killed and ate 2 opossums.

On the night of October 21, F17 moved into a finger of natural vegetation at the extreme northwest corner of the remaining

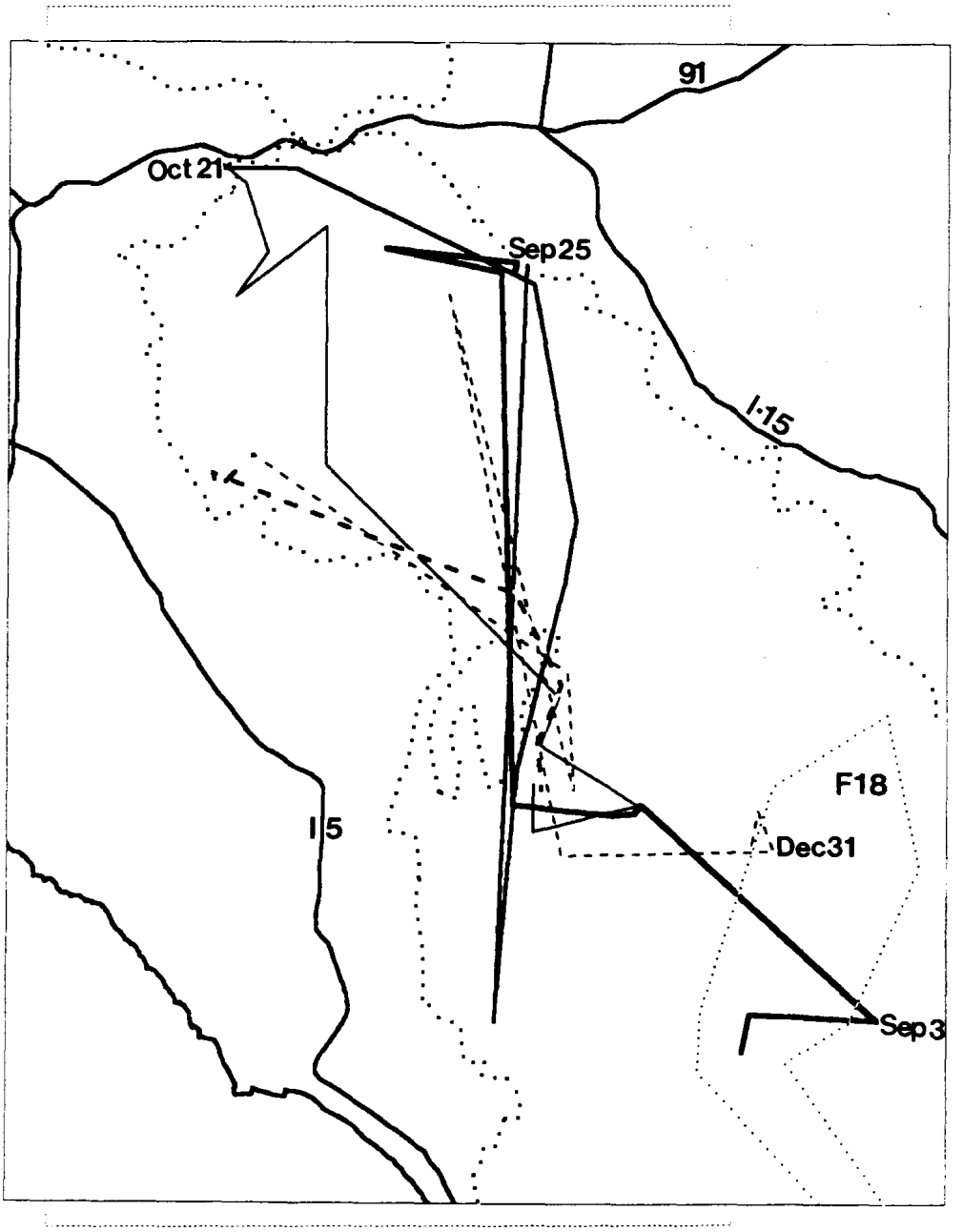

Figure 21: Dispersal Movements of F17. Dotted polygon indicates home range of her mother (**F18**). Heavy dotted line indicates limits of cougar habitat. The sequence of F17's travels are indicated by progressively thinner solid lines, then by progressively thinner dashed lines.

habitat, surrounded by the encroaching urban growth of the Anaheim Hills. She daybedded in the small canyon that contained a small horse stables and The Garden Church, sandwiched south of these facilities and north of a huge area where graders were ripping the terrain for new housing tracts. The Riverside Freeway was 400 m north at the mouth of the canyon. On the ridge to her west carpenters were framing houses on Star View Street. F17 had been exploring the urban edge that night, and had to wait until dark to extricate herself. Dozens of people and machines surrounded her all day long. This is yet another example of the remarkable ability of cougars to explore marginal habitat, habitat peninsulas, and habitat corridors without being detected by humans.

On about December 31 1991, F17 returned to her mother's home range for the first time since her dispersal began. On that date F17 and F18 were located together at the north edge of F18's home range. By January 6 1992, F18 had moved south into the interior of her home range, but F17 was still near her December 31 location. She died there during January 6-9 1992, apparently of natural causes (Chapter 4).

Dispersal of M5

M5 was captured and radio-tagged on August 3 1990 after he was treed by domestic dogs in a Temecula back yard. The capture site was near the tip of the "Temecula cul-de-sac" of the Pechanga Corridor (Figure 7: M5; Figure 22: C). M5 was a dispersing yearling and his presence there was our first evidence that dispersers were attempting to use that corridor. His tracks confirmed that he had moved up Temecula Creek from its confluence with Pechanga Creek, but we could not determine if he had reached that confluence from the west (Santa Ana Mountain Range) or the east (Palomar Range).

M5 was released 22 km (14 miles) west

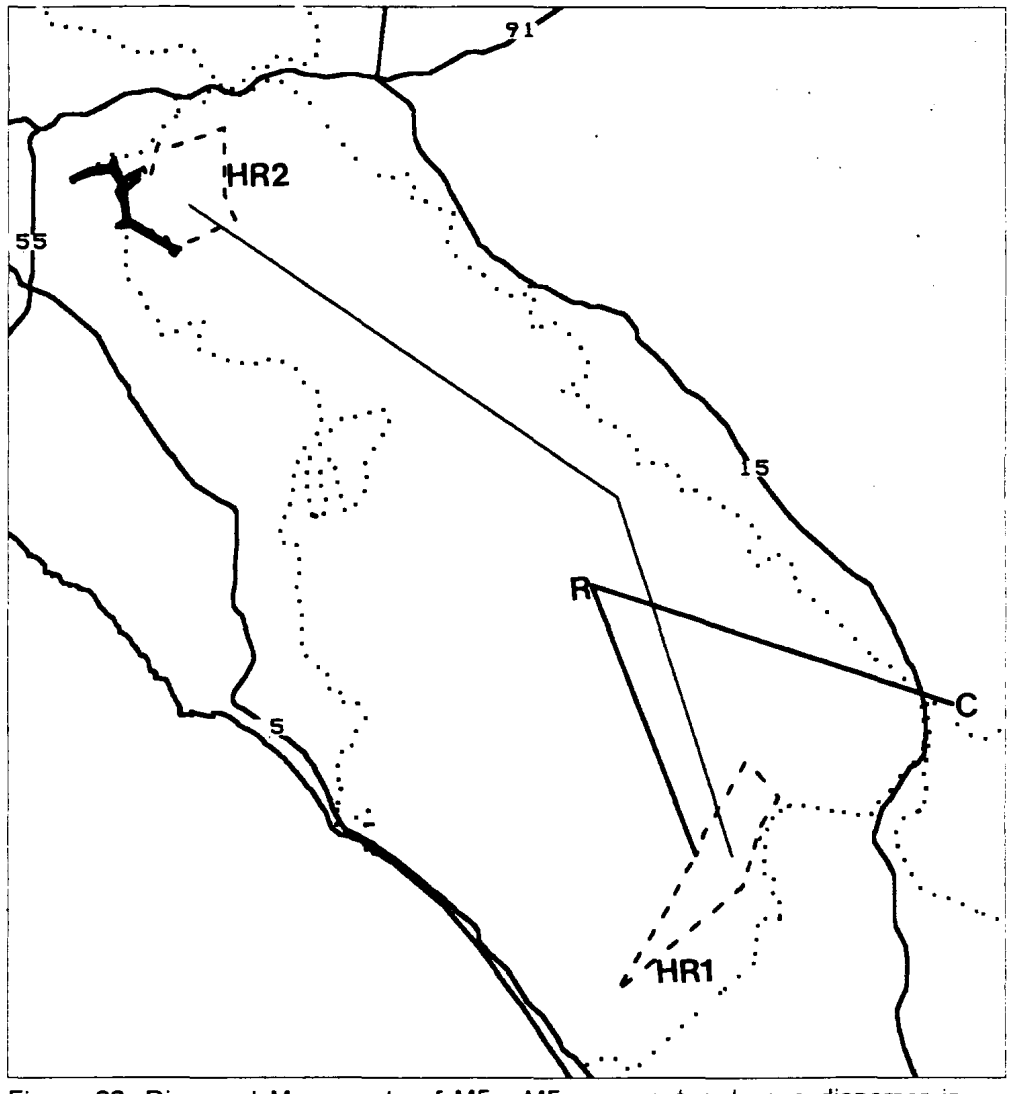

Figure 22: Dispersal Movements of M5. M5 was captured as a disperser in Temecula at **C** and released at **R**, from which he promptly moved to **HR1**. After 6 weeks there, he moved to **HR2** in less than 15 days. After M5 was crippled in an auto accident, he used a very small area (thick solid-edged polygon at west border of HR2) until his death 5 months later. The heavy dotted line indicates limits of cougar habitat.

of his capture site (Figure 22: R). By August 12, he had moved to the Santa Margarita River, another 22 km south of the release site. He used a transient home range there for the next 6 weeks (Figure 22: HR1). Like other transient ranges, this was elongate along the habitat edge. After exploring the southern habitat edge, and finding no route further south, M5 rapidly moved north, covering at least 32 km (20 mi) in a 5-day interval, and at least 40 km (25 mi) in the next 10-day interval. By October 7, he had reached Peters Canyon Reservoir, and thus in less than 15 days had moved from the extreme southeast to the extreme northwest edges of habitat in the Santa Ana Mountain Range.

M5 established a medium-sized home range (Figure 22: HR2) in this area, with a favorite daybed in the large willow forest in the Villa Park Dam impoundment area in Irvine Park. This area was adjacent to housing tracts or the developed areas of Irvine Park along nearly half of its periphery. On November 15, we treed M5 and he appeared to have gained about 15 pounds since initial capture. During diel monitoring on December 10-11, M5 began and ended his night movements in the willow forest, but spent most of the night hunting in nearby Weir Canyon, never approaching the housing tracts or the developed parts of the park.

After 6½ months in this home range, M5 was severely injured in an a vehicle accident and died 5 months later (Chapter 4). During his last 5 months he used an extremely small home range pressed up against the urban edge (Figure 22: thick dashed polygon along west edge of HR2). Despite being crippled and within a stone's throw of tract homes for most of those 5 months, M5 was never a threat to human property or safety (Chapter 9).

Dispersal of M6

M6 (like M5) was captured as a disperser and thus we do not know his natal home range. He was captured in lower San Mateo Creek on August 27 1990, weighing 80 pounds and in excellent condition. After release he moved steadily southeast along the coastal hills and coastal plain of Camp Pendleton for 10 days, moving a net distance of 4-6 km per day until he reached the lower Santa Margarita River September 8 or 9 (Figure 23: thick line segments). He used a small home range centered on the river delta for about 2 weeks (Figure 23: HR1), and then moved back northwest along the coastal plain. When he reached the north edge of Camp Pendleton on October 7, M6 began a rapid move north (Figure 23: thin line segments).

Between October 10 and October 15 1990, M6 moved 27 km (17 mi) north to the highlands of O'Neill Regional Park near Oso Lake. He had left this vicinity by October 17 and we were unable to locate him again despite intense ground searches and weekly air searches of all areas wouth of SR-91. M6 suddenly reappeared near the mouth of Gypsum Canyon on May 6 1991. On the night of May 26-27, he moved north across the Riverside Freeway using the Coal Canyon culvert to cross under SR-91. Over the last 1½ years of the study, M6 moved between the Chino Hills and the Santa Ana Mountain Range at least 22 times (Figure 8). Because we searched the lands south of SR-91 so thoroughly during October 1990-May 1992, we conclude that M6 spent that 6½ months in the Chino Hills.

Over the last 1½ years of the study, M6 spent increasingly longer periods of time south of the Riverside Freeway, with increasingly shorter stays in the Chino Hills. On each of 18 crossings, we found M6's tracks in the Coal Canyon culverts. On the other 4 crossings, there were no tracks in any culvert, and we conclude that he used the vehicle

underpass at Coal Canyon. The frequency with which M6 crossed the freeway is precisely the intensity with which that corridor must be used by an adult male to insure that female cougars in the Chino Hills are bred. These data provide yet another striking example of the ability of dispersing cougars to find and use corridors.

The size of M6's home range (Figure 23: HR2) approached that of M2 and M9, both fully territorial adult males. His pattern of movement and his occasional associations with adult females suggest that he was an adult male at the end of the study. However, if he lives, we expect that his home range will continue to increase in size.

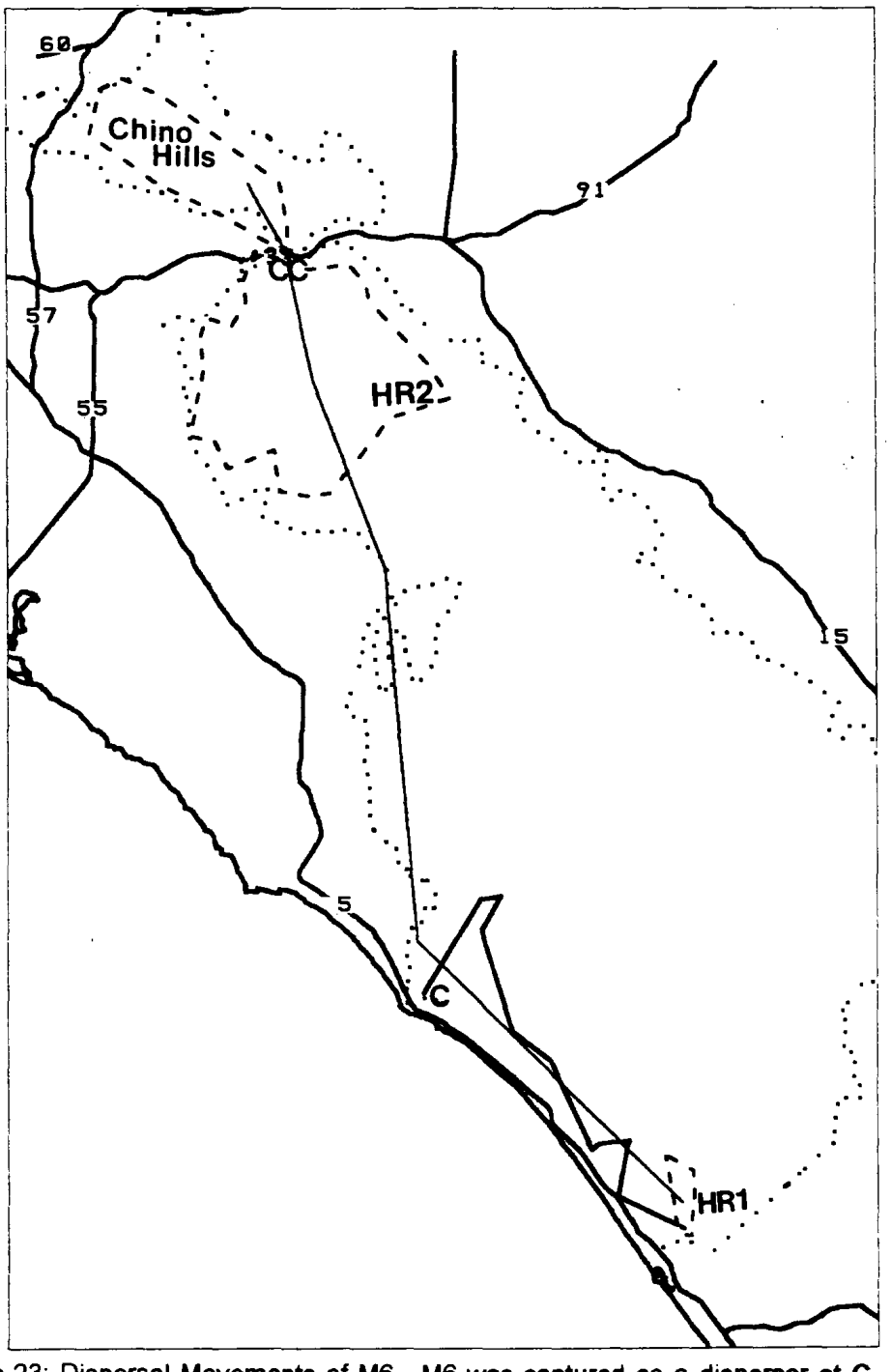

Figure 23: Dispersal Movements of M6. M6 was captured as a disperser at **C** and then he travelled (thick line segments) to **HR1**. After 2 weeks there, he moved rapidly (thin line segments) to the **Chino Hills** where he spent 5½ months before expanding this area into an hourglass-shaped home range (**HR2**). The 2 lobes of HR2 are connected by the Coal Canyon Corridor (**CC**). The heavy dotted line indicates limits of cougar habitat.

CHAPTER 7. PREY RELATIONSHIPS

Prey use based on prey remains

In the course of our routine monitoring activities, we examined 145 cougar-killed prey carcasses. About 59% of these carcasses were deer, and the main secondary prey were coyotes and opossums (Figure 24). Deer were also the largest prey item regularly taken (calves were larger but rarely taken). In terms of mass, the prey carcass data suggest that deer were 78% of the prey biomass eaten, followed by calves (8%), coyotes (3%), and all other species at less than 3% each (using approximate live weights listed in Encyclopedia of Mammals, Fact on File Inc., New York, 1984).

All 3 common species of livestock were taken by cougars. The 4 calves taken were all young animals, and all were killed by male cougars. The chart excludes about 12 killed goats that we learned about when livestock owners reported the losses to state or county authorities. Including these goats would have greatly inflated the apparent importance of goats to cougars because these livestock losses were much more detectable than other carcasses. Only 1 goat and no sheep were present in 176 cougar scats (see below)

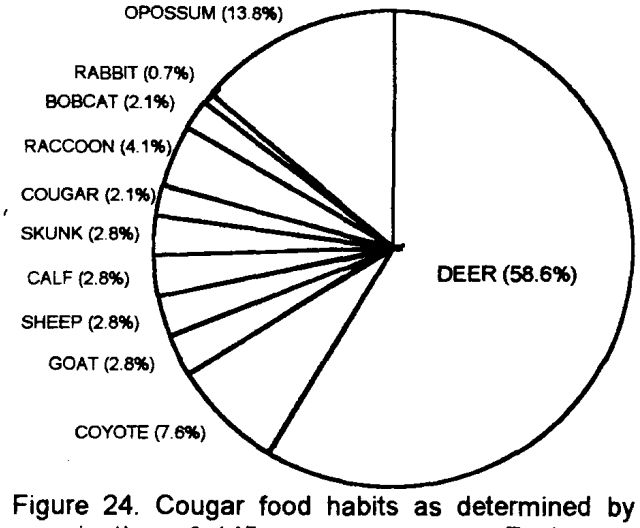

Figure 24. Cougar food habits as determined by examination of 145 prey carcasses. Each prey item = 0.7% of the sample.

suggesting that there is a strong detectability bias even for those livestock carcasses we found without reports. Nonetheless, the impact on the livestock owner is greater than our data indicate, because in many depredations, several goats and sheep would die in addition to the 1 or 2 animals eaten. Most of these surplus victims were killed by the cougar; a few others died with no apparent injury, perhaps due to shock.

The 3 cougar carcasses (F6, M4, and a cub of F3) were consumed almost completely, and 2 of them (F6 and the cub) showed clear evidence that they were killed by a cougar. M4 may have died of other causes, but his fresh carcass was eaten by his mother and brother. In addition, a 4th cougar (F1) died of cougar-inflicted injuries but is not included here because she was not fed upon. These data greatly overestimate the importance of cannibalism because the radio-collars made cougar carcasses 100% detectable. The 160 scats we collected (see below) contained small amounts of cougar fur, apparently from grooming, but no scats contained enough cougar fur to suggest cannibalism.

Almost ¼ the 85 deer carcasses were fawns (table below). Because many fawns, especially those only a few days or weeks old, were consumed completely and left no carcass for us to find, cougars prey much more heavily on fawns than these data suggest. Of the 63 deer carcasses for which we could determine sex, 36 (or 57%) were males. In contrast, adult males comprised only about 20% of live deer in our spotlight surveys (see below: "Deer density estimates and deer herd composition"). Clearly male deer were more susceptible than female deer to predation by cougars. Although capturing the relatively larger male deer yields more food energy per kill, we do not believe that cougars actively select males for that reason. It is more likely that the behavior of male deer (e.g., wide-ranging movements, or lowered vigilance while scouting female deer

and sparring with other males) makes males more vulnerable to predation.

Table 9: Age and sex composition of 85 cougar-killed deer in the Santa Ana Mountain Range, 1988-1992.

Sex of deer	Age of Deer (years) 0	1	2	3-10	Adult (age unknown)	Total
Females	2	1	2	12	10	27
Males	4	7	4	17	4	36
Sex unknown	14	0	1	1	6	22
Total	20	8	7	30	20	85

For 12 deer killed by cougars in the dry season (Jun-Dec), the average fat content of the femur marrow was 41%, with a standard error of 7%. For 3 deer killed by cougars in the wet season (Jan-May), the average fat content was 49%, with a standard error of 8%. These fat contents indicate fair to poor condition. However, this does not necessarily indicate that cougars are taking weaker deer, because these fat levels may be typical for deer in this mountain range.

Of the 145 cougar-killed prey carcasses, we examined 130 carcass within a few hours or days of the kill. We found that cougars generally followed a very predictable pattern of prey consumption:

1. Cougars usually spent 3-4 days consuming a deer, and usually ate the entire carcass, often including the brain and some bone marrow. Generally the heart, lungs, and liver were eaten immediately after the kill, and major muscles were eaten over the next few days.

2. Deer were usually dragged a short distance from the kill site to the site where they were consumed; these sites were generally cool canyon bottoms with good hiding cover.

3. Prey consumption was almost entirely at night. Deer carcasses were usually covered with leaves and twigs at dawn and left covered all day. The deer's rumen (major stomach) was almost always buried in a separate leaf mound several feet away from the rest of the carcass; the rumen was never consumed.

4. The cougar usually bedded down for the day near the carcass, but sometimes up to 1.5 km away.

5. Smaller prey, like opossums, raccoons, and skunks, were usually consumed in 3-5 hours; sometimes these carcasses would also be covered.

In contrast to this general pattern, we occasionally observed unusual behavior with respect to prey carcasses. We present several of these anecdotes below:

1. Six of the 145 prey carcasses were abandoned or only slightly fed upon: (A) F2 killed a pregnant 8-year-old doe at 1AM on March 2 1989 and stayed on the kill until the night of March 7, thus spending 5 nights consuming the carcass. During this time she consumed nearly 100% of the carcass, but left the fully-developed deer fetus virtually untouched and left an opossum carcass, with the head and tail and feet neatly bitten off, but otherwise intact. (B) F7 killed a mule deer fawn on July 9 1989, ate less than half the carcass on the night of the kill, and abandoned it in the morning with no attempt to cover it from the sun's heat or scavengers. She did not return to the kill. (C) During overnight monitoring on April 15-16 1992, M9 killed a doe and 2 fawns at about 10:30 PM. He stayed on the kill until about 06:45AM, when he moved 500 m into a nearby canyon. He had consumed 1 fawn and less than 1/4 of the doe, covering the doe and 1 uneaten fawn as if he intended to return. M9 did not return to these kills. (D) During overnight monitoring on May 26 1992, M13 fed on a large buck all night

long, but left most of the carcass unconsumed. In this case, the carcass had been dragged from an open hillside into a narrow canyon where the carcass became wedged before it could be dragged further downstream to a shady location. Quite likely the carcass was so tightly wedged that M13 could not turn it over for feeding. (E) On January 17-19 1991, M8 killed 2 deer and consumed only 1 of them; this occurred early in his dispersal. (F) On June 15 1989, F1 killed a raccoon and an opossum at the same site. She ate the raccoon, but the intact possum was left buried under grass and covered with ants.

2. Almost all prey carcasses had been freshly killed by the cougar. We documented only 1 clear case of scavenging. On the nights of January 21 and 22 1990, F4 fed upon the badly decomposed carcass of a male fawn that had died 1-2 weeks earlier. F4 buried the carcass carefully with grass and leaves for daytime storage and buried the excised rumen separately. F4 avoided eating the most rotten meat (ribs and backstrap), and fed only on the (moderately rotten and maggoty) major limb muscles. This carcass was also in an unusual location, only 50 m from a golf course fairway in San Clemente.

3. The longest distance we documented

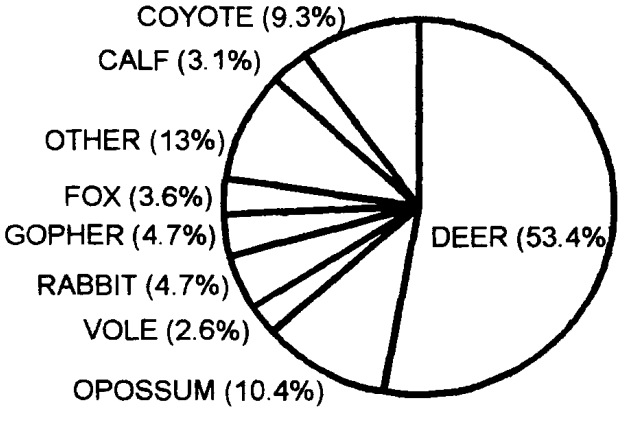

Figure 25. Cougar food habits as determined by frequency of occurrence of fur, claws, and bones in 178 scats (fecal droppings). There were 2 prey in each of 15 scats, for a total of 193 prey items. "Other" prey were raccoons, unidentified canids, domestic cats, unidentified rodents, beavers, badgers, skunks, goats, and moles (each < 2%).

a deer carcass being dragged was 250 m. In that case (F5, 18 Nov 1989), this distance was necessary to get the deer into a canyon with suitable cover. F5 disemboweled the deer after dragging it about 70m, discarding the rumen at that point. The consumption site was in dense chaparral about 4 feet tall, and in the bottom of a minor drainage. Given the low shrubs and grassy openings in the kill area, she had dragged the deer to the nearest good (or at least marginal) consumption site. In this case F5 daybedded next to the carcass.

Prey use based on cougar scats

We collected a total of 204 scats (fecal deposits), 28 of which yielded no identifiable cougar prey. Dr. Joel Weintraub of California State University at Fullerton identified 193 prey items in the other 178 scats. Deer were the most common prey item in these scats, comprising just over half the total; the scats contained fur, bones, or claws from 17 other taxa (Figure 25). However, most of these other species weigh a great deal less than deer, and are less important than suggested by the number of animals eaten. In terms of biomass, deer made up 81% of the weight of these 193 prey items. The only other species contributing at least 1% of biomass were domestic cattle (11%), coyotes (3.8%), and opossums (1.0%); the remaining 12 species combined contributed only 3.2% of the total biomass (using approximate live weights listed in MacDonald 1984). All scats containing cow-calf hair were from the early calving season and had reddish short hairs suggesting that young calves were taken.

The data based on prey carcasses are obviously biased toward larger prey items, because smaller prey will often leave no carcass, or only a few tufts of fur that we overlooked in searching for prey remains. Thus scats are a less biased sample of cougar food habits. Nonetheless both sources of data give the same ranking both in terms of prey numbers

(deer, opossums, coyotes, and calves) and in terms of biomass (deer, calves, coyotes, opossum). As expected, several smaller prey were found in scats but not as carcasses, namely, voles, gophers, gray foxes, badgers, beaver, moles, domestic cats, and 1 woodrat. Several larger species that were present in the carcass tally were not found in scats, namely bobcats, sheep, goats, and cougars.

Two scats contained remains of domestic cats and 3 others contained remains of unidentifiable canids, which could have been domestic dogs. The geographic locations of these scats suggest that these animals were not backyard pets but were either feral or had been abandoned in the country.

Deer density estimates and herd composition

Deer were clearly the most important prey species for cougars in this study. To better understand cougar-deer relationships, we attempted to estimate deer density and the age-sex composition of the deer population using spotlight transects, data from CDFG helicopter surveys, and data from the deer capture effort carried out by CDFG for the Tollway studies.

Our spotlight surveys for deer covered over 125 km of roads in south Orange County (Rancho Mission Viejo, Starr Ranch, Caspers Park, and adjacent areas) and in north Orange County (Weir, Blind, upper Gypsum, and parts of Fremont and Blackstar Canyons, and Loma Ridge). We repeated these transects on 6 occasions: November 1988, March 1989, June 1989, September 1989, January 1990, and September 1992, covering only the south Orange County areas on the first 2 efforts. Analyses of these data using program TRANSECT (Laake et al. 1979, Burnham et al. 1980) indicated that there were about 1.1 to 2.2 deer per square kilometer (2.8-5.5 deer/mi^2). We believe that these estimates are invalid due to gross violations of the assumptions of the line-transect procedure. Line-transect analysis assumes that detectability of the deer depends mainly on distance from the transect line and that 100% of deer on or near the line are detected. But detectability of deer on our transects depended mainly on topography and vegetation, both of which changed greatly along each transect and were far more important than distance from the transect line. We could have failed to detect deer 5 m from the transect line. As a result, our data yielded a declining function of deer numbers versus distance only after several attempts at reclassifying distance classes, and the resulting detection function was sensitive to these arbitrary classes. In turn, program TRANSECT's estimates are highly sensitive to the shape of the detection function. The line transect estimates are certainly invalid, and we believe they lay far below the true number of deer in these areas.

We suggest that somewhat better estimates are provided by 2 other sets of data: (1) In late October 1990, CDFG observers ran helicopter surveys to determine the age-sex composition of the deer herd in several areas in the Santa Ana Mountains. (2) In January 1990, Blind Canyon (Irvine Ranch) was intensely surveyed from a helicopter just after 14 deer were captured and radio-collared there. Although the surveys were not designed to estimate deer numbers, the observer felt that virtually all deer in Blind Canyon, and at least 70% of the deer in the other areas, were counted. We estimated minimum density by dividing the deer counts by the area surveyed as calculated from maps provided by Esther Burkett (CDFG biologist-observer on all the flights). The Blind Canyon survey was conducted over a period of several hours by a very skilled and aggressive pilot, with more wildlife experience than the pilot on the other surveys. Thus it is quite likely that nearly 100% of the deer in Blind Canyon were seen. The other surveys were conducted in less time

per unit area by a less experienced pilot, and it is certain that some deer were not seen.

Our analyses of these data suggest that true deer density was about 5 deer per km^2 (13 deer per mi^2) in the better habitat and about 1.9-2.3 deer per km^2 (5-6 deer per mi^2) in the poorer habitat (Table 10). We feel this is a much more realistic estimate, and one which is more consistent with our estimates of deer mortality rates due to cougars (next section).

The high density estimate for Blind Canyon was not solely a result of survey methods, but probably also reflects the fact that Blind Canyon contained some of the best deer habitat in the Santa Ana Mountain Range (oak trees, coastal sage, chaparral, grasslands, and water well-distributed throughout). Starr Ranch, Caspers Park, the southern parts of Rancho Mission Viejo, Loma Ridge, and Gypsum and Coal Canyons were probably similar to Blind Canyon in habitat quality and deer density, i.e., about 13 deer per square mile. If adults were about 76% of the population (see end of this section), the adult population density was about 9.9 adults/mi^2 on better habitat.

The chaparral-dominated areas at higher elevation in the mountain range probably supported lower deer densities. Although the estimates are very sensitive to assumptions about the number of deer not counted, these areas probably supported about 5.5 deer per square mile, assuming that half the deer were counted. If adults were about 76% of the population (see end of this section), the adult population density was about 4.2 adults/mi^2 on poorer habitat. It is important to note that most of the protected habitat in Orange and Riverside Counties (i.e., the Trabuco Ranger District) lies in these areas of low deer density. Relatively little of the area with the highest deer density (and consequently little of the best cougar habitat) is protected from urban growth.

These deer density estimates are very crude. We would recommend that future efforts should not use spotlight transects, and that any future helicopter counts should use a skilled and aggressive pilot concentrating on a few target areas that can be clearly delineated both from the air and on maps. The results of the Blind Canyon survey suggest that near-total counts are possible.

Although they provided low density

Table 10: Deer density estimates based on intensive helicopter surveys in Blind Canyon (January 1990) and less-intensive helicopter surveys in other areas (October 1990).

Location	Area (mi2)	# deer seen	Deer/mi2 Minimum[a]	Deer/mi2 Estimate[b]
Blind Canyon (Irvine Ranch)	2.33	30	6.0	12.9
upper Blackstar Canyon[c]		0	0	0
Tin Mine Canyon	1.86	6	3.2	6.4
Silverado Burn[d] (Brown, Anderson, and Coldwater Cyns)	12.1	17	1.4	2.8
Cañada Chiquita	5.94	12	2.0	4.0
Wagon Wheel Canyon & west Cañada Gobernadora	3.49	9	2.6	5.2
Average (excluding Blind Canyon and upper Blackstar)			2.25	5.5

[a] based on actual number of deer counted, except for Blind Canyon, which is based on 14 deer captured and collared.

[b] based on the assumption that 50% of the deer present were observed, except for Blind Canyon, which is based on the total number observed in an intense survey.

[c] E. Burkett suspects that overgrazing and poaching in upper Blackstar contribute to this zero count.

[d] The Silverado burn occurred in 1987. The Ortega and San Mateo Burns of 1989-1990 were briefly surveyed and appeared to have very few deer.

Table 11: Deer herd composition in Orange County as determined by spotlight counts. The March 1989 counts are excluded because age and sex of deer were difficult to discern in that season. The total and mean values for fawn:doe ratio excludes the June 1989 counts because most fawns hide during June.

Date	Males	Females	Fawns	Male:Female	Fawns : 100 Females
November 1988	3	18	6	14%:86%	33
June 1989	10	(38)	(8)	21%:79%	(21)
September 1989	10	43	17	19%:81%	40
January 1990	5	23	9	18%:82%	39
September 1992	17	58	28	23%:77%	48
Total	45	180(142)	68 (60)	20%:80%	42
Unweighted mean				19%:81%	40

estimates, the spotlight surveys probably accurately estimated the relative proportions of deer in the fawn, adult male, and adult female classes. Although these numbers varied seasonally and among years, the adult population was about 20% males and 80% females (Table below), and about 76% (187/247) of the population were adults. As mentioned above ("Prey use based on prey remains"), 57% of deer carcasses were males, indicating that males were much more vulnerable to cougar predation.

Estimation of deer harvest rate and cougar kill rate on deer

Thirty (30) deer were radiotagged and monitored in the northwestern part of the Santa Ana Mountain Range during March 1990-December 1991 (Anonymous 1992) and an additional 11 deer were radiotagged and monitored in south Orange County from Fall 1990 through December 1991 (D. Padley, project leader, pers. comm.). From January through December 1992, we continued to monitor these radio-tagged deer, and we investigated deer mortalities to determine cause of death.

To compute the probability of a deer being killed by a cougar during a year, we analyzed these data using 1-month time intervals and the product limit procedure with staggered entry (Pollock et al. 1989). The product of 12 monthly rates yielded an estimate of annual rate of not being killed by a cougar, and the average of these running products yielded a single point estimate. Subtracting this rate from 1.00 yielded a harvest rate. We analyzed the data to provide separate estimates for adult males (through March 1992, at which time only 3 male radiotags were functioning) and adult females (through December 1992, at which time 19 female radiotags were functioning). Following these procedures, cougars annually killed about 10% of adult male deer and 6% of adult female deer. These harvest rates are considerably lower than we had expected. However, harvest rate of fawns is undoubtedly much higher than on adults, and the harvest rate for all age classes is therefore higher than 6-10%.

Twelve (12) radio-tagged deer died during March 1990-December 1992, and 6 of these mortalities were due to cougar predation. Thus cougar predation accounted for about half of adult deer deaths over this period.

In Chapter 6, we noted that cougars killed deer on about 10% of the intensive monitoring sessions. This yields a rate of about 1 deer killed per 10 days, or 36 deer killed per cougar per year.

Inconsistency among our estimates

Finally, it is instructive to evaluate the consistency among our various results. In particular, we have estimated:

- **C** = population density of Cougars = 2.5 adults/100 mi^2
- **K** = the Kill rate, or frequency at which cougars kill adult deer = about 1 deer per 10 days = 36 deer/year
- **D** = population density of adult Deer = 990 adult deer/100mi^2 on better habitat and 420/100mi^2 on poorer habitat, probably about 600/100mi^2 on average.
- **H** = % of adult deer Harvested by cougars per year = 7%, sexes combined

Obviously the number of adult deer killed by cougars per 100 square miles per year should be given by either the quantity $\mathbf{C} \cdot \mathbf{K}$ or by the quantity $\mathbf{D} \cdot \mathbf{H}$. Thus we can state:

$$\mathbf{C} \cdot \mathbf{K} = \mathbf{D} \cdot \mathbf{H}$$

However, when our estimates are inserted into this identity, we obtain:

$$(2.5)(36) = (600)(0.07)$$
$$90 = 42.$$

Clearly one or more of our estimates is in error. This inequality can be turned into an identity by 1 of the following (or by some combination of changes in the indicated directions):

halving our estimate of cougar density, **C**
halving our estimate of kill rate, **K**
doubling our estimate of deer density, **D**
doubling the harvest rate, **H**

Of these 4 factors, we feel that **D** is based on the weakest data, and that **H** was much lower than we had expected. It would be impossible to halve **C** without going below the numbers radio-tagged in 1991, and our **K** is based on extensive data that agrees closely with other published reports. We believe it is most likely that our estimates of **D** and **H** are too low.

CHAPTER 8. IMPACT OF URBAN GROWTH

Habitat loss and fragmentation

The cougar population is the Santa Ana Mountain Range is clearly in jeopardy of becoming extinct due to habitat loss and fragmentation (Chapters 2, 3, & 4; Beier 1993). Vehicle mortalities associated with increased highway traffic due to urban growth also impact the population (Chapter 4). However, even if vehicle-caused deaths were eliminated, the population will not survive continued massive loss of habitat. If the critical Pechanga corridor is enhanced and most of the other important corridors are preserved (Chapter 3), then considerable areas of cougar habitat can be converted into urban uses without significantly increasing the extinction risk (Chapter 4; Beier 1993). However, if the Pechanga corridor is not protected, every new parcel of habitat lost will add to the risk of extinction (Chapter 4).

There is no evidence that habitat loss and fragmentation cause cougars to become aggressive toward humans, or habituated to humans (Chapters 6 and 9).

Six freeways threaten to fragment habitat

Six major freeway projects have great potential to fragment cougar habitat and induce urban growth that eliminate habitat. Fragmentation could occur due to the physical obstacle provided by the freeway itself, due to the urban growth induced by the freeway, or a combination of these 2 factors. The 3 most important and immediate threats are:

1. The southern half of the Foothill Transportation Corridor (FTC-s) slices deeply through an area with no human residents and only 1 approved urban project. It could potentially isolate several small protected parcels (Arroyo Trabuco, Wagon Wheel Park, the Cañada Gobernadora wetland mitigation area, and the Rancho Mission Viejo Conservancy) from the main block of habitat to the east of the Tollway alignment. The Transportation Corridor Agency (TCA) solicited our comments on these potential impacts. In response to our comments, TCA has planned bridged undercrossings at sites along 5 routes that radio-tagged cougars used to access these smaller parcels. Due to an apparent misunderstanding, our proposed bridge crossing on upper Christianitos Creek northeast of the Rancho Mission Viejo Conservancy was omitted from TCA's modified map in late 1991, but we were assured at that time that this bridge would be added. If no urban growth occurs along FTC-s, these undercrossings would effectively mitigate the impact of the FTC-s on cougar movements. However the Tollway will induce massive urban growth that will block these undercrossings unless further mitigations are implemented. In its EIR for this project, TCA's worst case scenario for predicting impacts presumed that the project area (except 1 parcel) would not be built to greater densities than permitted by the Open Space designation in the general plan.

2. The Eastern Transportation Corridor (ETC) would potentially isolate Irvine Regional Park and the proposed Weir Canyon Regional Park from the main habitat block. We provided comments regarding impacts to wildlife movements on 2 occasions. Our second set of comments reflected our knowledge that the only promised crossing area led into a planned community of 13,000 homes (instead of toward the central habitat block), and newer data indicating that the main cougar crossing area was in upper Blind Canyon. As of spring 1992, the TCA had not modified their plans to reflect these conditions.

3. State Route 91 widening project: CalTrans and a private corporation are co-

operating to add additional lanes to SR-91 (Riverside Freeway) from the Riverside County Line to SR-55. At least 9,500 homes cannot be built or sold without this widening project (City of Anaheim conditions of approval); these homes include the Cypress Canyon project that would occlude the critical Coal Canyon Corridor (Chapter 3). Despite being informed of these impacts at a meeting on February 6 1992, later that same month CalTrans prepared a statement that the project did not require an EIR on the grounds that the widening project would not be growth inducing, and that, moreover, the urban growth in the project area would occur with or without the project.

In addition, 3 other highway projects have potential impacts that are either less severe or less immediate. Carbon Canyon Road (SR-142) has been proposed for widening, and a superstreet has also been proposed to run through Soquel Canyon just south of SR-142. Such roads would probably break the Chino Hills habitat into 2 halves. However, this impact is overshadowed by the potential loss of the Coal Canyon Corridor, which would eliminate cougars from the entire Chino Hills. A freeway proposed by Riverside County and generally referred to as the "Cajalco Road Extension" would cut east-west across the Trabuco Ranger District at Santiago Canyon, just north of Saddleback Mountain. This road is so early in the proposal stage that it is difficult to determine if there is any chance that it would be built. It would have a severe impact on cougars. Finally, there have been several proposals (one version was called the Santa Rosa Expressway) for freeways to run from either Fallbrook or Temecula, around the north side of Camp Pendleton (traversing the San Mateo Canyon Wilderness Area), and into south Orange County. The impact of this road on cougars, other wildlife, federally-designated wilderness, and Camp Pendleton would be so severe that it is difficult to justify.

CHAPTER 9. COUGAR-HUMAN ENCOUNTERS

A history of cougar-human encounters

We have previously summarized the record of cougar attacks on humans in the U.S. and Canada during 1890-1990 (Beier 1991, included as Appendix 2 in this report) and updated these observations for 1991 and early 1992 (Beier 1992, inlcuded as Appendix 3 in this report). These 2 papers should be consulted for details beyond this brief summary. During 1890-1990 (101 years) there were 9 attacks resulting in 10 human deaths and at least 44 nonfatal attacks. Attacks on humans have increased markedly during the last 2 decades, probably because cougar numbers and human use of cougar habitats also increased during this time. Most victims (64%) were children; the modal age class was 5-9 years. Of 37 child victims, 35% were alone, 37% in groups of children, and 22% were accompanied by adults; 11 of 17 adult victims were alone at the time of the attack. We believe these data show that attacks are more likely for children, especially unaccompanied children, and more likely for solitary adults than adults in groups. However, the data also clearly show that children accompanied by adults, and even adults in groups, are at some risk of being attacked.

The data also suggest that aggressive human responses appear to be effective in averting an imminent attack and do not support the notion that one should avoid loud shouting or avoid eye contact with the cougar when attack appears imminent. An aggressive response may also be effective in causing a cougar to retreat after an attack has been initiated. There is no empirical support for the efficacy of "playing dead" once an attack has begun. The data suggest that yearling and underweight cougars were more likely to attack humans, but some attackers were healthy adults.

Finally, although attacks were much rarer in previous decades when cougar prey (deer) were market hunted and cougars were aggressively persecuted, the risk was always greater than zero. There has been at least 1 attack in every decade since 1890. It is impossible to reduce this small risk to zero without eliminating either cougars or humans from cougar habitat.

The habituation hypothesis

One popular hypothesis to explain recent cougar attacks is that cougars have become habituated to humans because they are no longer bountied predators, and because in many areas (e.g., wilderness parks, all of California since 1971) cougars are no longer subject to sport hunting. The hypothesis is that as cougars learn to accept humans as a non-threatening part of their environment, they may be more likely to treat humans as prey. However, hunters and animal control agents annually kill about 6-10% of the cougars on Vancouver Island annually (Hebert 1989), a rate that is probably higher than harvest rates in any western state (see references in Smith 1989). Compared to other North American populations, Vancouver's cougar population may be the least habituated to humans and the most subject to aversive conditioning. Nonetheless Vancouver Island has by far the highest concentration of cougar attacks on humans (Beier 1991). This fact is inconsistent with the habituation hypothesis. There is no substantial evidence that habituation has played a role in any particular attack nor in the general recent increase in attacks.

Our study yielded no evidence to suggest that cougars in the Santa Ana Mountain Range are habituated to humans. Cougars entered urban areas with astonishing rarity and were generally unseen by the

thousands of potential human observers in their midst.

The "repeat offender" hypothesis

The data provide weak support for the "repeat offender hypothesis," which speculates that once a cougar has attacked a human, it is more. likely to attack again. Beier (1991, 1992) lists 10 cases in which no cougar was removed after an attack. In 3 of these cases there was a subsequent attack within 80 km and 2 years of the initial attack; in the other 7 cases the offending animal did not attack again. Thus when an attacking cougar was not removed, there was a 30% chance of a second attack within 80 km and 2 years. We believe that for a random set of dates and locations in the current range of cougars, there is a far less than a 30% rate of cougar attacks within the same time and distance. Due to small sample size and the lack of a rigorous test (i.e. actually selecting some random dates and locations), this must be considered weak support for the hypothesis.

Use of garbage and artificial food sources

During this study we had no evidence that cougars directly used artificial food sources. Although the cougar killed in Caspers Park after the attack on Laura Small was reported to have aluminum foil in its stomach, no suggestion of anything other than wild prey has been found in any of the scats we collected and examined.

A possible secondary influence of artificial food sources could occur at garbage dumps where raccoons and opossums and coyotes may feed in considerable numbers, thus offering an abundant and reliable prey base for cougars. We have no evidence for this occurring at the San Juan Capistrano or Irvine Lake landfill sites, both of which are accessible to cougars. It is unlikely that such attraction occurred without detection, because many radio-tagged animals lived near these landfills and we monitored these areas frequently both day and night. In both cases, the extremely open terrain around the landfills probably acted as a deterrent to cougars. It is possible that a landfill in or adjacent to wooded areas could attract cougars to feed on the raccoons and opossums.

We documented 4 occasions when cougars fed on raccoons and opossums near the urban edge; these raccoons and opossums probably did feed from nearby trash cans or other human refuse. Shortly before her death F2 spent about 1 week along the Arroyo Trabuco, just north of the I-5 bridge, feeding on opossums and raccoons within 70 m of a residential area. For the several months after breaking both legs in a vehicle accident, M5 relied mainly on opossums and raccoons in Peters Canyon Reservoir and lower Santiago Creek, almost always within 300 m of residential areas, and on the night of November 18 1990, M3 also killed and ate a raccoon just outside the kitchen house of the Lazy W Camp in Hot Springs Canyon. During her dispersal movements, F17 killed and ate 2 opossums in an abandoned avocado orchard (with much more ground cover than in a maintained orchard) in Main Street Canyon near Corona. In all of these cases, unlike the 2 landfills, the kills were consumed (and presumably made) in dense woody cover close to the artificial food sources.

We conclude that cougars are not directly attracted to artificial food sources, but in rare cases they may secondarily be attracted to areas where raccoons and opossums rely on garbage.

Aversive conditioning was infeasible

Our original contract suggested testing the use of aversive conditioning to make cougars avoid humans. Such work was not practical on wild cougars, because we did not have the sort of control necessary to (a) apply the aversive conditioning, and (b) monitor its efficacy. We reached this conclusion in our first annual report (May 1989) and indicated at that time that we would not make progress on this objective.

In any event, the cougars in our study were remarkably adept at avoiding contact with humans (next section), and it is difficult to imagine that their behavior could have been more reclusive if we had been able to apply aversive conditioning. The experience of being chased by hounds, and then drugged and handled by humans, may have provided some aversive conditioning to our radio-tagged cougars. However, radio-tagged cougars always returned to the capture site, usually within a few days. Thus apparently they did not associate the negative experience with the location.

The aversive conditioning of being chased by hounds is apparently of limited effectiveness on Vancouver Island, where cougar attacks are relatively frequent despite heavy use of hounds to chase cougars (Beier 1991). Also, a yearling cougar attacked a person in Big Bend National Park 4 months after being chased and handled by humans for radio-tagging (Beier 1991). Aversive conditioning (shooting the cougar with rock salt at close range) was tried deliberately on another cougar after a near-attack in Big Bend NP. That animal returned to aggressive behavior 2 weeks later and had to be removed.

Public warnings

Some wildland parks now offer warnings to visitors about the risk of attacks. Such a policy may be appropriate as part of a park's educational program, or for other reasons. We offer 3 observations:

1. There are serious consequences to consider if parks are *required* to post such warnings. If cougars are dangerous enough to merit a warning, then warnings for many other hazards -- from rattlesnakes to cliffs to poison oak -- seem equally appropriate for thousands of square miles of wildlands, including national parks, national forests, and other public lands. This raises the specter of wilderness areas blighted with guardrails and warning signs or, worse yet, wildlands sanitized of all hazards.

2. It is not clear that a warning reduces the risk to wildland visitors. If a visitor is warned that "There are mountain lions in this wildland; they could bite or kill you," the only risk-reducing action he can take, based solely on this warning, is not to enter the area. After several attacks over a decade, Big Bend National Park (Texas) during 1990-91 attempted to warn every person entering their Visitor Center about the potential for cougar attacks. In the first year of this program, the park is unaware of a single visitor who has turned back because of this warning (P. Koepp, Big Bend NP Director, pers. comm., August 14 1991). In 1 case, a cougar walked through the main campground in Big Bend National Park in daylight, confronting a camper briefly before retreating. After the incident, park rangers warned everyone in the campground about cougars and specifically mentioned the recent incident; no camper (except the person involved in the confrontation) left the Park. Similarly, Caspers Regional Park required every visitor during 1988-92 to sign a statement that he or she had been warned of the potential risk of cougar attacks. Our conversations with Park employees indicate that fewer than 10 people in

5 years chose not to enter the Park due to this warning.

3. A broad public education effort is an alternative to simple warnings. Recently several public entities have started to educate the public about cougars in a balanced way that includes mention of the aesthetic and ecological role of cougars, the potential risk of attack, and suggestions for how to respond if one encounters a cougar. Within the past 5 years, Colorado Division of Wildlife, Montana Department of Fish Wildlife and Parks, and Big Bend National Park have produced helpful and accurate brochures on cougars. The first 2 agencies provide information targeted not only at wildland visitors but also at people who live in cougar habitat. California Department of Fish and Game has also prepared a similar brochure which is available for distribution.

Cougar use of areas on the urban fringe

Cougars were remarkably adept at using habitat along the urban-wildland edge. In particular, all 9 dispersing juvenile cougars encountered at least one urban area during their explorations. There were no instances of cougars behaving aggressively to humans or taking pets in any of these urban edge settings. (Cougars did take pet goats near rural homes).

The sections of Chapter 6 dealing with dispersal movements of juveniles offer many anecdotes illustrating cougar behavior at the urban edge. Several additional anecdotes follow:

M5 in East Orange. Probably the most dramatic case is presented by M5. After breaking both hind legs (Chapter 4: highway injuries) in a vehicle collision on Santiago Canyon Road on April 23 1991, M5 used a very small home range, and stayed in very level terrain eating mainly raccoons and opossums until his death 5 months later. During this 5 months, his locations were almost entirely within 300m of the urban edge. His favorite haunts were the Villa Park Dam impoundment area, Peters Canyon Reservoir, Santiago Oaks Regional Park, and Santiago Creek *downstream* from Santiago Oaks Regional Park as far as the small (10-ha) forest on the north side of Santiago Canyon Road at Hewes St.

In overnight monitoring at Peters Canyon Reservoir on June 12-13 1991, and in Santiago Creek near Hewes St. on July 29-30 1991, M5 moved in a manner suggesting that he was feeding on small prey. On neither occasion did he enter the surrounding residential areas. We had only 2 reported sightings of M5 by a human, in both cases brief glimpses of M5 moving away from the human. At death M5 was grossly normal except for the healed leg injuries and being markedly underweight. M5 never behaved in a manner suggesting a threat to public safety.

M10 in the Anaheim Hills. During overnight monitoring on June 23-24, June 25-26, and July 6-7 1992, M10 spent the night in a thin shard of habitat north of Santiago Oaks Regional Park, close to residential areas, and in a heavily-used recreational area. This area consisted of a ridgetop and small canyon, and was mostly grassland with some coastal scrub and a few eucalyptus trees. Although the area had less woody cover than is typical for cougar habitat locally, it contained abundant prey. Nearby to the southwest were new homes along Serrano and Maybury Streets. More new homes and powerlines lay upslope (north) of this habitat fragment, and tanks and powerlines occupied much of the artificially-flattened north-south ridge.

In each of the 3 nights that we monitored M10 in this area, many hikers, bikers, and joggers passed close to him. However, there were no reported sightings of M10 by people, no indication that M10 was

interested in humans as prey, and only 1 occasion when he got close enough to a residential area to cause a dog to bark.

In the late afternoon of June 24-25, and continuing into the twilight, many joggers and bikers passed near M10 without incident. Just before 10 PM the Disneyland fireworks show began, and 2 people watched the fireworks from the ridge above (north of) M10. After the fireworks these people walked south passing within 250 m of M10. At 0130, M10 walked into the mouth of the draw and approached Serrano Road, at which point the neighborhood dogs erupted with barking and howling, apparently getting scent of the cat before he entered the residential area. M10 promptly retreated to the draw and apparently hunted there the rest of the night (our followup in the morning did not reveal any prey remains).

Two nights later (June 25-26), M10 started out in the same small canyon and stayed there until about 8 PM, while several joggers and bikers again passed nearby. From 1830-2030 the radio-tracker watched M10 from a nearby rock outcrop. During most of this time M10 was resting in a patch of rather open grassland about 300 m from the observer, semi-hidden by his brown color, laying posture, and immobility. The cat raised his head and looked around in response to nearby barking dogs, singing birds, and perhaps scents carried on the wind (on 2 occasions he sniffed the wind and then looked around). At one point M10 started walking but then stopped when 2 women with 2 small dogs jogged on a trail about 200m away. He sat and calmly watched them pass by, but never crouched or appeared aggressive. During the night, he moved gradually east, and by dawn he had moved into Weir Canyon.

We monitored M10 a third night (July 6-7) in the same area. Once again he hunted close to residential areas, and within 200m of joggers and bikers during the evening hours. He again ended the night in Weir Canyon, far from developed areas.

F2 in San Juan Capistrano. On the night of February 7-8 1991, F2 moved down Trabuco Creek to I-5, and spent the next several days there, north of the Freeway and south of 3 residences (including a small ranch with horses and goats) built right on the creek. This site was 3 km south of that portion of Trabuco Creek that F2 normally uses. This portion of the Creek lay in a channel with cut banks 8-12 feet deep. About 8 homes on the eastern blufftop were less than 200m from F2's daybeds and the large "Village San Juan" housing tract was less than 100 m from the western bluff top.

On February 11, we found remains of 2 raccoons and 2 opossums that F2 had killed along Trabuco Creek. One opossum was extremely large and perhaps it had thrived by raiding nearby garbage cans. There were no reported sightings of F2 from nearby residents, and no indication that she was a threat to the nearby pets, goats, or residents. In 3 visits to the creek we were unable to see or hear her despite approaching to within 10 feet of her, so strong was her determination not to leave the protection offered by the dense bamboo thickets.

M13 in Coto de Caza. During overnight monitoring of M13 on September 25-26 1992, M13 traveled north up Cañada Gobernadora into an area of estate lots at the southern end of Coto de Caza. At about midnight he killed a deer in the creek bottom, near the chain-link fence marking the estate boundary. The kill site was about 50m from the road and a similar distance from a light illuminating the estate grounds. He stayed in this location feeding on the deer until 0530, at which time he traveled south and east about 2 km, skirting the south edge of a freshly graded area and traveling through the northern part of

the new Gun Club site, into Bell Canyon to daybed.

Urban intrusion. Most radio-tagged cougars had urban areas abutting part of their home range, and several cougars experienced urban growth within their home ranges during the study. The cougars did a remarkable job of keeping out of areas immediately after the bulldozers removed the native vegetation. In several cases cougars moved into newly-initiated construction sites during the night, and remained bedded near them while heavy machinery operated nearby the following day. For instance, in early January 1990, F2 made her first visit to the lower Arroyo Trabuco in over 2 years, during which time many changes had occurred. On January 11, she was daybedded in a small canyon on the east rim of the Arroyo Trabuco. To her east, a street sign ("Antonio Parkway") stood incongruously in a grassland and bulldozers were busy making a street for the street sign to mark, with the road cut about 150m east of F2. To the north the cat could easily see golfers on the newly-built Rancho Santa Margarita. To the west (across the Arroyo) hundreds of hammers clattered on hundreds of house frames in Mission Viejo. And less than 1 km south bulldozers were scraping the Arroyo to put in footings for the Oso bridge. During all daylight hours the cougar was surrounded by construction activity. Shortly after dusk she quickly moved back east to the central part of her range.

Human structures in rural areas. Cougars in more remote areas also encountered humans regularly. For instance, within F3's home range were Los Amantes Camp (used for large outdoor parties), the TRW ("Star Wars") plant, the Ford munitions testing facility, and a very large sand mining and processing operation. F3 used all of these facilities when human activity was low, and showed no apparent aversion to passing near isolated buildings or vehicles at night. During one overnight monitoring session, she passed within 200m of Los Amantes Camp when a large outdoor party was in progress, showing no apparent interest in the activity.

Cougars also passed close to rural homes and occasionally ate goats there.

Cougars in parks and near wilderness trails

On several occasions, we documented a cougar (on different occasions: F1, F2, M2, M5, M6, M8, and M10) bedded for the day a few feet off of well-used park trails in Caspers Park, O'Neill Park, the Arroyo Trabuco (closed trails regularly used by trespassers), Whiting Ranch Regional Park, Chino Hills State Park, or Santiago Oaks Regional Park. The cougar doubtless was aware of the hikers, the hikers were completely unaware of the cougar and therefore were at risk of being ambushed. The only reported sighting in all these cases was a single incident in which F2 scrambled up a tree as an equestrian approached.

Given the high human use of Santiago Oaks Regional Park, there is a potential for human-cougar encounters in that Park. Although there may be greater risk at other parks that are more regularly used by cougars, park visitors are probably less aware of the potential for encountering a cougar in Santiago Oaks Regional Park. Because most people approach the park from the heavily-urbanized west, many park visitors tend to regard it (despite its oak forest and other wild traits) as a "city park," disregarding any efforts to make them aware of a potential cougar encounter. A similar disparity between public perception and biological reality exists at Irvine Park.

Many County Parks were cougar habitat (Chapter 3), and thus each had the potential for a cougar attack, although this risk is very low. Neither the historical record nor our data on radio-tagged animals provide a basis for assigning a greater degree of risk to a

particular park. As long as a park is cougar habitat, it has a small amount of risk.

Management practices related to cougars differed greatly among the above County Parks, from signed warnings and a prohibition on minors in Caspers Wilderness Park, to busloads of school children in Santiago Oaks Regional Park, to a largely unpatrolled Wagon Wheel Regional Park. The Parks as a group also differed from adjacent National Forest lands that were open to all visitors.

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GLOSSARY

adult - a cougar over 24 months of age and exhibiting a stable home range.

carrying capacity - the average number of animals that a given habitat area can support in the long term. For cougars, it is usually expressed in numbers of adults per 100 km^2 or per 100 mi^2.

corridor (wildlife corridor) - a linear habitat used by animals or plants to move between 2 larger habitat areas.

cub - a cougar from birth until dispersing out of its mother's home range at 13-27 months of age

depredation - the killing of domestic livestock or pets by a wild predator

dispersal - Movement of an animal away from its place of birth to establish a new home range elsewhere. For cougars, the process of dispersal takes several weeks to months, during which the animal searches for suitable habitat with minimum risk of conflict with other resident adults of the same sex. Cougars in this population dispersed at 13-27 months of age.

hectare (ha) - hectares, a unit of area equal to 10,000 m^2 (e.g., a square 100 m on a side) or about 2.471 acres. To convert ha to acres, multiply ha by 2.471; to convert acres to ha, multiply acres by 0.4047. see also kilometers

home range - The area used by animal in the course of its normal activities of feeding, breeding, resting, and raising young. Home range excludes rare excursions to locations not later revisited.

intensive monitoring - radio-tracking sessions starting before sunset and continuing until after sunrise. During each session, we determined the location of a single cougar (the focal animal) every 15 minutes. also called "overnight monitoring"

juvenile - a term that includes both cubs and subadults, i.e., any cougar that is not yet adult.

kilometer (km) - a unit of length equal to 1000 meters, or about 0.625 miles. To convert km to miles, multiply km by 0.625; to convert miles to km, multiply miles by 1.6. To convert km^2 to mi^2, multiply by 0.386; to convert mi^2 to km^2, multiply by 2.59.

overnight monitoring - *see* intensive monitoring

parturition - the act of giving birth

Santa Ana Mountain Range - The study area, including the Santa Margarita Mountains, the Santa Rosa Plateau, and the Chino Hills. See Figure 1.

scat - fecal dropping

subadult - a cougar from the age of dispersal until a stable home range is established, usually by 36 months of age

transient (home range) - (a home range) used for several weeks or months by a dispersing juvenile cougar and then abandoned. Transient home ranges were smaller than adult home ranges, and were usually elongate and pressed up against the urban edge.

Determining Minimum Habitat Areas and Habitat Corridors for Cougars

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Abstract: *I simulated population dynamics of cougars to predict the minimum areas and levels of immigration needed to avoid population extinction caused by demographic and environmental stochasticity for a period of 100 years. Under most plausible parameter values, the model predicted very low extinction risk in areas as small as 2200 km², and (in the absence of immigration) increasing risk as area decreased below 2200 km². If as few as one to four animals per decade could immigrate into a small population, the probability of population persistence increased markedly. Thus a corridor for immigration will benefit a small population in an area where further loss of habitat will occur.*

The model was applied to the cougar population in the Santa Ana Mountain Range of southern California (2070 km², with about 20 adults). Field data support the model's conclusion that this population is demographically unstable. There will be a high risk of extinction if the habitat is reduced to currently protected and connected areas (1114 km²). A movement corridor allowing immigration from the adjacent population and intra-range corridors would greatly enhance the prognosis. However, the last corridor for immigration has been degraded by recent human activity. Within the mountain range, cougars recently became extinct in a 75-km² habitat fragment recently isolated by development, and cougars will become extinct in another 150-km² of habitat if a proposed housing project occludes a critical corridor. Radio tracking has confirmed use of this and other important corridors.

Neither the model nor the field data alone would have much influence in the face of development pressure; together they have stimulated interest in restoring and protecting critical corridors in this range. Nonetheless, the long-term prognosis for this population is bleak, because 22 local governments review potential impact on a case-by-case basis.

Determinando áreas mínimas de hábitat y hábitat en corredes para pumas

Resumen: *Simulé la dinámica de la población de pumas para predecir áreas mínimas y niveles de inmigración necesarios para evitar la extinción de la población debido a estocasticidad demográfica y ambiental por un período de 100 años. Usando los parámetros más viables, el modelo predice riesgos de extinción muy bajos en áreas tan pequeñas como 2200 km², y (en ausencia de inmigración) un riesgo creciente a medida que el área decrece por debajo de 2200 km². Si tan solo 1–4 animales por década pudiesen inmigrar a una pequeña población, la probabilidad de persistencia se incrementaría marcádamente. Por consiguiente, un corredor para la inmigración puede beneficiar una pequeña población en un área dónde ocurrirá una mayor pérdida del hábitat.*

El modelo fue aplicado a la población de pumas en la cadena Montañosa de Santa Ana, al Sur de California (2070 km², con unos 20 adultos aproximádamente). Datos de campo apoyan las conclusiones del modelo, que indican una población demográficamente inestable. Si el hábitat es reducido a las actuales áreas protegidas y conectadas (1114 km²) habría un alto riesgo de extinción. La prognosis se podría mejorar ampliamente con un corredor de movimiento que permitiera la inmigración desde poblaciones en áreas adyacentes y corredores dentro del área de distribución. Sin embargo, el último corredor para la inmigración ha sido degradado por el reciente impacto humano. Dentro de la cadena montañosa, los pumas se han extinguido recientemente en un fragmento de hábitat de 75 km² aislado a causa del desarrollo; los pumas se extinguirían en otros 150 km² de hábitat si un proyecto de viviendas propuesto obstruye un corredor crítico. El uso de este y otros importantes corredores ha sido confirmado a través de telemetría.

Ni el modelo ni los datos de campo por si solos tendrían mucho impacto ante la presión por el desarrollo; juntos han estimulado el interés en restaurar y proteger corredores que son críticos en esta cadena. A pesar de todo, la prognosis a

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Effective land-use planning must be spatially explicit and regional in scope. Because cougars need corridors and because telemetered cougars can quickly identify movement corridors, cougar research is an efficient and appropriate way to inject biological data into such planning efforts.

largo plazo para esta población es yerma ya que 22 gobiernos locales revisaron los impactos potenciales caso por caso. Una effectiva planificación del uso de la tierra debe ser explícita espacialmente y regional en extensión. La investigación sobre pumas es una vía eficiente y apropiada de introducir datos biológicos en los esfuerzos de planificación. Esto es así porque los pumas necesitan corredores y al estar marcados telemétricamente permiten identificar rápidamente los corredores de movimiento.

Introduction

As landscapes are fragmented into ever-smaller patches of habitat isolated by high-speed barriers (Harris & Gallagher 1989), it has become important to determine the minimum area needed to preserve functioning ecosystems. Because there are no methods to determine the minimum areas of reserves with reference only to ecosystem properties, biologists are forced to conduct viability analyses for a few "indicator" or "umbrella" species as an efficient way to address the viability of the whole system (Soulé 1987*a*:8; Noss 1991).

Species such as the grizzly bear (*Ursus arctos horribilis*), the wolf (*Canis lupus*), and the cougar or mountain lion (*Felis concolor*) make ideal candidates for such analysis because they exist at low density and require large areas. Of these, only the cougar plays a significant ecological role in much of the lower forty-eight states. Therefore, viability analysis for this species would have widespread utility. Shaffer (1983) presented an analysis for the grizzly bear. In this paper, I present such an analysis for the cougar.

I focus solely on the issue of identifying the minimum area and immigration rate needed to avoid extinction caused by demographic and environmental stochasticity, ignoring inbreeding effects. Previous analyses have shown that the areas needed to avoid inbreeding depression in the long term are so large "that the only recourse in most situations will be to establish the species in several sites since there won't be enough space in any given site" (Soulé 1987*b*:177). My analyses address the issue of how large each of these "several sites" must be so that management intervention can be limited to that needed to maintain genetic variability.

Simulation models are superior to analytic models when addressing a particular species, because the analytic calculations are possible only for unduly simplified models (Ewens et al. 1987:67). But there are pitfalls to the simulation approach, especially with small populations. For example, most simulation models account only for females and make no allowance for an "Allee effect" whereby animals at low density may have difficulty finding mates. This creates an inverse density-dependence in fecundity when numbers of one sex are very low (Begon & Mortimer 1981:30), which has been documented in a cougar population (Padley 1990). Another problem is that most subroutines for incorporating stochastic variation in survival rates introduce crucial errors when simulated populations become small (see Methods section). Most important, even though "habitat fragmentation ... is the primary cause of the present extinction crisis" (Wilcox & Murphy 1985: 884), few simulation models allow analysis of the effects of movement corridors; such analysis requires explicitly modeling various levels of immigration.

In this paper I describe a model that realistically simulates the population dynamics of small populations of cougars. My goal was to predict the conditions under which a cougar population can avoid extinction in the short term (100 years), ignoring inbreeding effects. My main conditions of interest were those that humans can control, namely, area of habitat (controlled by restrictions on human development) and the amount of immigration into the population (controlled via provision for wildlife movement corridors to adjacent populations). In addition, I examined how estimates of extinction risk depends on estimates of life history parameters, many of which vary geographically or are difficult to measure.

Finally, I apply the model to the cougar population in the Santa Ana Mountains of southern California, which I have studied since 1988, and I summarize some of the relevant field observations from that study. This real-world application illustrates that model results have little impact on land-use decisions unless they are supplemented by field study to identify actual or potential movement corridors. My goals in this illustration are to promote the use of data from telemetered cougars to identify and protect wildlife corridors, and to advocate that regional planning efforts based on geographic information systems (GIS) replace current piecemeal approaches.

Methods

Simulation Model

The simulation model used standard Leslie-matrix computations, with subroutines that controlled immigration

and adjusted survival and fecundity rates for density-dependence, demographic and environmental stochasticity, and an Allee effect. For each combination of input conditions, the population dynamics were simulated 100 times; each simulation was 100 years in duration. In each case, the initial number of adults (animals 2 or more years of age) was set equal to the carrying capacity and evenly distributed among age classes. Initial numbers of 0-year-olds and 1-year-olds were set at a half and a quarter, respectively, of the number of adult females.

The question of what constitutes preservation is "the most crucial and least addressed" issue in conservation biology: "Does a 95% probability of persistence for 100 years make extinction sufficiently remote or all too immanent?" (Shaffer 1987:81,84). I advocate planning for an extinction risk of less than 1%, and I label "significant" any extinction risk 2% or more.

For each set of 100 runs, the program recorded the population trajectory by sex and age class, the number of runs on which the population went extinct, mean population size in year 100, and other summary statistics.

INPUT CONDITIONS

The main factors of concern were area of habitat and level of immigration. Simulations were run with habitat areas as small as 200 km^2 and in increments of 200 km^2 until extinction risk declined to less than 2%. Four levels of immigration were considered. The first level depicted no wildlife movement corridor (no immigration). The second and third levels reflected a marginal corridor, allowing immigration of one or two males per decade, respectively. The fourth level of immigration was three males plus one female per decade. These levels reflect the finding that about 80% of juvenile males, but only about 25% of juvenile females, dispersed out of their natal mountain range, often crossing inhospitable desert habitat to reach another range (Ashman et al. 1983).

For each combination of habitat area and level of immigration, simulations were run under many combinations of estimates for life history and environmental attributes (Table 1). We have poor estimates for some of these parameters (for example, male and female equilibrium densities, juvenile survival rates) and some parameters may vary geographically, so I used many combinations initially. A smaller subset was obtained by dropping values that produced unrealistic outcomes and variables that did not influence the results.

Litter size. Mean litter size (Table 1) was based on reports of Robinette et al. (1961), Ashman et al. (1983), and Anderson's (1983:34) compilation of data from 407 litters. In the simulations, up to 40% of the 2-year-old females bred each year and no kittens or yearling females bore young, based on minimum and mean ages of primiparous females of 25 and 32 months (Ashman et al. 1983). Because the mean interval between births (except when a litter dies) is usually about 24 months (Hornocker 1970:16, Robinette et al. 1961:215), the model excluded from breeding those females with surviving litters from the previous year. The model assumed that a female whose litter dies comes into estrus and breeds the next year (Hornocker 1970:16; Seidensticker et al. 1973:56; Eaton & Velander 1977:65).

Juvenile survival rates. There are few estimates of survival of 0-year-olds. Comparing mean litter sizes near birth and at 12 months (not the same litters followed through time) Ashman et al. (1983) suggested a value of 0.78. Similar data in Robinette et al. (1961:213, inferring age from weight) suggested a survival rate of 0.73. To the extent that entire litters died, this is a high estimate (Robinette et al. 1961:213); it is also higher than the adult survival rate reported by Lindzey et al. (1988). Survival rates of African felid cubs (lion, cheetah) are about 0.50 (Schaller 1972:191,300). Preliminary analy-

Table 1. Input states for biological parameters used in simulating population dynamics of cougars.

Parameter	*Possible States*
Mean litter size	2.4[a]
	2.8
	3.2[b]
Juvenile[c] survival	0.55 (0.50)[d]
	0.65 (0.60)
	0.75 (0.70)
Adult[c] survival	0.65[a]
	0.75
	0.85
Carrying capacity (breeding adults per 100 km^2)	Sex ratio of 2 femles per male:
	0.4 females, 0.2 males
	0.6 females, 0.3 males
	0.8 females, 0.4 males
	1.0 females, 0.5 males
	1.2 females, 0.6 males
	Sex ratio of 3–4 females per male:
	0.8 females, 0.2 males
	1.2 females, 0.4 males
	Sex ratio near unity:
	0.4 females, 0.4 males
	0.8 females, 0.6 males
	None (constant carrying capacity)
Severity of catastrophe (loss of carrying capacity)	20% in years 25–27, 50–53, 75–77
	40% in years 25–27, 50–53, 75–77[f]

[a] *This value was dismissed because it produced unrealistically low population sizes even when used in concert with optimistic estimates for other variables. See first section of Results.*
[b] *This value was dismissed because it produced extinction probabilities that did not differ from those under a mean litter size of 2.8, and this value is best supported by field studies. See first section of Results.*
[c] *0- and 1-year olds of both sexes, and 2-year-old males.*
[d] *Survival of 1-year-old males indicated in parentheses.*
[e] *Females ≥2 years old and males ≥3 years old.*
[f] *This value was dismissed because extinction probabilities varied only trivially from the 20% case. See first section of Results.*

sis of 172 cougar-months of telemetry data (0- and 1-year-olds combined) suggests an annual survival rate for cougar cubs of 0.48 (Beier, unpublished data). Hemker et al. (1986) reported a survival rate of 72% for cubs between 3 and 10 months of age in an area of extremely low cougar density (gross density of 0.5 cougars per 100 km^2); this rate may reflect density-dependent enhancement of survival rates at low density. In any event, if additional mortality during 0–3 months of age is considered, 0.75 is probably a high estimate and was used as the highest estimate in the simulations.

There are no published estimates of survival of 1-year-olds. Hemker et al. (1986) reported a survival rate of 92% for cubs from 10 months to dispersal at 16–19 months, from the same low-density population. This figure ignores higher post-dispersal mortality (Hornocker 1970:18). Lacking better evidence, I set yearling survival rates equal to 0-year-old survival rates. In the simulations kittens died when orphaned in the year of birth, but kittens orphaned in the year after birth had the same survival rate as nonorphans.

Adult survival rate. I used adult survival rates of 65% (Robinette et al. 1977:123, Ashman et al. 1983), 75% (Lindzey et al. 1988), and 85% (Anderson et al. 1989).

Longevity. A maximum longevity of 12 years was used in all simulations. The longest lifespan reported for a wild cougar is 13–15 years (Hopkins 1989:23); I found no other reports of wild cougars living past 12 years of age. Extreme longevities for captive cougars are 12, 15, and 18 years (Young 1946:59), and 12 and 19 years (Eaton & Velander 1977:56). My preliminary analyses showed that risk of extinction decreased only slightly as maximum longevity increased past 12 years, especially in the critical right tail (Figs. 3–6) of the extinction curve.

Carrying capacity. Although they are not territorial, social intolerance among adult females is thought to regulate their density, whereas territoriality among males separately regulates male density (Seidensticker et al. 1973). Apparently female density is calibrated to vegetation, topography, and prey availability, whereas males compete for access to females (Seidensticker et al. 1973:59,56). To model density-dependent survival rates, separate estimates of carrying capacity for males and females were needed.

Estimates of densities for male and female adult cougars vary widely (Hornocker 1970; Seidensticker et al. 1973; Sitton & Wallen 1976; Currier et al. 1977; Shaw 1977; Hemker et al. 1984; Logan et al. 1986; Neal et al. 1987; Hopkins 1989). Because many study sites were selected because of expected high cougar density, some reported densities are atypically high. Also, not all studies reported how many of these adults were nonbreeding transients as described by Hornocker (1970) and Seidensticker et al. (1973).

In light of these uncertainties, I ran the model under a variety of carrying capacities (Table 1). Because most studies (excluding male-biased summaries of hunting returns) report a 2:1 ratio of breeding adults (females: males) (Seidensticker et al. 1973:17, first 3 years; Currier et al. 1977; Ashman et al. 1983; Murphy 1983; Hemker et al.1984; Logan et al. 1986; Neal et al. 1987; Hopkins 1989:23), most simulations used this ratio between carrying capacities for males and females. However, other adult sex ratios have been reported, for example, 3:1 (Currier et al. 1977; Shaw 1977; Quigley et al. 1989; M. Jalkotzy and I. Ross, Calgary, Alberta, unpublished data), 1.3:1 (Hornocker 1970:15), and 1:1 (Seidensticker et al. 1973:17, last 3 years; Hopkins 1981). Therefore I also used similar ratios (Table 1).

I excluded high densities due to winter concentration. The markedly lower gross density of 0.4/100 km^2 reported by Hemker et al. (1984) and the markedly higher adult density of 3/100 km^2 reported by Neal et al. (1987) were also excluded as outliers which may deviate from the actual long-term carrying capacity.

Catastrophic reductions in carrying capacity. On each run, simulated carrying capacity decreased by either 0%, 20%, or 40% during years 26–28, years 51–53, and years 76–78. This modeled prey die-offs due to droughts or severe winters.

DENSITY-DEPENDENCE IN FECUNDITY

Because the gestation period is only 92 days and neonates weigh only 500 grams (Anderson 1983:33–34), cougar pregnancy is relatively cheap; therefore simulated litter sizes were independent of density and maternal age. When the simulated number of adult females was less than carrying capacity, all females over 2 years old (except those with a surviving litter from the previous year) and 40% of 2-year-old females (Ashman et al. 1983) bore litters. The program allowed females in excess of carrying capacity to breed with probability equal to 0.20, and assigned the youngest females to nonbreeding status, reflecting the inhibition of reproduction in young females until home range establishment (Seidensticker et al. 1973).

The probability of a female breeding was inversely density-dependent when numbers of breeding males were below the carrying capacity for adult males. When there were vacant male territories, the proportion of adult females that were bred was reduced by a factor of

$$\frac{KM - \#AdM}{KM} * 1.15^{KM - \#AdM},$$

where KM = carrying capacity for breeding males and #AdM = number of adult males. Under this expression, each adult male increases his home range size by 15% for each "deficit male"; thus the effect is very mild ex-

cept at very small population sizes; for example, when KM = 5 and #AdM = 4, 92% (not 80%) of the females are bred.

DENSITY DEPENDENCE IN SURVIVAL RATES

In preliminary analyses, some simulations were run without any density dependence in survival rates; resulting extinction rates were about ten times higher than those produced using density-dependent survival rates for all ages. Other simulations were run with mild density dependence in juvenile survival rates (Fig. 1, curve A) and density independent adult survival rates, producing extinction rates about five times higher than when survival rates for all ages were density-dependent. In simulations lacking density-dependent survival rates, the mean number of adults in year 100 (in surviving populations) far exceeded carrying capacity. Because density independence produced such unrealistic ending population sizes, I ran all remaining simulations with density-dependent survival rates (Fig. 1, Table 2).

In the model, density dependence operated most strongly on 0- and 1-year-olds, whose survival rates depended on the number of adult females; survival of 1-year-old males also varied with the number of adult

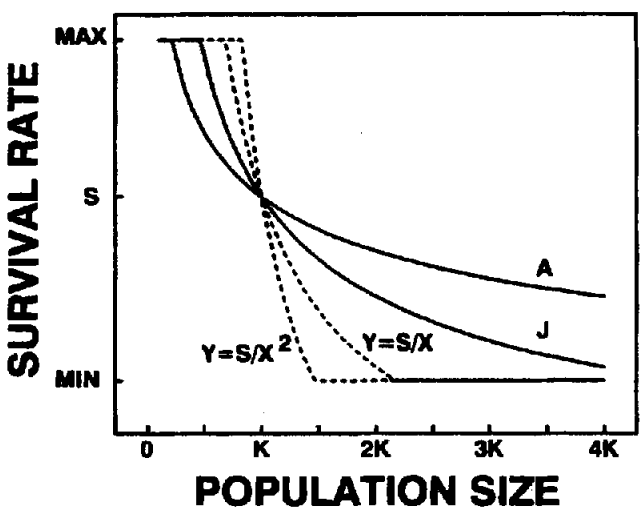

Figure 1. Density-dependent functions relating survival rates to population density. Lines A and J, respectively, illustrate the adult and juvenile survival functions (Table 2) used in all simulations illustrated in Figures 3–7. Simulations using stronger density-dependent functions (dashed lines) did not change the risk of extinction. In all simulations the juvenile survival function was one line steeper than the adult survival function. K = Carrying capacity for the appropriate sex. Max = 0.95 (adults) or 0.9 (juveniles). Min = 0.5 (adults) or 0.3 (juveniles). S = Survival rate at carrying capacity.

Table 2. Equations used to create density-dependence in cougar survival rates. S = the 12-month survival rate at carrying capacity; KF and KM = carrying capacity for breeding females and males respectively; #AdFemales and #AdMales = number of ≥2-year-old females and males, respectively.

Age	*Sex*	*Expression for Density-Dependent Survival Rate*[a]
0	both	$S * (KF/\#AdFemales)^{0.5}$
1	F	$S * (KF/\#AdFemales)^{0.5}$
	M	Minimum of: $S * (KF/\#AdFemales)^{0.5}$ or $S * (KF/\#AdFemales)^{0.5} * (KM/\#AdMales)^{0.5}$
2	F	$S * (KF/\#AdFemales)^{0.5}$
	M	$S * (KM/\#AdMales)^{0.5}$
3+	F	$S * (KF/\#AdFemales)^{0.25}$
	M	$S * (KM/\#AdMales)^{0.25}$

[a] *To avoid unrealistic results that the above expressions yield under certain conditions (such as when a divisor approaches or equals zero), the program truncated all survival rates to values between 0.3 and 0.9 for animals under 3 years of age, and between 0.5 and 0.95 for adults.*

males, reflecting density-dependent mortality of young males during dispersal. Density-dependence was relatively mild for animals less than 2 years old. There is no empirical data to support these particular functions (Table 2); they were chosen for computational simplicity. In light of the markedly changed outcomes when density dependence was added to the model (above), I tested the model using more severe density-dependent functions. Neither risk of extinction nor ending population size varied among the functions illustrated in Figure 1.

STOCHASTIC VARIATION

Most simulation models introduce stochastic variation into survival rates by randomly selecting a rate from a normal distribution and then multiplying this rate by the number of individuals in an age-sex class. When there are only one or two animals in a sex-age class, this approach introduces rounding errors that increase the survival rate to near 100% and, ironically, eliminate stochastic variation (Beier, unpublished data). To avoid this problem, the model applied the appropriate probability to each individual animal in the population. For example, if the survival rate for yearling males was 0.60 and there were two yearling males in a given year, all outcomes (2, 1, or 0 survivors) were possible (with binomial probabilities 0.36, 0.48, and 0.16, respectively) in a biologically realistic manner.

Similar procedures introduced stochasticity into primary sex ratio, litter sizes, and immigration rates. Each newborn had a 50% chance of being male. Each litter had two, three, or four cubs with probabilities appropriate to the specified mean value. Each year one male or one female immigrated with the appropriate probability, and the immigrant was assigned to the 1-year,

2-year, or 3-year age class with probability equal to 0.3, 0.5, and 0.2, respectively.

Field Work in the Santa Ana Mountains

The cougar population in the Santa Ana Mountain Range of southern California consists of about twenty adults on about 2070 km^2 of habitat (Fig. 2) (Beier & Barrett 1992*b*). The surrounding urban areas do not offer even marginal cougar habitat. About 1270 km^2 of this habitat (61%) is protected from urban uses, primarily within lands owned by the U.S. Forest Service and U.S. Navy (Table 3). Of the protected land, about 1114 km^2 forms a contiguous block; if all private lands were developed,

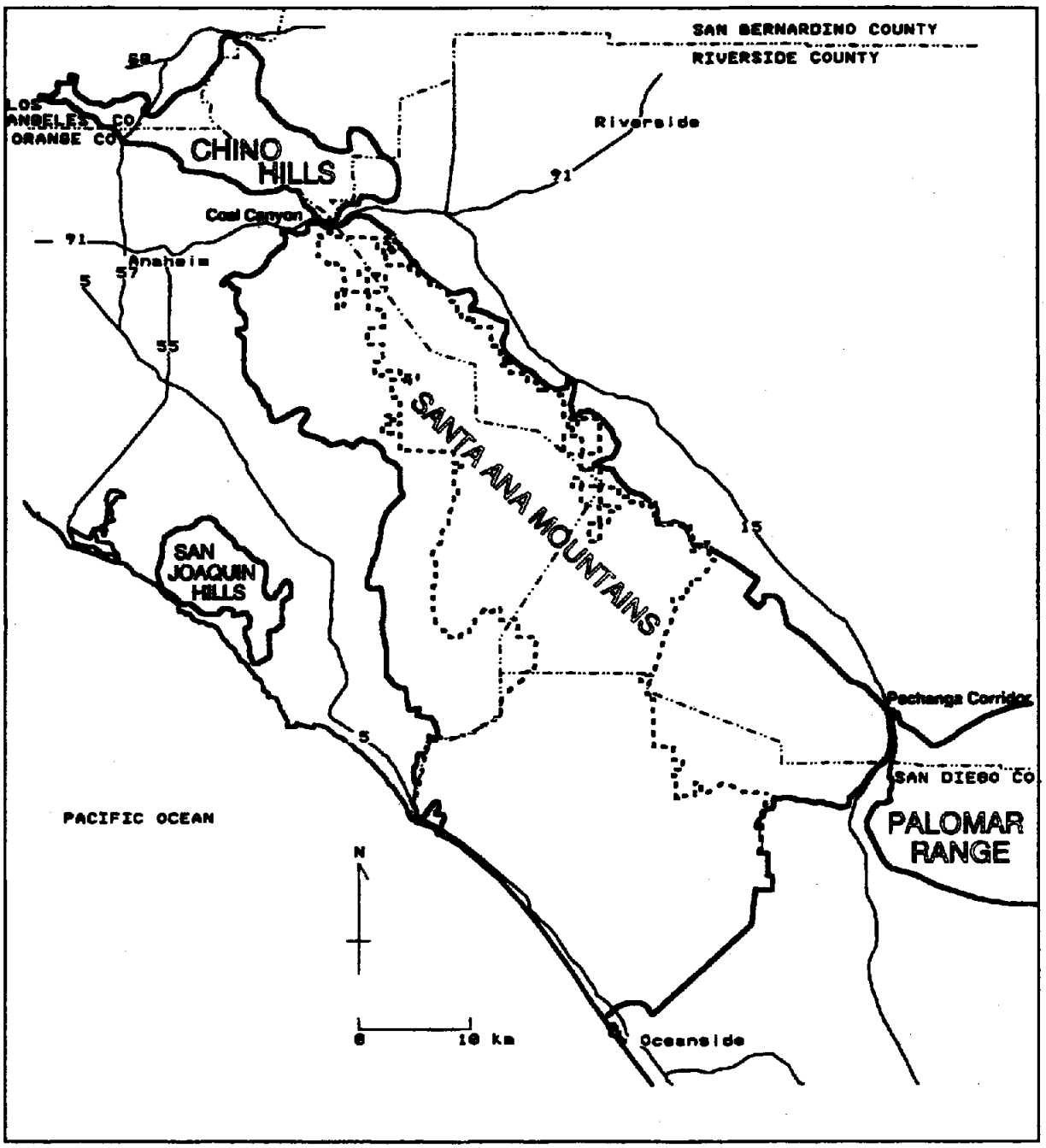

Figure 2. The heavy solid line encloses three areas: 2070 km^2 of cougar habitat in the Santa Ana Mountain Range (including the Chino Hills); 75 km^2 of suitable habitat in the San Joaquin Hills (recently extinct); and (east of Highway 15) a portion of the habitat in the adjacent Palomar Range. The heavy dashed line encloses 1114 km^2 of protected and connected parcels (Table 3). All roads shown are 6- to 10-lane freeways.

Table 3. Area in hectares of protected lands contained within cougar habitat in the Santa Ana Mountain Range, California.

Ownership and Parcel Name	*Areas Forming a Large Contiguous Block*	*Areas Surrounded by Unprotected Land*
Federal		
Cleveland National Forest	53,604[a]	
Cleveland National Forest (6 parcels)		626
Camp Pendleton	49,292[b]	
Fallbrook Naval Weapons Station	3,099	
Bureau of Land Management (7 parcels)		550
Bureau of Land Management (1 parcel)	364	
State		
Chino Hills State Park		5,059
San Diego State University Field Station		1,805[c]
Dept Fish & Game Coal Canyon Preserve	385	
Orange County Parks		
Caspers	3,085	
Limestone Canyon		2,169[d]
O'Neill		805
Whiting Ranch		632
Irvine		193
Wagon Wheel		178
Santiago Oaks		142
Private Reserves		
Santa Rosa Plateau Preserve		2,803[e]
National Audubon Society Starr Ranch	1,578	
Rancho Mission Viejo Conservancy		486
Total	111,407	15,448

[a] *Excludes private inholdings.*
[b] *Includes land leased to San Onofre Beach State Park; excludes 1700 hectares in urban use and airfield; includes some severely affected bombing ranges that may not be suitable habitat.*
[c] *Includes 510 hectares of Bureau of Land Management land administered by the field station.*
[d] *Expected to be transferred to county from private ownership.*
[e] *Administered by The Nature Conservancy (TNC); includes lands owned by TNC, State of California, and Riverside County.*

the other 154 km^2 of protected land would be isolated into fragments unusable by cougars.

The six counties of southern California contain 5% of the U.S. human population. The human population of the eastern half of Orange County and the western sixth of Riverside County is projected to grow from 1.15 million in 1987 to 2.09 million by 2010 (Anonymous 1989). Most of this growth is expected to occur in tract homes built in privately-owned open spaces, including most of the best cougar habitat. In addition to outright habitat destruction, some wildlands are lost to the cougar population because they become isolated by freeways and other development. For example, after urbanization isolated a 75-km^2 fragment of cougar habitat (Fig. 2, San Joaquin Hills) in the late 1970s, cougars became extinct there by June 1990 (Beier & Barrett 1990*a*).

In early 1988, field work began in the southern half of the range, focusing on seven telemetered adult females. In January 1988, one such female had 3-month-old triplets and a second had a single yearling cub at heel. After the death of a mature male cougar in February 1988, there was no additional reproductive activity and no sign of a breeding male for over 12 months (Padley 1990:40–43). When two young males established themselves as breeders in early 1989, their tracks and vocalizations were obvious. In April 1989 we heard copulatory vocalizations involving four telemetered females, and that summer six of the seven females bore cubs (Padley 1990). The presumed sires of these litters (two adult males subsequently captured and radio-tagged) were both 2 years old at the time they became breeders. Therefore, all evidence suggests that there was no adult male and no reproduction in the southern half of the range for a full year.

In 1989 the study expanded to include the entire mountain range. We intensified our efforts to collar predispersing animals, and four times per month we selected a focal animal whose location was determined every 15 minutes from 1 hour before sunset until 1 hour after sunrise. This research has focused on (1) identification of existing or potential corridors for immigration into the population as a whole; (2) identification of lands within the mountain range that connect nearly-isolated patches of habitat; and (3) documentation of the travel paths used by cougars, especially dispersing animals, and especially paths between areas designated as permanent open space. If protected, such paths can be expected to become corridors as future human activities affect the adjacent habitat.

Results

Rejection of Unrealistic or Uninformative Parameter Values

To reduce the results to a digestible mass, I first rejected parameter values that produced unrealistic outcomes or that did not influence the results. For example, the mean number of adults in year 100 was 70–80% of carrying capacity whenever adult survivorship equalled 0.65, even with a habitat area of 3000 km^2 and the highest estimates for juvenile survival rate, mean litter size, and carrying capacity. If carrying capacity is ever to be observable in nature, it should be so under these conditions, so I excluded the adult survival rate of 0.65 from consideration.

Similarly, because a mean litter size of 2.4 tended to produce ending population sizes about 15% below carrying capacity, this litter size was excluded. Extinction rates decreased only trivially when mean litter size increased from 2.8 to 3.2. Because available data best support a mean litter size of 2.8, the mean litter size of 3.2 was also excluded from further consideration. Finally, extinction risk increased only trivially as the severity of the catastrophe (temporary loss of carrying capacity) increased from 0% to 20% to 40%. All results reported herein used the 20% reduction.

Influence of Habitat Area and Level of Immigration

The main factors of interest were those under human control, i.e., area of habitat and the presence (or absence) of a corridor allowing various levels of immigration. As expected, both factors influenced the probability of extinction (Figs. 3–5).

Despite variation in model predictions due to uncertainty in biological parameters, 98% or more of simulated populations persisted for 100 years when there was 2200 km^2 or more of habitat available, except under the most pessimistic estimates of biological parameters (carrying capacity of 0.4 or fewer adult females and 0.2 adult males per 100 km^2, in concert with adult survivorship of 0.75 or less).

As expected, the probability of extinction increased as area of habitat decreased. With only 1000 km^2 of habitat and no immigration, simulated populations had 98% persistence only under the most optimistic estimates of biological parameters (carrying capacities of 1.0 or more adult females and 0.5 adult males per 100 km^2, in concert with adult survivorship of 0.85 or more and juvenile survivorship of 0.65 or more). In the absence of an immigration corridor, therefore, the critically small habitat area lies between 1000 and 2200 km^2. Within this range, the critical size depends on demographic parameters (next section).

Immigration improved the probability of survival at surprisingly low levels—as low as one male per decade. For any given combination of biological parameter estimates, the critical habitat area was 200–600 km^2 smaller with an immigration corridor than without. Immigration had no influence on the mean size of the adult population in year 100 for populations that survived.

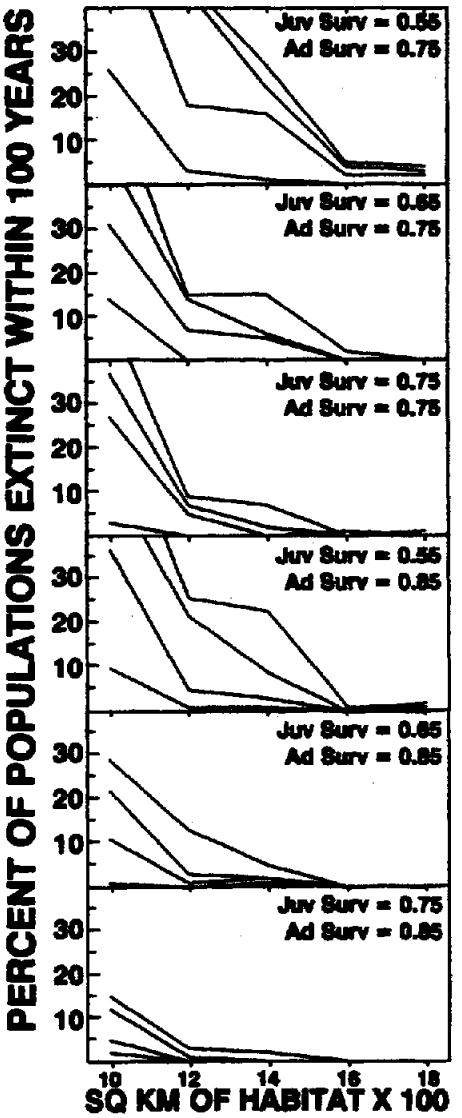

Figure 3. Effect of habitat area and immigration on cougar population persistence, given a carrying capacity of 0.6 breeding adult females and 0.3 breeding adult males per 100 km^2. In each graph the top through bottom lines give the percent of simulated populations that went extinct within 100 years when the numbers of immigrants per decade were 0, 1 male, 2 males, or 3 males and 1 female, respectively. Juv Surv (juvenile survival rate) and Ad Surv (adult survival rate) are defined in Table 1.

Influence of Biological Parameters

Predictions were sensitive to all of the biological parameters, especially the estimates of carrying capacity (Figs.

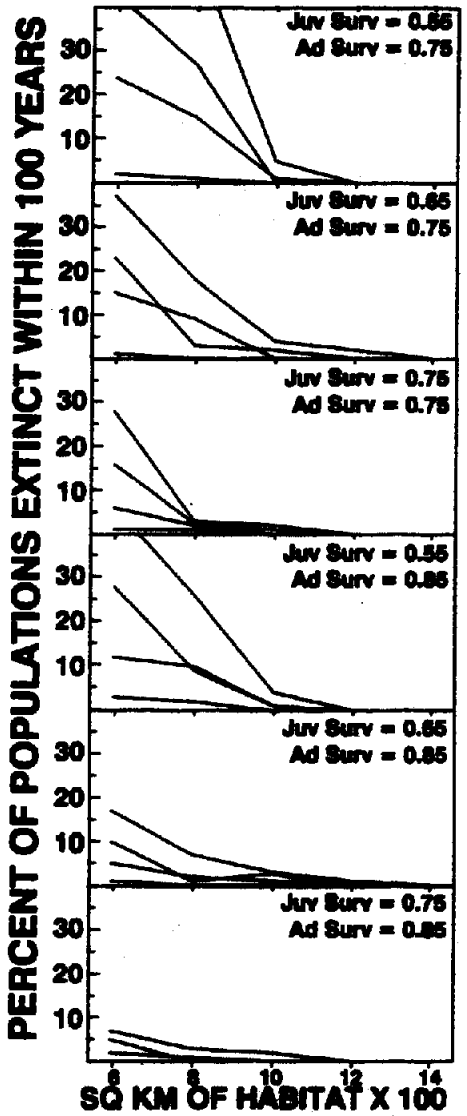

Figure 4. Effect of habitat area and immigration on cougar population persistence, given a carrying capacity of 1.2 breeding adult females and 0.4 breeding adult males per 100 km². In each graph the top through bottom lines give the percent of simulated populations that went extinct within 100 years when the numbers of immigrants per decade were 0, 1 male, 2 males, or 3 males and 1 female, respectively. Juv Surv (juvenile survival rate) and Ad Surv (adult survival rate) are defined in Table 1.

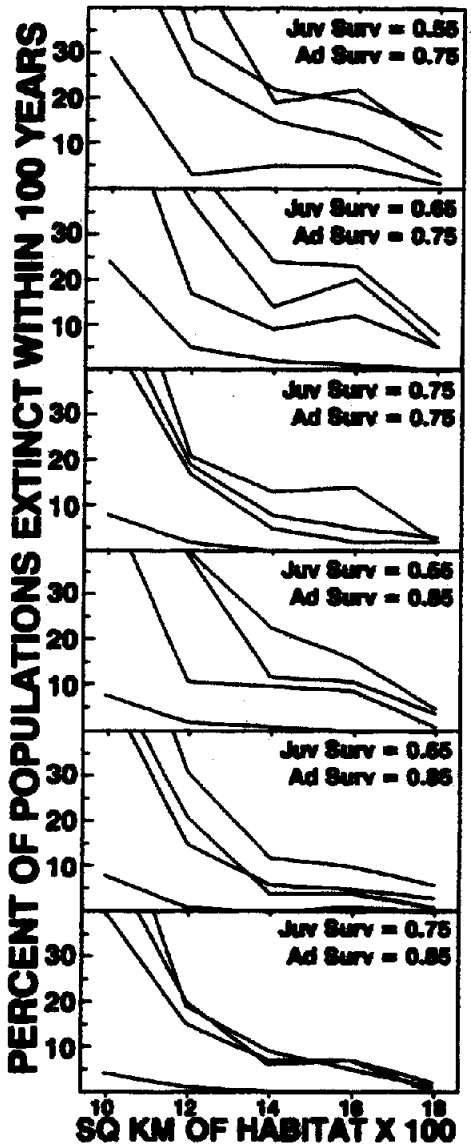

Figure 5. Effect of habitat area and immigration on cougar population persistence, given a carrying capacity of 0.4 breeding adult females and 0.4 breeding adult males per 100 km². In each graph the top through bottom lines give the percent of simulated populations that went extinct within 100 years when the numbers of immigrants per decade were 0, 1 male, 2 males, or 3 males and 1 female, respectively. Juv Surv (juvenile survival rate) and Ad Surv (adult survival rate) are defined in Table 1.

3–5; graphs for carrying capacities listed in Table 1 but not illustrated herein are available on request). Both juvenile and adult survivorship values also had important influences on model results (Figs. 3–5).

The adult sex ratio (the ratio of carrying capacity for females to that for males) was also important. When the adult sex ratio was skewed toward females (Figs. 3–4), immigration of one or two males per decade had the most pronounced rescue effects. This was most evident with a highly skewed sex ratio (Fig. 4). In contrast, immigration of one or two males had a relatively muted rescue effect on populations with equal sex ratios. These populations, however, benefited dramatically from a corridor that allowed four immigrants (including one female) per decade (Fig. 5).

Population Trajectory

For populations with low extinction risk, the population trajectory on a run of 100 years fluctuated near carrying capacity (for example, see Fig. 6A). Despite this relative stability, the age and sex composition of the simulated population showed considerable variation, even when smoothed by taking 5-year running means (Fig. 6B). Surprisingly, most trajectories showed no response to the simulated "catastrophes," despite 20–40% reductions in carrying capacity in years 26–28, 51–53, and 76–78 (see Fig. 6A).

Populations at greater risk of extinction showed even greater demographic instability (Fig. 6C). When the sex ratio was skewed toward females, the most common extinction scenario was loss of breeding males at a time when no male cubs survived.

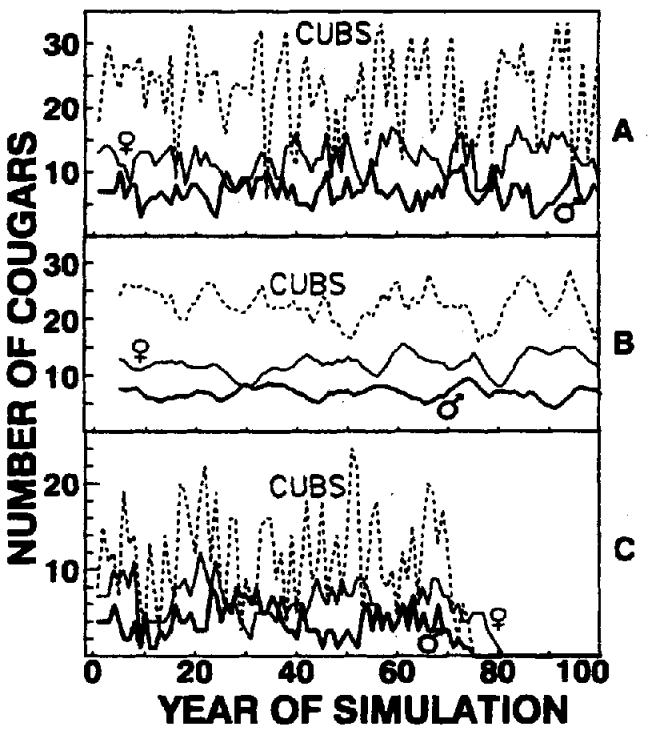

Figure 6. Trajectories of simulated cougar populations with juvenile survivorship = 0.55, adult survivorship = 0.85, carrying capacity = 0.6 female and 0.3 male adults/100 km², no immigration, and a 20% loss of carrying capacity lasting 3 years every 25 years. **A.** *With 2200 km² of habitat, all populations persisted. As in this typical trajectory, age and sex composition of the population varied markedly over time.* **B.** *Five-year running means from panel A, showing that even with five years of observation, population demographics varied considerably.* **C.** *With 1200 km² of habitat, demographic instability increased and 25% of the simulated populations went extinct. As in this typical trajectory, extinction was usually initiated by loss of adult males.*

Applying the Population Model in the Santa Ana Mountains

Given the best local estimates for survivorship rates and carrying capacity, the model predicted that the cougar population in the Santa Ana Mountains is clearly endangered. Although there is less than 3% risk of extinction in the next 100 years with the current 2070 km² of habitat and no immigration, every parcel of habitat lost increases the risk of extinction (Fig. 7). If the population is confined to the 1114-km² block of contiguous protected lands, extinction risk rises to about 33%; an immigration corridor, necessarily including some lands now in private ownership, would greatly improve the prognosis.

Inter-Range Corridor

The only population that can potentially supply immigrants to the cougar population in the Santa Ana Mountain Range is that in the Palomar Range. Interstate Highway 15 and the urban developments along it present the most formidable barrier to wildlife movements between these ranges. A bridged river provides the only safe undercrossing of Highway 15, and there is only one potential corridor between the Palomar range and this un-

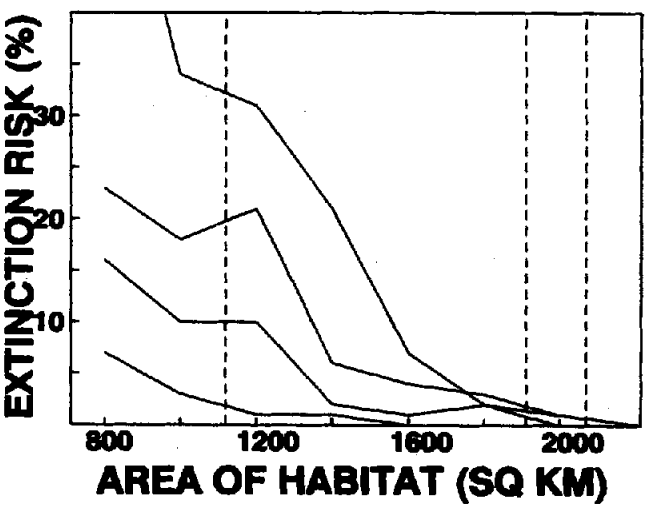

Figure 7. Extinction risk for the cougar population in the Santa Ana Mountains. The top through bottom lines give the percent of simulated populations that went extinct within 100 years when the numbers of immigrants per decade were 0, 1 male, 2 males, or 3 males and 1 female, respectively. From right to left, the vertical lines indicate total available habitat in 1992, total available habitat if the Chino Hills is lost, and total area of the protected and interconnected habitat block. Simulations were run with the following estimates: carrying capacity = 0.7 adult females and 0.35 breeding adult males/100 km², juvenile survivorship = 0.50, and adult survivorship = 0.80.

derpass (Beier & Barrett 1990*b*, 1992*b*). The potential corridor is about 4.5 km long and follows an intermitent watercourse (Pechanga Creek) and the wooded ridges south of this creek (Fig. 2: Pechanga Corridor). Although creeks tend to be natural travel corridors, the utility of lower Pechanga Creek as a corridor is compromised by night lighting from adjacent tract homes, streambed degradation by recent construction, a concrete embankment on portions of the north bank, and removal of woody vegetation for golf courses on the south bank. There are also several residences, an abandoned quarry, a two-lane paved road, and a golf course in the wooded ridges south of the creek.

Although no single one of these obstacles occludes the corridor, collectively they probably prevent immigration by mountain lions into the Santa Ana Range. Field evidence suggests that the corridor *almost* works. On 3 August 1990, a dispersing male mountain lion failed to negotiate the corridor, wandering into a rural residential area where he was captured by wardens. On 29 October 1990, another cougar was killed on I-15 just south of the bridged underpass. On 21 January 1992, a telemetered dispersing male successfully used the corridor to emigrate from the Santa Ana Mountains to the Palomar Range. However, he avoided the bridged undercrossing and the lower 4 kilometers of Pechanga Creek, and was lucky not to have been struck crossing I-15. The pattern of topography and habitat degradation makes it even less likely that a west-bound immigrant would successfully find the undercrossing (Beier & Barrett 1992*b*).

Intra-Range Corridors and Travel Paths

Our data on cougar travel paths (including detailed observations on dispersal routes) have identified specific areas that now prevent intra-range fragmentation. The most threatened link is that connecting the Chino Hills (about 150 km^2 of cougar habitat, including a 57-km^2 state park) to the rest of the mountain range (Fig. 2: Coal Canyon Corridor). State Route 91 and adjacent developments present the greatest obstacle to movement between these areas. The Coal Canyon corridor provides an excellent natural travel route to the freeway and two usable passageways under it (Beier & Barrett 1990*a*, 1991). At least two (probably three) cougars successfully used the Coal Canyon corridor and its underpasses to cross Route 91 into the Chino Hills. In addition, one telemetered cougar was struck by a vehicle attempting to cross the freeway at the mouth of Coal Canyon. One telemetered male dispersed from over 60 kilometers away to establish a home range that now straddles Route 91; he has used the Coal Canyon corridor to cross the freeway at least 16 times during May–December 1991. A pending proposal to build 1500 homes on a 150-ha parcel in Coal Canyon would sever this link, eliminating cougars from the Chino Hills.

Discussion

Population Model

In the absence of immigration, a habitat area of 1000–2200 km^2 (depending on the demographics of a particular population) is needed to support a cougar population with a 98% or more probability of persistence for 100 years; these minimum areas would hold about 15–20 adult cougars. These areas are far smaller than the area assumed necessary to support a population of large carnivores for several centuries without loss of genetic variability (Franklin 1980). It must therefore be stressed that provision of the minimum areas suggested by this model will not guarantee long-term survival of a population. In cases where no immigration corridor is provided, populations confined to such small areas will require monitoring and perhaps periodic intervention—such as introduction of new genetic material through translocation.

The attempt to eliminate some of the values for biological parameters (Table 1) yielded two biological insights. First, natural catastrophes of moderate severity (up to 40% loss of carrying capacity), frequency (every 25 years), and duration (3 years) appear unimportant to cougar population persistence. Shaffer (1983) similarly concluded that catastrophes were relatively unimportant to the population dynamics of grizzly bears. Future modeling efforts can investigate whether this surprising result also holds for disturbances of greater severity and frequency. Second, because adult survivorship of 0.65 or less prevented simulated populations from reaching carrying capacity, management of small populations should include attempts to control factors—such as depredation permits, construction of road undercrossings—that might influence adult survival rate.

These minimum areas and the number of cougars present therein are comparable to the minimum area and number suggested by Shaffer (1983) for grizzly bears. Both my model and Shaffer's incorporated density dependence and produced minimum areas and populations much smaller than predicted by analytic models (see Belovsky 1987) or simulation models lacking density dependence (Captive Breeding Specialists Group 1989; Ginzburg et al. 1990; this paper, Methods).

Ginzburg et al. (1990) advocated use of density-independent models to generate conservative estimates of extinction risk when it is highly sensitive to the shape of the density-dependent function (assuming the true function is unknown). However, to the extent that a density-independent analysis misclassifies viable populations as "hopelessly" small, it can be a *less* conservative approach. Furthermore, extinction risk in my model was not sensitive to the shape of the density-dependent function (Fig. 1). Therefore I chose a density dependent model because it is more realistic. In general, "all natural populations are ... influenced by density-dependent

processes" (Begon & Mortimer 1981:162). For cougars in particular, long-term observation in Idaho (Hornocker 1970; Seidensticker et al. 1973; Quigley et al. 1989) and the Ruby Mountains of Nevada (Ashman et al. 1983) show the stability characteristic of populations with density-dependent regulation. The data of Quigley et al. (1989) also suggest that cougar numbers track major long-term changes in carrying capacity (prey abundance). Finally, simulated populations with density-independent survival rates (when they persisted) often had unrealistically high ending densities (see Methods, Density-Dependence in Survival Rates).

If a wildlife movement corridor is available to allow immigration of up to three males and one female per decade, an area as small as 600–1600 km^2 (depending on the demographics of a particular population) can support a cougar population without significant extinction risk in 100 years. Doubtless higher levels of immigration would allow even smaller areas to support cougars. Thus, in areas where isolation or fragmentation of a cougar population appears imminent, protection and enhancement of any remaining corridor is valuable.

The model predicts that south Florida, with 8800 km^2 of occupied range and an adult density of about 0.6 adults per 100 km^2 (Maehr 1990) has adequate habitat for demographic persistence. Captive Breeding Specialists Group (1989), also using a simulation approach, concluded that the Florida population faced a high risk of extinction. These predictions do not necessarily conflict, however, because the CBSG model included extinctions caused by inbreeding effects and excluded enhancement of survival rates when populations were below carrying capacity. In any event, the best panther habitat in Florida is privately owned (Maehr 1990), and rapid agricultural and urban development could soon fragment this habitat into dangerously small parcels. The aggressive protection of habitat and movement corridors is essential to ensure the persistence of Florida panthers.

Two Caveats in Applying this Model

Two caveats apply to this model. First, the model is sensitive to the estimates for carrying capacities for adult males and females. Uncritical use of estimates from a different area or habitat type should be avoided. Because cougars are K-selected, it is probably reasonable to estimate carrying capacity from locally observed densities. However, the great variation in sex and age composition in simulated populations suggests that at least five years of study are needed for reliable estimates (Fig. 6A–B). Also, the carrying capacities used in this model must be estimated by numbers of breeding adult males and females, excluding the pool of nonbreeding male and female transients that characterize most populations (Seidensticker et al. 1973). Categorizing all individuals over 1 year of age as adult breeders would lead to overly optimistic predictions.

Second, survival rates observed for a population occupying a large area will probably decrease as area decreases and degree of isolation increases, due to increased highway mortality (Beier & Barrett 1992*a*) and decreased dispersal success. A conservative approach necessitates use of lower-than-observed survival rates in making projections for a population that has not yet been fragmented or isolated.

Application to the Santa Ana Mountain Range: Site-Specific Data along with Model Conclusions Can Save Land

If survival of this population is a goal, the model yields several clear conclusions (Fig. 7). Developments that isolate or destroy large tracts of habitat should be avoided. A corridor for immigration is of paramount importance. Within the mountain range, corridors are also needed to interconnect the protected parcels (Table 3).

Unfortunately, these conclusions alone have little power to save land in the prodevelopment political climate of southern California. For example, although the admonition to "avoid destroying large tracts" can be implemented without additional data, few planning decisions involve tracts that are "large" relative to the habitat needed to support a cougar population. The other conclusions cannot be heeded without additional data, especially on the location of movement corridors.

Field data suggest that habitat degradation probably prevents any regular inflow via the last potential corridor for immigration (Fig. 2: Pechanga Corridor). Except for the 15-year-old freeway, the obstacles to the Pechanga Corridor are less than 5 years old. If a regional, spatially-explicit land-use plan had been in place in 1986, the importance of this corridor would have been obvious and the obstacles preventable. Strict protection of the remaining habitat and additional habitat modification and restoration will now be necessary if the Pechanga Corridor is to function (Beier & Barrett 1992*b*). The Nature Conservancy is actively interested in taking such steps but faces an uphill struggle.

Our work has also spotlighted a critical corridor necessary to prevent intra-range fragmentation (Fig. 2: Coal Canyon). The City of Anaheim is now considering approval of a housing project that would destroy this corridor. Our documentation of both the importance and use of this corridor should result in a scaled-back project that leaves the corridor intact. The population model convincingly predicts that loss of this corridor would guarantee the extinction of cougars from the 150 km^2 of habitat north of the freeway, reducing by 7.5% the total habitat available to our population and pushing the population leftward to the steeply rising part of the risk curve (Fig. 7). The field work shows that the corridor is in fact used. Thus the model and the field work

together may provide sufficient documentation to protect this corridor; certainly neither could do so alone.

In another application, the model and complementary fieldwork are having limited success in mitigating the effects of a planned freeway; its proposed route slices through a pristine area with no human residents along its 21-kilometer length (Anonymous 1990). This freeway would affect wildlife movement between the bulk of habitat on one side of the road and five smaller areas of dedicated open space on the other side. By all-night radio-tracking of individual focal animals, we have learned the actual routes by which cougars travel among these areas. Although these routes now traverse pristine open space, they will become corridors (at best) as freeway-induced growth removes the adjacent habitat. The transportation agency has responded to this information by planning bridged undercrossings at the five most important crossing points. Previously, the agency had planned on only one of these bridges, and the location was based on geological rather than biological considerations.

Unfortunately, preserving a corridor is not as simple as building a bridge at one point along the corridor. The road-building agency has acknowledged that the freeway, by providing "critical infrastructure to large expanses of open space," will induce massive urban growth (Anonymous 1990:5.13); such growth could sever all of the wildlife corridors, rendering the underpasses pointless. The agency has refused requests to purchase easements to the three most important corridors as mitigation for this induced growth, and it currently faces a lawsuit on this issue.

Conclusions

The cougar is an ideal species for identification of movement corridors for two reasons. First, cougars are an area-sensitive species; therefore a corridor identified on the basis of cougar use will benefit at least one species. Second, a hunting cougar travels an average of 5.5 miles per night (Beier, unpublished data) and thus generates a lot of corridor data in a short time. Collection of comparable data for a less wide-ranging species may take years or generations.

I do not advocate using cougars as a proxy for all species of concern. However, management decisions will not await the conclusion of long-term studies on more sedentary species. In western North America, use of data from telemetered cougars may be the most expedient way to interject biological facts into the analysis of environmental impact and mitigation related to movement corridors. It is certainly a big step above current practices, which include (1) looking at aerial photos in an office and guessing where a corridor ought to be; or (2) labeling the leftover shards of habitat, or the bridge built according to geological constraints, as the "wildlife corridor."

Effective protection of wildlife corridors requires *putting them on the map.* Unfortunately, the current mechanism for such protection is for concerned citizens to detect and force mitigation on each proposed project that threatens the corridor. For the cougar population in the Santa Ana Mountains, this requires monitoring and being prepared to litigate decisions made by five county governments, seventeen municipal governments, two transportation authorities, and the world's largest water district. Because a corridor is only as strong as its weakest link, a single oversight or failure on the part of conservationist volunteers is sufficient to lose the linkage.

Putting wildlife corridors and critical habitat on a planner's map can best be done through a geographic information system covering a *regional* landscape. Although General Plans are mandated for each county in California, such plans are rarely site-specific in any recommendations and are almost never tied to a GIS. Furthermore, as the present case illustrates, a single population or wildland may span several counties, and land-use planning is nonexistent at the regional level.

A spatially-explicit planning tool such as a GIS is essential because it provides the only efficient means of addressing cumulative impact and an accessible forum on which developers, conservationists, and other citizens express their vision of the regional landscape at build-out. Scott et al. (1990) describe a GIS-based approach that would admirably serve a regional plan, and Hollings (1978) gives practical advice that should inspire such planning.

Acknowledgments

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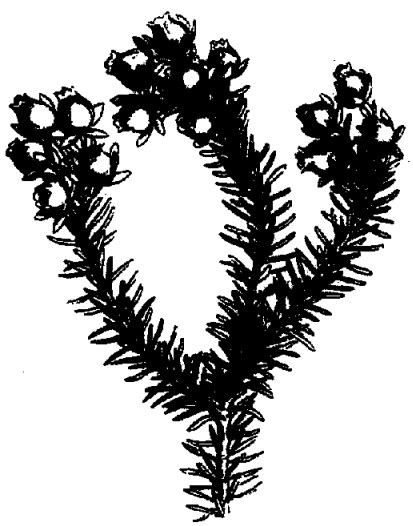



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DISPERSAL OF JUVENILE COUGARS IN FRAGMENTED HABITAT

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Abstract: There is little information on the spatiotemporal pattern of dispersal of juvenile cougars (*Felis concolor*) and no data on disperser use of habitat corridors. I investigated dispersal of radio-tagged juvenile cougars (8 M, 1 F) in a California landscape containing 3 corridors (1.5, 4.0, and 6.0 km long) and several habitat peninsulas created by urban growth. Dispersal was usually initiated by the mother abandoning the cub near an edge of her home range. The cub stayed within 300 m of that site for 13–19 days and then dispersed in the direction opposite that taken by the mother. Mean age at dispersal was 18 months (range 13–21 months). Each disperser traveled from its natal range to the farthest part of the urban-wildland edge. Dispersing males occupied a series of small (<30% the area used by ad M in the same time span), temporary (10–298 days) home ranges, usually near the urban-wildland interface, and often with its longest border along that edge. Each of the 3 corridors was used by 1–3 dispersers, 5 of the 9 dispersers found and successfully used corridors, and 2 dispersers entered but failed to traverse corridors. Dispersing cougars will use corridors that are located along natural travel routes, have ample woody cover, include an underpass integrated with roadside fencing at high-speed road crossings, lack artificial outdoor lighting, and have <1 dwelling unit/16 ha.

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Key words: California, corridors, cougar, dispersal, *Felis concolor*, habitat fragmentation, mountain lion, population dynamics, urban.

For carnivores, dispersal is the movement of an individual away from its natal range upon reaching the age of independence (Bekoff 1989: 104). Dispersal plays an important role in cougar population dynamics because recruitment into a local population occurs mainly by immigration of juveniles from adjacent populations, while the population's own offspring emigrate to other areas (Seidensticker et al. 1973). Dispersal enables cougars to expand their ranges and recolonize habitats where chance local extinction has occurred (Hemker et al. 1984). However, most studies of cougar dispersal have been limited to reports of age at onset of dispersal and net distance moved from the predispersal home range (except Hornocker 1970:16, Maehr et al. 1991*b*, Seidensticker et al. 1973:18, Anderson et al. 1992).

Cougars have been used as a focal species in planning habitat corridors to facilitate animal movement between larger habitats in a regional landscape (Harris and Scheck 1991, Beier and Loe 1992, Royte 1992). However, corridors decrease extinction risk only if they aid dispersal (Beier 1993), and there is no evidence on whether cougars use corridors during dispersal. My objectives were to (1) describe movements of mother and offspring just before dispersal, juvenile movement patterns during dispersal, and characteristics of transient home ranges (THRs) used by dispersers, and (2) document how dispersers negotiate the urban-wildland interface, including corridors and habitat peninsulas.

This paper is dedicated to colleagues working on the Paseo Pantera, a 7-nation effort to link wildlands in the Central American isthmus. Research was supported by California Agricultural Experiment Station Project 4326-MS, California Department of Fish and Game (CDFG), Orange County, and the U.S. Marine Corps. D. Choate, K. Drewe, D. Krucki, W. D. Padley, T. Tennant, and D. Wroe were radio trackers. I thank CDFG telemetry pilots R. Anthes and J. Veal, and especially pilots R. C. Chipman, J. T. Hornacek, and J. Williams, who donated their services. Friends of Tecate Cypress, the Mountain Lion Foundation, The Nature Conservancy, Sierra Club, and others have struggled to maintain connectivity in the Santa Ana Mountains. I thank B. B. Ackerman, T. H. Hemker, R. F. Noss, D. S. Maehr, and an anonymous reviewer for comments. This study operated under Animal Use Protocol R139-0394 issued by the Animal Care and Use Committee at the University of California at Berkeley.

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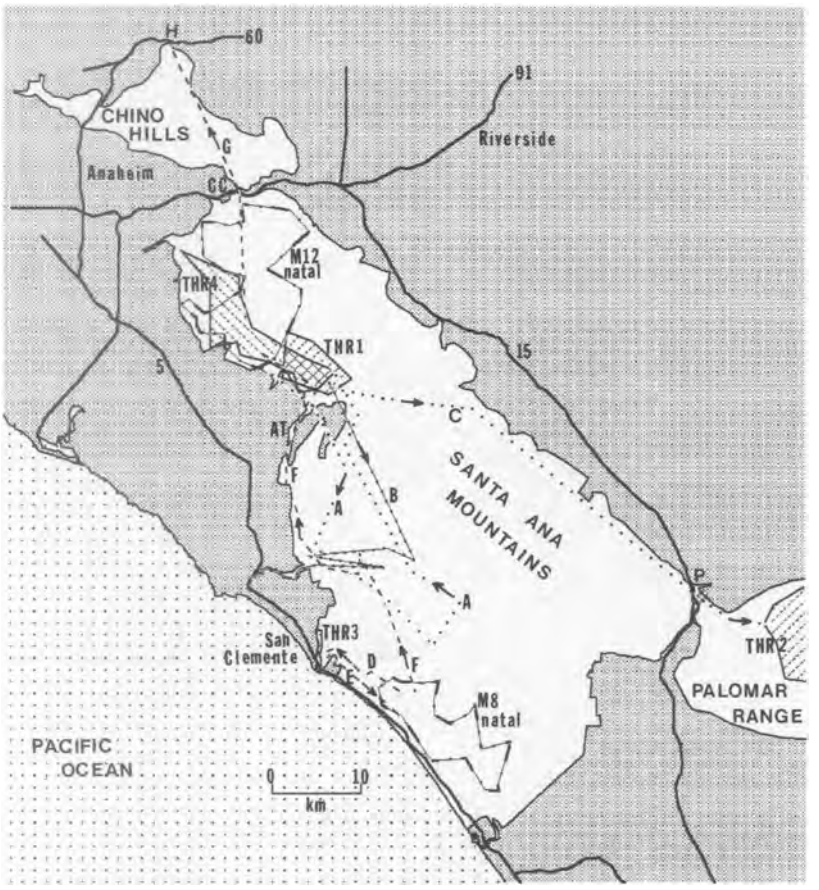

Fig. 1. Santa Ana Mountains study area and dispersal movements of cougars M8 and M12 in southern California, 1990–92. Urban (nonhabitat) areas are indicated by dark stippling, transient home ranges (THR) by diagonal hatching. All roads shown are 6- to 10-lane freeways. The 3 habitat corridors are designated CC (Coal Canyon), AT (Arroyo Trabuco), and P (Pechanga, with the Temecula Creek habitat peninsula extending east from the label). All thin habitat peninsulas shown were explored by dispersers. Natal ranges (natal) enclose mothers' locations for 12 months before dispersal. A (35 days, 94 km): M12 abandoned natal range and wandered before establishing THR1. B (16 days, 87 km): During an excursion from THR1, M12 explored this 6-km habitat peninsula, then returned to THR1 within 48 hours. C (8 days, 59 km): Abandoning THR1, M12 used the Pechanga Corridor to reach THR2 (partially shown) in the Palomar Range. D (12 days, 16 km): M8 abandoned natal range and moved to THR3 for 18 days. E (2 days, 17 km): M8 abandoned THR3, returned to natal range for 7 days. F (17 days, 67 km): M8 used the Arroyo Trabuco Corridor en route to THR4 (used 70 days). G (2 days, 20 km): M8 abandoned THR 4, moved into the Chino Hills via Coal Canyon Corridor. H: 20 days later he was killed in a vehicle accident at the end of a habitat peninsula.

STUDY AREA

I studied cougars in the Santa Ana Mountains of southern California (Fig. 1) from May 1988 through December 1992. Radio-tagged juveniles dispersed only during the final 27 months (Beier and Barrett 1993). The cougar population (approx 20 ad) used about 2,070 km^2 of habitat (Fig. 1). Over 1.1 million people lived in the 17 cities and 7 unincorporated towns surrounding the mountain range. About 61% of cougar habitat in the area was protected within Cleveland National forest, Camp Pendleton, and several smaller reserves (Beier 1993). Terrain was rugged, with elevation varying from 0 to 1,680 m, and vegetation included chaparral, coastal scrub, oak (*Quercus agrifolia* and *Q. engelmannii*) woodlands, and annual grasslands. Small areas of coniferous forest occurred at higher elevations, mainly on north-facing slopes. Few drainages had perennial aboveground water flow, but seeps and springs were well distributed throughout the range. Cougars were born in all seasons, with a peak in summer.

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METHODS

Corridors and Habitat Peninsulas

Before radiotracking dispersers, I identified 3 potential corridors (Coal Canyon, Pechanga, and Arroyo Trabuco) connecting larger habitat parcels in the area (Fig. 1). These 3 areas were not designed as wildlife movement corridors, but were simply habitats made linear by urban growth.

The Coal Canyon Corridor provided the only potential habitat link between the Santa Ana Mountain Range and the Chino Hills, and was the shortest of the 3 corridors, with 1.5 km separating the large blocks of intact habitat on either end. Habitat in the corridor was degraded, containing 2 shrubless golf courses and a horse stable devoid of understory. The corridor was intersected by an 8-lane freeway (State Route 91) with heavy night traffic that precluded any at-grade road crossing. The only potential freeway undercrossings were a vehicle underpass (not used at night, but devegetated, brightly lit, and noisy at all hours) and a 2.6- × 3.3-m concrete box culvert 200 m long. Although home ranges of several radio-tagged adult cougars abutted the corridor, none used it.

The Pechanga Corridor was about 4.0 km long. The main impediments to movement were the 6-lane Interstate 15 freeway (I-15) and 2 golf courses. A bridge over the Santa Margarita River provided the only freeway undercrossing, and the area under it was characterized by riparian vegetation, little traffic noise, and minimal light pollution. However, to use the underpass, a cougar had to cross >400 m of golf course and skirt 2 fences along a driving range. If it skirted east of the driving range, it would encounter a habitat peninsula (Temecula Creek), which offered habitat for 900 m but then ended in a residential area. The Pechanga Corridor was the last potential habitat link between the Santa Ana Mountains and the Palomar Range, and was not used by any radio-tagged adult.

In 1990, nonurban habitat along the Arroyo Trabuco was 400–600 m wide for 6.0 km of its length. Tract homes lined both sides of the arroyo, but steep bluffs (20–70 m deep) minimized urban vistas, noise, and light pollution in the arroyo. The relatively undisturbed vegetation was dominated by an oak-sycamore (*Platanus racemosa*) riparian forest, with shrub and grassland communities on slopes and in smaller side canyons. In 1990–91, a 4-lane bridge was being built over the southern arroyo, with grading, excavating, and storage of steel beams, tractors, and other equipment in the arroyo. Unlike the other 2 corridors, the arroyo was not the sole link between the large habitat area at either end (Fig. 1).

In addition, several habitat peninsulas extended into urban areas. Because these peninsulas contained habitats avoided by adults (e.g., open grasslands, cut and fill slopes bordering tract homes), I did not try to identify and list them a priori. Instead we monitored dispersers near the urban-wildland interface and observed several dispersers explore these peninsulas.

Radio Telemetry

I captured and radiotagged 6 juvenile (9–18 months old) offspring of previously radio-tagged females when they were still in their mother's home range. Because the mothers were radiotagged before births of these juveniles, their birth dates were known within 4 days. One juvenile was radiotagged simultaneously with her mother (1 month before dispersal), and 2 others (mothers not radiotagged) were captured as dispersers; I estimated their birth dates from tooth wear, pelage, and mass (Ashman et al. 1983:19–27).

We obtained single locations, ≤1/day/animal, from the ground (54% of locations) or aircraft (46%) using standard triangulation or homing techniques (Mech 1983). We determined locations almost every day when dispersers moved through new terrain, and as rarely as every 2 weeks when home ranges were stable for >1 month. We also monitored animals overnight, determining the focal animal's location by ground triangulation every 15 minutes starting 1 hour before sunset and continuing until 1 hour after sunrise or until 1 hour of stasis, whichever came last.

I could not establish a network of precisely located receiving stations. Ground triangulation was by a single observer using a vehicle to take successive bearings in as brief a time as possible. Under these conditions, it is impossible to assess precision of locations (White and Garrott 1990: 90–93), but we minimized location errors by using only azimuths that differed by 60–120° and by getting close to the animal (White and Garrott 1990:58, 109). In obtaining 715 single locations on dispersers, we took 77% of the bearings from ≤500 m of the focal animal and 88% from within 1 km. These percentages increased

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Table 1. Dispersal timing, fate, distance traveled, and intensity of radiotracking for 1 female and 8 male juvenile cougars in southern California, 1990–92.

ID	Dispersal age (month)	Dispersal duration[a] (days)	Dispersal month	Fate	Dispersal distance (km)	Max. possible distance[b] (km)	Intensity of radiotracking: Single locations	Intensity of radiotracking: Overnight monitoring sessions
F17	20	128	Sep	Died (natural cause)	48	48	39	5
M3	18	20	Jan	Died (disease)	19	42	14	0
M5	19[c]	414	Aug[d]	Died (vehicle)	69	75	163	3
M6	19.5[c]	475	Aug[d]	Recruited	75	75	117	2
M7	19.5	392	Apr	Recruited	56	61	97	1
M8	18.5	148	Dec	Died (vehicle)	77	67	73	8
M10	22	536	Mar	Died (vehicle)	66	67	155	8
M11	17	41	Jan	Died (shot)	69	64	20	1
M12	13.5	195	Sep	Died (natural cause)	75	64	37	4
$\bar{x}$	18[e]	278[e]		2 of 9 recruited	63[e]	64[e]	84.5	3.4
SD	2.8	201			19	10		

[a] Until death, or until disperser (M6 and M7) occupied a stable home range.
[b] The distance from the centroid ($\bar{x}$, $\bar{y}$) of the natal home range to the most distant habitat edge that could be accessed without using the Coal Canyon or Pechanga corridors or (for M5 and M6, captured as dispersers) the longest straightline distance between any animal location and the most distant habitat edge without using those 2 corridors.
[c] Age cougar was captured as a disperser (excluded from $\bar{x}$).
[d] Month cougar was captured as a disperser.
[e] Excludes F17.

to 83 and 96%, respectively, during the 31 night monitoring sessions.

I computed home range size by the minimum convex polygon (MCP) method (Hayne 1949) excluding locations isolated by >7 km from the other locations. I monitored each disperser until death or until it occupied a stable adult home range, defined as an area ≥250 km² (for M) or ≥75 km² (for F) used for ≥3 consecutive months without a subsequent change in location. I defined dispersal as a movement >7 km beyond the boundary of a juvenile's natal range (mother's MCP for the previous 12 months) for >7 days. A THR was an area that an animal used after leaving its natal range, but later abandoned.

To compare THRs with ranges of adults of the same sex, I computed ≥3 MCPs for each radio-tagged adult for the same time span as each THR. Because I did not monitor adults as intensively, in most cases I computed the adult range from fewer locations. In the other cases, I randomly deleted points from adult samples if necessary, so that the adult ranges matched THRs in duration and number of locations.

I estimated time of dispersal, death, or entry into a home range by the midpoint between the closest known dates before and after the event. I defined dispersal date as the midpoint between the last date a juvenile was located within its natal range and the first date it was located off the natal range. I calculated dispersal distance as the maximum distance between a disperser's location and the centroid ($\bar{x}$, $\bar{y}$) of its mother's home range (for the 7 with radio-tagged mothers) or the maximum distance between centroids of THRs (for the 2 captured as dispersers). I contrasted each dispersal distance with a maximum possible distance, calculated as the distance from the centroid of the natal home range to the most distant habitat edge that could be accessed without using the Coal Canyon or Pechanga corridors (for the 7 with radio-tagged mothers) or as the longest straight-line distance between any animal location and the most distant habitat edge without using those 2 corridors (for the 2 captured as dispersers).

RESULTS

Dispersal Patterns

Age and Direction.—Eight male and 1 female juvenile cougar were radiotagged and survived to dispersal age; all 9 dispersed (Table 1). Mean dispersal age for 6 male cougars of known age was 18 months (Table 1). Littermates (2 pairs: M8 and M10, and M11 and M12) did not disperse at the same age but did disperse in the same direction.

Behavioral Initiation.—In 5 of 7 cases, dispersal was initiated by the mother leaving the cub 0–3 km from an edge of her home range while she moved to or just beyond the opposite edge of her home range, remaining there for 2–

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Table 2. Characteristics of transient home ranges (THR; range 1–4) of 7 dispersing juvenile male cougars in southern California, 1990–92.

Cougar	THR	Area (km^2)	Day entered[a]	Day abandoned[a]	Distance from previous range[b] (km)
M5	1	52.0	8	50	24
	2	51.5	64	262	63
	3	21.2[c]	262	414	2
M6	1	1.8	13	26	23
	2	77.0	50	242	75
	3	292.0	242	Through Dec 1992	10
M7	1	404.0	12	300	13
	2	260.0[d]	301	Through Dec 1992	27
M8	1	10.0	12	31	15
	2	112.0	56	126	36
	3	77.0	128	148	14
M10	1	1.4	4	23	12
	2	7.4[c]	40	69	52
	3	89.0	116	290	19
	4	135.0	300	536	32
M11	1	78.0[c]	17	36	46
M12	1	30.0	35	112	10
	2	97.0	121	195	66

[a] Days after capture for M5 and M6 (captured as dispersers with unknown dispersal date); days after start of dispersal for all others.
[b] Air line distance between centroids ($\bar{x}$, $\bar{y}$) of home ranges. For each animal, the first distance is the distance from centroid of mother's home range or (M5, M6) distance from release site.
[c] Home range after automobile collision.
[d] Abutted previous range with no overlap.

3 weeks. In 2 cases the cub was abandoned in the central part of the natal range. Each cub (n = 7) used a <50-ha area, centered on the abandonment site, for 13–19 days, then moved out of its mother's home range. Each male (n = 6) dispersed in the direction opposite (range 150–210°) that taken by his mother, but the female dispersed 45° from the direction taken by her mother.

Movements and Transient Ranges.—The female disperser wandered throughout the northern half of the Santa Ana Mountains, changing directions ≥5 times upon encountering the urban-wildland interface, and covered ≥342 km without establishing a THR. Four months after her dispersal date, she returned to the edge of her natal range and bedded near her mother for 1 day, dying near that location 5 days later of unknown causes.

Each male dispersed over several weeks to months, during which as many as 4 THRs were occupied sequentially (Table 2). For each disperser, the first THR was small and occupied for 7–20 days. On average, successive THRs were larger and occupied longer (0.5–8 months). Generally THRs were 2–30% as large as areas used by adult males over the same time span (Table 3). Thirteen of 18 THRs abutted the urban-wildland interface, and 11 of these 13 THRs had their longest border along that interface (Fig. 1). Three THRs were the result of restricted movements after vehicle collisions. Occasionally a disperser made an excursion from a THR, but returned to it; the 2 longest round trips were 87 km in 16 days and 89 km in 13 days.

Dispersers usually moved from 1 THR to the next in 1–16 days. In the only marked exception, M12 wandered 94 km over 35 days before entering a THR that abutted his natal range (Fig. 1: line A). Two of 6 dispersing males returned to their natal ranges 32 days (M8, traveling 15 km; Fig. 1: line E) and 87 days (M10, traveling 57 km) after dispersal and stayed there for 7 and 10 days, respectively, and then departed without a second return. One juvenile (M3) died 21 days after dispersal and traveled only 19 km. All other male dispersers moved from their natal range or capture site to the most distant corner of suitable habitat in the Santa Ana Mountains (Tables 1 and 2, Figs. 1 and 2).

Fates.—Seven of the 9 dispersers died before

Table 3. Size (km^2, based on minimum convex polygon) of male transient home ranges (THR) compared with the home ranges (HR) of adult M2 and adult M9, for similar durations and sampling intensities, in the Santa Ana Mountain Range, California, 1990–92.

Duration (days)	Transient home ranges				M2 home ranges				M9 home ranges			
	n	Locations/THR	$\bar{x}$	SD	n	Locations/HR	$\bar{x}$	SD	n	Locations/HR	$\bar{x}$	SD
13–20	5	7–15	23	32	7	7	134	83	5	7	182	42
29–43	2	12–21	30	22	7	11	176	84	7	11	259	89
70–77	3	10–31	80	36	13	10–28	278	75	5	11	416	78
152–198	4	42–83	60	26	5	50	439	70	4	36	585	114
236–288	2	35–53	270	134	5	35	487	16	4	44	673	76
360–366	2	32–145	276	16	3	35	506	61	3	35	704	32

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establishing a stable home range, with 3 deaths due to vehicle collisions. One (M11) followed a habitat peninsula into an urban area, where he was killed by police. Another (M3) died of apparent intestinal disease, and F17 and M12 apparently died of natural causes (no external trauma, not emaciated). Dispersers recovered from 2 other vehicle accidents.

The 2 successful dispersers obtained territories by expanding their last THRs. One (M6) occupied a transient range in the Chino Hills for 187 days before he expanded this range to the south via the Coal Canyon Corridor (Fig. 2). He used the Coal Canyon Corridor 12 times during the next 140 days, 65% of which were spent in the Chino Hills. Over the next 433 days, he crossed the freeway 10 times. During the latter period, his stays in the Chino Hills continued to average 14 days, but his stays south of the freeway increased to an average of 60 days.

Use of Corridors

Five of the 9 dispersers used corridors, and 1 used 2 corridors (Fig. 1). Two dispersers failed to traverse corridors that they entered (M10 was hit by a vehicle in Coal Canyon Corridor; midway through the Pechanga Corridor, M5 entered the Temecula Creek habitat peninsula and was captured).

Coal Canyon.—Two dispersers successfully used the Coal Canyon Corridor, and a third was hit by a vehicle there. One (M6) used the Coal Canyon Corridor ≥22 times over 19 months to establish a home range that included both the Chino Hills and the northern part of the Santa Ana Mountains (Fig. 2). When crossing under the freeway in this corridor, his tracks indicated he used the culvert 18 times and the vehicle underpass 4 times. In the only 2 radio-tracked passages, he started from daybeds <1 km south of the freeway, began walking north about 1 hour after sunset, used the culvert, and reached Chino Hills State Park (2 km) within 2 hours. In addition, tracks indicate that an uncollared juvenile cougar used the Coal Canyon culvert under the freeway.

Pechanga.—Three dispersers encountered the Pechanga Corridor. One (M7) apparently did not enter it, another (M12) traversed it in a single night, and a third (M5) was halfway through the corridor when he entered a habitat peninsula (Temecula Creek), following it into a residential area where he was captured by animal control officers. Between October 1990 and December 1992, 4 uncollared cougars were killed by vehicles where I-15 crosses the Pechanga Corridor. Three of these deaths occurred where M12 crossed successfully, and 1 occurred 4 km south at the only other place where unlighted cougar habitat fronted both sides of the freeway. In 9 track searches, we found no evidence of a cougar crossing under the Santa Margarita Bridge.

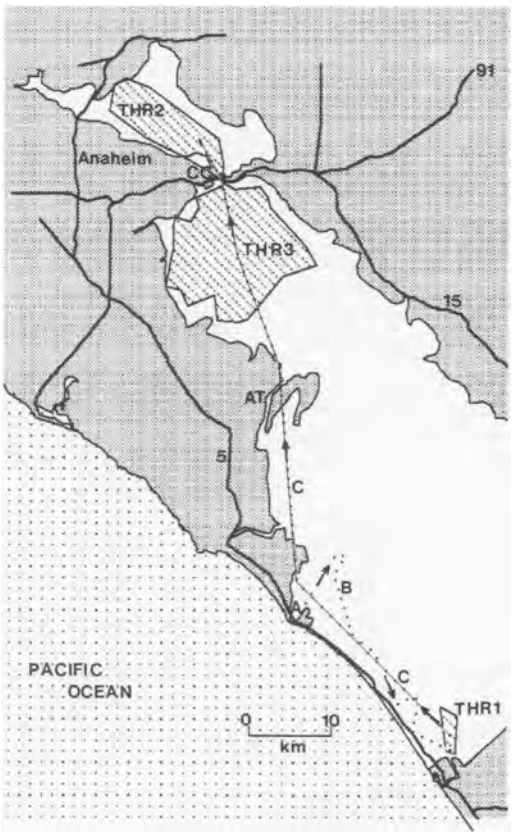

Fig. 2. Example of dispersal of a cougar (M6). A: M6 captured here as a disperser. B (10 days, 27 km): After release M6 traveled to THR1 (used 13 days). C (24 days, 85 km): M6 moved to the Chino Hills (perhaps using the Arroyo Trabuco [AT]), covering the final 52 km in <9 days. He spent 5.5 months in THR2 before expanding into an hourglass-shaped home range (THR2 and THR3). The 2 home range lobes are connected by the Coal Canyon Corridor (CC), which M6 used >22 times in 19 months.

Arroyo Trabuco.—Three dispersers successfully used the Arroyo Trabuco, taking 7 days (M8), 3–4 days (M10), and <48 hours (M11) to travel its length. Unlike the other 2 corridors, the arroyo was occasionally used by radio-tagged adults. Two of these adults were older than the corridor, having been born before the first housing tracts appeared east of the arroyo in 1986.

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The third adult first encountered the arroyo in late 1988, when the constricted area was shorter and wider than in 1990.

Movements at the Wildland-Urban Interface

All dispersers frequently encountered the urban-wildland interface. Except for the short-lived M3, each disperser encountered at least 3 of the 4 habitat edges. Although all dispersers came within 100 m of urban areas and heavily peopled parklands for several hours to several weeks, only 5 sightings (involving 3 dispersers) were reported to local authorities. There were no instances of dispersers behaving aggressively toward humans or their pets in urban edge settings, although M12 took pet goats near 4 rural homes.

Seven of the 9 dispersers explored to the tips of habitat peninsulas, making a total of 10 such forays, averaging 2.9 km in 1-way length (range 0.8–7.0, SD = 2.3). All peninsulas extended into dense urban areas, and most were heavily used during the day by humans. One juvenile (M8) spent 14 days in a 350-ha riparian forest at Trestles Beach in San Clemente, and M5 explored Santiago Creek for 4.5 km into Orange and Anaheim, bedding for the day in a 10-ha riparian forest at Katella Street. Despite intense monitoring (149 overnight monitoring sessions and >10,000 single locations on 20 radio-tagged adults during 1988–92), there was no evidence that any adult cougar, tagged or untagged, visited any of the 10 habitat peninsulas. On 4 of the 10 explorations, the disperser bedded for the day near the tip of the cul-de-sac and returned to the main habitat block the following night. On 4 occasions, dispersers entered the urban area beyond the terminus of the peninsula, resulting in 2 dispersers being treed by domestic dogs (both were captured and released back into the wild), and 2 dispersers being killed (1 by police, 1 by a vehicle).

All travel in corridors and habitat peninsulas occurred at night. During overnight monitoring, the disperser usually avoided artificial lights when in the corridor or peninsula. For example, M12 consistently used dark areas as he rapidly (<4 hr) traveled the grassy ridge (6.0 × 1.5 km) separating San Juan Capistrano from San Clemente (Fig. 1). Also M12 seemed to use light cues when he negotiated the tightest part of the Pechanga Corridor; his consistent movements in the direction of the darkest horizon caused him to miss the only bridged undercrossing of I-15.

Overnight monitoring showed that dispersers especially avoided night-lights in conjunction with open terrain. On M12's initial encounter with a well-lit sand factory and adjacent sand pits, he took 2 hours and 4 attempts to select a route that skirted the facility, after which he rested on a ridgetop for 2 hours. During 2 nights in the Arroyo Trabuco, M8 explored several small side canyons lacking woody vegetation. He followed each canyon to the ridgetop, where city lights were visible 300–800 m west. He stopped at each canyon ridgetop for 15–60 minutes before returning to the arroyo, without moving >100 m into the grasslands west of the ridgeline in view of the city lights.

Dispersers readily approached highways, but usually stopped 50–100 m from a newly encountered freeway until daylight. The following evening the cougar would either cross the freeway or retrace its route. As an example, M12 encountered a freeway at the tip of a 6-km peninsula of marginal habitat before 0400, stopping in an oak grove <30 m from the freeway. Across the freeway lay a dark industrial park with an unlit ridge beyond. By sunrise, the buildings were visible from his location, and after the following sunset, M12 traveled back to his THR (29 km away) within 48 hours.

Dispersers regularly crossed under highway bridges built to accommodate watercourses. For example, M8 crossed I-5 under the San Mateo Creek bridge ≥6 times, M6 crossed I-5 under the Las Flores Creek Bridge ≥2 times, and 3 dispersers made ≥8 crossings under the 2 bridges that spanned the Arroyo Trabuco.

Cougars (dispersers and adults) usually avoided large and small culverts under freeways or 2-lane rural highways. In 5 overnight monitoring sessions, the focal cougar used a drainage bottom, climbed out of the canyon, crossed the 2-lane road at grade, and re-entered the drainage. However, in 2 other sessions, 1.8-m box culverts were used to pass under 2-lane roads. Providing a striking exception to the pattern of culvert avoidance, M6 used the Coal Canyon box culvert to cross under an 8-lane freeway in 18 of his 22 known crossings.

In corridors and in the main habitat block, the most frequently used travel routes for dispersers and adults were scour zones in stream channels, followed by ridgeline routes and dirt roads. Dirt roads and hiking trails were es-

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pecially favored as routes through dense chaparral. Adult and dispersing cougars occasionally bedded for the day 20–100 m from trails heavily used by hikers, bicyclists, and equestrians. Dispersers showed no aversion to parked vehicles, occasionally walking within 2 m of a researcher sitting in a vehicle on a dirt road with the engine off. They also passed within 30 m of isolated homes and buildings with no outdoor lighting.

DISCUSSION

Dispersal Patterns

The mean age for dispersal of males (18 months) was older than the mean of 13.3 months in previous studies (summarized by Anderson et al. 1992:61, 66), but lies well within the range of those reports, and is close to the 17.9 months reported by Maehr et al. (1991*b*) who used a similar definition of dispersal. Dispersal was initiated by the female abandoning the cubs within her home range, as also reported in Idaho by Seidensticker et al. (1973).

As was the case in the Santa Ana Mountains, Anderson et al. (1992:61 and Colo. Div. Wildl., Montrose, pers. commun.) found that all 9 radio-tagged juvenile males dispersed in Colorado. However, they found that 2 of 6 juvenile females failed to disperse. Additional reports are needed to determine how frequently juveniles fail to disperse. Although the mean dispersal distance for males in this study (63 km) was shorter than the average of 85 km reported in previous studies (Anderson et al. 1992:61, 66), cougars moved as far as possible within the Santa Ana Mountain Range. In Florida, where cougar habitat was limited, mean dispersal distance for males was 59 km (Maehr et al. 1991*b*).

In this fragmented landscape, 2 of 9 dispersers lived to establish stable adult home ranges. In the only comparable report, Anderson et al. (1992) found that 2 of 12 dispersers survived to establish stable home ranges in western Colorado. Although vehicles killed 4 of 9 dispersers in the Santa Ana Mountains (compared with zero cougars of any age in all other reported mortality rates in the west. U.S.), this vehicle mortality was apparently compensated by lack of other mortality factors, such as hunting. Maehr et al. (1991*a*), studying cougars in urban southern Florida, reported that 47% of deaths were due to vehicles.

Each male disperser used a series of small, elongate THRs along the urban-wildland edge and moved rapidly from 1 THR to the next. Because adult male cougars tend to exclude other males from their territories (Anderson et al. 1992:70, Beier and Barrett 1993), these home range traits are probably due to dispersers attempting to avoid conflict with territorial adult males.

Maehr et al. (1991*b*) reported that the single female disperser in their study raised 1 litter within her mother's home range and then dispersed only 16 km, and Laing and Lindzey (1993) reported that vacated ranges of resident females were filled by their daughters or those of adjacent females. Because young females are more readily integrated into the resident adult population, females may not follow the pattern of THRs exhibited by males.

MANAGEMENT IMPLICATIONS

Use of Corridors and Habitat Peninsulas

Cougars will disperse via habitat corridors in a landscape fragmented by urbanization, and some dispersers will use corridors containing unnatural features such as golf courses and major freeways. Significantly, 2 of the 3 corridors—Coal Canyon and Pechanga—were the only potential links between the large habitat blocks on either end and were important to persistence of this cougar population (Beier 1993). Corridor skeptics point out that a low quality corridor is a potential population sink and could decrease the size of a metapopulation (Simberloff et al. 1992). However, in this study no radio-tagged disperser was killed in the 2 low quality corridors (although 1 was injured), compared with 2 deaths in habitat peninsulas and 5 deaths inside the main habitat block. Furthermore, in this urban area, the only alternative to corridors is isolation, which might increase mortality because dispersers would be unable to escape the urban-wildland interface. Finally, even if some mortality occurs in corridors, it only takes a few successful dispersers per decade to benefit a cougar population (Beier 1993). For cougars, any connection between 2 isolated patches is better than no connection.

Implications for Corridor Design

A cougar cannot use a corridor unless its normal travel pattern causes it to encounter the corridor entrance. Conversely, a corridor along a natural travel route is likely to be used even

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if habitat conditions within the corridor are suboptimal (Foster and Humphrey 1992:17). Radio telemetry is ideal for identifying such routes if data are gathered when matrix lands are still intact (Beier 1993, Beier and Barrett 1993). If such data are not available for a particular area, scour zones in canyon bottoms are the most probable travel routes for cougars, followed by ridgelines free of artificial light.

Dispersers exploring new terrain and navigating corridors apparently oriented toward dark areas and away from city lights. Lights are especially detrimental in a road undercrossing or in open habitats. Lighting could also be an effective tool to deter an animal from entering a habitat peninsula that dead-ends in an urban area.

Traffic can kill or injure dispersers and may preclude an at-grade crossing. Where a heavily used road crosses a corridor, a bridged undercrossing is preferable to a culvert (Foster and Humphrey 1992, this study). A wide median should be open rather than covered (Foster and Humphrey 1992, Mock et al. 1992), but a narrow median should be covered to minimize noise, debris, and traffic light (Reed et al. 1975). Mock et al. (1992) recommended that noise in the underpass not exceed 60 db during expected time of use.

Vehicle accidents within corridors may have been prevented if the freeways had fencing to guide animals away from the roads and into underpasses. Foster and Humphrey (1992) found that a 3.1-m-high chain link fence topped with 3 strands of barbed wire helped Florida panthers stay off freeways and use underpasses. On first approaching busy freeways, dispersers stopped until daylight, perhaps to visually assess the habitat on the opposite side. I agree with Foster and Humphrey (1992:25) that the approach to the underpass should give the animal a good view of the habitat on the other side.

Cougars frequently used dirt roads and trails. Where dense woody vegetation impedes cougar travel, a trail or dirt road running the length of the corridor can facilitate use by cougars and discourage travel into adjacent urban areas. Mock et al. (1992) found that all functional wildlife corridors in urban San Diego County, California, had a path, drainage, railroad, or other linear feature, and speculated that these features helped guide animals through the corridor.

Unrestrained pets should be excluded from corridors because pet owners almost always demand the death of a cougar that preys on a pet animal. Because cougars showed no aversion to hikers, bicyclists, equestrians, isolated unlit buildings, or parked vehicles, I conclude that corridors are compatible with such activities. However, there is a low risk of an attack on humans (Beier 1991).

In the Santa Ana Mountains, there was no housing within any of the 3 corridors or in most of the central habitat block. Where housing did occur, cougars readily moved through low density areas (about 1 dwelling/16 ha) and found dense areas (>20 dwellings/ha) impassible. I could not observe cougar movement in areas of intermediate housing density.

A corridor between the Santa Ana Mountains and the Palomar Range needs to accommodate only 2–4 immigrants/decade (Beier 1993), with each animal making a single passage. In contrast, because Chino Hills is smaller than an adult male home range, it requires a better linkage that will allow a breeding male to find and repeatedly use the corridor to breed with resident females (Fig. 2). Protected areas smaller than an adult female home range would require high quality, preferably multiple linkages, to enable a resident adult to use them as part of a home range.

Some native woody vegetation should be present to provide visual cover. I observed cougars move ≤400 m across unlit open terrain when the surrounding areas were in native woody vegetation, but they did not cross this span of open terrain with urban areas nearby on either side. Because some dispersers waited 12–24 hours near a freeway crossing point, woody cover is especially important near road crossings. In this study, cougars avoided row crops and orchards.

Lacking empirical data on corridor use, Harrison (1992) suggested that long corridors be ≥1 home range wide (about 5 km for cougars), and Noss (1992) recommended that regional corridors exceed 1.6 km in width with no bottleneck <400 m wide. Working on a smaller landscape, I documented that cougars will use corridors as narrow as 400 m for distances <7 km, with bottlenecks as narrow as 3.3 m for road undercrossings. Similarly, Mock et al. (1992) documented cougar use of 1 corridor 500 m long and 100–160 m wide and found that cougars did not use 8 potential corridors in which the most constrained sections were <100 m wide for >200 m. If disturbance level, cover, and the other factors discussed above are suitable, I suggest

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that a corridor designed for use by cougars should be >100 m wide if the total distance to be spanned is <800 m, and >400 m wide for distances of 1–7 km. To the extent that other factors are suboptimal, and as the corridor length increases, corridor width should be increased.

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Systematic review

The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis

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ABSTRACT

Biodiversity is being lost at an increased rate as a result of human activities. One of the major threats to biodiversity is infrastructural development. We used meta-analyses to study the effects of infrastructure proximity on mammal and bird populations. Data were gathered from 49 studies on 234 mammal and bird species. The main response by mammals and birds in the vicinity of infrastructure was either avoidance or a reduced population density. The mean species abundance, relative to non-disturbed distances (MSA), was used as the effect size measure. The impact of infrastructure distance on MSA was studied using meta-analyses. Possible sources of heterogeneity in the results of the meta-analysis were explored with meta-regression.

Mammal and bird population densities declined with their proximity to infrastructure. The effect of infrastructure on bird populations extended over distances up to about 1 km, and for mammal populations up to about 5 km. Mammals and birds seemed to avoid infrastructure in open areas over larger distances compared to forested areas, which could be related to the reduced visibility of the infrastructure in forested areas. We did not find a significant effect of traffic intensity on the MSA of birds. Species varied in their response to infrastructure. Raptors were found to be more abundant in the proximity of infrastructure whereas other bird taxa tended to avoid it. Abundances were affected at variable distances from infrastructure: within a few meters for small-sized mammals and up to several hundred meters for large-sized mammals.

Our findings show the importance of minimizing infrastructure development for wildlife conservation in relatively undisturbed areas. By combining actual species distributions with the effect distance functions we developed, regions sensitive to infrastructure development may be identified. Additionally, the effect distance functions can be used in models in support of decision making on infrastructure planning.
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1. Introduction

Global biodiversity is changing at an unprecedented rate as a result of several human-induced changes in the global environment (Vitousek, 1994; Pimm et al., 1995; Sala et al., 2000; MEA, 2005). Biodiversity loss at the species level tends to result in the so-called homogenisation process (Lockwood and McKinney, 2001). This process is generally characterised by a decrease in the abundance of many species, culminating into an increase in the number of threatened species and the extinction of others, in combination with a simultaneous increase in the abundance of a few species. The main drivers of biodiversity change are land-use and land-cover change, climate change, pollution, fragmentation and infrastructure development (UNEP, 2001; Sala et al., 2000; Sanderson et al., 2002; Alkemade et al., 2009).

The ubiquity of road networks and the growing body of evidence of the negative impacts that roads and other linear infrastructure have on wildlife and ecosystems suggest that infrastructure represents a major driving factor of biodiversity loss. The most commonly reported impacts from roads and utility corridors include habitat loss, intrusion of edge effects in natural areas, isolation of populations, barrier effects, road mortality and increased human access (Andrews, 1990; Forman and Alexander, 1998; Spellerberg, 1998; Trombulak and Frissell, 2000; Forman et al., 2003). Road construction leads to habitat destruction and creates open spaces in otherwise closed forests (Gullison and Hardner, 1993; Reed et al., 1996; Santos and Tabarelli, 2002). The open spaces may fragment populations (barrier effect), attract light-demanding species and may be avoided by others (edge effect)

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(Kroodsma, 1984; Vos and Chardon, 1998; Bolger et al., 1997; Ortega and Capen, 1999). Additionally, the use of infrastructure by cars or trains increases the risk of collisions with wildlife and the stress on (breeding) individuals (due to noise and visual stimuli), both of these risks affecting animal populations (Van der Zande et al., 1980; Reijnen et al., 1996; Romin and Bissonette, 1996; Boarman and Sazaki, 2005; Parris and Schneider, 2009).

Besides roads, other types of infrastructure, such as railways, powerlines, pipelines, hydroelectric developments, oil wells, seismic lines and wind parks, have an impact on wildlife populations (Dunthorn and Errington, 1964; McLellan and Shackleton, 1989; Cameron et al., 1992; Van Dyke and Klein, 1996; Mahoney and Schaefer, 2002; Nellemann et al., 2003a; Barrios and Rodriguez, 2004). All these impacts may influence the long-term viability of populations and, eventually, biodiversity.

Qualitative reviews provide a broad understanding of the ecological effects of infrastructure that affect a range of taxa and ecosystems, but lack quantitative evidence (Trombulak and Frissell, 2000; Forman et al., 2003). However, the few attempts to quantify the effects of infrastructure (UNEP, 2001; Nellemann et al., 2003b; Fahrig and Rytwinski, 2009), or to model the vulnerability of animal populations to road effects (Jaeger et al., 2005), are not based on meta-analysis, which is the statistical procedure for combining the results of independent studies in a quantitative way (Arnqvist and Wooster, 1995). In this study, we aim at estimating the decline of animal populations in relation to proximity to infrastructure by using a meta-analytical approach.

Among all animal taxa, mammal and bird populations were chosen for our analysis since both have been widely reported to be declining in relation to their distance from infrastructure. However, large differences in disturbance sensitivity seem to exist between and within these groups. Bird populations seem to be affected within a few hundred metres from infrastructure, whereas a reduction in mammal populations has been found at distances of a few hundred metres up to several kilometres from infrastructure (McLellan and Shackleton, 1989; Cameron et al., 1992; Ortega and Capen, 1999; Nellemann et al., 2003a). Additionally, traffic intensity seems to play a role in the decline of both bird and mammal populations close to roads (Van der Zande et al., 1980; Reijnen et al., 1995, 1996; Dyer et al., 2001; Rheindt, 2003; Gagnon et al., 2007).

To quantify the patterns of reduced population densities in relation to infrastructural development, we searched the scientific and non-scientific literature for quantitative data on mammal and bird populations at varying distances from infrastructure. As the metric of effect size, we calculated the ratio between the species abundance at varying distances to infrastructure (Disturbance or Effect distance) relative to the species abundance at the largest (control) distance reported in the study. This ratio is a form of the biodiversity indicator mean species abundance (MSA) which represents the mean abundance of (remaining) original species in an area related to an undisturbed situation (Alkemade et al., 2009). Meta-analysis was used to combine the effect sizes (MSA values) across all studies for several distance intervals and test their level of significance. Furthermore, meta-regression was applied to model the relationship between distance to infrastructure and MSA for birds (MSA_B) and mammals (MSA_M) (infrastructure–distance effect), and to examine sources of heterogeneity in this relationship.

2. Methods

2.1. Search and selection of published studies on infrastructural effects

Relevant studies were searched by using the following electronic databases: Ebsco, ISI Web of Knowledge, JSTOR, Omega (Utrecht University Digital Publications Search Machine), Science Direct, Scopus, Springer Link and Wiley InterScience. The search terms were: road* AND impact* AND biodiversity OR mammal, bird; infrastructure AND impact* AND biodiversity OR mammal, bird; road* AND distance AND biodiversity OR mammal, bird; road-effect zone AND mammal abundance, bird abundance; road* AND disturbance* and biodiversity OR mammal, bird; powerline AND impact AND biodiversity OR mammal, bird; wind park AND biodiversity OR mammal, bird; road traffic* AND impact* AND biodiversity* OR mammal, bird; infrastructure AND disturbance AND biodiversity OR mammal, bird. An Internet search was also performed using the meta-search engine Google scholar. Bibliographies of articles viewed at full text were searched for relevant secondary articles. Authors and recognized experts in the field of infrastructure development, road establishment and effects on biodiversity (Christian Nellemann, UNEP-Grid Arendal, and Rien Reijnen, Alterra) were also contacted for further recommendations, and for provision of any unpublished material or missing data that may be relevant (grey literature). Foreign language searches were undertaken by using cross-reference.

2.2. Study inclusion criteria

From this bulk of literature we selected those studies of which title and keywords were associated to the objective of this review. Subsequently, information contained in the abstracts was examined to further narrow down the selection to those studies that met the following criteria:

- Relevant study objects: Populations of any mammal or bird species. Studies were included irrespective of habitat or spatial scale.
- Types of intervention: Disturbance distances or distances close to infrastructure at which mammal and bird populations might be reduced compared to larger distances or control distances (see Types of comparator).
- Types of outcome: Species abundance (density and/or counts) at varying distances to infrastructure.
- Types of comparator: Control distances or distances at which mammal and bird populations are unaffected by infrastructure and roads.

2.3. Data extraction

Finally, 49 studies met the selection criteria for data extraction, from which 90 datasets were extracted and stored in a database, resulting in 2107 data points. The data included the mean abundance at disturbance distances close to infrastructure and at a larger control distance; furthermore we recorded the sample size, the variance, and standard deviation or standard error, depending on the study. These data were used to estimate an effect size and its variance as required in meta-analysis (Osenberg et al., 1999). Additionally, we stored data on location, habitat, infrastructure type, taxon (order) and traffic intensity to explore sources of heterogeneity (see Table 2 in Supplementary material, available at http://www.environmentalevidence.org/SR68.html). These variables are considered biologically meaningful and could affect the way different taxa respond to infrastructure. Thus, we expected that different taxa would respond differently to different infrastructure types (linear and clustered) and in different habitat types according to varying visibility of infrastructure, while traffic intensity could affect the response due to the influence of noise and visual stimuli.

2.4. Effect size calculation: Mean Species Abundance (MSA)

For each study, individual effect sizes were calculated as the ratio between the abundance of each species close to the infrastructure

(Disturbance distance) and the abundance of the same species at the largest (control) distance, as reported in the study. Individual effect sizes were aggregated for each study and distance, resulting in an estimate of the mean species abundance (MSA), which is the metric of effect size for the meta-analysis (see Eq. (1))

$$\mathrm{MSA}_{sd} = \frac{\sum_i R_{isd}}{N_s}; \quad (1)$$

where MSA_{sd} is the relative mean species abundance estimated in study s at a distance d; R_{isd} is the ratio between the abundance or density of species i at distance d and the abundance or density of species i at the control distance, calculated as: A_{isd}/A_{isc} for $A_{isc} > 0$. N_s is the number of species considered in study s. MSA values ranged from 0 to 1 and declined at shorter distances from infrastructure. For species with higher densities at short distances from infrastructure compared to the control distance, the MSA value was truncated to 1; therefore, if $A_{isd} > A_{isc}$, then $R_{isd} = 1$.

2.5. Estimation of variation in MSA values

The variance of the MSA value for each distance and study was estimated by calculating the variance of the external error (2), and of the internal error (3), which are both forms of the variance of a sample mean (Mood et al., 1973). The largest variance was used in the meta-analysis, thus taking into account the largest error associated with each data point (DerSimonian and Laird, 1986). For single species' studies, only the variance of the internal error could be calculated.

The variance of the external error was calculated as:

$$\sigma^2_{ext} = \frac{\sum (MSA_{sd} - R_{isd})^2}{N_s(N_s - 1)} \quad (2)$$

The variance of the internal error was calculated as:

$$\sigma^2_{int} = \frac{\sum \sigma^2_{R_{isd}}}{N_s^2}; \quad (3)$$

where $\sigma^2_{R_{isd}}$ is the individual variance for each ratio, which was calculated by using the Delta Method (4), a first-order approximation of the variance of a ratio of two random variables (Oehlert, 1992; Winzer, 2000).

$$\sigma^2_{R_{isd}} = \frac{A^2_{isd}}{A^2_{isc}}\left[\frac{A^2_{isd}}{\sigma^2_{A_{isd}}} + \frac{A^2_{isc}}{\sigma^2_{A_{isc}}} - \frac{2\rho \cdot \sigma_{A_{isd}} \cdot \sigma_{A_{isc}}}{A_{isd} \cdot A_{isc}}\right] \quad (4)$$

In this equation $\sigma^2_{A_{isd}}$ and $\sigma^2_{A_{isc}}$ are the variances of A_{isd} and A_{isc}, respectively, and ρ their correlation coefficient. We assume A_{isd} and A_{isc} to be independent and, therefore, the correlation coefficient ρ to be zero. Variances of A_{isd} and A_{isc} were obtained from studies, when available; where this was not the case, the data was assumed to follow a Poisson distribution, in which $\mu = \sigma^2$ and, therefore, $A_{isd} = \sigma^2_{A_{isd}}$, and $A_{isc} = \sigma^2_{A_{isc}}$ (Sokal and Rohlf, 1981).

Finally, as some species had a density of zero at the disturbance distance ($A_{isd} = 0$), a continuity correction factor ($k = 1/2$) was added to the numerator and denominator of the ratio of all species, resulting in slightly higher variance estimates (Cox, 1970; Sweeting et al., 2004).

2.6. Study quality assessment

Study characteristics were summarized and experimental design (control and treatment plots) and data availability for extraction (means, standard errors and sample sizes) were used as criteria for determining study quality (low; medium–low; medium; medium–high; high) (Supplementary material available at http://www.environmentalevidence.org/SR68.html). A sensitivity analysis was done by removing studies scoring "medium–low" or "low".

2.7. Data analyses

Meta-analyses were performed separately for mammal and bird studies by using the package "metafor" in R 2.9.1 software (Viechtbauer, 2009). A random effects meta-analysis was done to derive a pooled effect size for all datasets allowing pseudoreplication. Additionally, meta-analyses were done per distance interval containing non-duplicated independent datasets.

Heterogeneity was assessed by inspection of Forest plots and formal tests of heterogeneity Q and I^2 (Thompson and Sharp, 1999). Publication bias was also assessed using Funnel plots of asymmetry along with formal tests (Egger et al., 1997; Supplementary material available at http://www.environmentalevidence.org/SR68.html).

To explore factors introducing heterogeneity we built several Generalized Linear Mixed Models (GLMM), accounting for several alternative nested ecological hypotheses that included the following a priori selected explanatory variables: distance to infrastructure (DIST or LOGDIST when log-transformed), presence of forest cover (FOR), infrastructure type (INFTYP) and traffic intensity (TRAF). All GLMM were built in S-Plus 7.0 and fit by restricted penalised quasi-likelihood (Pinheiro and Bates, 2000). Each MSA value was weighed by its variance. Study was introduced as random effect since we expected similar but not identical effects of infrastructure across studies.

Models were compared and selected by means of information theoretic criteria, including Akaike's Information Criterion corrected for sample size (AICc) and Akaike weights. AIC corrected for overdispersion (QAIC) was not needed since the random effects of the GLMM accommodate any possible overdispersion in the data. This was *ad hoc* checked by calculating a scale parameter (sigma) for our models using package "lme4" in R 2.9.1. (Bates and Maechler, 2009). The model selected was that minimizing the loss of Kullback–Leibler information.

Additionally data was disaggregated and GLMM were built to examine differences in the relationship between MSA and distance for different habitats, for forested and non-forested habitats, for different infrastructure types (linear and clustered) and for different taxa.

3. Results

3.1. Data availability and selected studies: review statistics

More than 600 studies contained relevant titles and abstracts. Of these, 50 studies corresponded to the selected criteria for data extraction. Two studies referred to the same data and were treated as one (Noel et al., 2004; Joly et al., 2006), resulting in 49 studies used for the meta-analysis. Some geographical bias was found since most of the studies were from either North America (21) or Europe (23), while a few studies from Africa (3) and Oceania (2) were found.

Twenty-seven studies included 201 bird species, and 49 independent datasets were extracted for the meta-analysis. The other 22 studies included 33 mammal species, and 41 independent datasets were extracted. Some species were repeated more than once (Appendix 3, Supplementary material available at http://www.environmentalevidence.org/SR68.html). Of the 49 datasets for birds, 10 contained relevant information on traffic intensities. Of the 41 datasets for mammals, five included information on traffic intensity, which was considered insufficient for the inclusion of this variable in the analysis (Supplementary material available at http://www.environmentalevidence.org/SR68.html).

Bird datasets frequently included a large number of species (mean = 9.1 (1–54)), compared to mammal datasets, which (with some exceptions, e.g. Newmark et al., 1996; Goosem and Marsh, 1997; Yost and Wright, 2001) usually focused on a single species (mean = 3.7 (1–11)). The most represented habitat types within the bird datasets were grasslands and agricultural lands (each of them in 15 datasets), and the least represented was boreal forests (1 dataset). The most represented habitat type in the mammal datasets was arctic tundra (12 times) and the least represented habitat types were grasslands and semi-arid habitats (1 time each).

The most represented bird taxon was Passeriformes (21 datasets) and the least represented bird taxa were Coraciiformes, Psittaciformes and Trochiliformes (1 dataset each). The most represented mammal taxon was Artiodactyla (25 datasets) and the least represented mammal taxa were Lagomorpha and Perissodactyla (1 dataset each).

Reported distances in bird datasets were in the range of 0–2580 m whereas data points for mammals were obtained within a range of 0–17,000 m.

3.2. Meta-analysis

3.2.1. Combination of all distances with pseudorreplication

The pooled effect size derived from an all-encompassing meta-analysis of MSA values for birds indicated that bird abundance declined within ca. 2600 m from infrastructure (MSA_B = 0.678; 95% CI 0.636–0.720, $P < 0.0001$; Table 1). Likewise for mammals, MSA_M decreased within 17,000 m from infrastructure (MSA_M = 0.675; 95% CI 0.608–0.742, $P < 0.0001$). However, for both meta-analyses there was large heterogeneity and publication bias within the datasets (Q_B = 16938.28, $P < 0.0001$; Egger $test_B$ = 5.785, $P < 0.0001$; Q_M = 3466.80, $P < 0.0001$; Egger $test_M$ = 3.684, $P < 0.0001$; Tables 1 and 2). Fail-safe numbers indicated that a large number of studies reporting neutral or positive effects of the proximity of infrastructure on species abundance would be needed to overturn these results and so even with some publication bias, the results for mammals and birds can be considered a reliable estimate of the true effect (Rosenthal, 1979).

Sensitivity analyses were performed and the results remained similar after removing studies that scored "medium–low" in the study quality assessment. The pooled effect size for bird data increased slightly, heterogeneity was lower but still statistically significant and there was evidence of publication bias (MSA_B = 0.683; 95% CI 0.627–0.740, $P < 0.0001$; Q = 2653.70, $P < 0.0001$; Egger test = 4.699, $P < 0.0001$; Appendix 4, Supplementary material available at http://www.environmentalevidence.org/SR68.html). For mammals the pooled effect size was similar, heterogeneity decreased slightly and there was publication bias (MSA_M = 0.678; 95% CI 0.6086–0.7472, $P < 0.0001$; Q = 3401.70, $P < 0.0001$; Egger test = 4.006, $P < 0.0001$; Appendix 4, Supplementary material available at http://www.environmentalevidence.org/SR68.html).

3.2.2. Effect size per distance interval

Pooled effect sizes calculated per distance interval for independent datasets were significant for mammal and bird data, but considerable heterogeneity and publication bias existed for most of the intervals. Lower MSA values were obtained at shorter distance intervals to infrastructure for both mammals and birds.

Table 1
Results of the meta-analysis for bird species at different distance intervals.

Distance (m)	*n*	Effect size (MSA)	SE	CI (lb)	CI (ub)	*P* (e.size)	Q	*P*(Q)	I^2 (%)	Egger's test intercept	*P*(*t*) Egger	Fail-safe *N*
0–2580	288[a]	0.6777	0.0215	0.6355	0.7200	**<0.0001**	16938.28	**<0.0001**	96.6	5.785	**<0.0001**	**11,23,452**
<10	10	0.3983	0.1290	0.1455	0.6512	**0.002**	62.7322	**<0.0001**	94.4	2.625	**0.0026**	**245**
15–35	18	0.4855	0.0893	0.3105	0.6605	**<0.0001**	223.89	**<0.0001**	93.3	4.336	**<0.0001**	**2233**
38–65	20	0.5339	0.0905	0.3566	0.7112	**<0.0001**	370.28	**<0.0001**	95.2	3.639	**<0.0001**	**1939**
70–80	16	0.5923	0.0896	0.4165	0.7680	**<0.0001**	33.19	**0.007**	54.5	2.561	**0.0002**	**689**
90–100	16	0.6218	0.0722	0.4802	0.7634	**<0.0001**	38.42	**0.0004**	68.4	3.993	**0.0003**	**1494**
110–125	13	0.6673	0.1022	0.4671	0.8676	**<0.0001**	40.99	**<0.0001**	65.7	3.072	**0.0001**	**577**
130–140	5	0.7070	0.1592	0.3950	1.0190	**<0.0001**	45.79	**<0.0001**	85	4.981	**0.0222**	**225**
150–160	16	0.5978	0.0788	0.4434	0.7522	**<0.0001**	79.12	**<0.0001**	83.8	4.874	**0.0002**	**1946**
170–180	10	Fisher scoring algorithm did not converge										
190–200	13	0.6292	0.0908	0.4512	0.8072	**<0.0001**	301.50	**<0.0001**	95.7	6.786	**0.0015**	**2864**
210–240	12	0.6734	0.1281	0.4223	0.9246	**<0.0001**	428.83	**<0.0001**	95.3	5.434	**0.0124**	**1560**
250–280	17	0.6676	0.0963	0.4789	0.8563	**<0.0001**	331.47	**<0.0001**	96.5	9.347	**0.0122**	**9320**
300–320	15	0.7454	0.1062	0.5374	0.9535	**<0.0001**	8769.78	**<0.0001**	99.4	15.540	0.202	**20,053**
340–375	10	0.6432	0.0943	0.4583	0.8281	**<0.0001**	34.74	**0.0001**	75.2	4.828	**0.0161**	**851**
380–480	16	0.7495	0.0888	0.5755	0.9236	**<0.0001**	1052.78	**<0.0001**	96.9	8.952	**0.0003**	**7820**
490–550	14	0.6946	0.1004	0.4978	0.8914	**<0.0001**	86.19	**<0.0001**	87	5.331	**0.0073**	**2013**
565–645	9	0.7182	0.0929	0.5361	0.9003	**<0.0001**	27.72	**0.0005**	75.8	6.594	**0.0436**	**1294**
650–785	11	0.7564	0.1203	0.5206	0.9921	**<0.0001**	581.18	**<0.0001**	94.1	5.980	**0.0451**	**1588**
800–860	3	0.6869	0.1968	0.3011	1.0728	**<0.0001**	12.75	**<0.0001**	81.1	4.640	**0.0124**	**69**
900–915	4	0.9152	0.1043	0.7108	1.1196	**<0.0001**	0.2687	0.9658	0	4.1168	**0.0189**	**97**
1000–1075	11	0.8363	0.0791	0.6812	0.9913	**<0.0001**	17.23	0.0695	46.7	4.585	**0.0050**	**930**
1100–1175	3	0.9696	0.1275	0.7198	1.2195	**<0.0001**	0.0722	0.9645	0	4.052	0.0780	**52**
1200–1290	4	0.8308	0.1097	0.6158	1.0459	**<0.0001**	5.011	0.171	47	5.426	**0.0344**	**171**
1300	1	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
1400	2	0.9098	0.0515	0.8090	1.0107	**<0.0001**	0.0398	0.842	0	10.941	0.321	**176**
1500–1505	7	0.8511	0.0677	0.7183	0.9838	**<0.0001**	13.894	**0.0308**	71.7	10.572	0.0516	**2018**
1600	1	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
1700–1750	4	0.9294	0.0992	0.7349	1.1239	**<0.0001**	0.5252	0.9133	0	4.4439	**0.0148**	113
1800–2000	4	1.0000	0.0483	0.9053	1.0947	**0.0000**	0	1.0000	0	7.868	0.136	362
2150	1	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
2365	1	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
2580	1	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.

[a] Total number of MSA values included in the meta-analysis for bird species. The total number of studies is 27, from which 49 datasets were extracted containing 288 MSA calculated values for different distances.

Table 2
Results of the meta-analysis for mammal species at different distance intervals.

Distance (m)	*n*	Effect size (MSA)	SE	CI (lb)	CI (ub)	*P* (e.size)	*Q*	*P*(*Q*)	I^2 (%)	Egger's test intercept	*P*(*t*) Egger	Fail-safe *N*
0–17,000	151[a]	0.6746	0.0342	0.6076	0.7415	**<0.0001**	3466.80	**<0.0001**	90.7	3.6843	**<0.0001**	**114,151**
1	6	0.1528	0.1005	−0.0442	0.3498	>0.1	12.74	**0.0259**	71.9	1.0862	0.0937	10
10–25	11	0.7110	0.0451	0.6227	0.7993	**<0.0001**	4.38	0.9284	0	4.300	**<0.0001**	**816**
30–50	16	0.5651	0.0726	0.4229	0.7073	**<0.0001**	28.65	0.0178	55.8	2.9972	**<0.0001**	**834**
75–100	7	0.3957	0.1831	0.0369	0.7545	**<0.05**	10.87	0.0925	47.7	1.4193	**0.0016**	**362**
110–180	16	0.8374	0.0520	0.7354	0.9394	**<0.0001**	7.42	0.9448	0	3.4069	**<0.0001**	**1083**
200	2	0.6104	0.2382	0.1435	1.0774	**0.0104**	0.02	0.878	0	1.464	0.402	2
250–300	9	0.8470	0.0627	0.7241	0.9698	**<0.0001**	7.78	0.4557	7.8	4.059	**0.0037**	**485**
350–600	19	0.6222	0.1115	0.4035	0.8408	**<0.0001**	206.68	**<0.0001**	91.9	3.3561	**<0.0001**	**1485**
750–1000	6	0.8669	0.1052	0.6608	1.0731	**<0.0001**	9.23	0.1002	50.2	4.8430	**0.0036**	**307**
1050–2200	20	0.5786	0.0806	0.4207	0.7366	**<0.0001**	75.49	**<0.0001**	74.1	3.0049	**<0.0001**	**1316**
2500	8	0.8233	0.2098	0.4121	1.2345	**<0.0001**	0.9453	0.9957	0	1.2516	**0.0020**	30
3500–4000	7	0.9807	0.1276	0.7307	1.2308	**<0.0001**	0.2907	0.9995	0	1.9095	0.0775	**60**
4500–5000	8	0.8666	0.1099	0.6512	1.0820	**<0.0001**	6.06	0.5323	30.8	3.395	**0.0255**	**265**
5500–7000	8	0.8049	0.1983	0.4163	1.1936	**<0.0001**	0.8083	0.9974	0	1.2467	**0.0039**	29
7500	2	0.8730	0.0118	0.8498	0.8962	**<0.0001**	0.0084	0.9272	0	37.35	0.494	**2047**
8500	1	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
9500–11,000	4	1.0000	0.0131	0.9744	1.0256	**<0.0001**	0	1	0	76.122	**<0.0001**	**2527**
17,000	1	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.

[a] Total number of observations points or MSA values included in the meta-analysis for mammal species. The total number of studies is 22, from which 41 datasets were extracted containing 151 MSA calculated values for different distances.

The number of datasets per distance interval decreased as the distance from infrastructure increased (Tables 1 and 2).

Sensitivity analyses for mammal and bird data resulted in similar MSA values per distance interval with the exception of the distance intervals 300–320, 340–375 and 380–490 m for the bird data, which had larger MSA values (Appendix 4, Supplementary material available at http://www.environmentalevidence.org/SR68.html). Heterogeneity was not statistically significant in these intervals, but there was publication bias.

3.2.3. Exploration of reasons for heterogeneity: meta-regression

The relationship between MSA and distance to infrastructure was positive for both mammals and birds (Fig. 1 and 2). When the data was subgrouped per habitat, all relationships were also positive except for temperate forests in the case of mammal species, and Mediterranean forests in the case of bird species (Tables 6 and 7). In forests both bird and mammal species abundances were affected in the proximity of infrastructure whereas in non-forested areas the effect extended over a larger distance (Tables 6 and 7). All relationships had lower AICc when "LOGDIST" was chosen as explanatory variable, except for Tundra.

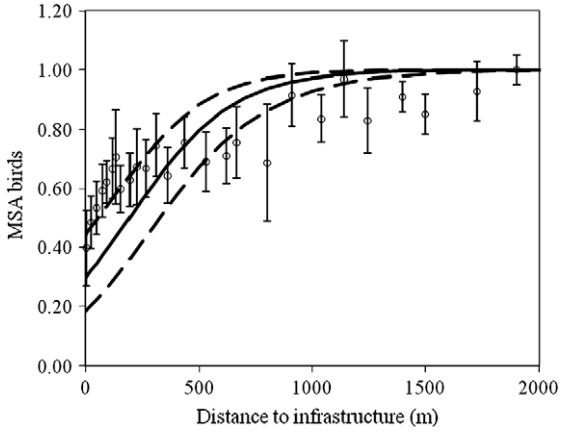

Fig. 1. Logistic regression between mean species abundance of birds and distance from infrastructure. Open dots represent the pooled results of the meta-analysis per distance interval ± S.E. The black line denotes the estimated curve for the decline of MSA, related to distance. Dashed lines are the 95% upper and lower limits of the confidence bands of the curve.

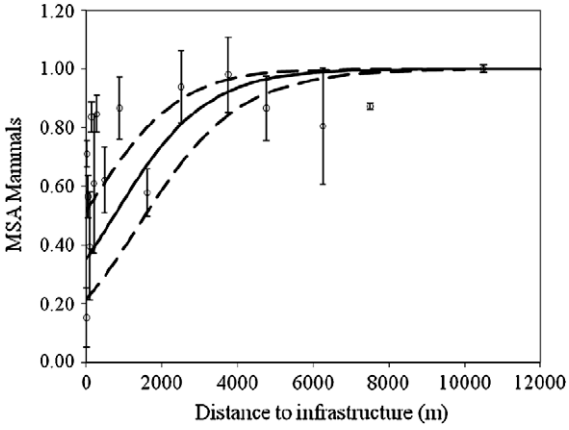

Fig. 2. Logistic regression between mean species abundance of mammals and distance from infrastructure. Open dots represent the pooled results of the meta-analysis per distance interval ± S.E. The black line denotes the estimated curve for the decline of MSA, related to distance. Dashed lines are the 95% upper and lower limits of the confidence bands of the curve.

There existed also differences in the relationship between MSA and distance to infrastructure for different taxa. Accitriformes and Falconiformes were the only bird taxa which were unaffected or positively affected by the presence of infrastructure, whereas for other bird taxa proximity to infrastructure seemed to exert a negative effect on species abundance, or the magnitude of the effect was unknown due to low sample size (Supplementary material available at http://www.environmentalevidence.org/SR68.html). From all mammal taxa, a positive relationship between MSA and distance to infrastructure could only be found for Artiodactyla and Rodentia, but abundances of the latter were only reduced at short distances from infrastructure while this effect extended over a large distance for the former.

Several *ad hoc* models were built to explore the high heterogeneity between effect sizes. We worked on several biological hypotheses to explain the variability in the relationship between MSA and distance to infrastructure. For bird species the most parsimonious model was that containing only the explanatory variable "LOGDIST" (Akaike weight: 0.78, Table 3). For mammal

Table 3
Models expressing different biological hypotheses on the influence of infrastructure distance, infrastructure type and infrastructure visibility (forest) on the mean species abundance of birds. The selected model appears in bold.

Model (birds)	AICc	*K*	*n*	Δ_iAICc	w_i
LOGDIST + FOR + INFTYP + LOGDIST * INFTYP + LOGDIST * FOR + FOR * INFTYP + LOGDIST * INFTYP * FOR	No model convergence				
LOGDIST + FOR + LOGDIST * FOR	1630.78	6	288	3.04	0.17
LOGDIST + INFTYP + LOGDIST * INFTYP	1636.04	6	288	8.30	0.01
LOGDIST + FOR	1633.96	5	288	6.21	0.03
LOGDIST + INFTYP	1637.29	5	288	9.54	0.01
LOGDIST	**1627.75**	**4**	**288**	**0.00**	**0.78**
FOR	1647.18	4	288	19.43	<0.01
INFTYP	1646.40	4	288	18.65	<0.01
DIST + FOR + DIST * FOR	1762.19	6	288	134.45	<0.01
DIST + FOR	1744.61	5	288	116.86	<0.01
DIST	1739.98	4	288	112.23	<0.01

AICc = Akaike Information Criterion corrected for sample size;
K = No. of estimable parameters: Intercept, log (effect distance), effect distance, forest, infra type, interaction term, study and error term;
n = No. of data points;
Δ_iAICc = Delta AICc value;
w_i = Akaike weight.

Table 4
Models expressing different biological hypotheses on the influence of infrastructure distance, infrastructure type and infrastructure visibility (forest) on the mean species abundance of mammals. The selected model appears in bold. See Table 3 for explanation of coefficients.

Model (mammals)	AICc	*K*	*n*	Δ_iAICc	w_i
LOGDIST + FOR + INFTYP + LOGDIST * INFTYP + LOGDIST * FOR + FOR * INFTYP + LOGDIST * INFTYP * FOR	889.18	10	151	3.59	0.14
LOGDIST + INFTYP + LOGDIST * INFTYP	963.06	6	151	77.50	<0.01
LOGDIST + FOR + LOGDIST * FOR	900.02	6	151	14.46	<0.01
LOGDIST + LOGDIST	919.67	5	151	34.12	<0.01
LOGDIST + FOR	911.34	5	151	25.79	<0.01
LOGDIST	923.42	4	151	37.87	<0.01
INFTYP	896.93	4	151	11.38	<0.01
FOR	899.30	4	151	13.75	<0.01
DIST + FOR + INFTYP + DIST * INFTYP + DIST * FOR + FOR * INFTYP + DIST * INFTYP * FOR	1081.87	10	151	196.28	<0.01
DIST + FOR + DIST * FOR	964.56	6	151	79.01	<0.01
DIST + INFTYP	893.28	5	151	7.73	0.02
DIST + FOR	**885.54**	**5**	**151**	**0.00**	0.84
DIST	897.99	4	151	12.45	<0.01

Table 5
Models expressing different biological hypotheses on the influence of infrastructure distance, traffic intensity (noise) and infrastructure visibility (forest) on the mean species abundance of birds. The selected model appears in bold. See Table 3 for explanation of coefficients.

Model (birds)	AICc	*K*	*n*	Δ_iAICc	w_i
LOGDIST + FOR + TRAF + LOGDIST * TRAF + LOGDIST * FOR + FOR * TRAF + LOGDIST * TRAF * FOR	583.52	10	87	10.87	<0.01
LOGDIST + TRAF + LOGDIST * TRAF	512.30	6	87	31.65	<0.01
LOGDIST + TRAF	503.06	5	87	22.40	<0.01
TRAF	537.10	4	87	56.44	<0.01
LOGDIST	**480.66**	**4**	**87**	**0.00**	**0.99**

species the most parsimonious model was that including the explanatory variables "DIST" and "FOR" (Akaike weight: 0.84, Table 4).

The most parsimonious model for the subset of bird data containing information on traffic intensity was that including only "LOGDIST" as explanatory variable (Akaike weight: 0.99, Table 5).

4. Discussion

4.1. Effect of distance from infrastructure on bird and mammal species abundance

Our analyses suggest that infrastructure can have a negative impact on bird and mammal abundance and that this impact is more evident in the proximity of the infrastructure. Pooled results for pseudorreplicated data indicated a decline in species abundance of 28–36% and 25–38% for birds and mammals within 2.6 km and 17 km from infrastructure, respectively. Pooled results per distance interval showed that MSA of birds and of mammals became higher for distance intervals far away from infrastructure. The meta-regression also indicated a positive relationship between MSA of birds and mammals and distance to infrastructure. A second conclusion that can be obtained from these results is that bird populations are likely to be more affected at short distances from infrastructure while the effect on mammal populations seems to extend over larger distances. These results confirm the effect distances reported in other studies, which were larger for mammals (Cameron et al., 1992; Newmark et al., 1996; Nellemann et al., 2003a; Joly et al., 2006) than for birds (Van der Zande et al., 1980; Madsen, 1985; Reijnen et al., 1996; Rheindt, 2003). However, considerable heterogeneity was found in our results, especially for birds, and also publication bias, both limiting the robustness of these conclusions.

Table 6
Univariate meta-regression coefficients for the relationship between MSA and distance for bird species in different habitats. Models with log-transformed distance as explanatory variable are more parsimonious than without transformation for all habitats.

Bird species							
Explanatory variable	Habitat	*b*	Intercept	*k*	*n*	*K*	AICc
LOGDIST	Agricultural lands	1.523	−7.933	15	109	4	626.29
	Temperate forests	0.761	−2.868	8	35	4	192.57
	Boreal forests	No model convergence		1	2		
	Mediterranean forests	27.020	−136.950	2	4	4	−12.28
	Grasslands	1.014	−5.193	15	97	4	417.24
	Scrublands	1.174	−4.853	5	35	4	200.84
	Tropical forests	18.834	−61.705	3	6	4	80.13
	All forests	0.826	−2.770	14	47	4	263.04
	Non-forested habitats	1.333	−6.712	35	241	4	1361.75
DIST	Agricultural lands	0.005	−1.777	15	109	4	779.75
	Temperate forests	No model convergence		8	35	4	
	Boreal forests	No model convergence		1	2		
	Mediterranean forests	0.046	3.222	2	4	4	0.45
	Grasslands	0.002	−0.759	15	97	4	488.01
	Scrublands	No model convergence		5	35	4	
	Tropical forests	0.522	−17.254	3	6	4	97.57
	Forests	0.011	−0.894	14	47	4	301.93
	Non-forested habitats	0.004	−1.218	35	241	4	1478.68

Table 7
Univariate meta-regression coefficients for the relationship between MSA and distance for mammal species in different habitats. Models with log-transformed distance as explanatory variable are more parsimonious than without transformation for all habitats except for tundra.

Mammal species							
Explanatory variable	Habitat	*b*	Intercept	*k*	*n*	*K*	AICc
LOGDIST	Agricultural lands	No model convergence		2	9		
	Temperate forests	0.260	0.103	4	15	4	67.99
	Boreal forests	1.526	−7.742	9	34	4	162.23
	Grasslands	Only 1 dataset		*1*	*5*		
	Scrublands	2.133	−6.773	3	11	4	59.19
	Tropical forests	0.681	−1.136	5	22	4	81.39
	Semi-arid lands	Only 1 dataset		*1*	*8*		
	Arctic tundra	2.854	−21.429	12	52	4	364.50
	All except for Tundra	0.978	−3.670	25	104	4	528.05
	Forests	0.860	−3.151	18	71	4	313.90
	Non-forested habitats	1.142	−7.089	19	85	4	548.28
DIST	Agricultural lands	No model convergence		2	9		
	Temperate forests	0.002	0.850	4	15	4	75.91
	Boreal forests	No model convergence					
	Grasslands	Only 1 dataset		*1*	*5*		
	Scrublands	No model convergence		4			
	Tropical forests	0.003	0.592	5	22	4	107.21
	Semi-arid lands	Only 1 dataset		*1*	*8*		
	Arctic tundra	0.001	−1.832	12	52	4	332.68
	All except for Tundra	0.004	−0.478	25	104	4	614.09
	Forests	0.003	−0.026	18	71	4	397.21
	Non-forested habitats	0.001	−1.659	19	85	4	561.76

The sensitivity analyses resulted in a slightly (but not statistically significant) larger pooled effect size for pseudorreplicated data in the case of bird species. Sensitivity analyses per distance interval showed similar results to the full meta-analyses except for the distance intervals between 300 and 480 m from infrastructure, with larger effect sizes. Yet, fail-safe numbers indicate that a large number of non-significant studies would be needed to overturn the pooled effect sizes calculated for these distance intervals. Thus, we decided to maintain these studies in the meta-regression following Wolf and Guevara (2001), who advocate for the use of all available data when doing meta-analysis.

The high heterogeneity underlying the results of our meta-analysis indicates that infrastructure development can have negative impacts on bird and mammal abundance within a certain distance depending on a number of factors which we further explore in Section 4.2.

4.2. Exploration of sources of heterogeneity

Meta-regression helped us to elucidate that "LOGDIST" was the main explanatory variable for the decline in abundance of bird populations due to infrastructure. For mammals, "DIST" was the main variable but the variable "FOR" seemed to add important information to the model. Meta-regression on subgroups divided by habitat type and taxa indicated that in open habitats, both mammal and bird populations seem to avoid infrastructure over larger distances, compared to those in forested biomes, which could probably be related to reduced visibility of infrastructure. Forman and Deblinger (2000) showed similar results for breeding birds in open grasslands and in woodlands (data adapted from Reijnen et al. (1995, 1996)).

For the subset of bird data including information on traffic intensity, the most parsimonious model was that which contained

only "LOGDIST" as explanatory variable. Therefore it seems that traffic intensity has no effect on the reduction of bird populations nearby roads. These results are contrary to the findings of a number of authors that have highlighted the pernicious effects of traffic intensity and noise on bird populations (Reijnen and Foppen, 1994; Reijnen et al., 1995, 1996, 1997; Forman et al., 2002; Rheindt, 2003). However, there are other studies which found a decline in bird populations near roads with low traffic intensity (Räty, 1979; Madsen, 1985; Develey and Stouffer, 2001) and others which found no clear relationship (Peris and Pescador, 2004). Finally, some authors claim that there exists a trade-off between traffic intensity and velocity, with low traffic intensity being related to higher velocities (Martínez-Abraín, 1994; Drews, 1995). Yet, traffic velocity seems to be related to bird mortality, which occurs on the road itself. To the best of our knowledge, studies that deal with this topic usually do not report on bird densities at increasing distances from roads (or include a control distance for comparison). As none of the studies included in our analysis contained data on traffic velocity, the influence of this variable could not be evaluated.

Not all species showed a decline in abundance nearby infrastructure: species abundance of Accipitriformes and Falconiformes was larger in the proximity of infrastructure. This was not a surprising outcome since other studies have reported the presence of raptors nearby roads searching roadkill carrion (Forman and Alexander, 1998; Lambertucci et al., 2009) and hunting (Dónazar et al., 1993; Fajardo et al., 1998; Dean and Milton, 2003), with some exceptions during the breeding season (Martínez-Abraín et al., 2008).

In the case of mammals, we could detect that Rodentia populations were slightly affected within few meters from infrastructure. By contrast, Artiodactyla species were affected up to distances of several hundred meters. Within Artiodactyla wild reindeer (*Rangifer tarandus*) was one of the most studied and sensitive species, with their population abundance being reduced up to several kilometres from infrastructure (Nellemann and Cameron, 1996; Nellemann et al., 2001, 2003a,b). These outcomes are consistent with the fact that small-sized mammals usually have smaller home ranges and migration distances compared to medium- and large-sized mammals, the latter being more sensitive to infrastructure development and habitat fragmentation (Harestad and Bunnel, 1979; Buskirk, 2009).

4.3. Review limitations

Only some of the included studies used Before-After-Control-Impact (BACI) experimental designs, so we decided to use the largest reported distance in the study as control distance. Although the sensitivity analyses allowed us to remove some of the studies of lower quality and indeed the results did not vary in most of the cases, we acknowledge that our conclusions are restricted by the lack of proper comparators in some of the studies.

The identified publication bias is another of the weaknesses of our review. A few studies did not find negative effects of infrastructure on bird and mammal populations and were not included due to lack of proper data on the selected variables (e.g. Adams, 1984; Evans and Gates, 1997; Ballard et al., 2000); and there may exist many others that were never published due to non-significant results or that we were unable to obtain (grey literature). However, fail-safe numbers indicated that our results are sufficiently robust.

Many of the studies initially considered in our systematic review lacked suitable data for extraction and had to be left out of the analysis. Therefore we may have excluded potentially relevant studies and included lower quality studies due to availability of data on the selected variables.

The scope of the study was intended to be global and covered different types of biomes and habitats; nevertheless there is a geographical bias in the studies included in our review. Most studies were done in Europe and North America and therefore the applicability of the results to other geographic areas remains unknown.

4.4. Conclusions and management implications

Changes in wildlife populations in the proximity of infrastructure have been reported for decades in a number of studies (see Table 2 in Supplementary material, available at http://www.environmentalevidence.org/SR68.html), and have been pointed out in relevant authors' reviews (Spellerberg, 1998; Trombulak and Frissell, 2000; Forman et al., 2003). Additionally, there have been previous attempts to quantify wildlife population decline in relation to distance from infrastructure, either locally (Forman and Deblinger, 2000) or at the global scale (UNEP, 2001; Nellemann et al., 2003b; Fahrig and Rytwinski, 2009), but none of them followed the guidelines for systematic reviews (Pullin and Stewart, 2006) or summarized the information by means of a meta-analysis. Our study represents a step forward within the field of road ecology research that may contribute to the understanding of the magnitude of the pernicious effects of infrastructure development on animal populations. Reported effects for most bird populations extend over distances up to about 1 km, and for most mammal populations up to about 5 km, with variation according to taxa and habitat type (Fig. 1 and 2). However, the evidence shown by our results is somewhat hampered by the limitations mentioned in Section 4.3. We therefore encourage researchers to perform BACI studies whenever possible and make their data available for researchers pursuing a systematic review. Should new studies that include these recommendations be released in the future, the review can be updated by including the new available evidence.

Although the patterns found in our analysis are clear, we would like to emphasise that these only represent a partial estimate of the actual effect of infrastructure on wildlife. Therefore, we highlight the importance of broadening the analysis to other taxonomic groups, such as herpetofauna, plants and invertebrates (e.g. Przybylski, 1979; Angold, 1997; Auerbach et al., 1997; Haskell, 2000; Shine et al., 2004; Barrows et al., 2006). Further research on these taxonomic groups would add up to the current models presented in this study, contributing to eventually produce a model that would provide an accurate estimate of the effects of infrastructure development on biodiversity.

The results of our meta-analysis will be implemented in the next version of the GLOBIO3 model, which is used to estimate the biodiversity loss at global, regional and national level at current state and for possible future scenarios and policy options (Alkemade et al., 2009). The results of the GLOBIO3 model have been reported in global assessments such as the second Global Biodiversity Outlook and the fourth Global environmental Outlook and are aimed to support policy makers on the elaboration of biodiversity conservation policies (sCBD and MNP, 2007; UNEP, 2007). The method is also used at the regional level (Verboom et al., 2007) and at the country level (e.g. in Viet Nam, Ecuador and Nicaragua).

Our study shows the importance of minimizing infrastructure development for wildlife conservation in relatively undisturbed areas. By combining actual species distributions with the effect distance functions we developed as a form of dose–effect relationship, regions sensitive to infrastructure development may be identified. More specifically, the effect distance functions can be used in models in support of decision making on infrastructure planning. This would mean a substantial improvement of the current situation in which, in most cases, results of previous studies on ecological impacts are barely taken into account (OECD, 2002; Roedenbeck et al., 2007).

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Supplementary material

Supplementary material available at http://www.environmentalevidence.org/SR68.html. Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.02.009.

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Interactions between demography, genetics, and landscape connectivity increase extinction probability for a small population of large carnivores in a major metropolitan area

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The extinction vortex is a theoretical model describing the process by which extinction risk is elevated in small, isolated populations owing to interactions between environmental, demographic, and genetic factors. However, empirical demonstrations of these interactions have been elusive. We modelled the dynamics of a small mountain lion population isolated by anthropogenic barriers in greater Los Angeles, California, to evaluate the influence of demographic, genetic, and landscape factors on extinction probability. The population exhibited strong survival and reproduction, and the model predicted stable median population growth and a 15% probability of extinction over 50 years in the absence of inbreeding depression. However, our model also predicted the population will lose 40–57% of its heterozygosity in 50 years. When we reduced demographic parameters proportional to reductions documented in another wild population of mountain lions that experienced inbreeding depression, extinction probability rose to 99.7%. Simulating greater landscape connectivity by increasing immigration to greater than or equal to one migrant per generation appears sufficient to largely maintain genetic diversity and reduce extinction probability. We provide empirical support for the central tenet of the extinction vortex as interactions between genetics and demography greatly increased extinction probability relative to the risk from demographic and environmental stochasticity alone. Our modelling approach realistically integrates demographic and genetic data to provide a comprehensive assessment of factors threatening small populations.

1. Introduction

Understanding factors that influence extinction in wild populations is a fundamental challenge for population ecology and conservation biology [1–3]. Habitat fragmentation can result in small, isolated wildlife populations within which extinction risk may be elevated by interactions between environmental, demographic, and genetic factors, often referred to as the extinction vortex or small-population paradigm [4–5]. Stochasticity in demography from sampling variance within small populations (demographic stochasticity) causes variation in realized vital rates, even in a constant environment, which can greatly increase extinction risk. Small, isolated populations also lose genetic diversity over time,

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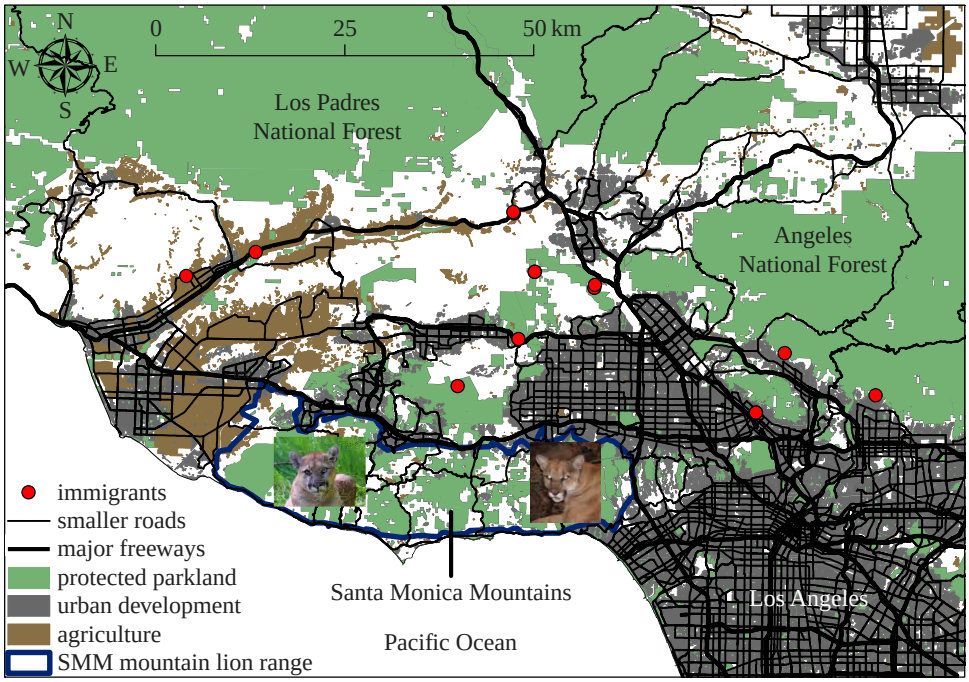

Figure 1. Santa Monica Mountains (SMMs) and adjacent areas in the greater Los Angeles metropolitan area, California. The blue polygon is the composite home range for mountain lions tracked from 2002 to 2015 within the SMMs. Red circles are locations of mountain lions captured or otherwise sampled in adjacent areas used to simulate immigration in our model.

principally through inbreeding and genetic drift, which may further increase extinction risk if demographic performance becomes compromised by inbreeding depression [4,6,7].

The importance of inbreeding depression in influencing extinction of small populations is theoretically robust, but empirical support remains scant as few studies have documented the causes of extinction in nature [3,5,8]. Theory also predicts that when populations become small enough for inbreeding depression to occur, demographic and environmental stochasticity are likely to cause extinction before inbreeding will play an important role [5,9,10]. These conflicting predictions have led to a considerable debate regarding the relative influence of demographic and genetic factors on the viability of small populations [6,10–12]. There is now substantial evidence that inbreeding depression can strongly influence demographic performance of individuals and populations [8,13–15]. Fagan & Holmes [1] retrospectively characterized the decline to extinction of 10 wild vertebrate populations providing key insight into the extinction process; however, they could not demonstrate the importance of inbreeding depression and associated demographic consequences directly because they lacked genetic data. Thus, the relative influences of demographic and genetic factors on the extinction of wild populations remain poorly understood and controversial [3,8,16,17]. Modelling dynamics of small populations with empirical demographic and genetic data may be effective to elucidate the mechanisms of the extinction vortex for wild populations [18].

Large carnivores, and specifically mountain lions (*Puma concolor*), are excellent study species with which to investigate interactions between demography and genetics, and their influence on extinction risk in fragmented landscapes. Large carnivores occupy large home ranges and exist at low density, making them sensitive to habitat fragmentation and anthropogenic barriers to connectivity [19]. Recently, there have been examples of small populations of felid and canid top predators in North America being pushed to the brink of extinction by negative consequences of low genetic diversity [14,15]. For mountain lions, a relatively small number of males often dominate breeding opportunities in wild populations, which can further reduce the effective population size [14,20]. Recent work showed that major freeways and development represent substantial barriers to movement of mountain lions between areas of formerly connected habitat and documented strong genetic structuring, high rates of inbreeding, and low genetic diversity in isolated populations in southern California [20,21].

Another population of mountain lions, Florida panthers (*Puma concolor coryi*), declined rapidly in the twentieth century owing to overhunting and habitat loss until a small, isolated population of 20–30 animals persisted in south Florida [14]. This population exhibited low genetic diversity and poor demographic performance resulting from inbreeding depression [14]. Detailed research on the near-extinction and subsequent genetic restoration of panthers provided quantitative predictions for (i) levels of genetic diversity at which inbreeding depression may occur in mountain lion populations and (ii) demographic consequences of inbreeding depression for this species [14,22,23]. Mountain lion populations isolated by habitat fragmentation and major freeways in the greater Los Angeles area have the lowest levels of genetic diversity documented for this species aside from Florida panthers [20,21], causing concern regarding inbreeding depression.

We developed an individual-based population model with empirical data from a 13 year (2002–2015) study during which we quantified survival, reproduction, movements, and multilocus genotypes of individual mountain lions ($n = 45$) within and adjacent to an isolated population in the Santa Monica Mountains (SMMs) west of Los Angeles [20] (figure 1). We constructed a starting population of individuals that reflected the age, sex, and genetic structure of the 2015 population and projected the model forward to estimate stochastic population growth, extinction probability, and measures of genetic diversity over the next 50 years. We used genotypes of mountain

lions captured or otherwise sampled in areas adjacent to the SMMs to simulate individual-level immigration events and additional gene flow into the SMMs. We used the model to address the following questions. (i) Is the population currently demographically vigorous? (ii) What is the probability of extinction due purely to stochastic demography? (iii) At what rate will genetic diversity decline under a range of immigration scenarios reflecting potential future variation in landscape connectivity? (iv) If the model predicts rapid declines in genetic diversity, how would reductions in vital rates proportional to those documented in Florida panthers experiencing inbreeding depression influence population growth and extinction probability of SMM mountain lions?

2. Material and methods

(a) Capture and monitoring

We captured mountain lions using Aldrich foot-snares or cable restraints, baited cage-traps, or by treeing them with trained hounds. We deployed global positioning system (GPS) collars (Followit AB, Simplex and Tellus models, Stockholm, Sweden; North Star Science and Technology LLC, Globalstar Tracker model, King George, VA; or Vectronic Aerospace, GPS Plus model, Berlin, Germany) on adults. We also captured three- to five-week-old kittens at natal dens by hand and implanted very high-frequency (VHF) transmitters (Telonics, IMP/200/L, Mesa, AZ) in their peritoneal cavities (details in [24]). We monitored the survival of GPS-collared adult and subadult mountain lions daily via remote download and VHF instrumented kittens greater than or equal to three times per week using ground telemetry. When we detected mortality, we hiked into the locations to retrieve carcasses and attempted to determine cause of death. Additionally, all carcasses were necropsied by experienced veterinarians to confirm our field diagnoses and to gain additional information. We monitored reproduction of all collared females, using GPS telemetry to locate natal dens and capture, count, sex, and mark kittens [24].

(b) DNA genotyping

We genotyped all captured mountain lions at 54 microsatellite loci using laboratory methods and markers described previously [20]. We also genotyped mountain lions from samples obtained in areas adjacent to the SMMs (figure 1).

(c) Estimating demographic parameters

We separated mountain lions tracked within the SMMs into three age classes for parameter estimation: kittens, subadults, and adults. Kittens were dependent offspring with their mothers. Subadults were independent animals prior to reproduction, whereas adults were resident, reproducing animals. Kittens in the SMMs became independent from their mothers at a mean of 408 days (range = 348–515, $n = 12$). Thus, we considered mountain lions of both sexes to be kittens from 0 to 14 months. We considered females to be subadults from 14 to 25 months (age of youngest known-age female documented breeding). We considered males to be subadults from 14 to 42 months (age of the youngest known-age male documented breeding). We estimated sex and age-class-specific survival rates using the Kaplan–Meier estimator generalized for staggered entry [25] and the Greenwood method for estimating variance implemented in R v. 3.1.3 (R Development Core Team 2015) with the 'survival' package. We pooled sexes for kitten survival estimates owing to relatively small sample sizes ($n = 16$). We allowed females in the model to breed in the first month after reaching adulthood. Females raising kittens within the model were not eligible to breed again until they either lost the entire litter to mortality or the kittens became independent, whichever came first. Females in the model bred in the first month following loss or independence of kittens as all females we tracked in the SMMs bred within 25 days (mean = 17 days, range 11–25, $n = 4$) of losing kittens to mortality or independence. Mean litter size was 2.88 in the SMMs (range 2–4, $n = 8$ litters). We estimated the probability of a female having two (0.375), three (0.375), or four (0.250) kittens in a litter based on the proportion of these litter sizes documented in our study.

(d) Model overview

We developed an individual-based population model for mountain lions that incorporated demographic and environmental stochasticity, as well as a simple form of density-dependence (figure 2). Individual-based population models differ from classical models in that population-level processes are explicitly modelled as the outcome of the variable performance of individuals, which are tracked through time and allowed to differ in important ways [26,27]. We began the model with a starting population that reflected the sex, age, and genetic structure of the current (2015) population and projected the model forward to estimate the demographic and genetic structure of future populations (figure 2). Specifically, both adult males (including the sole known breeder) and three of the (presumed) four to six adult females residing in the SMMs during 2015 were included in the starting population. Two additional females that had been captured in the SMMs and subsequently died were included as adults. Eight additional mountain lions born in the SMMs during 2012–2015 were included as kittens and subadults (two males and two females of both age classes). Thus, the starting population comprised 15 SMM mountain lions (nine females, six males) with empirical genotypes at 54 loci. Offspring produced in the model were assigned genotypes derived through simple Mendelian genetics (i.e. one allele randomly inherited from each parent at each loci).

We ran simulations consisting of 5000 population projections of 50 years, unless noted otherwise. The population dynamics simulated by the model was a reflection of individual-based demographic processes specified by empirical probability distributions estimated with data collected from wild mountain lions in the SMMs. Population size was updated at each monthly time step by subtracting individuals lost through mortality and adding individuals gained through reproduction or immigration (figure 2). We imposed mortality (survival senescence) on all mountain lions of both sexes in the model that reached 15 years of age as mountain lions have rarely been documented living beyond that age in the wild [28]. We incorporated density-dependence by imposing a maximum number of adult males ($n = 2$) and females ($n = 6$) that could exist in the population at any given time. When all of the adult slots of a given sex were occupied, we eliminated individuals of that sex that would have otherwise transitioned from subadults to adults. This process simulated density-dependent population regulation through death or dispersal. This density-dependence provided an important limitation on population growth, which otherwise would have resulted in population sizes larger than the SMMs could realistically support given the limited space and barriers to movement [20]. Although the upper limits for adult males and females were fixed, the number of adults varied stochastically during model projections owing to variation in survival and reproduction. The sex-specific maximum values reflected our understanding of the size and space limitations of the population based on intensive monitoring with telemetry, genetic analysis, and remote cameras for more than 13 years. See additional details of the modelling procedures in electronic supplementary material, appendix A.

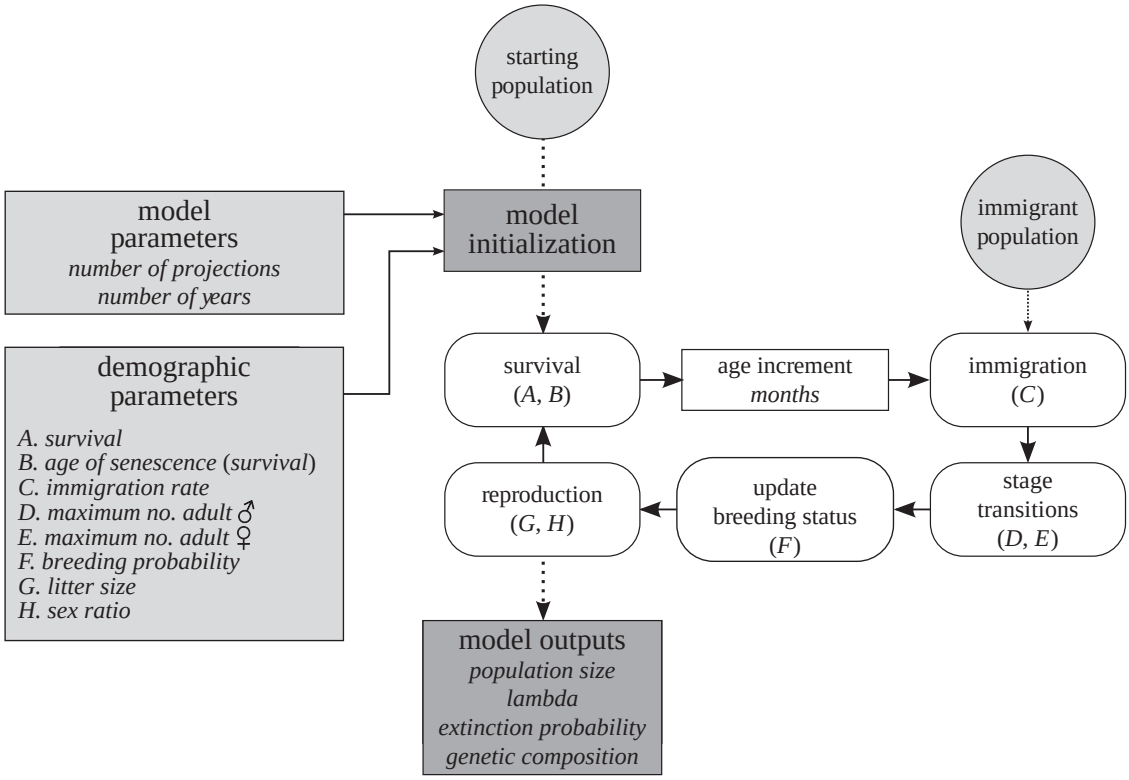

Figure 2. Flow diagram shows demographic parameters, population model loop (in white boxes) and model outputs. Demographic parameters are labelled with letters (A–H) to indicate which parameters are relevant to each portion of the main population model loop.

(e) Submodel structure

(i) Survival

We generated environmentally stochastic monthly survival probabilities by transforming estimated Kaplan–Meier survival rates and their standard deviations into beta shape parameters, using the betaval function in the R package 'popbio' [29]. At each monthly time step, we drew a random survival value from this beta distribution which was used as the environmentally stochastic survival probability for all individuals of the same sex and age class during that time step. We then assessed demographically stochastic survival of each individual, using a Bernoulli trial with the monthly survival probability as the threshold between survival and mortality.

(ii) Immigration

We assigned a fixed annual immigration rate prior to starting a simulation. This annual rate was transformed into a monthly probability and was assessed stochastically, using Bernoulli trials during each monthly time step. For our main analysis, we restricted immigration to subadult males. In addition to being more likely to disperse, males are also more likely to undertake longer and riskier dispersal events [30,31]. Indeed, the single immigration event documented into the SMM population during our study was a radio-collared subadult male that crossed the 101 freeway [20]. Although we expect most immigrants into the SMMs will be males, we also ran simulations where both subadult males and females immigrated with equal probability to investigate the influence of female immigration. We assigned genotypes to immigrants from mountain lions captured or otherwise genotyped in adjacent areas north and east of the SMMs ($n = 18$). The model sampled immigrant genotypes without replacement from the 18 genotypes available. If all genotypes were used during a given population projection, the pool of potential immigrants was reset and once again populated with all 18 available genotypes from north and east of the SMMs. Each immigrant was randomly assigned an age from 14 to 42 months (for males) or 14–25 months (for females). Once in the SMM population, these immigrants were subjected to the same demographic procedures as other subadults in the model.

(iii) Age class adjustment

We allowed some flexibility in the age that subadults of both sexes transitioned to adults. For females, we incorporated stochasticity into the age of first reproduction (and therefore in their transition to adulthood) by sampling each individual's age of transition from a uniform distribution between 25 and 33 months. Males transitioned to adulthood at 42 months if there was room for an additional adult male in the population based on our density-dependent limit. However, if there were no adult males present in the population, then subadult males greater than or equal to 36 months of age were eligible to transition to adulthood and begin breeding. We implemented this flexibility because breeding for male mountain lions in wild populations is probably delayed beyond the age of sexual maturity. Thus, when no adult males were present, we assumed younger males would begin breeding sooner.

(iv) Breeding status

We designated reproductive males and females in the starting population and, thereafter, the model randomly selected breeding animals from subadults eligible to transition to adults when openings became available. Males reaching breeding status remained reproductive for the remainder of their lives. Breeding females were eligible to become pregnant throughout the remainder of their lives whenever they did not have dependent offspring. New offspring were produced three months after pregnancy to simulate the gestation period for mountain lions.

(v) Reproduction

Females produced offspring at any time of the year consistent with mountain lion reproductive ecology and our documentation of litters throughout the year in the SMMs. When one breeding

male was present in a simulated population, he mated with all adult females. When two males were present, they each mated with half the adult females. When an odd number of females were present, one was designated as a 'floater' that could mate with either male randomly. Litter size varied stochastically by generating a random, uniform value between 0 and 1 for each reproductive female and comparing the value to a cumulative probability distribution for litter sizes of 2, 3, and 4 based on the proportion of these litter sizes documented during our study. We determined the sex of each offspring using a Bernoulli trial with a probability of 0.5.

We documented either one or two adult males in the population at any one time throughout the 13 year field study. Thus, the number of breeding males may have fluctuated between one and two males at different times during the study. However, we never confirmed that two males were ever breeding simultaneously in the population with genetic data. In fact, parentage analysis indicated that only two males were responsible for all known reproduction from 2002 to 2015 with sequential breeding periods that did not overlap. To account for this uncertainty we modelled the two possible scenarios separately: (i) a situation where less than or equal to two adult males could be present but only a single male bred at any one time, and (ii) a situation where less than or equal to two adult males were present and both bred with half of the females present. We present both sets of results because both were plausible and had consequences for the rate at which genetic diversity eroded in our simulations.

(f) Model outputs

(i) Demography and extinction

We estimated λ at time t as N_t/N_{t-1}, where N_t = total population size at time t. We estimated λ_s (stochastic lambda) across time periods of interest with the formula

$$\frac{\sum^{N\text{years}} \ln(\lambda_t)}{N_{\text{years}}}.$$

We report median λ_s from the distribution of values across all 50 year projections for simulations of interest. We estimated credible intervals for λ_s using the highest posterior density (HPD) derived using the R package 'coda' (v. 0.17–1). We estimated probability of extinction as the proportion of projections that went extinct during a given simulation and derived estimates of variability by conducting a non-parametric bootstrapping procedure implemented in the R package 'boot' (v. 1.3–17). We ran 1000 bootstraps of 5000 population projections to estimate uncertainty regarding extinction probability, which we present with 95% HPD intervals. We estimated the effective population size based on a census of the breeding animals in simulated populations using the formula: $N_e = (4 \times N_{BF} \times N_{BM})/(N_{BF} + N_{BM})$. Where N_e is effective population size, N_{BF} is number of breeding females, and N_{BM} is number of breeding males.

(ii) Genetic parameters

We estimated measures of genetic diversity for starting populations and simulated populations 1–50 years in the future using mean values from genotypes of individuals across all projections in a given simulation. We estimated expected (H_e) and observed (H_o) heterozygosity, individual inbreeding coefficient (F_{is}), the mean number of alleles per loci (N_A), and the proportion of polymorphic loci using the R package 'adegenet' v. 2.0.0 [32].

(g) Elasticity analysis

We investigated sensitivity and proportional sensitivity (elasticity) of λ_s estimated by our model to small (5%) increases in vital rates [29]. We conducted these analyses with the density-independent model to investigate which demographic parameters had the greatest influence on λ_s in the absence of density-dependent limitations. We calculated sensitivity values (S) for 5% increases in each demographic parameter following Morris & Doak [29]

$$S = \frac{\text{Log } \lambda_s(\text{adjusted}) - \text{Log } \lambda_s(\text{original})}{\text{parameter(adjusted)} - \text{parameter (original)}}.$$

Where 'adjusted' refers to demographic rates increased by 5% and the resulting value of λ_s, and 'original' refers to the original demographic rates and resulting value of λ_s prior to these increases. We then calculated elasticity values (E) for each demographic parameter following Morris & Doak [29]

$$E = S \times \left(\frac{\text{parameter}_{\text{original}}}{\text{parameter}_{\text{adjusted}}}\right).$$

(h) Simulating inbreeding depression

We simulated inbreeding depression by running population projections with input parameters reduced to reflect proportional changes in age and sex-specific survival rates consistent with differences documented between Florida panthers experiencing inbreeding depression and outbred panthers following the genetic restoration programme [14,22,23]. These adjusted input parameters are provided in electronic supplementary material, table S3.

3. Results

Demographic parameters estimated from SMM mountain lions used to construct the model are summarized in electronic supplementary material, table S1. Density-independent λ_s over 25 years was 1.19 [1.13, 1.23] and was most sensitive to changes in adult female survival (electronic supplementary material, table S2). Probability of extinction from the density-independent model was 0.009. More realistic, density-dependent simulations predicted stable median population growth ($\lambda_s = 1.01$) over the next 50 years, regardless of the level of immigration (table 1 and figure 3*a*). However, there was a 15–22% probability of extinction owing to demographic stochasticity with no or low immigration into this small population (table 1). Moderately higher levels of immigration (one every 2–4 years) reduced probability of extinction due purely to demographic factors to 2–8% (table 1 and figure 3*a*).

With little or no immigration, which reflects our understanding of the current level of isolation of this population [20], heterozygosity decreased precipitously (table 2; figures 3*b* and 4). However, when we simulated increased connectivity, heterozygosity declined much more slowly and was largely (73–94%) maintained (table 2; figures 3*b* and 4). Other measures of genetic diversity such as per cent polymorphism, inbreeding coefficient (F_{is}), and the number of alleles per loci (N_A) responded to variation in male immigration similarly (table 2). Allowing both males and females to immigrate yielded similar results, although loss of heterozygosity was slightly greater and extinction risk was slightly higher than when only males immigrated (electronic supplementary material, tables S3–S4). When we simulated inbreeding depression by reducing age-class-specific survival rates proportional to reductions documented between inbred and outbred Florida panthers (electronic supplementary material, table S5), the population declined dramatically ($\lambda_s = 0.88$ [0.76, 0.98]) with an estimated probability of extinction of 99.7% in 50 years and an estimated median extinction time of 14.5 years (4.25, 30.25; electronic supplementary material, table S6).

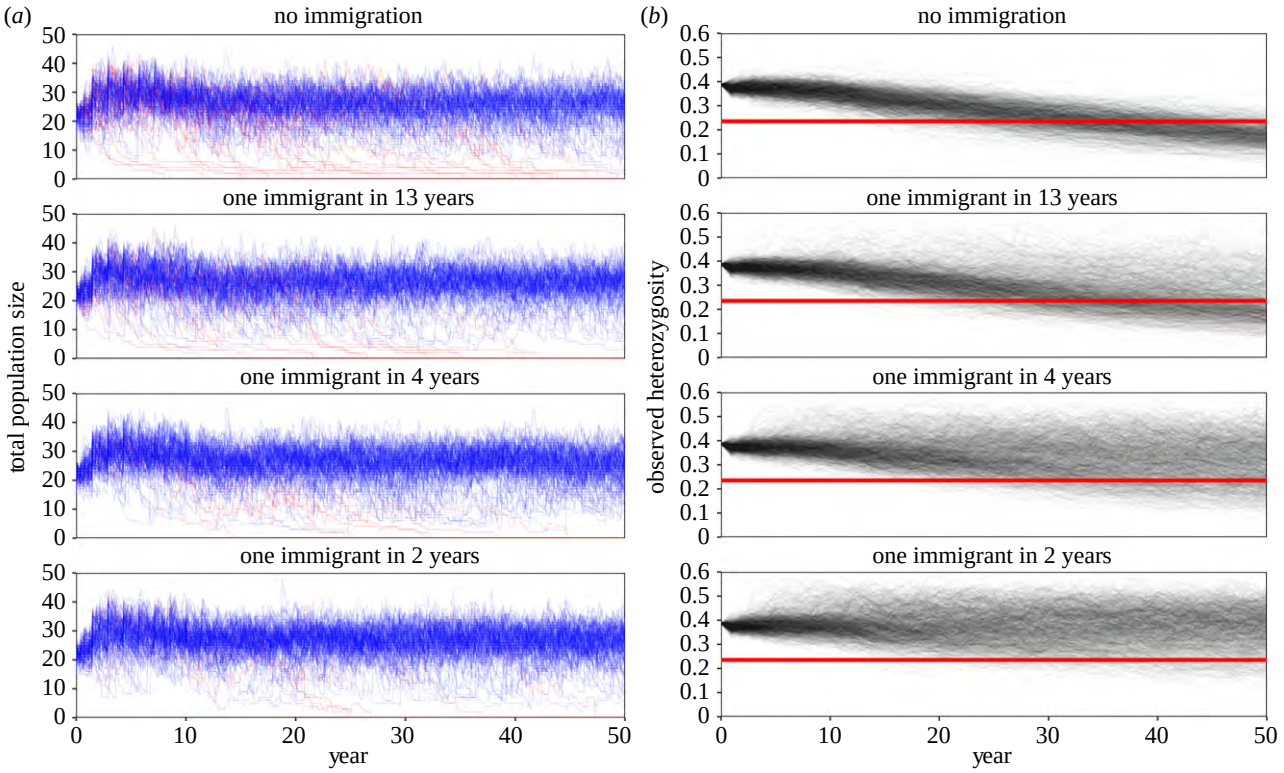

Figure 3. Results from individual-based population model for mountain lions projected 50 years showing predictions for population size and genetic diversity. Darker and lighter colours in the plots reflect highest and lowest probability of predicted values, respectively. (*a*) Population projections showing generally stable population size and growth, regardless of immigration and a 3–22% probability of extinction. Persistent projections shown in blue, projections going extinct shown in red. (*b*) Predicted values of observed heterozygosity (H_o) declined rapidly with no or low (one every 13 years) immigration, whereas H_o was largely maintained with moderate increases in immigration (one every 2–4 years). Red bands indicate the level of H_o documented in Florida panthers experiencing inbreeding depression (from Johnson *et al*. [14]), calculated as proportional loss of heterozygosity relative to outbred pumas (additional details in Discussion).

Table 1. Demographic results predicted by individual-based population model for Santa Monica Mountain lions, Southern California. Values are mean (unless otherwise noted) estimates at year 50 based on 5000 population projections.

	no immigration		one immigrant per 13 years		one immigrant per 4 years		one immigrant per 2 years	
	estimate	95% HPD[a]	estimate	95% HPD[a]	estimate	95% HPD[a]	estimate	95% HPD[a]
one male breeding								
λ[b]	1.01	(0.91, 1.02)	1.01	(0.92, 1.02)	1.01	(0.95, 1.02)	1.01	(0.99, 1.02)
extinction prob.	0.211	(0.200, 0.222)	0.156	(0.145, 0.165)	0.078	(0.07, 0.09)	0.024	(0.020, 0.029)
extinction time	30.79	(12.83, 49.20)	30.37	(12.08, 49.17)	32.44	(12.58, 49.67)	31.87	(11.50, 48.67)
adults (*n*)	5.20	(0, 8)	5.60	(0, 8)	6.23	(0, 8)	6.68	(0, 8)
N_E	2.91	(0, 3.43)	2.94	(0, 3.43)	3.00	(0, 3.43)	3.09	(0, 3.43)
two males breeding								
λ[b]	1.01	(0.91, 1.02)	1.01	(0.93, 1.02)	1.01	(0.96, 1.02)	1.01	(0.99, 1.02)
extinction prob.	0.220	(0.208, 0.231)	0.150	(0.140, 0.160)	0.066	(0.058, 0.072)	0.030	(0.025, 0.035)
extinction time	30.79	(12.08, 47.33)	30.37	(12.08, 49.17)	30.48	(12.08, 48.42)	33.55	(12.67, 49.75)
adults (*n*)	5.16	(0, 8)	5.66	(0, 8)	6.30	(0, 8)	6.69	(4, 8)
N_E	3.95	(0, 6)	4.060	(0, 6)	4.21	(0, 6)	4.45	(0, 6)

[a]95% highest posterior density credible intervals.
[b]Median stochastic population growth rate.

4. Discussion

The SMM mountain lion population is currently demographically vigorous with no indication of inbreeding depression as evidenced by estimated survival and reproductive rates that were mostly similar or slightly higher than other unhunted mountain lion populations across North America [22,23, 28,33]. The lone exception was subadult survival, which was

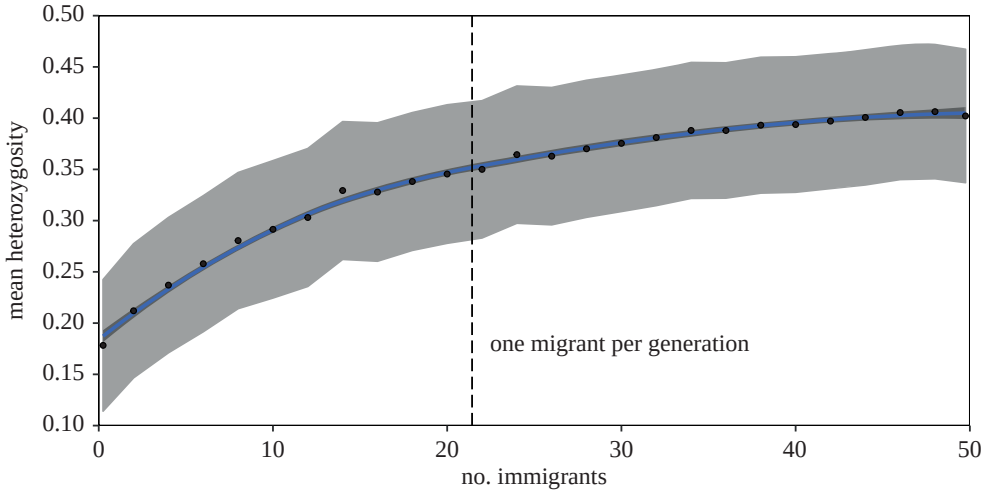

Figure 4. Relationship between genetic diversity and immigration predicted by individual-based model for mountain lions projected forward 50 years. Blue trend line depicts mean (with 95% confidence interval in grey) relationship between immigration and observed heterozygosity derived by simulating a range of immigration (0–50 immigrants over 50 years) reflecting variation in connectivity and gene flow for mountain lions between the Santa Monica Mountains and surrounding areas. (Online version in colour.)

Table 2. Genetic results predicted by individual-based population model for Santa Monica Mountain mountain lions, Southern California. Values are mean estimates at year 50 based on 5000 population projections.

	starting population		no immigration		one migrant per 13 years		one migrant per 4 years		one migrant per 2 years	
	estimate	s.e.	estimate	s.e.	estimate	s.e.	estimate	s.e.	estimate	s.e.
one male breeding										
H_e	0.352	0.032	0.143	0.027	0.189	0.027	0.248	0.028	0.297	0.029
H_o	0.388	0.040	0.165	0.032	0.217	0.033	0.283	0.034	0.337	0.034
N_A	2.220	0.123	1.431	0.074	1.624	0.082	1.882	0.093	2.098	0.100
F_{is}	0.127	0.022	0.191	0.022	0.184	0.019	0.172	0.020	0.127	0.021
polymorphic (%)	0.778	—	0.400	—	0.527	—	0.674	—	0.776	—
two males breeding										
H_e	0.352	0.032	0.156	0.027	0.206	0.028	0.276	0.028	0.328	0.029
H_o	0.388	0.040	0.178	0.032	0.234	0.033	0.311	0.034	0.366	0.034
N_A	2.220	0.123	1.468	0.077	1.669	0.085	1.960	0.096	2.190	0.104
F_{is}	0.127	0.022	0.186	0.018	0.179	0.019	0.168	0.020	0.159	0.021
polymorphic (%)	0.778	—	0.429	—	0.556	—	0.715	—	0.814	—

lower than other populations, likely because dispersal of subadults was frustrated and many were killed by adult males [20]. The population has strong growth potential as the density-independent model predicted a rapidly increasing population and an extremely low (less than 1%) probability of extinction over the next 25 years. In the absence of inbreeding depression, and with no or low immigration, the density-dependent model predicted a stable median growth rate and a 15–22% probability of extinction over the next 50 years owing to demographic stochasticity (figure 2*a*). However, without additional gene flow, the predicted erosion of genetic diversity within 50 years warrants concern regarding inbreeding depression and the potential for rapid extinction.

In the context of population viability analysis (PVA), 5–10% reduction in mean heterozygosity has been suggested to be the maximum acceptable loss over 100–200 years to avoid inbreeding depression in wild populations [34,35]. Our model predicted much greater reduction in heterozygosity (40–57%) over only 50 years. Predicted observed heterozygosity in 50 years with no or low immigration were similar to values reported for inbred Florida panthers prior to genetic introgression [14], although these values may not be directly comparable owing to the use of different microsatellite loci between studies. To account for differences in the panel of loci, we compared the proportion of heterozygosity retained in inbred panthers and SMM mountain lions relative to values quantified for outbred populations using the same loci. In the years prior to genetic introgression, inbred Florida panthers exhibited 54–58% of the observed heterozygosity of outbred pumas from Texas released into south Florida during the genetic restoration programme [14]. For comparison, mountain lions in our model at year 50, with no or low immigration, exhibited 39–56% of the

observed heterozygosity documented in mountain lions sampled east and north of the SMMs in southern California [20]. Thus, our results suggest mountain lions in the SMMs will lose as much or more genetic diversity within 50 years, relative to outbred populations, than was lost by the panther population that nearly went extinct from consequences of inbreeding depression. Not surprisingly for a population of five to eight adults, the model predicted rapid extinction of SMM mountain lions when we simulated inbreeding depression. More optimistically, our simulations predicted that modest increases in immigration would allow mountain lions in the SMMs to retain 67–87% of the heterozygosity exhibited by outbred mountain lions in southern California.

Our model predictions were consistent with empirical genetic data collected within this population to date as genetic diversity declined and inbreeding increased from 2004 to 2010 [20]. In 2010, the single immigrant documented entering the population arrived, and there was a brief (2 years) increase in genetic diversity and reduction in inbreeding [20]. However, the positive influence of this rare immigration event was short-lived as the immigrant male began to breed with his daughters and genetic diversity began to decline again [20]. Thus, the low level of immigration occurring under the current landscape conditions appears to be insufficient to reduce inbreeding and maintain genetic diversity for the long-term. In addition to concern over the absolute loss of heterozygosity predicted by our model, the rapid rate of this loss may further exacerbate extinction probability. Populations experiencing slower erosion of genetic diversity may be more likely to maintain evolutionary potential and responsiveness to environmental change [36,37].

The SMM mountain lion population has persisted at a very small population size for at least several decades and is predicted to exhibit generally stable population growth in the absence of inbreeding depression. Importantly, our model predicts a much lower probability of extinction (2–22%) due purely to demographic and environmental stochasticity compared with the probability of extinction following inbreeding depression (100%). Thus, our results support the central tenet of the extinction vortex that demography and genetics interact to elevate extinction risk in small, isolated populations [4,6], and do not support previous contentions that demographic stochasticity and deterministic factors generally cause extinction before inbreeding depression can negatively influence viability [5,10,11]. Our results also provide insight into the one migrant per generation (OMPG) rule, which suggests that OMPG is sufficient to minimize the loss of polymorphism and heterozygosity [38]. Simulating OMPG (generation time = 28–36 months) resulted in the population retaining 76–97% of its observed heterozygosity and 86–105% of its polymorphism over 50 years (table 2 and figure 3).

Large carnivores persisting within a metropolitan area as large as Los Angeles is extremely rare and our model elucidated interactions between inbreeding and demography that substantially elevated extinction probability. However, the interactions themselves are not rare and are likely to become more common in wild populations as activities of the growing human population increasingly isolate populations of wildlife in small patches of otherwise highly suitable habitat. Indeed, wolves (*Canis lupus*) on Isle Royale appear to be on the brink of extinction following increased isolation associated with decreased frequency of sufficient winter lake-ice formation to allow immigration of wolves from mainland populations, which has been linked to global climate change [15]. Florida panthers nearly went extinct from consequences of inbreeding depression after being isolated from other mountain lion populations due to overhunting and habitat loss in eastern North America. Following restoration of genetic variability through an intentional introgression programme, demographic performance of panthers improved and the population rapidly expanded numerically [14]. Inbreeding depression may be less important in influencing extinction than deterministic factors when populations continue to decline rapidly, because the rate of decline is faster than the effects of inbreeding depression [16]. For example, high mortality in endemic bird populations from introduced predators on islands is a situation where inbreeding depression is predicted to be less likely to influence viability than deterministic factors [39]. However, inbreeding depression can strongly influence extinction in cases where the deterministic decline has been slowed or halted and small populations persist in isolated patches of suitable habitat, as with Florida panthers and SMM mountain lions.

Despite wide recognition of the value of explicitly incorporating interactions between demographic, genetic, and landscape processes into PVA, and using measures of genetic diversity to improve estimates of extinction probability, these goals have remained elusive [40]. This limitation has persisted despite the increasing availability of detailed genetic data accompanying demographic studies of wildlife populations of conservation concern. Our results provide managers with an opportunity to develop proactive conservation strategies that could prevent inbreeding depression and extinction. A highway crossing structure to facilitate immigration into the SMMs could increase gene flow sufficiently to minimize the loss of genetic diversity, as well as reduce extinction probability due purely to demographic stochasticity. Mountain lions readily use highway crossing structures [41] and are known to traverse areas immediately adjacent to the SMMs [20]. If a crossing structure is implemented, mountain lions entering the SMMs via the structure should be monitored with remote cameras in conjunction with continued demographic and genetic monitoring of the population to test the predictions of our model. Alternatively, translocation of mountain lions into the SMMs from other areas could be considered in the future to facilitate genetic restoration or recolonization. However, a crossing structure might eliminate the need for translocation and, importantly, would also benefit other species for whom these freeways represent significant barriers [42]. Furthermore, although genetic rescue through translocation can be an effective short-term solution, previous work has highlighted the importance of addressing environmental factors that threaten small populations in a comprehensive manner to achieve long-term genetic restoration and viability [43,44].

Maintaining healthy populations of native top predators within greater Los Angeles, the second largest metropolitan area in the USA, would provide a model for successful large carnivore conservation within highly fragmented, urban landscapes. This would have broad implications given the rapid rate of global urbanization and importance of carnivores as critical elements of healthy ecosystems [19]. We show that demography and genetics can be modelled synergistically within PVA to provide a comprehensive assessment of factors threatening small populations with extinction. This framework can be applied globally to other small populations for which detailed demographic and genetic data are available to increase understanding of these processes and improve wildlife conservation in fragmented landscapes.

Ethics. Animal capture and handling protocols were approved by the National Park Service Institutional Animal Care and Use Committee.

Data accessibility. Data analysed in this paper are accessible through Dryad: http://dx.doi.org/10.5061/dryad.82pm0 [45].

Authors' contributions. Designed the study: J.F.B., P.J.M., J.A.S., S.P.D.R. Collected data: J.A.S., L.E.K.S., J.P.P., H.B.E., S.P.D.R. Analysed data: J.F.B., P.J.M. Wrote manuscript: J.F.B. Revised manuscript: J.F.B., P.J.M., J.A.S., L.E.K.S., J.P.P., H.B.E., S.P.D.R.

Competing interests. We declare we have no competing interests.

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RESEARCH ARTICLE

Individual and Population Level Resource Selection Patterns of Mountain Lions Preying on Mule Deer along an Urban-Wildland Gradient

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Data Availability Statement: Data are owned by the National Park Service and data sufficient to reproduce the authors' analyses will be available upon request. However, given that mountain lions are a specially protected species in California, specific animal location data will not be made available. Requests for data may be directed to: Seth P.D. Riley, National Park Service Santa Monica Mountains National Recreation Area 401 W. Hillcrest Dr. Thousand Oaks, CA 91360 (805) 370-2358; (seth_riley@nps.gov)

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Abstract

Understanding population and individual-level behavioral responses of large carnivores to human disturbance is important for conserving top predators in fragmented landscapes. However, previous research has not investigated resource selection at predation sites of mountain lions in highly urbanized areas. We quantified selection of natural and anthropogenic landscape features by mountain lions at sites where they consumed their primary prey, mule deer (*Odocoileus hemionus*), in and adjacent to urban, suburban, and rural areas in greater Los Angeles. We documented intersexual and individual-level variation in the environmental conditions present at mule deer feeding sites relative to their availability across home ranges. Males selected riparian woodlands and areas closer to water more than females, whereas females selected developed areas marginally more than males. Females fed on mule deer closer to developed areas and farther from riparian woodlands than expected based on the availability of these features across their home ranges. We suggest that mortality risk for females and their offspring associated with encounters with males may have influenced the different resource selection patterns between sexes. Males appeared to select mule deer feeding sites mainly in response to natural landscape features, while females may have made kills closer to developed areas in part because these are alternative sites where deer are abundant. Individual mountain lions of both sexes selected developed areas more strongly within home ranges where development occurred less frequently. Thus, areas near development may represent a trade-off for mountain lions such that they may benefit from foraging near development because of abundant prey, but as the landscape becomes highly urbanized these benefits may be outweighed by human disturbance.

Conservation at UCLA, California State Parks, the Santa Monica Mountains Fund, Santa Monica Mountains Conservancy/Mountains Recreation and Conservation Authority, and the Calabasas Landfill. The funding from the La Kretz Center for California Conservation came in the form of a postdoctoral fellowship for JFB made possible by an endowment from Morton La Kretz to UCLA through the Institute of the Environment and Sustainability. This fellowship was co-funded by the National Park Service. The other organizations noted above provided funding for mountain lion research that were not connected to specific grants. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

Introduction

Identifying environmental conditions associated with specific activities that influence fitness of animals, such as foraging, is a fundamental pursuit in ecology and conservation biology [1, 2]. Understanding extrinsic influences on the acquisition of food resources is especially critical for the management of small populations in human-altered landscapes because suitable habitat may be limited, and fluctuations in demography due to environmental stochasticity can have serious, rapid consequences for extinction risk [3–5]. Thus, quantifying habitat and landscape features associated with successful foraging provides valuable information regarding the spatial ecology and habitat requirements of populations of conservation concern.

Large carnivores, such as mountain lions (*Puma concolor*), are sensitive to habitat fragmentation because they occupy large home ranges within which they must acquire sufficient large prey [6]. However, mountain lion populations are able to persist within urbanized landscapes in some situations, especially where protected lands exist within or adjacent to developed areas [7–9]. In these situations, it becomes imperative to understand predator-prey interactions and how they may be influenced by development and other landscape features encountered by mountain lions while foraging for preferred prey along urban-wildland gradients. Despite considerable interest in maintaining populations of mountain lions in ecosystems altered by anthropogenic activities (e.g., [7, 10, 11]), there is little information about predator-prey interactions and resource selection of mountain lions at predation sites within and adjacent to highly urbanized landscapes.

Ecologists are increasingly recognizing the importance of considering individual-level variation in resource selection studies [12]. A common source of variation for mountain lions are sexual differences, as males and females often use space and select resources differently [13–14]. However, most studies of resource selection specifically at foraging sites of mountain lions have not investigated sex-specific patterns [15–18], but see [14]. Another common source of individual variation in resource selection stems from spatial variation in the distribution and abundance of resources. For instance, selection of a resource may vary as a function of its availability on the landscape, often referred to as a functional response in resource selection [19]. Several studies have found that large carnivores exhibit functional responses to anthropogenic landscape features or activity, which may represent trade-offs between mortality risk and foraging success (e.g., [13, 20]). Knopff et al. [20] suggested that mountain lions in Alberta, Canada benefited from human-altered landscapes primarily through prey acquisition and found that mountain lions selected some anthropogenic features more strongly in areas where these features were more prevalent. Recently, Smith et al. [21] found that male and female mountain lions responded differently to increasing development in terms of kill rates and handling time of prey. Thus, both intrinsic (sex) and extrinsic (resource availability) sources of individual-level behavioral variation may influence mountain lion-prey interactions and resource selection in human-altered landscapes. Investigating mountain lion predation in more highly urbanized landscapes than previous studies, such as in areas within and adjacent to major metropolitan areas, may identify novel behavioral responses of these top predators to human disturbance.

We quantified selection of natural and anthropogenic landscape features at sites where mountain lions consumed mule deer (*Odocoileus hemionus*) across home ranges in and adjacent to the city of Los Angeles. Specifically, we addressed several questions. 1) What natural and anthropogenic landscape features were selected and avoided by mountain lions at foraging sites? 2) Were there differences in resource selection patterns between males and females? 3) Was there substantial additional individual-level variation in the responses of mountain lions to anthropogenic land-uses due to spatial variation in the level of human disturbance? Our

results are important because they provide novel information about environmental conditions that facilitate successful predation by mountain lions in a highly urbanized landscape. This information will be valuable for managers attempting to conserve healthy populations of mountain lions, and naturally-functioning ecosystems, along urban-wildland gradients surrounding metropolitan areas.

Methods

Ethics statement

Animal capture and handling protocols were approved by the National Park Service Institutional Animal Care and Use Committee. We conducted research according to the conditions of animal capture and handling protocol PWR_SAMO_Riley_Mt.Lion_2014.A3. Mountain lions are not an endangered species in California. However, they are a specially protected species that cannot be legally killed in California except under specific circumstances with a state approved permit.

Study area

We conducted research in and adjacent to the city of Los Angeles in Los Angeles and Ventura Counties, California (Fig 1). The study was focused on the Santa Monica Mountains National Recreation Area (SMMNRA; 34°05'N, 118°46'W), a unit of the National Park Service, and surrounding areas. Most research was carried out on public lands managed by the National Park Service who granted us access to the properties. When access was needed to private land this was obtained from private landowners in advance. The SMMNRA encompassed 600 km^2 and included an assemblage of federal, state, and privately-owned lands largely in the Santa Monica Mountains. The Santa Monica Mountains were bordered by the Pacific Ocean to the south; by US 101, an 8–10 lane freeway, and various urban and suburban communities to the north; by the highly urbanized Los Angeles basin to the east; and by agricultural and developed areas in Ventura County to the west. Additionally, we studied mountain lions in areas north and east of the Santa Monica Mountains in the Simi Hills, the Santa Susana Mountains, Griffith Park, and the Verdugo Mountains (Fig 1). Griffith Park was a municipal park lying within the city of Los Angeles in the western portion of the Santa Monica Mountain range (Fig 1). The Verdugo Mountains were a small, rugged mountain range spanning several cities adjacent to Los Angeles including Glendale and Burbank (Fig 1). All patches of natural habitat in the study area were bordered by major freeways, urbanization, or agricultural development. The study area was characterized by a Mediterranean climate, with cool, wet winters and hot, dry summers. There were multiple land uses throughout the area including federal, state, and local parklands, urban and suburban areas with commercial and residential (both high and low density) development, and agricultural areas (Fig 1). Natural vegetation consisted of mixed chaparral, coastal sage scrub, oak woodlands and savannas, riparian woodlands, and non-native annual grasslands. Bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) occurred throughout most of the study area and the only wild, large ungulates were mule deer.

Capture and telemetry

We captured mountain lions using Aldrich foot-snares or cable-restraints, baited cage-traps, or by treeing them with trained hounds during 2002–2015. We immobilized mountain lions with ketamine hydrochloride combined with either xylazine hydrochloride or medetomidine hydrochloride administered intramuscularly. Animals were monitored for the duration of the time they were immobilized. We deployed global positioning system (GPS) collars (Followit AB,

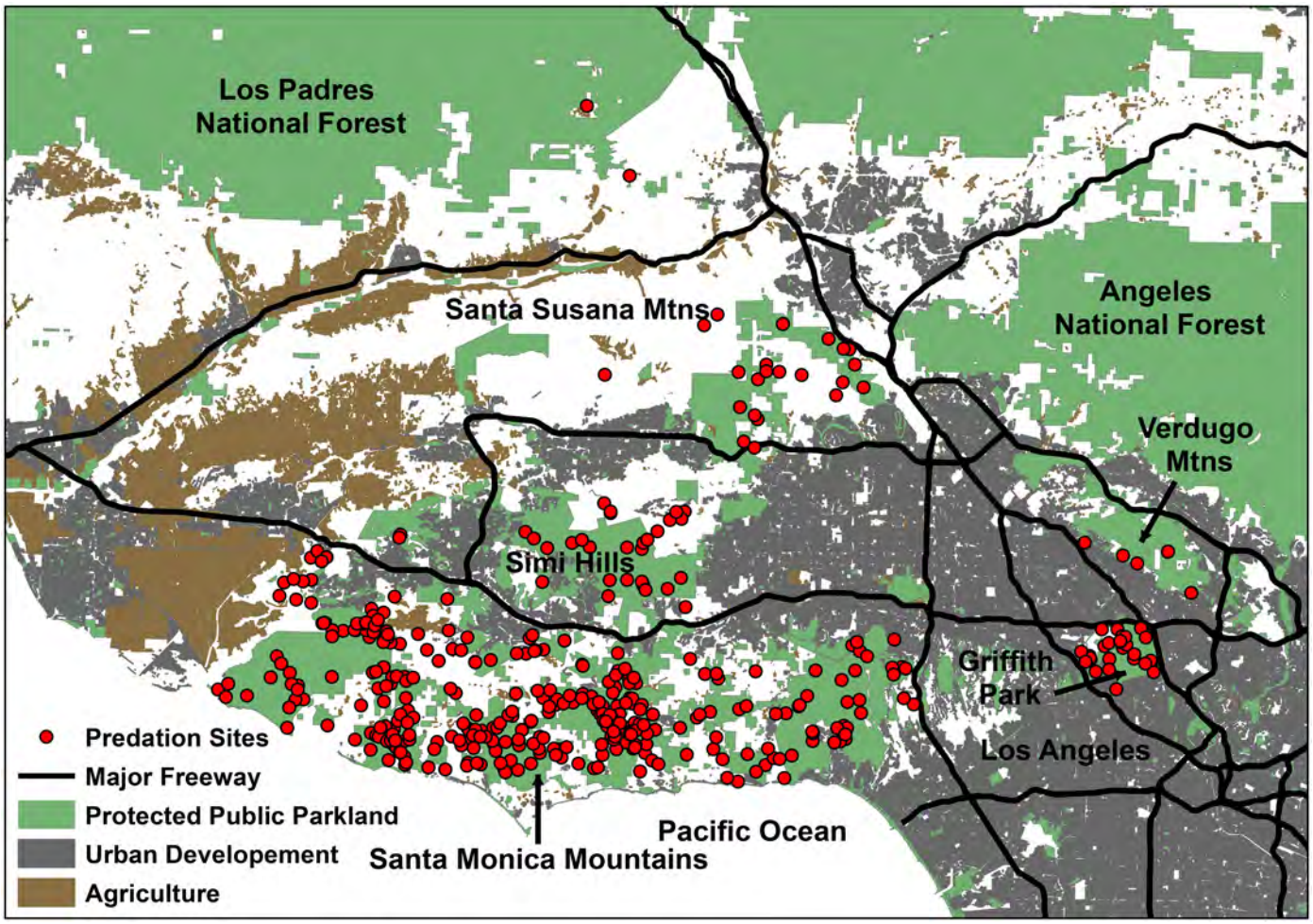

Fig 1. Greater Los Angeles area in southern California where we studied mountain lion predation on mule deer. Shown are sites where mountain lions fed on mule deer (Predation Sites), major freeways, protected parklands, areas of urban development, and agricultural areas.

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Simplex and Tellus models, Stockholm, Sweden; North Star Science and Technology LLC, Globalstar Tracker model, King George, Virginia, USA; or Vectronic Aerospace, GPS Plus model, Berlin, Germany) equipped with VHF beacons on adults. Fix schedules of GPS collars varied but we programmed most collars to obtain 1–2 day locations and 5–7 night locations per 24/hour period. Additional details of our capture, handling, and tracking of mountain lions are available elsewhere [8].

Feeding site investigations

We found carcasses of prey eaten by mountain lions by visiting clusters of GPS or VHF telemetry locations (n = 520) and searching the area for prey remains. When we found prey remains (n = 473) we identified the species, sex, and age of the prey when possible. We obtained coordinates at the prey remains with a handheld GPS unit. Previous research has indicated that clusters of mountain lion locations with locations from >1 night had a high probability of containing a kill, and that increasing numbers and the proportion of night locations in GPS clusters were strong predictors of sites where mountain lions fed on kills [18, 21, 22, 23]. Our protocol for finding prey remains was to visit clusters of telemetry locations that contained ≥ 2

night (sunset-sunrise) locations within $\leq$ 50 meters of each other and spanning periods $\geq$ 24 hours. We found prey remains at 91% of the clusters we visited. We reduced the likelihood of bias in the location of these carcasses with respect to landscape features because we visited clusters of locations regardless of the topography or their proximity to habitat features or roads.

A previous study of mountain lions in southern California found that large prey are generally dragged 0–80 m from the kill site [24]. Thus, we recognize that most of the locations where we found carcasses were probably not the exact locations where the deer were killed. However, our distance-based analysis was robust to location error [25] which ensured that our results should provide reliable inferences regarding areas where deer were killed and consumed. Nonetheless, we refer to the locations where we found carcasses as feeding sites to reflect that the deer were not necessarily killed exactly at these sites.

Resource use and availability

We investigated resource selection with an approach similar to Johnson's (1980) 3rd order of selection by comparing locations used by mountain lions at feeding sites to those available within their annual home ranges. The use-available design for resource selection models estimates the relative probability of use of resource variables (i.e. relative to their availability). For the used locations, we identified 30 m pixels (30 x 30m) on the landscape within which we found carcasses of mule deer preyed upon by mountain lions. We also occasionally found carcasses of smaller prey species (n = 54, 11% of kill sites) but we chose to focus our analysis on deer because they comprised the majority of carcasses and because mountain lions rely on large ungulates to survive and reproduce [13]. We had small sample sizes for smaller prey species ($n \leq 33$ for each individual prey species smaller than deer). Additionally, given that mountain lions likely spent considerably less time at sites where smaller prey items were consumed, we assumed we missed more of the smaller prey.

To estimate availability, we estimated adaptive local convex hull home ranges in R version 2.15.1 with the package 'adehabitat' using GPS telemetry data for each mountain lion included in our analysis. We set the 'a' parameter as the maximum distance between any 2 points in each dataset [26]. In total, we estimated 49 home ranges for 26 mountain lions with telemetry data (mean number of locations = 1814, range = 166–5507) collected across 1–12 months (mean number of monitoring days = 247, range = 30–365). In most (90%) cases we estimated home ranges with data specific to a single calendar year that matched the year of the feeding sites identified for that mountain lion. In the remaining cases (10%) we combined continuous data from 2 consecutive calendar years (if $<$ 40 days of data were available within a single year) to provide a better estimate of space use for that individual. We used calendar year as our temporal unit rather than season because seasonal variation in climate and conditions was relatively subtle in our southern California study area.

We systematically sampled 30 m pixels separated by 150 m throughout each annual home range resulting in 44 pixels/ km^2 to estimate resources available to each mountain lion [27]. We calculated distances to habitat types, land use designations, and roads from the centroid of all 30 m pixels used by (feeding sites) and available to (systematic locations across each individual's home range) mountain lions while preying on deer. Additionally, we classified the slope and elevation values associated with used and available pixels. We modified 2 existing habitat/ vegetation layers (Santa Monica Mountains National Recreation Area Vegetation Layer, 2007 and the CALVEG—South Coast Layer [CALVEG, USDA-Forest Service, Pacific Southwest Region, 2013]) by combining similar habitat types to produce a layer with 6 broad habitat classes: chaparral, coastal sage scrub, prairie/meadow, upland woodland, riparian woodland, and water (Table 1). For areas where natural habitat was developed or otherwise altered for

Table 1. Resource variables included in resource selection function models for feeding sites used by mountain lions preying on mule deer in southern California, 2002–2015.

Resource variable	Type	Range (units)	Description
Slope	Continuous	0–70 (%)	Inclination of terrain from horizontal
Elevation	Continuous	0–2432 (m)	Vertical distance above sea level
Chaparral	Continuous	0–3027 (m)	Dense, drought and fire-adapted evergreen shrubs
Riparian woodland	Continuous	0–8645 (m)	Diverse riparian forest and shrubs along canyon bottoms and drainages
Upland woodland	Continuous	0–8008 (m)	Oak, walnut, and other woodlands on slopes, shaded ravines, and canyons
Prairie/Meadow	Continuous	0–5396 (m)	Open grasslands
Water	Continuous	0–9817 (m)	Lakes, ponds, creeks, reservoirs
Trail	Continuous	0–7878 (m)	Unpaved roads and trails
Developed areas	Continuous	0–11545 (m)	Residential and commercial development
Altered-open areas	Continuous	0–5858 (m)	Areas modified by humans but less so than developed areas
Male	Categorical	0–1	Female (0) or male (1)

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anthropogenic activities, we generalized a digital land-use map for 2 classes of anthropogenic land use: developed areas (3% of mountain lion home ranges) and altered-open areas (9% of home ranges). Developed areas included commercial and residential areas with ≥1 house/acre. Altered-open areas were modified by humans to a lesser extent than developed areas and included golf courses, schools, landscaped areas such as city parks, low-density residential areas (<1 house/acre), cemeteries, horse ranches, and other moderately developed areas. We calculated distances from the centroid of all used and available pixels to the closest pixel of the 6 habitat classes and 2 land-use classes using the 'Euclidean Distance' tool in the Spatial Analyst toolbox in ArcGIS 10.2.2 (ESRI, Redlands, CA, USA) using Geographic Information System (GIS) methods described by Benson [27]. We also estimated distances from used and available locations to 3 classes of paved roads, as well as a single class of unpaved roads and trails (hereafter referred to as trails). Additionally, we estimated slope and elevation from digital elevation models (DEM) in ArcGIS (Table 1). DEM data were estimated at 9.5 m resolution, but we averaged these data across 30 m used and available pixels for our analyses. These distance and classification based values allowed us to compare resources used by and available to lions while preying on deer.

Distance-based variables are effective for assessing habitat selection [28] and using continuous, distance-based variables for habitat classes (rather than categorical variables) also eliminated the need to base inference on subjectively chosen reference categories in our regression models [29]. Distance-based approaches for habitat selection analysis are also robust to error in location data [26] and mitigate GIS error. Thus, even though mountain lions likely dragged carcasses short distances from the actual kill sites, our distance-based analysis should capture selection of areas where lions killed and consumed deer. Distance-based analyses are especially effective for assessing resource-selection at individual sites on the landscape, such as feeding sites, because the proximity to specific resource variables (e.g., water or developed areas) is quantified even if the sites of interest rarely or never actually fell within the habitat types or land-use types being considered.

Resource-selection models

We modeled resource selection at feeding sites with generalized linear mixed models (GLMMs) implemented in the R (version 3.1.1) package 'lme4'with a binary (0 = available, 1 = used) response variable. We included random intercepts for individual and year in each model, with year nested in individual. Including random intercepts for individuals mitigated

the effects of the unbalanced feeding site data across individuals (range 1–77) and the lack of independence between used locations from the same individual [30]. The random intercept of year accounted for correlation between sites used within a given year by a given individual and paired the year-specific used and available data appropriately within our models. We did not include the paved road classes in our resource selection models because of 1) the infrequency of major highways (primary roads) within mountain lion home ranges, and 2) correlation of intermediate-sized paved roads (secondary roads) and smaller paved roads (tertiary roads) with developed ($r = 0.53$) and altered-open ($r = 0.57$) areas, respectively. Secondary and tertiary roads were also correlated with each other ($r = 0.55$). Finally, we excluded the coastal sage-scrub habitat class because it was correlated ($r = 0.63$) with elevation. We were more interested in investigating and accounting for the general influence of elevation on selection of feeding sites than the influence of the specific habitat-type of coastal sage-scrub. Correlation between other predictor variables was modest or low ($r < 0.44$) so we included all remaining variables in our global model (Table 1). Prior to modeling, we rescaled values for all continuous variables by subtracting their mean and dividing by 2 standard deviations following Gelman [31].

The terms "selection" and "preference" have sometimes been used synonymously or inconsistently in the resource selection literature [29, 32]. To avoid confusion, we use the term selection throughout to indicate 1) that used locations (feeding sites) were significantly closer to distance-based resource variables (habitat types, land-use types, trails) than were available locations, or 2) that values of classification-based resource variables (elevation and slope) were significantly greater at used locations relative to available locations. Specifically, we inferred selection or avoidance of resource variables when 95% or 90% confidence intervals of fixed-effect beta coefficients did not overlap 0.

We investigated potential sex-specific patterns in resource selection at feeding sites by including a dummy-coded 'male' variable (0 = female, 1 = male) and fitting interactions between 'male' and each resource variable. We compared the fit of the null model, the global model with all resource variables, a model with interactions between 'male' and each resource variable, and a reduced interactions model retaining only interactions that indicated or approached significance (i.e. when 85% confidence interval did not overlap 0) using Akaike's Information Criteria (AIC; [33]). This allowed us to evaluate support for models of varying complexity by calculating differences (Δ) in AIC values (lower values indicate better fit). We concluded there was strong empirical support for more complex models if $\Delta AIC > 5$. We investigated the significance and marginal significance of fixed effects and interactions in strongly supported models with 95% and 90% confidence intervals, respectively.

We tested the predictive ability of our models using k-fold cross validation implemented in 'lme4' as described by Boyce et al. [34]. Specifically, we used 80% of the data (training data) to build a model that was then used to predict the relative probability of use of the remaining 20% (test data). This procedure was repeated 5 times until all data had been used as both training and test data. We ran Spearman rank correlations to assess relationships between the frequency of cross-validated feeding site locations and 10 probability bins of equal size representing the range of predicted values. A model with good predictive ability is expected to show a strong correlation with higher numbers of locations falling into higher probability bins [34].

Functional responses to human disturbance

We also explored additional individual variation in selection of areas modified by humans. Specifically, we hypothesized that distance of mule deer feeding sites to developed or altered-open areas might vary as a function of the availability of these areas, consistent with a functional response in resource selection as defined by Mysterud and Ims [19]. To test these

hypotheses, we constructed resource-selection proportions by dividing the mean distance at used locations by the sum of the mean used and available locations (mean used distance / [mean used + mean available]). Proportions of 0.5 represented no difference between used and available, proportions < 0.5 indicated mountain lions were closer to the feature than expected, and proportions > 0.5 indicated mountain lions were farther from the feature than expected. We averaged selection proportions and availability values across years for individuals with feeding sites documented in multiple years. We only constructed these proportions for mountain lions for which we documented ≥ 5 feeding sites ($n = 19$). We explored potential functional responses by modeling these resource-selection proportions (response variable) as a function of distance-based resource availability of the same resource (predictor variable, i.e. mean distance to the feature of interest across home ranges) using beta regression models with a 'probit' link which is appropriate for conducting regression on a proportional response variable. We fit 2 separate models for developed and altered-open areas using generalized additive models (GAMs) in the R package 'mgcv' version 1.8–0. We specified predictor variables as non-parametric smooth functions (splines) in the GAMs to allow for the possibility of non-linear relationships, which are often observed with functional responses [12]. However, if the relationship between the response and predictor variables was better modeled as linear (i.e. estimated degrees of freedom [edf] = 1) then predictor terms were included as parametric fixed effects [35]. Thus, because semi-parametric GAMs do not assume a linear response, they allowed us to evaluate whether selection of anthropogenic resources by individual mountain lions varied as a linear or non-linear function of availability. Small samples precluded testing for differences in functional responses between sexes. However, we visually inspected plots of the raw data to ensure that pooling sexes was not disguising obvious differences and that these relationships were qualitatively similar between sexes.

Results

Feeding sites

We included the locations of 420 mule deer killed by 26 mountain lions (16 males, 10 females) in our analysis. We found 229 mule deer killed by mountain lions in chaparral (55%), 91 in coastal sage-scrub (22%), 52 in upland forest (12%), 14 in prairie-meadow (3%), 8 in riparian-woodland (2%), 8 in disturbed areas (2%), 8 in altered-open areas (2%), 5 in exotic vegetation (1%), 2 in rocky outcrops (<1%), 2 in developed areas (<1%), and 1 in water (<1%). In reality, the 1 kill classified as being in water was located close to (rather than in) water. This kill was < 5m from the edge of a water patch in our habitat layer and was classified as water because it fell within the boundary of a pixel classified as water.

Population-level and sex-specific resource selection

Model fit for models with resource variables was considerably better than for the null model, indicating that the resource variables provided substantial information regarding resource selection at mule deer feeding sites (Table 2). There was also support for considering differences in resource selection at feeding sites between male and female mountain lions (Table 2). Model fit was best with the reduced interactions model which accounted for sex-specific differences in selection of riparian woodland, water, and developed areas (Table 2). Males selected riparian woodland and water more than females, whereas females selected developed areas marginally more than males (Table 3, Figs 2 and 3). Main effects for the resource variables fit with interactions indicated that females significantly selected developed areas, whereas they avoided riparian woodlands (Table 3). Females did not select or avoid water (Table 3). There were not significant sex-specific differences for other resource variables. Mountain lions

Table 2. Comparison of model fit between models of varying complexity. Shown are Akaike's Information Criteria (AIC) and differences between best model and competing models (ΔAIC).

Model	AIC	ΔAIC
3 resource × sex interactions*	5927.7	0
All resource variables, no interactions	5934.4	6.7
All possible resource × sex interactions	5937.2	9.5
Null model	6014.1	86.4

* Riparian woodland × male, water × male, developed areas × male

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avoided higher elevations, whereas they selected steeper slopes, chaparral, and upland forests at mule deer feeding sites (Table 3). Mountain lions also marginally selected trails at mule deer feeding sites (Table 3). Sex-specific maps of the relative probability of use of mule deer feeding sites by males and females are shown in Figs 2 and 3. The best resource-selection model, with 3 sex-specific interactions, had good predictive ability as the frequency of cross-validated locations within probability bins were highly correlated with bin ranks ($r_s = 0.85$).

Functional response modeling

Mountain lions exhibited a functional response to developed areas at feeding sites as there was a significant, negative relationship between selection of developed areas and mean distance to developed areas within individual home ranges ($\chi^2 = 7.89$, $P = 0.005$, Deviance explained = 32.7%, $n = 19$) which did not differ from a linear trend (edf = 1.0; Fig 4). In general, mountain lions selected developed areas at mule deer feeding sites more within home ranges where developed areas were less common (Fig 4). Mountain lions did not select altered-open areas as a function of their availability ($\chi^2 = 1.0$, $P = 0.541$, edf = 1.6, $n = 19$).

Table 3. Results of mixed-effect resource selection models for mountain lions at mule deer feeding sites in and adjacent to Los Angeles in southern California, 2002–2015. Shown are β coefficients and 95% and 90% confidence intervals. Significant and marginally significant fixed effects, based on 95% and 90% confidence intervals, respectively, shown in bold. Note that for classification-based variables (elevation and slope) positive β indicate selection, negative β indicate avoidance. All other variables are distance-based, so negative β indicate selection, positive β indicate avoidance. Also shown are the mean values at mule deer feeding sites used by mountain lions.

	β	95% LCL	95% UCL	90% LCL	90% UCL	Mean used value
Intercept	-6.84	-7.71	-5.98	-7.57	-6.10	——
Male	-0.76	-1.88	0.36	-1.70	0.18	——
Elevation	**-0.93**	**-1.28**	**-0.58**	**-1.22**	**-0.63**	372 (m)
Slope	**0.23**	**0.03**	**0.44**	**0.06**	**0.41**	24 (%)
Water	-0.04	-0.45	0.38	-0.39	0.30	2523 (m)
Riparian woodland	**0.74**	**0.09**	**1.39**	**0.19**	**1.28**	808 (m)
Chaparral	**-0.97**	**-1.46**	**-0.37**	**-1.43**	**-0.51**	54 (m)
Prairie-meadow	-0.02	-0.26	0.23	-0.22	0.19	578 (m)
Upland woodland	**-0.58**	**-0.97**	**-0.18**	**-0.91**	**-0.4**	273 (m)
Altered open	0.06	-0.23	0.34	-0.18	0.30	651 (m)
Developed	**-1.05**	**-1.61**	**-0.48**	**-1.52**	**-0.58**	1325 (m)
Trails	**-0.43**	-0.80	0.06	**-0.74**	**-0.12**	459 (m)
Riparian woodland × male	**-1.06**	**-1.84**	**-0.28**	**-1.71**	**-0.40**	——
Water × male	**-0.62**	**-1.15**	**-0.09**	**-1.06**	**-0.18**	——
Developed × male	**0.66**	-0.04	1.37	**0.07**	**1.26**	——

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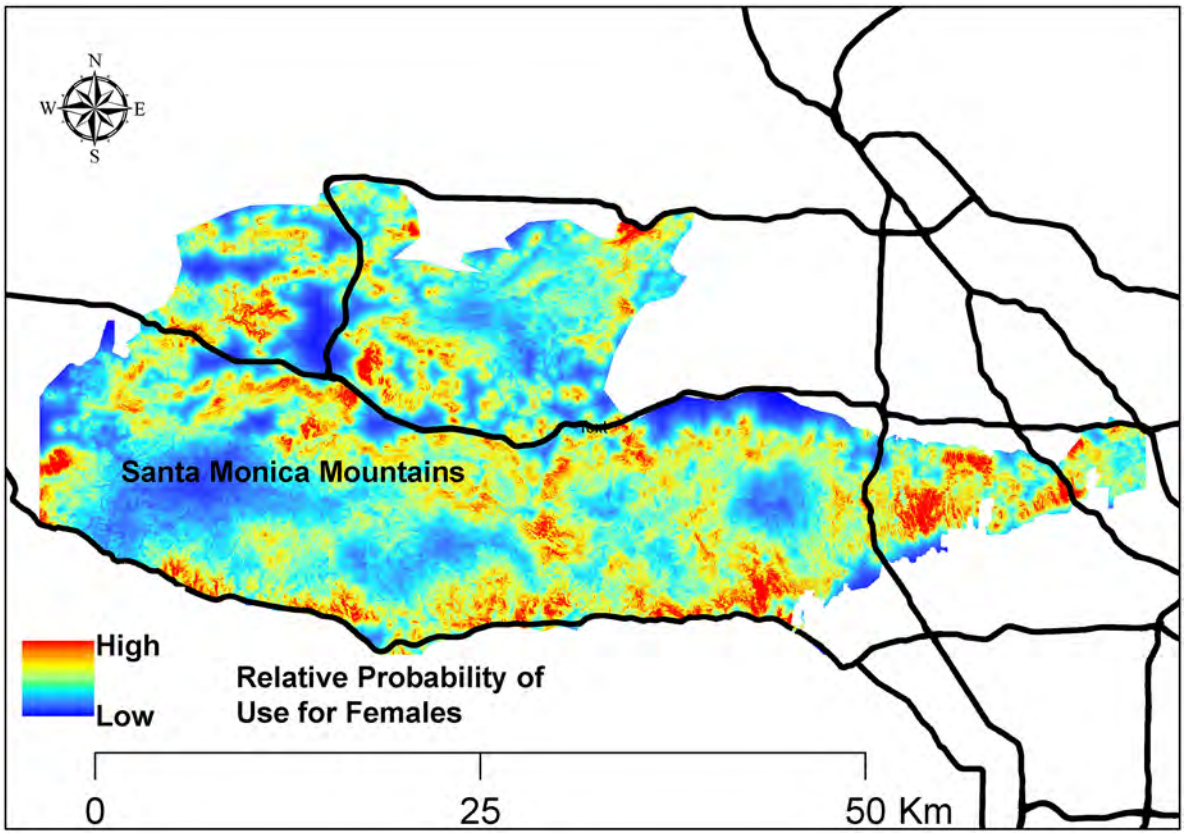

Fig 2. Relative probability of use of mule deer feeding sites by female mountain lions in the Santa Monica Mountains and Simi Hills, southern California, 2002–2015. Relative probability of use predicted by generalized linear mixed model of resource selection.

doi:10.1371/journal.pone.0158006.g002

Discussion

Our results indicate that multiple environmental variables influence the location of mountain lion-mule deer predation events in the fragmented landscape along the urban-wildland gradient in the greater Los Angeles metropolitan area. Unfortunately no studies of mule deer have been conducted within our study area, so there is little information about mule deer abundance and distribution relative to habitat types and other environmental variables. Nonetheless, our results clearly reflect areas where mule deer were present, as well as where they were vulnerable to predation by mountain lions. Given the importance of obtaining sufficient large ungulate prey for maintaining healthy populations of mountain lions [13], understanding where mountain lions are able to kill mule deer is a valuable first-step in understanding the spatial ecology and resource selection of mountain lions in and adjacent to the Santa Monica Mountains.

Females selected mule deer feeding sites closer to developed areas at the population-level, and fed on deer marginally closer to developed areas than males, relative to availability. We point out that this selection was in a distance-based context and that no feeding sites for females were actually located within developed areas (mean distance to developed areas = 1316 m, range = 95–5165 m, n = 186 sites from 10 females). Thus, female mountain lions fed on mule deer closer to developed areas than expected, rather than within developed areas. We did find 2 feeding sites for males within developed areas (mean = 1304 m, range 0–4773, n = 234 sites from 16 males). Wilmers et al. [14] also documented female mountain lions selecting

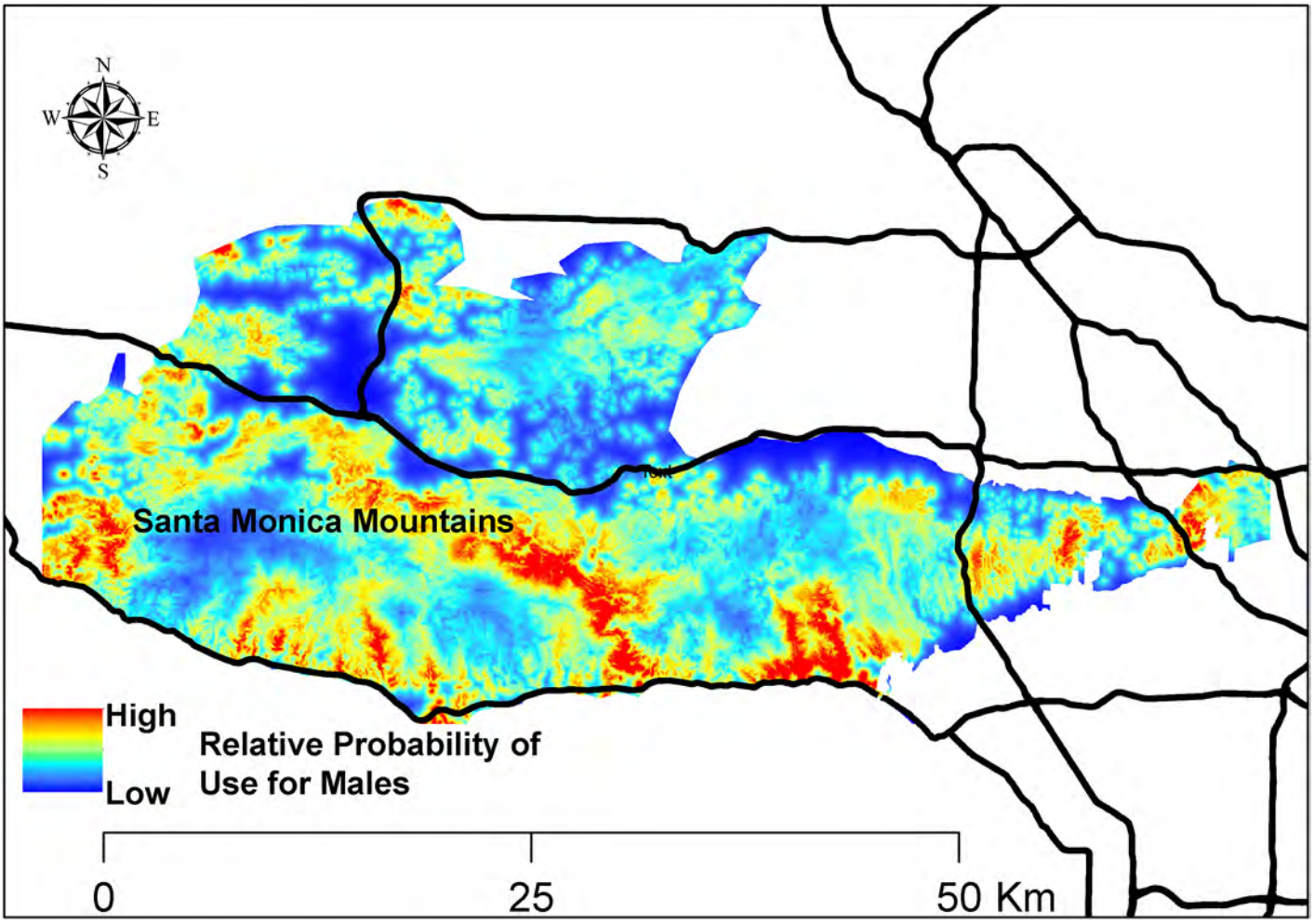

Fig 3. Relative probability of use of mule deer feeding sites by male mountain lions selection in the Santa Monica Mountains and Simi Hills, southern California, 2002–2015. Relative probability of use predicted by generalized linear mixed model of resource selection.

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developed areas more than males (while traveling) and suggested that deer may be more abundant in developed areas in central California. Indeed, deer are often attracted to disturbed areas and cultivated vegetation [36]. In southern California, mule deer might also be abundant near developed areas due to the paucity of natural water sources, as residences provide water from sprinklers, swimming pools, and other sources. The extreme drought in southern California from 2012–2015 may have made these anthropogenic water sources, and the relatively lush vegetation they support, particularly important to deer.

However, there was additional individual variation in the selection of developed areas at the individual-level that was consistent with a functional response in resource selection. Mountain lions with home ranges with greater availability of developed areas selected developed areas less than those in more remote areas. This finding suggests that some developed areas can be beneficial to mountain lions and further supports previous contentions that anthropogenic disturbance is associated with greater prey availability [14, 20]. However, developed areas may also represent increased mortality risk for mountain lions [37]. Thus, there may be a trade-off for mountain lions associated with development as the potential negative effects of human disturbance appeared to outweigh the benefits at higher levels of urbanization. The developed

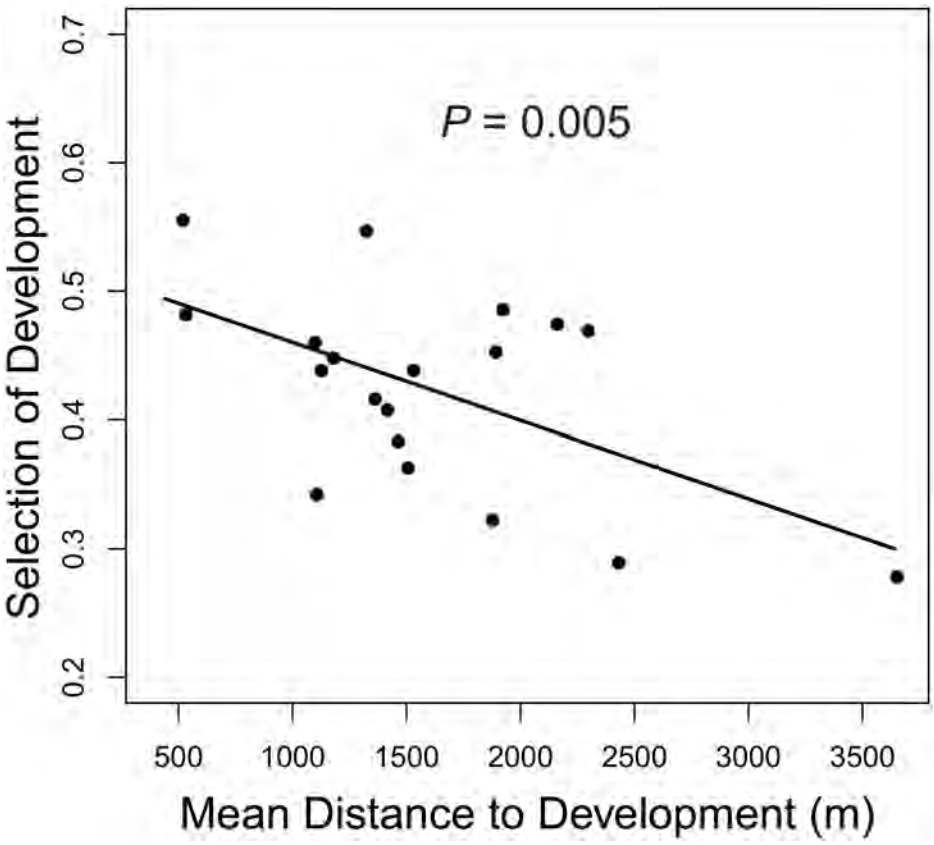

Fig 4. Functional response by mountain lions feeding on mule deer relative to development. Functional response is exhibited by the linear relationship between a selection proportion for developed areas (used distance/ used + available distance; y axis) and the mean distance to developed areas across each mountain lions home range (x axis). Selection proportions < 0.5 indicates mountain lions were closer than expected, whereas proportions > 0.5 indicate mountain lions were farther than expected from the resource relative to availability.

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areas in the highly urbanized portions of the study area, such as the densely populated neighborhoods surrounding Griffith Park and the Verdugo Mountains were characterized by higher levels of human activity and tended to be larger than developed areas in remote areas such as the Santa Monica Mountains (see Fig 1). Thus, both the size (as seen in Fig 1) and availability (quantified in our functional response analysis) of developed areas may influence where mountain lions kill mule deer. Killing and consuming deer farther from developed areas in more populated areas appears to be one way that mountain lions minimize interactions with humans in southern California.

The functional response we documented was contrary to the response exhibited by mountain lions in Alberta, where individuals decreased their avoidance of oil and gas pipelines and well sites as these features became more prevalent on the landscape [20]. There are several potential explanations for this apparent discrepancy. First, human populations and activity were considerably greater in the Los Angeles area (18.5 million people) than in west-central Alberta where populations in communities and rural areas ranged from 515–7231 people [20]. Thus, in rural areas that are relatively sparsely populated, mountain lions may select anthropogenic features more as these features become more abundant to compensate for reductions in natural habitat and to exploit potentially greater prey availability in these areas, as suggested by

Knopff et al. [20]. When human presence and development reaches higher levels, as in southern California, mountain lions may stop selecting these features or even avoid them. Second, although deer may be attracted to lower and intermediate levels of disturbance and development [14, 36], they may be less common in highly developed areas in southern California making these areas less attractive to mountain lions.

Mountain lions in general resource selection studies in Washington and central California did not exhibit functional responses to development [14, 38]. Although these studies were conducted in human-altered landscapes, the mountain lions they studied almost certainly did not encounter human population densities as high as those found within and adjacent to Los Angeles, the second largest metropolitan area in the United States. That our results differ from areas where human population sizes are lower highlights the important and unique nature of our study area where mountain lions can be studied across a steep gradient of human disturbance that spans areas from within the city of Los Angeles, to relatively remote areas of protected lands within the Santa Monica Mountains. Understanding the range of behavioral responses of mountain lions to varying levels of urbanization and human disturbance is critically important if we are to maintain healthy populations of top predators, and relatively intact ecosystems, as development, urbanization, and human populations continue to increase.

In the strongest intersexual difference documented by our analyses, males showed strong selection of riparian woodlands, whereas females avoided these areas. Riparian woodlands might be attractive to male mountain lions because they are visited by mule deer taking advantage of the relative abundance of lush vegetation in these habitat patches in the dry Mediterranean landscape. Indeed, previous studies have shown that mule deer select riparian habitat types and that they are distributed in close proximity to water and succulent vegetation [39–41]. Additionally, riparian woodlands may be used by males because they represent corridors that facilitate travel across their large home ranges as these woodlands offer vegetative cover and terrain that is likely easier to traverse than the steep ridges and rugged canyons that are common throughout the study area. Although riparian woodlands may also be attractive to females, we suspect females may have avoided them to minimize encounters with aggressive males. The leading cause of death for mountain lions in our study area is intraspecific aggression, as males often kill other mountain lions including females and their offspring [8]. Confrontations over prey carcasses are thought to be a major reason why male mountain lions kill conspecifics [13]. Interestingly, an earlier study of general habitat selection by mountain lions in the Santa Ana Mountains adjacent to Los Angeles showed that riparian woodlands were selected above all other habitats by a sample of mountain lions that was mostly females [42]. This apparent discrepancy may be explained by the fact that we studied feeding sites specifically, or because intraspecific aggression does not appear to be a major source of mortality for mountain lions in the Santa Ana Mountains [43]. Thus, the higher intraspecific mortality risk in our study area may lead to stronger intersexual differences in resource selection.

The difference in the use of water by males and females may also reflect a trade-off made by females between selecting feeding sites where prey are abundant and vulnerable, and avoiding encounters with males. Standing water in ponds and streams is relatively rare in our study area and these water sources, and the vegetation they support, likely attract abundant mule deer. Indeed, proximity to water sources was a strong predictor of mule deer fawn and doe distribution in San Diego County [40]. However, anthropogenic sources of water (e.g., pools and sprinklers) are available in our study area and also may attract deer. It is possible that males prey on deer closer to natural water sources, whereas females prey on deer closer to developed areas which represent alternative areas where water is available and deer congregate. Given that mountain lion hunting is illegal in California, and that human activity in many developed areas would be relatively low at night when mountain lions are killing and eating deer, this

trade-off could be beneficial from a fitness standpoint. However, Smith et al. [21] recently showed that females left mule deer kills sooner and compensated with higher kill rates in areas of greater development in central California. This suggests that there could be energetic costs for females preying on mule deer near developed areas. Although avoiding areas of natural habitat where deer are abundant and vulnerable may reduce intraspecific mortality risk, increased energetic expenditures associated with foraging near developed areas could potentially negatively influence fitness of females by lowering reproductive output or offspring survival.

Finally, previous studies have found that mountain lions select habitats with dense understory vegetation and noted the importance of adequate stalking cover to allow for successful hunting [14, 25, 38, 42]. Our results support these findings as chaparral, a habitat-type characterized by extremely dense shrubs, was selected by mountain lions at mule deer feeding sites and males strongly selected riparian woodlands which would also have dense stalking cover. Correlation between elevation and distance from coastal sage scrub habitat prevented us from completely separating avoidance of higher elevations and selection for coastal sage scrub. Exploratory analyses suggested both variables were important when included separately in different models, although the avoidance of higher elevation was considerably stronger than selection for coastal sage scrub. We chose to include elevation in our final model to avoid conducting regression with strongly correlated variables, but we do not suggest that coastal sage scrub is not potentially important foraging habitat for mountain lions in southern California. That 22% of the mule deer carcasses killed by mountain lions we documented were discovered in coastal sage scrub habitat highlights this point.

Our results and maps of relative probability of use of mule deer feeding sites should be incorporated into land management decisions in the Santa Monica Mountains National Recreation Area, as well as in other state, federal, city, and private parks and protected areas across the greater Los Angeles area to conserve mountain lions and naturally-functioning predator-prey dynamics. Our finding that mountain lions feed on their primary prey farther from development relative to availability as a function of increasing urbanization is broadly important because it extends understanding of how anthropogenic disturbance influences mountain lion resource selection at feeding sites with data in and around a major metropolitan area. Our results suggest that continued development in areas used by mountain lions adjacent to Los Angeles and other metropolitan areas could reduce the quality of foraging habitat for mountain lions, as they fed on mule deer farther from development when there was greater availability of developed areas within their home ranges. This functional response also indicates that, at least with respect to their behavior while preying on mule deer, mountain lions in and adjacent to Los Angeles appear to exhibit behavior that should reduce encounters and potential conflicts with humans. Our current results should be linked with analyses of resource selection by mountain lions during other activities, such as traveling and denning, to provide a more comprehensive understanding of how mountain lions use the landscape along the urban-wildland gradient in southern California. Our current model, combined with additional resource-selection analyses, could be used to evaluate the potential influence of new development projects on the relative probability of use of these areas by mountain lions.

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Author Contributions

Conceived and designed the experiments: JFB JAS SPDR. Performed the experiments: JAS SPDR. Analyzed the data: JFB. Wrote the paper: JFB JAS SPDR.

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Extinction vortex dynamics of top predators isolated by urbanization

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Abstract. Extinction risk is elevated in small, isolated populations due to demographic and genetic interactions. Therefore, it is critical to model these processes realistically in population viability analyses (PVA) to inform local management and contribute to a greater understanding of mechanisms within the extinction vortex. We conducted PVA's for two small mountain lion populations isolated by urbanization in southern California to predict population growth, extinction probability, and loss of genetic diversity with empirical data. Specifically, we (1) provide the first PVA for isolated mountain lions in the Santa Ana Mountains (SAM) that considers both demographic and genetic risk factors and (2) test the hypothesis that variation in abundance and mortality between the SAM and Santa Monica Mountains (SMM) result in differences in population growth, loss of heterozygosity, and extinction probability. Our models predicted 16–21% probability of local extinction in the SAM due purely to demographic processes over 50 yr with current low levels or no immigration. Our models also predicted that genetic diversity will further erode in the SAM such that concern regarding inbreeding depression is warranted unless gene flow is increased, and that if inbreeding depression occurs, rapid local extinction will be highly likely. Dynamics of the two populations were broadly similar, but they also exhibited differences driven by larger population size and higher mortality in the SAM. Density-independent scenarios predicted a rapidly increasing population in the SMM, whereas growth potential did not differ from a stable trend in the SAM. Demographic extinction probability and loss of heterozygosity were greater in the SMM for density-dependent scenarios without immigration. However, higher levels of immigration had stronger, positive influences on both demographic viability and retention of genetic diversity in the SMM driven by lower abundance and higher adult survival. Our results elucidate demographic and genetic threats to small populations within the extinction vortex, and how these vary relative to demographic structure. Importantly, simulating seemingly attainable increases in connectivity was sufficient to greatly reduce extinction probability. Our work highlights that conservation of large carnivores is achievable within urbanized landscapes, but requires land protection, connectivity, and strategies to promote coexistence with humans.

Key words: demographic stochasticity; extinction; heterozygosity; inbreeding; mortality; population viability analysis; Puma concolor; *urbanization.*

Introduction

Demographic and genetic processes, and interactions between them, influence probability of extinction for small, isolated populations (Saccheri et al. 1998, O'Grady et al. 2006). Specifically, deterministic stressors, demographic and environmental stochasticity, and inbreeding depression can all contribute to increased extinction probability (Mills and Smouse 1994, Beissinger et al. 2008). However, the relative influence of these processes in different wildlife populations remains difficult to predict and empirical demonstrations are rare (Palomares et al. 2012, Wootton and Pfister 2013). The predicted decline to extinction of small populations from these interacting processes is referred to as the extinction vortex (Gilpin and Soulé 1986). Modeling dynamics of small, isolated populations provides critical information to local conservation efforts and also

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contributes to a more general understanding of the forces influencing extinction.

All populations with small numbers of breeding individuals are likely to be destabilized by demographic stochasticity (Lande 1993, Morris and Doak 2002) and are also the most likely to suffer from inbreeding depression (Mills and Smouse 1994). However, variation in local environmental conditions, and resulting differences in demographic structure, can influence population growth, the rate at which genetic diversity is lost, and extinction probability (Stacey and Taper 1992, Reed 2005). Prior to the onset of inbreeding depression, some small populations continue to exhibit strong survival and reproduction (Benson et al. 2016a), while others suffer from poor demographic performance due to ongoing deterministic stressors (Caughley 1994). Comparing dynamics of isolated populations of the same species but of varying abundance, and with different vital rates and associated deterministic stressors, will increase our understanding of demographic and genetic processes of small populations.

Mountain lions (*Puma concolor*) exist at low density, have female-biased sex ratios, and often exhibit highly skewed male reproductive success (Johnson et al. 2010, Riley et al. 2014). These traits reduce effective population size (Mills and Smouse 1994) and have made mountain lions important study species for investigating small population dynamics (Johnson et al. 2010, Benson et al. 2016a). Indeed, one of the clearest demonstrations of inbreeding depression driving a population to the brink of extinction was with endangered Florida panthers (a subspecies of mountain lions, *Puma concolor coryi*; Johnson et al. 2010). Panthers exhibited reduced fitness from inbreeding depression and declined to fewer than 30 individuals; however, extinction was avoided and the population rapidly increased following genetic restoration (Johnson et al. 2010).

Small, isolated populations of mountain lions have also persisted within the highly urbanized landscape of southern California in the Santa Monica Mountains (SMM) and Santa Ana Mountains (SAM) northwest and southeast of Los Angeles. These two populations exhibit the lowest genetic diversity documented for the species aside from Florida panthers (Ernest et al. 2014, Riley et al. 2014). Recently, a population viability analysis (PVA) indicated that mountain lions in the SMM population exhibited strong survival and reproduction and predicted generally stable population growth for the next 50 yr (Benson et al. 2016a). However, this PVA also predicted potential for extinction due purely to demographic factors, as well as rapid loss of genetic diversity that raised concern about inbreeding depression (Benson et al. 2016a). An earlier PVA for mountain lions occupying the SAM indicated that the population was demographically unstable and that additional habitat loss would lead to a high risk of extinction (Beier 1993). This PVA explicitly considered the influence of corridors and habitat loss on extinction probability due to demographic processes, but ignored potential effects of inbreeding depression. Furthermore, most of the demographic rates came from the literature rather than from empirical data collected within the SAM (Beier 1993). Given the isolation and low genetic diversity documented for this population (Ernest et al. 2014, Gustafson et al. 2017), as well as additional fragmentation of the available habitat that has occurred (Burdett et al. 2010), an updated PVA constructed with empirical genetic and demographic data is needed for mountain lions in the SAM to evaluate the influence of interactions between genetics, demography, and landscape connectivity in this heavily human-dominated landscape.

The SMM and SAM are both occupied by small populations of mountain lions in similar habitats isolated by anthropogenic barriers and exhibiting low levels of genetic diversity (Ernest et al. 2014, Riley et al. 2014). However, there are notable differences in demographic structure of the two populations that could have consequences for population dynamics and viability. First, the estimated number of breeding adults in the SAM was approximately twice that estimated for the SMMs (Beier 1993, Ernest et al. 2014, Riley et al. 2014, Benson et al. 2016a). Differences in abundance were clearly related to the smaller patch of available habitat within the SMM relative to the SAM (Beier 1993, Benson et al. 2016a). Importantly, smaller population and habitat island size are strong predictors of reduced genetic diversity (Frankham 1995). Second, survival rate of radiocollared adult mountain lions in the SAM, where the main cause of death was collisions with vehicles, was lower than other unhunted populations (Vickers et al. 2015). In contrast, adult survival in the SMM was as high or higher than most unhunted populations and the main cause of death was intraspecific strife (Riley et al. 2014, Benson et al. 2016a). This could have important implications because mountain lion population growth is most strongly influenced by adult female survival (Lambert et al. 2006, Benson et al. 2016a). Thus, comparing the dynamics of these populations will inform conservation efforts and provide empirical insight into the influence of variation in demographic structure (i.e., abundance and survival rate) on the relative influence of demographic and genetic processes, and how they interact to influence extinction risk. Such research would represent an important case study for understanding the dynamics of isolated populations and provide insight into management strategies for maintaining viable populations of top predators within human-dominated landscapes.

We used the individual-based population model of Benson et al. (2016a) parametrized with empirical demographic and genetic data collected during long-term studies of mountain lions in our focal populations to model dynamics and viability. We constructed starting populations with empirical, multi-locus genotypes that reflected the age, sex, and genetic structure of the current populations and projected models forward to estimate

stochastic population growth, extinction probability, and measures of genetic diversity over the next 50 yr. We used these model projections to address multiple questions regarding the viability of populations of top predators in isolated mountain ranges within highly urbanized landscapes. First, we investigated the dynamics and viability of mountain lions in the SAM to evaluate the influence of demographic and genetic processes on probability of extinction. Second, we hypothesized that variation in population abundance and mortality patterns in small, isolated mountain lion populations would result in differences in population growth, the rate of loss of genetic diversity, and extinction probability. We predicted that reduced adult survival would result in lower population growth and greater extinction probability due purely to demographic processes (P1a). We also tested the alternative prediction that the greater number of breeding adults and carrying capacity in the SAM would offset the lower survival and result in similar growth and extinction probability between the two populations (P1b). Next, we predicted that genetic diversity would erode more quickly in the SMM population given the smaller number of individuals and smaller amount of available habitat (P2). Finally, we predicted that reductions in vital rates due to inbreeding depression would result in high probability of extinction for both populations (P3). We provide the first PVA for mountain lions in the SAM that explicitly models both demographic and genetic processes. More broadly, our results elucidate how variation in abundance, carrying capacity, vital rates, and sources of mortality influence mechanisms underlying the extinction vortex for isolated populations in fragmented landscapes. Thus, our work provides a case study that will help to inform conservation of isolated wildlife populations in human-dominated landscapes.

Materials and Methods

Study area

We studied mountain lions in two isolated mountain lion populations occupying mountain ranges southeast (SAM: Orange, Riverside, and San Diego Counties) and northwest (SMM: Los Angeles and Ventura Counties; Fig. 1) of the city of Los Angeles. The SAM population



Fig. 1. Greater Los Angeles, southern California, USA showing the location of the Santa Monica (blue polygon) and Santa Ana (red polygon) Mountains within which we studied population dynamics of mountain lions. Also shown are other nearby mountain ranges, major (white lines) and more minor (gray lines) roads, and areas where natural habitat has been replaced by urbanization (dark gray) and agriculture (lighter gray).

inhabited approximately 1,533 km^2 in the SAM, a portion of the Peninsular Ranges including federal, state, county, and private lands. The SMM population inhabited approximately 600 km^2 in the Santa Monica Mountains, part of the Santa Monica Mountains National Recreation Area, a unit of the National Park Service that included an assemblage of federal, state, and privately owned lands. The areas occupied by both populations were bordered by a combination of anthropogenic (freeways, development, agriculture) and natural (Pacific Ocean) barriers that have drastically restricted movement of mountain lions between the populations and surrounding areas. Both were characterized by a Mediterranean climate, with cool, wet winters and hot, dry summers. Vegetation consisted mainly of mixed chaparral, coastal sage scrub, oak woodlands and savannahs, riparian woodlands, and nonnative annual grasslands. Mountain lions were the only remaining large carnivore and the only wild ungulates were mule deer (*Odocoileus hemionus*). Both study areas have been described extensively elsewhere (Burdett et al. 2010, Riley et al. 2014, Vickers et al. 2015, Benson et al. 2016b).

Capture and monitoring

We captured mountain lions using Aldrich foot-snares or cable restraints, baited cage-traps, or by treeing them with trained hounds. We deployed global positioning system (GPS) or very high frequency (VHF) radio-collars on adult and subadult mountain lions. In the SMM, we also captured 3–5 week old kittens at natal dens by hand and implanted VHF transmitters in their peritoneal cavities (Moriarty et al. 2012). We monitored survival and determined causes of mortality of radio-instrumented mountain lions as described previously (Beier and Barrett 1993, Vickers et al. 2015, Benson et al. 2016a). We monitored reproduction of all collared females in the SMM using GPS telemetry to locate natal dens and count kittens (Moriarty et al. 2012). In the SAM, all capture and handling was conducted under Protocol 10950/PHS, Animal Welfare Assurance number A3433-01, with capture and sampling procedures approved in Protocol number 17233 by the Animal Care and Use Committee at the University of California, Davis, and Memoranda of Understanding and Scientific Collecting Permits from the California Department of Fish and Wildlife (CDFW). In the SMM, animal capture and handling protocols were approved by the National Park Service Institutional Animal Care and Use Committee under protocol PWR_SAMO_Riley_Mt.Lion_2014.A3.

Genotyping

We genotyped all captured mountain lions at 44 (SAM) or 54 (SMM) microsatellite loci using laboratory methods and markers described previously (Ernest et al. 2014, Riley et al. 2014). Briefly, we extracted DNA from blood or tissue using DNeasy Blood & Tissue Kit (QUIAGEN, Valencia, California, USA). The loci used for genotyping mountain lions in both populations conformed to expectations for Hardy-Weinberg and linkage equilibria (Ernest et al. 2014, Riley et al. 2014). We used many of the same genotypes analyzed by Ernest et al. (2014) and Riley et al. (2014) to parameterize our model but also included genotypes from mountain lions captured more recently. We also genotyped mountain lions from samples obtained from areas adjacent to our focal populations to simulate immigration in our models.

Demographic parameters

We separated mountain lions into three age classes for parameter estimation. Kittens were dependent offspring with their mother (0–14 months), subadults were independent animals prior to reproduction (females, 14–25 months; males, 14–42 months), and adults were breeding animals (females, >25 months; males, >42 months; Benson et al. 2016a). We estimated sex and age-class specific survival rates using the Kaplan-Meier estimator generalized for staggered entry (Pollock et al. 1989) implemented in R version 3.1.3 (R Development Core Team 2015) with the package "survival". We estimated survival for adults and subadults separately for the SMM and SAM using empirical data from each population. We used survival data collected during 1987–1993 (Beier and Barrett 1993) and 2003–2016 (Vickers et al. 2015; T. W. Vickers et al., *unpublished data*) for the SAM, and during 2002–2015 for the SMM (Riley et al. 2014, Benson et al. 2016a). Females in the model bred in the first month after reaching adulthood and again following loss or independence of kittens, consistent with documentation in our field study (Benson et al. 2016a). We estimated the probability of females having two, three, or four kittens in a litter based on the proportion of these litter sizes documented in the SMM during 2004–2017 (all input demographic parameters are shown in Appendix S1: Table S1). Although the samples sizes used to estimate demographic parameters were relatively small numerically, they should be representative given the small size of the populations.

Model overview

We used the individual-based population model for mountain lions of Benson et al. (2016a) that incorporated demographic and environmental stochasticity, as well as a simple form of density dependence. We did not have data to understand the influence of catastrophes on vital rates of mountain lions in these populations, so our model assumes these unpredictable events do not occur during our projections. We began models with starting populations of individuals that reflected the sex, age, and genetic structure of the populations and projected the models forward to estimate the demographic and genetic structure of future populations. In the SAM, we

combined information from published estimates of population density and available habitat, as well as information from our ongoing 15-yr field study to assemble the starting population. Beier and Barrett (1993) and Beier (1993) estimated 2,070 km^2 of available habitat for the SAM population. We adjusted this estimate by subtracting 506 km^2 to remove the Chino Hills that are now isolated from the SAM by highway 91 and no longer occupied by mountain lions (Fig. 1). We further reduced the available habitat by 2% to reflect habitat loss during 1993–2017 based on estimates of Burdett et al. (2010). Thus, our estimate of available habitat for mountain lions in the SAMs was 1,533 km^2. Beier and Barrett (1993) estimated mountain lion density to be 0.7 females and 0.35 males/100 km^2. We applied estimates of mountain lion density (0.7 females and 0.35 males/100 km^2; Beier and Barrett 1993) to our habitat area estimate, which yielded 11 adult females and 5 adult males. We also included 9 kittens and 4 subadults. Although we did not formally estimate population density in our study, the abundance:habitat area ratios we used from Beier and Barrett (1993) agreed with observations made using telemetry, genetic analysis, and camera trapping during our intensive 15-yr study. We assigned empirical genotypes at 44 loci to all starting individuals in the SAM. The starting population for the SMM population was 15 mountain lions (including 5 adult females and 2 adult males) with empirical genotypes at 54 loci as described by Benson et al. (2016a).

We ran simulations consisting of 5,000 population projections of 50 yr unless noted otherwise. Although researchers sometimes attempt to predict extinction probability farther into the future (e.g., 100 yr), we followed the recommendation of Morris and Doak (2002:452) to avoid projecting population viability far into the future because of the increased uncertainty of predictions made over longer time periods. The population dynamics simulated by the model were a reflection of individual-based demographic processes specified by empirical probability distributions estimated with data collected in both populations. We imposed mortality (survival senescence) on all mountain lions of both sexes in the model that reached 15 yr of age (Benson et al. 2016a). We incorporated density dependence by imposing a maximum number of adult, breeding males (SMM, $n = 2$; SAM, $n = 5$) and females (SMM, $n = 6$; SAM, $n = 11$) that could exist in the population at any given time. For the SMM, we felt confident that our estimates were the maximum numbers of breeding individuals that could occupy the available habitat. The greater area and size of the SAM population contributed to uncertainty in our carrying capacity estimates; thus, we also explored an alternate scenario with a greater carrying capacity of 7 adult males and 14 adult females. For all scenarios, when all the adult slots of a given sex were occupied, we eliminated individuals of that sex that would have otherwise transitioned from sub-adults to adults. This process simulated density-dependent population regulation through death or dispersal. Although the upper limits for adult males and females were fixed, the number of adults varied stochastically during model projections due to variation in survival and reproduction. When breeding occurred within the model, we assigned genotypes to resulting offspring based on principles of Mendelian genetics (i.e. 1 allele randomly inherited from each parent at each loci). Additional details of the model and submodels are provided by Benson et al. (2016a).

Submodels

Survival.—We incorporated environmental and demographic stochasticity into age-class-specific survival rates as in Benson et al. (2016a). Specifically, we generated environmentally stochastic monthly survival probabilities by transforming survival rates and their standard deviations estimated from each study population into beta shape parameters using the betaval function in the R package popbio. At each monthly time step, we drew a random survival value from this beta distribution, which was used as the environmentally stochastic survival probability for all individuals of the same sex and age class during that time step. We then assessed demographically stochastic survival of each individual using a Bernoulli trial with the monthly survival probability as the threshold between survival and mortality.

Reproduction.—We designated reproductive males and females in the starting population and, thereafter, randomly selected breeding animals from subadults eligible to transition to adults when openings became available. Female age at first reproduction varied stochastically between 25 and 33 months in our model. Males reaching breeding status remained reproductive until death. If no adult males were present in our simulated populations, males were allowed to begin breeding at 36 months as the reason for delayed breeding in males is presumably due to social constraints imposed by dominant adult males. Breeding females were eligible to become pregnant until death whenever they did not have dependent offspring. Litter size varied stochastically by generating a random, uniform value between 0 and 1 for each reproductive female and comparing the value to a cumulative probability distribution for litter sizes we documented. We determined the sex of each offspring using a Bernoulli trial with a probability of 0.5.

Immigration.—We assigned a fixed annual immigration rate prior to starting a simulation. We transformed this into a monthly probability and assessed immigration stochastically using Bernoulli trials during each monthly time step. We restricted immigration to subadult males. Subadult males are more likely to disperse and to undertake longer and riskier dispersal events than females (Sweanor et al. 2000). Indeed, all immigration documented into the SMM and SAM populations has involved subadult males (Riley et al. 2014, Gustafson

et al. 2017). We assigned genotypes to immigrants from mountain lions genotyped in adjacent areas north and east of the SMMs ($n = 18$) and east of the SAM ($n = 83$). We modeled different immigration scenarios ranging from no immigration to a rate of one immigrant per year for our main analyses. We also modeled immigration rates for both populations based on immigration observed with radio-tracking and genetic analysis of mountain lions within and adjacent to our focal populations. Specifically, we observed two immigrants in 15 yr in the SMM (Riley et al. 2014; S. Riley et al., *unpublished data*) and three immigrants in 15 yr in the SAM (Gustafson et al. 2017). We were conservative with respect to modeling how much additional immigration could occur in our main analyses so we limited these to 1 immigrant per year. However, we also conducted additional scenarios to explore the hypothetical influence of two immigrants per year. For additional details of all submodels see Benson et al. (2016a).

Model outputs

Demography and extinction.—We estimated λ_t (Lambda [population growth] at time t) as N_t/N_{t-1}, where N_t is total population size at time t. We estimated λ_s (stochastic lambda) across time periods of interest with the formula:

$$\frac{[\sum^{N_{\text{years}}} \ln(\lambda_t)]}{N_{\text{years}}}$$

We report median λ_s from the distribution of values across all projections for simulations of interest. We estimated credible intervals for λ_s using the highest posterior density (HPD) derived using the R package coda (v. 0.17-1). We estimated probability of extinction as the proportion of projections that went extinct during a given simulation and derived estimates of variability by conducting a nonparametric bootstrapping procedure implemented in the R package boot (v. 1.3-17). We ran 1,000 bootstraps of 5,000 population projections to estimate uncertainty regarding extinction probability with 95% HPD intervals. We estimated the effective population size based on a census of the breeding animals in simulated populations using the formula: $N_e = (4 \times N_{BF} \times N_{BM})/(N_{BF} + N_{BM})$ (Crow and Kimura 1970), where N_e is the effective population size, N_{BF} is the number of breeding females, and N_{BM} is the number of breeding males.

Genetic parameters.—We estimated measures of genetic diversity from genotypes of mountain lions in populations simulated by our models 1–50 yr in the future using mean values across all projections. Specifically, we estimated expected (H_e) and observed (H_o) heterozygosity, individual inbreeding coefficient (F_{is}), the mean number of alleles per loci (N_A), and the proportion of polymorphic loci using the R package adegenet v. 2.0.0. Our genetic predictions varied stochastically because they were realistically linked to the stochastic demographic processes we modeled. Thus, by running 5,000 projections for each scenario, our models captured considerable environmental, demographic, and genetic stochasticity.

Elasticity analysis.—We investigated proportional sensitivity (elasticity) of λ_s to small (5%) increases in vital rates (Morris and Doak 2002). We conducted these analyses with the density-independent model to investigate which demographic parameters had the greatest influence on λ_s in the absence of density-dependent limitations. We calculated sensitivity values (S) for each demographic parameter:

$$S = \frac{\text{Log}\lambda_s(\text{increased}) - \text{Log}\lambda_s(\text{original})}{\text{parameter}(\text{increased}) - \text{parameter}(\text{original})}$$

and elasticity (E) for each demographic parameter following Morris and Doak (2002):

$$E = S \times \left(\frac{\text{parameter}_{\text{original}}}{\text{parameter}_{\text{adjusted}}}\right).$$

Inbreeding depression.—We simulated inbreeding depression by running population projections with input parameters reduced to reflect proportional changes in age- and sex-specific survival rates documented between inbred and outbred Florida panthers following the genetic restoration program (Hostetler et al. 2010, Benson et al. 2011; see Appendix S2: Table S1).

Results

Population viability in Santa Ana Mountains

Density-dependent simulations predicted stable median stochastic population growth over the next 50 yr in the SAM, regardless of the level of immigration (Table 1). However, there was an 11–21% probability of extinction across all immigration scenarios in the density-dependent simulations, inversely related to the level of immigration (Table 1, Fig. 2). The scenarios without immigration, or with the low level observed in our study, resulted in substantial loss of genetic diversity (e.g., 28–49% of expected heterozygosity) over 50 yr (Fig. 3; Appendix S3, S4). Predicted loss of heterozygosity decreased with higher levels of immigration, and heterozygosity was largely maintained with one immigrant per year (Fig. 3; Appendix S3: Table S1, Appendix S4: Fig. S1). Other measures of genetic diversity including percent polymorphism, inbreeding coefficient, and the number of alleles per loci responded to varying degrees of isolation and immigration similarly over time (Appendix S3: Table S1). When we explored the influence of a larger carrying capacity in the SAM (7 adult males and 14 adult females), population growth

TABLE 1. Demographic results predicted by individual-based population model for mountain lions in the Santa Ana and Santa Monica Mountain, Southern California, USA.

	No immigration		Observed immigration		1 immigrant/2 yr		1 immigrant/1 yr	
Parameter	Estimate	95% HPD†	Estimate	95% HPD†	Estimate	95% HPD†	Estimate	95% HPD†
Santa Anas								
λ_s‡	1.00	0.89, 1.01	1.00	0.95, 1.01	1.01	0.93, 1.02	1.01	0.95, 1.02
Extinction probability	0.22	0.20, 0.23	0.16	0.15, 0.17	0.11	0.10, 0.11	0.08	0.07, 0.09
Time to extinction (yr)	31	12, 50	31	11, 50	33	13, 50	33	13, 50
Adults (*n*)§	8	0, 11	9	0, 15	9	0, 15	10	0, 15
N_E§	6	0, 11	6	0, 12	6	0, 12	7	3, 14
Santa Monicas								
λ_s‡	1.00	0.89, 1.02	1.01	0.93, 1.02	1.01	0.98, 1.02	1.01	1.00, 1.02
Extinction probability	0.29	0.28, 0.30	0.16	0.15, 0.17	0.04	0.04, 0.05	0.02	0.01, 0.02
Time to extinction (yr)	31	13, 50	31	13, 49	33	12, 50	32	11, 48
Adults (*n*)§	5	0, 8	5	0, 8	6	0, 8	7	4, 8
N_E§	4	0, 6	4	0, 6	4	0, 6	5	3, 6

Notes: Estimates are median or mean estimates at year 50 based on 5,000 population projections.
HPD, highest posterior density; λ_s, stochastic population growth.
† 95% highest posterior density credible intervals.
‡ Median value.
§ Effective population size (mean value).

rate was similar (λ_s = 1.01 [0.92, 1.02], but extinction probability was reduced (10% with observed level of immigration; Appendix S5: Table S1). All immigration scenarios with higher carrying capacity yielded lower probability of extinction, ranging from 12% with no immigration to 5% with one immigrant per year (Appendix S5: Table S1). Loss of genetic diversity slowed slightly and effective population size increased with greater carrying capacity, although diversity still declined substantially with no immigration or the observed level (Appendix S5: Table S2). Simulating inbreeding depression in the SAM by reducing age-specific survival rates proportional to reductions documented in inbred Florida panthers, resulted in rapidly declining population growth (λ_s = 0.84, [0.61, 0.96]), 100% probability of extinction over fifty years, and median time to extinction of 11.7 yr (5.2, 23.5; Fig. 4).

Comparing dynamics of SAM and SMM

Median stochastic population growth rate predicted by the density-dependent scenarios was similarly stable in the two populations (Table 1, Fig. 2). However, the density-dependent scenarios for both populations also predicted extinction probabilities of 16–28% over 50 yr with no or observed immigration (Table 1, Fig. 2). Extinction probability due purely to demographic processes was reduced for both populations with higher levels of immigration, but more so for the SMM (Table 1, Fig. 2). Density-independent scenarios predicted a rapidly increasing population in the SMM (λ_s = 1.17 [1.11, 1.22]), whereas the predicted trend in the SAM did not differ from stable (λ_s = 1.06 [0.89, 1.12]; Fig. 5). Sensitivity and elasticity analysis showed that adult female survival had the strongest influence on density-independent population growth in both populations (Appendix S6: Table S1). Female subadult survival, female kitten survival, and litter size had moderate influence on population growth for both populations, whereas male survival parameters had little influence (Appendix S6: Table S1). When we explored the influence of two immigrants per year, extinction probability was further reduced and genetic diversity increased beyond the starting values in 50 yr (Appendix S7: Tables S1, S2).

Genetic diversity declined rapidly in both populations with no or observed immigration (Fig. 3; Appendix S3, S4). No immigration resulted in a greater loss of genetic diversity for SMM (57% loss expected heterozygosity) compared with SAM (49% loss; Fig. 3; Appendix S3, S4). However, the SMM population responded more strongly to increased levels of immigration as with one immigrant every 1–2 yr, the SMM retained more of its genetic diversity over 50 yr relative to the SAM (Fig. 3; Appendix S3, S4). Similar to the SAM, simulating inbreeding depression in the SMM resulted in predictions of declining population growth (λ_s = 0.89, [0.75, 0.96]), high probability of extinction (>99%) over 50 yr, and rapid median time to extinction (15.1 yr; Fig. 4).

DISCUSSION

Our modeling predicted a 16–21% probability of local extinction for mountain lions in the SAM over the next 50 yr with the low level of immigration observed in our study or no immigration. Thus, demographic and environmental stochasticity leave the SAM population vulnerable to extinction even before considering inbreeding depression, consistent with earlier predictions for this population (Beier 1993). Furthermore, our results

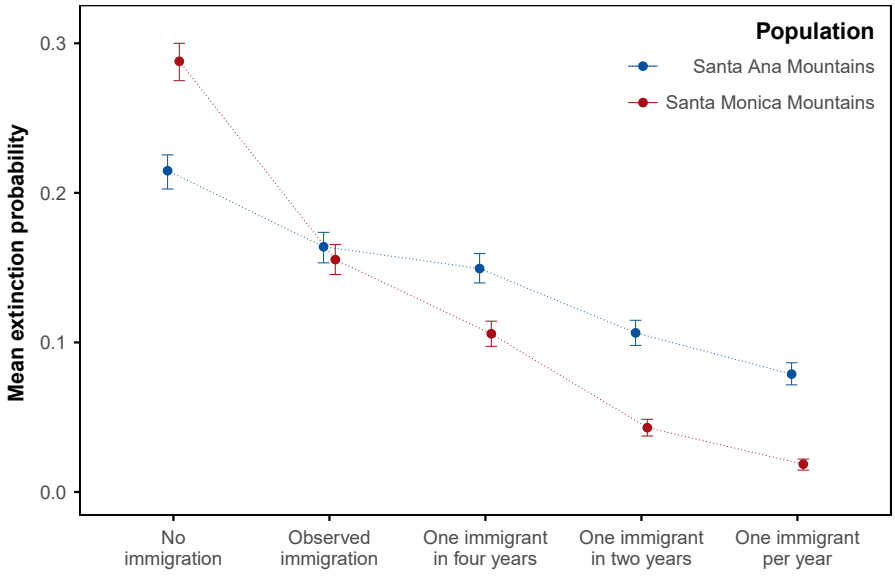

FIG. 2. Estimated extinction probability (without considering potential inbreeding effects) in 50 yr for mountain lion populations in the Santa Ana and Santa Monica Mountains from an individual-based population model based on 5,000 projections and varying levels of immigration.

suggest that, unless gene flow is increased, genetic diversity will rapidly erode in the SAM, and that, if inbreeding depression occurs rapidly, local extinction will be highly likely. We acknowledge that it is impossible to predict exactly when inbreeding depression will occur in a wild population, but our predictions with respect to genetic diversity are alarming and far surpass proportional losses of heterozygosity suggested by previous researchers to warrant concern regarding inbreeding depression (e.g., 5–10% loss in 100 yr; Soulé et al. 1986, Allendorf and Ryman 2002). Importantly, our predictions suggest that the loss of genetic diversity in SAM mountain lions in the next 50 yr will approach proportional losses experienced in another population of the same species (Florida panthers) that nearly went extinct due to poor demographic performance associated with inbreeding depression (Johnson et al. 2010; Appendix S4). Simulating a higher carrying capacity of 7 adult males and 14 adult females resulted in reduced extinction probability and slowed the loss of heterozygosity, highlighting benefits of even small increases in additional habitat and number of breeding adults (Frankham 1995). However, even with higher carrying capacity and abundance, the model predicted a 10% probability of extinction and 24% loss of expected heterozygosity over 50 yr.

Dynamics of the SAM and SMM populations were broadly similar, but our simulations revealed differences in their dynamics caused by variation in deterministic stressors, survival rates, and population abundance. The density-independent scenarios provided partial support for our prediction that lower survival in the SAM would negatively influence growth rate (P1a). Clearly, density independence is unrealistic given the space limitations experienced by both populations; however, these scenarios were instructive to compare growth potential and dynamics. Density-independent models predicted a rapidly increasing population for the SMM, whereas density-independent λ_s in the SAM did not differ significantly from a stable trend. Extinction probability was approximately three times greater (5.6%) in the SAM compared to the SMM (1.8%) in the absence of density dependence. Furthermore, in our density-dependent scenarios, higher levels of immigration (1–2 per year) in the SMM raised the credible interval of λ_s above 1, predicting a slightly increasing trend, whereas credible intervals overlapped 1 for all predictions of λ_s in the SAM, even with similarly high levels of immigration (Table 1; Appendix S7: Tables S1, S2). Clearly, realized population growth is limited by available habitat in both populations, but growth potential also appears to be limited by high human-caused mortality in the SAM. The leading cause of death for radiocollared mountain lions in the SAM was vehicle strikes, which did not differ in frequency by age or sex class, and resulted in high mortality of adults (Vickers et al. 2015). Although poor adult male survival had relatively little influence on density-dependent population growth, it influenced extinction probability by causing male extinction in some simulations for this small population with a female-biased adult sex ratio. These dynamics appear to be realistic as there was evidence of occasional male extinction in the SAM during previous research (Beier 1993). Conversely, adult survival of both sexes was high in the SMM where population growth appears to be mainly limited by the lack of additional habitat. Subadults survive poorly in the SMM due to the difficulty of successfully

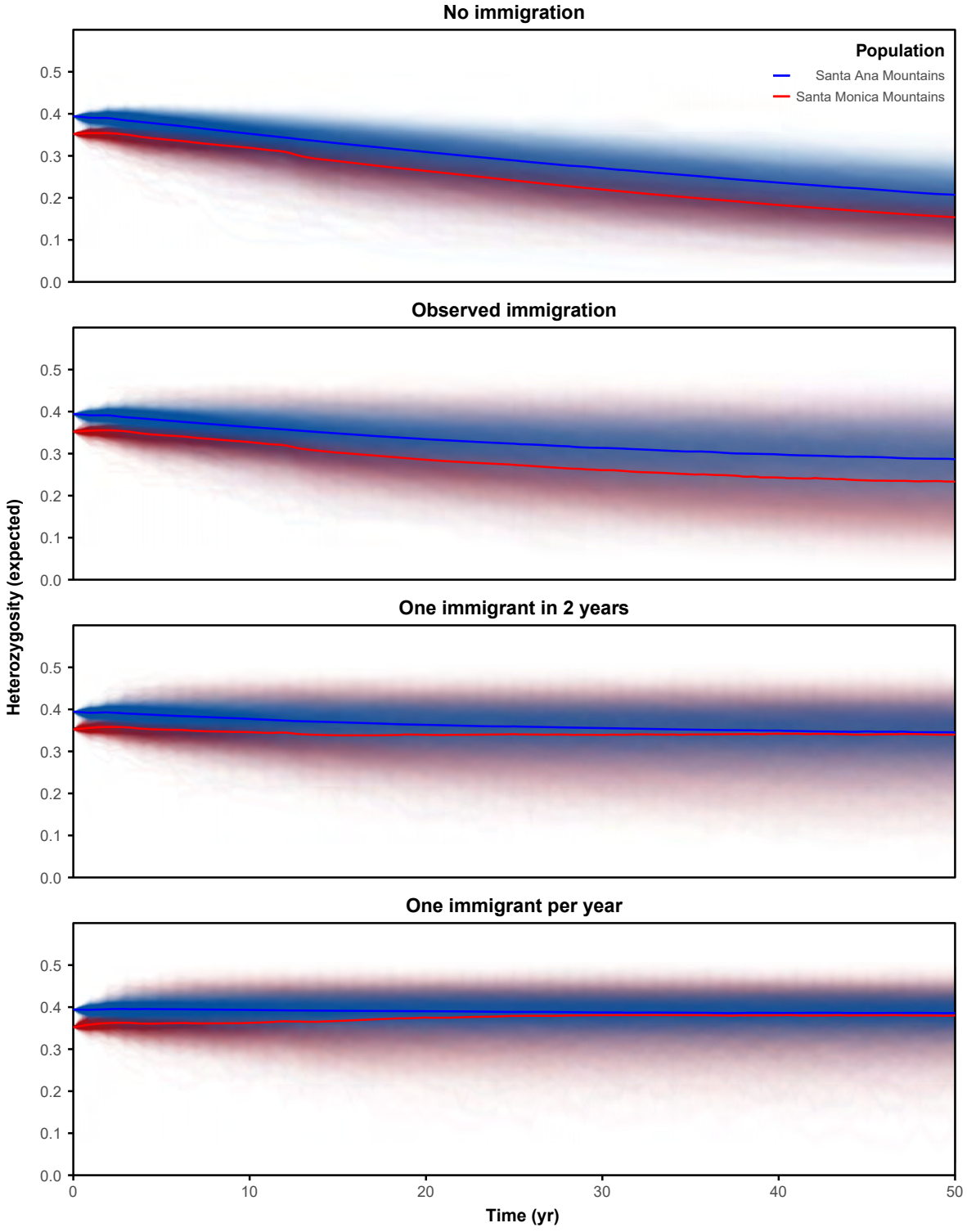

FIG. 3. Estimated expected heterozygosity over 50 yr for mountain lion populations in the Santa Ana and Santa Monica Mountains from and individual-based population model based on 5,000 projections and varying levels of immigration.

dispersing, as many young animals are killed by breeding males or hit by vehicles before or during dispersal (Riley et al. 2014). The difficulty of dispersal, combined with high survivalof breeding adults in a space-limited population provides few opportunities for mountain lions born in the SMM to breed.

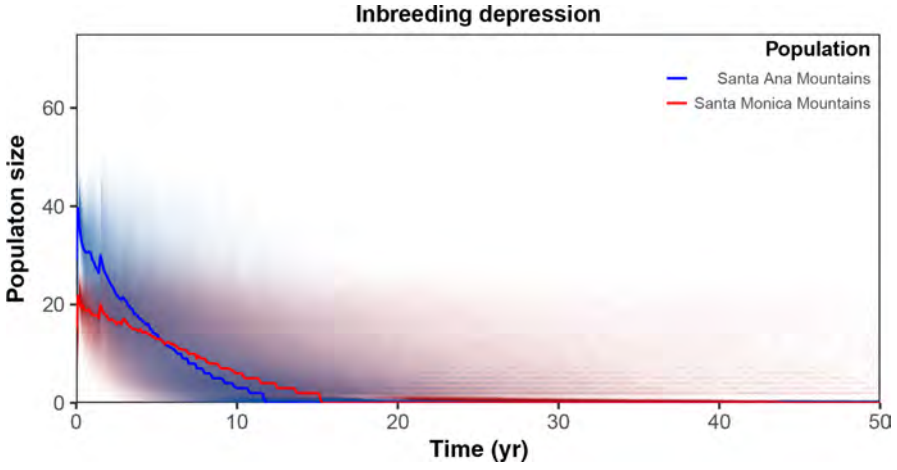

FIG. 4. Density-dependent demographic projections from individual-based population model showing predicted population sizes for mountain lions in the Santa Ana and Santa Monica Mountains over 50 yr based on 5,000 projections when we simulated inbreeding depression with the observed level of immigration.

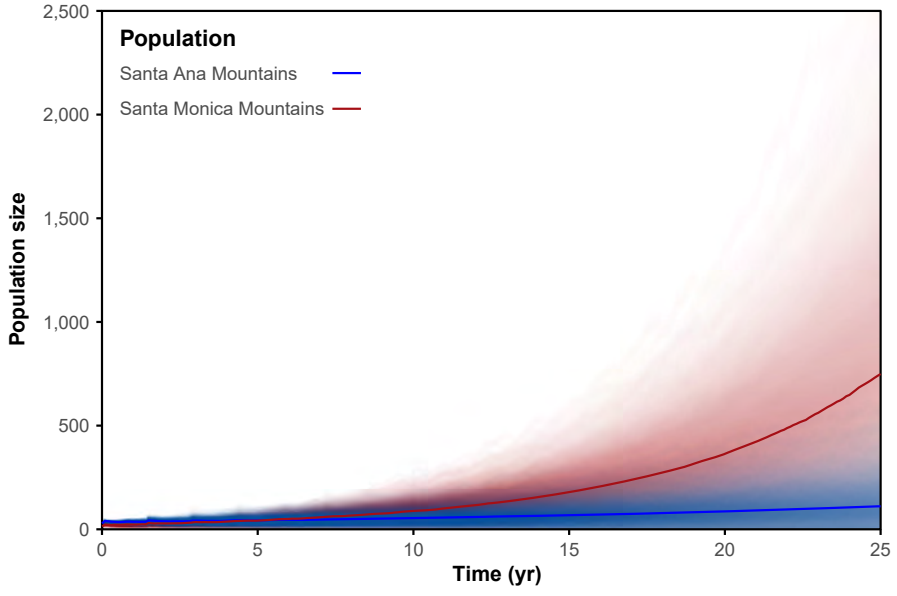

FIG. 5. Density-independent demographic projections from individual-based population model showing predicted mountain lion population size in the Santa Ana and Santa Monica Mountains over 25 yr based on 5,000 projections.

The SMM population had a slightly higher probability of extinction with no immigration than the SAM in our density-dependent scenarios, but increasing immigration resulted in a more pronounced reduction in extinction probability for the SMM. In fact, with one immigrant per year, extinction probability in the SMM did not differ from that predicted by the density-independent model suggesting that increased connectivity could largely mitigate the effects of isolation and limited habitat in the SMM, at least with respect to demographic extinction risk. The lesser positive impact of immigration on demographic extinction probability in the SAM was likely associated with the lower survival of adult males, which meant that tenure of immigrants successfully establishing as breeding adults was often short-lived. Although these comparisons were useful for evaluating the influence of variation in demographic structure on the dynamics of small populations, we recommend cautious interpretation of these differences for practical purposes. Indeed, predictions regarding extinction probability from PVA are probably best viewed as relative assessments (Morris and Doak 2002).

The greatest long-term threat to both populations appears to be the rapid loss of genetic diversity associated with their isolation from mountain lions in surrounding areas. With no immigration, the predicted rate

of loss of expected heterozygosity over 50 yr was greater for the smaller SMM population relative to the SAM population. This provided support for our prediction (P2) and is consistent with theoretical and empirical work indicating that population abundance and habitat island size are strong, positive predictors of genetic diversity (Crow and Kimura 1970, Frankham 1995). However, with immigration rates observed during the last 15 yr, predicted loss of heterozygosity was similar in the two populations. Importantly, simulating increased immigration and gene flow had a stronger positive influence on heterozygosity in the smaller SMM population. Thus, although heterozygosity is lost more rapidly in smaller populations, immigration events can also more quickly reverse these losses and restore diversity. In the SMM, only one or two males generally breed at any one time, such that when a radiocollared male immigrant entered the population in 2009 and began breeding it resulted in a rapid increase in population-level genetic diversity (Riley et al. 2014). A single breeding immigrant also positively influenced genetic diversity in the SAM (Gustafson et al. 2017), and relatively few immigrants have similarly influenced small populations of other large mammals (Vilà et al. 2003, Hogg et al. 2006, Adams et al. 2011). However, the key to maintaining diversity in small populations is to ensure that immigration occurs consistently (Mills and Allendorf 1996), to prevent reversal of short-term diversity gains as immigrants begin breeding with their offspring (Riley et al. 2014, Benson et al. 2016a). In addition to the larger population size, lower adult survival likely contributed to a reduced positive influence of immigration on genetic diversity in the SAM by limiting the reproductive success of immigrants. This finding further highlights the link between demographic and genetic factors in terms of influencing extinction in small populations. Despite interesting differences, we stress that our models predict rapid loss of diversity in both populations, indicating that viability will likely be compromised by interactions between genetics and demography unless gene flow is increased.

Mountain lions are not endangered in southern California and genetically diverse populations of mountain lions exist in areas such as the Sierra Nevada Mountains and other mountain ranges in southern California (Ernest et al. 2014, Riley et al. 2014). However, there is value to conserving viable populations of a native top predator within the SAM and SMM to maintain stable predator–prey dynamics and naturally functioning ecosystems within these isolated mountain ranges. This contention echoes growing recognition among ecologists and managers that conservation efforts should prioritize ecological function and maintaining ecosystem processes across extensive geographic areas, rather than simply preserving minimum viable populations somewhere across the range of a species (Soulé et al. 2003, Ritchie et al. 2012). Predators and other highly interactive species may be especially important to conserve in as many places as feasible to maintain important species interactions and ecosystem functions (Soulé et al. 2003, Lindenmayer et al. 2008, Cadotte et al. 2011). Indeed, research from around the world has begun to highlight the potential for conserving large predators within human-dominated landscapes (Athreya et al. 2013, Chapron et al. 2014, Riley et al. 2014). Our work suggests that conserving mountain lions in isolated mountain ranges in greater Los Angeles is feasible with relatively modest increases in landscape connectivity. If achieved over the long-term, this would be an important step toward maintaining intact, functioning ecosystems in these mountain ranges that lie within one of the most human-impacted landscapes in the world.

Our results suggest mitigation strategies for mountain lions in SAM and SMM should target two main threats: isolation and mortality. Increasing connectivity between both populations and the areas across the freeways should (1) decrease extinction probability due purely to demographic processes, and (2) maintain genetic diversity and prevent the onset of inbreeding depression. Translocation of outbred animals can be effective to quickly increase genetic diversity in threatened mountain lion populations (Johnson et al. 2010), but strategically located highway crossing structures (Gloyne and Clevenger 2001) allowing for dispersal and gene flow could be a more comprehensive long-term strategy. Our results suggest that maintaining genetic diversity in these populations would require at least one migrant every 1–2 yr. Given the expense of erecting highway crossing structures, translocation would certainly be a less expensive strategy, especially in the short-term. Indeed, the estimated cost for a bridge to connect the SMM population with habitat north of the 101 Freeway (Fig. 1) is approximately US$60 million. However, our results indicate that animals would need to be translocated frequently and indefinitely if connectivity is not improved, whereas a highway crossing structure would provide long-term connectivity once erected. Furthermore, populations of other species are also isolated by the freeways and other barriers surrounding these habitat islands (Delaney et al. 2010, Riley et al. 2006). Thus, construction of highway crossing structures, although unquestionably an expensive initial investment, would likely provide regular, consistent immigration of mountain lions and many other species that should increase the likelihood of maintaining healthy populations and intact ecosystems within these isolated mountain ranges. However, we certainly do not discount the value of translocation as a management tool. Translocation may be an especially valuable option if proposed development further degrades or prevents improvement of currently available passageways, and if the significant financial challenges delay construction of new crossing structures. As a specific example, extensive residential and resort development projects have been proposed for construction in the primary corridor area that has facilitated some movement of mountain lions between the SAM and habitat east of the

Interstate Highway 15 (Gustafson et al. 2017). Our results show that further reduction in immigration and gene flow, which are likely to occur with new development in corridor areas, would increase demographic extinction probability and hasten the loss of genetic diversity.

Our sensitivity analyses and inbreeding simulations show that increased mortality could have rapid, negative consequences for population growth and extinction probability in both populations, supporting our prediction (P3). Despite the smaller population size, predicted demographic extinction probability in the SMM was generally similar to that in SAM under the current levels of immigration largely because of the strong growth potential afforded by higher adult female survival. If female mortality increases in future years from the multitude of mortality agents documented in the SMMs (e.g., aggression from males, vehicle strikes, rodenticide poisoning) this could destabilize the population and increase extinction probability. Thus, reducing mortality in both populations is important and should decrease probability of extinction due to environmental and demographic stochasticity. In addition to highway crossing structures, exclusionary fencing strategically implemented along roadways where mountain lions are killed can be effective at reducing mortality (Foster and Humphrey 1995), such as that recently constructed along SR 241 in the SAM (Vickers et al. 2015). Strategies to promote best practices for housing domestic animals could reduce mortality from depredation permits issued to kill mountain lions threatening livestock (Vickers et al. 2015). To reduce mortality in the SAM and SMM from depredation mortality, the California Department of Fish and Wildlife (CDFW) has recently changed policies regarding depredation permit issuance in these two populations such that non-lethal deterrence methods must be attempted before lethal removal can occur (CDFW 2017).

Differences in demographic structure between the two populations revealed important aspects that have contributed to their persistence and highlighted management priorities for both populations. The greater demographic vigor of the SMM population is critical to its persistence, as a population with six to eight adults would clearly be at much higher risk of local extinction if survival and reproduction declined. Thus, in addition to management efforts to reduce mortality from documented causes such as vehicle strikes and rodenticide (Riley et al. 2014), it would be prudent to evaluate and monitor population dynamics of their main prey (mule deer) in the SMM to ensure the prey base remains adequate to support strong survival and reproduction. Greater population abundance in the SAM reduced demographic extinction probability and slowed the erosion of genetic diversity in simulations without immigration. Thus, the larger population size is beneficial to the persistence of mountain lions in the SAM, especially during periods when no immigration occurs. If additional habitat loss or fragmentation reduced the number of breeding adults that could occupy the SAM, this would have negative consequences for both demographic extinction risk and loss of genetic diversity. For instance, a population as small as the SMM population, but with the poor survival of the SAM would have a higher probability of extinction than we documented for either population. As noted above (see *Model overview*), both habitat loss and isolation appear to have reduced the population size over the last 25 yr. Our model results suggest it is critical to ensure that future habitat loss in the SAM is prevented and that fragmentation does not isolate portions of the current population.

Although our model realistically models demographic and genetic processes in these small populations with empirical data, we acknowledge that our model and data have limitations. For instance, although we were able to account for demographic and genetic processes, density dependence, and varying levels of immigration, we did not have sufficient data to understand the influence of catastrophes on the vital rates and viability of these populations. Two unpredictable forces that could potentially cause catastrophes include wildfires and disease outbreaks. Wildfires have become larger and more frequent in southern California shrubland ecosystems, and increasingly destructive wildfires appear to be linked to expansion of the urban–wildland interface (Keeley et al. 1999). Wildfires have directly caused mortality of mountain lions within our study populations (Vickers et al. 2015) and can also temporarily displace mountain lions (Jennings et al. 2016; S. P. D. Riley and J. A. Sikich *unpublished data*). Previous research on Iberian lynx (*Lynx pardinus*) has noted the potential that outbreaks of disease such as feline leukemia and reduced immune response associated with low genetic diversity could negatively affect population viability (Millán et al. 2009, Palomares et al. 2012). We note that catastrophic mortality associated with wildfires, disease, or other unpredictable events could substantially increase extinction probability above the predictions generated by our model.

Our results demonstrate that small populations isolated by freeways and urbanization are subjected to elevated extinction risk due to interactions between demography and genetics. We agree with previous authors that demographic and genetic risk factors for small populations should not be considered in isolation (Mills and Smouse 1994, Soulé and Mills 1998) and that both must be addressed in any comprehensive wildlife conservation strategy within urbanized landscapes (Benson et al. 2016a). Indeed, other small, isolated populations of felids are threatened by a combination of limited habitat and mortality, such as the highly endangered Iberian lynx (Ferreras et al. 2001). Inbreeding depression and extinction vortex dynamics are also concerns for Iberian lynx, and their conservation will require restoring habitat and improving demographic parameters (Palomares et al. 2012). As urbanization increases globally, it

will be necessary to (1) protect habitat patches large enough to facilitate persistence of populations of large carnivores, (2) mitigate anthropogenic deterministic stressors, and (3) restore and maintain connectivity within and between habitat patches if we are to maintain populations and ecosystem processes (e.g., predator–prey interactions) within urban landscapes (Crooks 2002). Our results also show that relatively small changes in abundance and key demographic parameters can influence loss of genetic diversity as well as extinction probability due to non-genetic processes. The difficulty of conserving top predators in the modern world are well documented (Woodroffe 2000, Ripple et al. 2014) and our work further details the demographic and genetic challenges facing large carnivores in human-dominated landscapes. Yet our results also provide reason for optimism, as seemingly realistic increases in gene flow appear sufficient to substantially reduce probability of extinction of top predators due to combined demographic and genetic threats within the second largest metropolitan area in the United States. Long-term conservation of mountain lions in greater Los Angeles would provide compelling evidence that large carnivores and abundant human populations are compatible, even within the most intensely developed landscapes.

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Short communication

Survival and competing mortality risks of mountain lions in a major metropolitan area

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ABSTRACT

Understanding natural and human-caused mortality for top predators persisting in human-dominated landscapes is critical for conserving their populations. We estimated survival and cause-specific mortality rates and investigated factors influencing mortality risk of mountain lions by radio-tracking 58 individuals (33 males, 25 females) across the highly fragmented landscape in greater Los Angeles, California from 2002 to 2019. Mortality risk did not differ strongly between subadults (annual survival [ŝ] = 0.68, SE = 0.08) and adults (ŝ = 0.81, SE = 0.04). However, the different age-classes were subjected to mortality risks from different sources as subadults were more likely to be killed by conspecifics, whereas adults were more likely to die from human-caused mortality. Male subadults were frequently killed by territorial adult males in the isolated Santa Monica Mountains, mortality that may be exacerbated by substantial anthropogenic barriers to dispersal in this landscape. We also tracked kittens tagged at natal dens in the Santa Monica Mountains and estimated survival to independence to be 0.63 (SE = 0.13). Higher mortality from anthropogenic causes for adults, whose survival has the greatest influence on population growth and extinction probability for mountain lions, highlights the importance of mitigation strategies to reduce human-caused mortality. Our work provides novel information about patterns of survival and mortality of mountain lions from the most urbanized landscape occupied by large carnivores in North America.

1. Introduction

Elucidating factors influencing survival and specific causes of mortality is fundamental to understanding the dynamics of animal populations (Lebreton et al., 1992). Managers in ecosystems strongly impacted by human activities require reliable estimates of mortality rates from natural and anthropogenic sources, as well as an understanding of factors that influence survival (Andrén et al., 2006; Goodrich et al., 2008). Age and sex are often strong predictors of mortality risk because parental care, access to resources, movement behavior, and interactions with conspecifics can vary widely across age and sex classes within the overall life-history patterns of a given species (Caughley, 1994). Large carnivores persisting in human-dominated landscapes are often especially sensitive to anthropogenic mortality, which increases stochasticity in vital rates and can magnify local extinction probability (Benson et al., 2016a). Detailed quantitative information on mortality patterns of large carnivores in urban areas is scarce in the literature because they are often absent or exist at low density in heavily human-impacted landscapes.

Consistent with their K-selected life history strategy and the importance of females to reproduction, adult female survival is the demographic parameter with the strongest influence on population growth for mountain lions (*Puma concolor*; e.g., Lambert et al., 2006; Benson et al., 2016a). Kitten survival can also be influential, but is a difficult parameter to measure directly (Hostetler et al., 2013; Clark et al., 2015). Survival of mountain lions is often influenced by sex and age, and can also vary spatially, especially in landscapes where landscape features and human disturbance are highly heterogeneous (Newby et al., 2013; Moss et al., 2016). Thus, a comprehensive understanding of survival and mortality patterns for mountain lions in human-dominated landscapes requires consideration of a number of intrinsic and extrinsic factors.

Mountain lions have persisted as a top predator within and adjacent to the human-dominated landscape of greater Los Angeles, the second

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Fig. 1. Greater Los Angeles, California study area where we studied survival and mortality of 58 mountain lions from 2002 to 2019. Blue polygon is composite home range from mountain lions we tracked in the Santa Monica Mountains, red polygon are composite home ranges from mountain lions tracked in the Santa Susana Mountains, Simi Hills, Griffith Park, and Verdugo Mountains.

largest metropolitan center in the United States (Riley et al., 2014; Ernest et al., 2014). Vickers et al. (2015) estimated annual survival, identified causes of mortality, and investigated factors influencing mortality risk for mountain lions in the Santa Ana Mountains and Eastern Penisular Range southeast of Los Angeles where human-caused mortality was high (Vickers et al., 2015). Riley et al. (2014) described causes of mortalities of mountain lions occupying a steep gradient of human disturbance north and west of Los Angeles that included isolated mountain ranges, as well as areas within and directly adjacent to urban areas, including the city of Los Angeles. However, Riley et al. (2014) did not estimate survival or model mortality risk.

We tracked mountain lions of all age and sex classes in greater Los Angeles, from the Santa Monica Mountains (SMMs) to areas within the city of Los Angeles to estimate survival and cause-specific mortality rates and model factors influencing mortality (Fig. 1). We used these analyses to address three important questions. First, we investigated the relative influence of sex, age-class, and location on mortality risk of independent-aged mountain lions. Some female (approximately 50%) and virtually all male mountain lions disperse from their natal areas in other populations (Logan and Sweanor, 2001; reviewed by Choate et al., 2018). Thus, we predicted that males and subadults might be at greater mortality risk due to the difficulties of dispersal in this fragmented landscape, which may put them at risk of both human (e.g., vehicles) and natural (e.g., strife) mortality (Riley et al., 2014). Movement of mountain lions within the SMMs was largely constrained by formidable anthropogenic and natural barriers, whereas mountain lions in areas adjacent to the SMMs were more often in close contact with densely populated neighborhoods and regularly crossed busy freeways or other large roads (Riley et al., 2014). Thus, we also predicted that mortality risk would be higher for mountain lions outside of the SMMs. Second, we evaluated whether different age-classes with varying degrees of influence on population growth differed with respect to vulnerability to human and natural mortality causes within a competing risks framework. Third, we estimated kitten survival rates, which has only been done occasionally for mountain lions tracked from a young age, and considered these relative to previous work (e.g., Logan and Sweanor, 2001; Ruth et al., 2011; Robinson et al., 2014; Clark et al., 2015; Elbroch et al., 2018). Our research was conducted within the largest metropolitan area occupied by large carnivores in North America and provides novel information regarding mortality patterns of top predators persisting in a human-dominated landscape.

2. Materials and methods

2.1. Study area

We studied mountain lions in and adjacent to the city of Los Angeles in Los Angeles and Ventura Counties, California (Fig. 1). The study was focused on Santa Monica Mountains National Recreation Area, a unit of the National Park Service, and surrounding areas within and adjacent to the Santa Monica Mountains (SMMs). The mountain lions we tracked used approximately 600 km^2 of the SMMs, an area bordered by the Pacific Ocean to the south, by US 101 (an 8–10 lane freeway) and various urban and suburban communities to the north, by the highly urbanized Los Angeles basin to the east, and by agricultural and developed areas in Ventura County to the west. Additionally, we studied mountain lions in areas north and east of the SMMs in the Simi Hills, the Santa Susana Mountains, Los Padres National Forest, Griffith Park, and the Verdugo Mountains (Fig. 1). Mountain lion hunting was illegal throughout California as a result of Proposition 117 which was passed in 1990. Additional details of our study area have been described extensively elsewhere (e.g., Riley et al., 2014; Benson et al., 2016a, b).

2.2. Capture and mortality tracking

We captured mountain lions using Aldrich foot-snares or cable restraints, baited cage-traps, or by treeing them with trained hounds from 2002 to 2019. We deployed global positioning system (GPS) radiocollars on adult and subadult mountain lions (Appendix A). We estimated age of captured animals based on size and tooth characteristics. We captured 3–5 week old kittens in the SMMs (n = 19) at natal dens by hand and implanted very high frequency (VHF) transmitters in their peritoneal cavities (Moriarty et al., 2012; Appendix A). We also captured and radio-collared 3 older, dependent kittens in the SMMs. We were able to accurately estimate the age of kittens tagged at dens (86% of kitten dataset) by the date that the females localized at natal dens and by physical characteristics at capture. We estimated the age of the 3 older kittens to the closest month and we acknowledge these ages were less certain. We obtained permission for capturing and handling mountain lions from the California Department of Fish and Wildlife. Animal capture and handling protocols were approved by the National Park Service Institutional Animal Care and Use Committee. We mainly tracked survival of adults and subadults using remotely accessed GPS telemetry data. We tracked kittens, and older mountain lions whose GPS units had failed, using ground-based VHF telemetry. We generally responded to GPS and VHF mortality signals within 24 h of detection. We attempted to locate all kittens with VHF transmitters ≥3 times a week and investigated immediately if a mortality signal was detected. We investigated all mortality sites for evidence of cause of death and submitted carcasses for necropsy by experienced veterinarians when remains were sufficient (California Animal Health and Food Safety Labs, San Bernadino, CA).

2.3. Estimation of survival and cause-specific mortality rates

We estimated survival rates for mountain lions using the nonparametric Kaplan Meier product limit estimator (Therneau and Grambsch, 2000). We estimated survival separately for 3 age-classes which represent 3 distinct life history stages for mountain lions: kittens (birth to independence from mother), subadults (independence to breeding age; 25 months for females, 42 months for males), and adults (breeding age; Logan and Sweanor, 2001; Benson et al., 2016a, 2019; Appendix A). For adults and subadults, we estimated and modeled survival using an annual recurrent timescale (Fieberg and DelGiudice, 2009). Animals entered the model in a staggered manner (Pollock et al., 1989) on the day of the year (1 Jan - 31 Dec) on which they were fit with a GPS or VHF transmitter. Animals exited upon death (coded 1) or were right-censored if the monitoring period ended prior to death (coded 0). Monitoring periods ended prior to death due to collar failure, timed release of GPS collars, or the end of the study period (20 September 2019). Additionally, we censored all animals alive with an active collar on the last day of the year (31 December) and re-entered them on the first day of the following year (1 January). Our sample sizes were modest within individual years (range 1–12 independent-aged animals tracked per year) and were insufficient to estimate year-specific survival rates (Appendix B). Thus, we made no inference about year-specific survival. The annual recurrent timescale essentially pools survival data across years and provides plots of survival curves that allow for visual assessment of seasonal patterns of mortality across the annual period. For adults and subadults, some animals were tracked in multiple years so we clustered all individuals by their unique IDs and estimated robust standard errors (Therneau and Grambsch, 2000; Fieberg and DelGiudice, 2009). For kittens, we estimated survival rates with an age-based timescale (Fieberg and DelGiudice, 2009) since their birthdates could be accurately estimated. Kittens entered the model on the day they were captured relative to their date of birth (e.g., day 28 for a 4-week old kitten). Kittens exited upon death (coded 1) or were right-censored if their transmitter failed or upon independence from their mother, whichever came first. Thus, we estimated survival of kittens across the period from capture at 3–5 weeks to independence (range 11–17 months) but we did not have survival or mortality information for kittens from birth to 3 weeks. Survival of individual kittens is likely not independent between littermates (e.g., Ruth et al., 2011), so we clustered kitten survival data by litter and estimated robust standard errors (Therneau and Grambsch, 2000).

To evaluate the relative importance of different, mutually exclusive causes of mortality, we estimated cause-specific mortality rates for independent-aged mountain lions (adults and subadults) using the nonparametric cumulative incidence function estimator (Heisey and Patterson, 2006) with the annual recurrent timescale. Specifically, we estimated rates of natural mortality (i.e. intraspecific strife), 2) human-caused mortality (vehicle collisions, rodenticide poisoning, poaching, or human-ignited wildfire), and unknown causes. We pooled human causes because sample sizes were small for specific causes.

2.4. Mortality and competing risks modeling

We investigated factors influencing mortality risk of independent-aged mountain lions (adults and subadults) with semiparametric Cox proportional hazards regression modeling (Therneau and Grambsch, 2000). We investigated the potential influence of sex, age-class (adult or subadult), location (inside or outside of the SMMs (Fig. 1)) on mortality risk of mountain lions with discrete, dummy-coded predictor variables. The actual dummy-coded variables included in the models were male (reference: female), SMMs (reference: areas outside of SMMs), and adults (reference: subadults). We used our study location variable to investigate whether differences in landscape across these locations led to obvious differences in mortality risk. We acknowledge that our relatively small sample sizes of mountain lions tracked outside of the SMMs (Table 1) precluded a definitive test for differences in mortality risk across study areas, but at a minimum this variable accounted for potential spatial differences in mortality risk.

We compared the relative fit of these mortality risk models with all combinations of ≤ two variables hypothesized to influence mortality risk (sex, age-class, and location) using Akaike's Information Criterion corrected for small samples (AICc; with n = number of events; Burnham and Anderson, 2002). We did not fit the model with all 3 variables together to avoid overfitting models by ensuring we had at least 10 events per variable (Peduzzi et al., 1996). Some individuals had > 1 record in the input data (those tracked in multiple calendar years, those that transitioned from subadults to adults, and those that moved between the SMMs and adjacent areas). Thus, we estimated robust ("sandwich") standard errors and P-values for parameter estimates, clustered by individual, to account for the lack of independence of these records (Therneau and Grambsch, 2000).

For adults and subadults, we also modeled the influence of age-class on mortality risk from specific causes of mortality (natural vs. human causes) in a competing risks framework (Lunn and McNeil, 1995; Benson et al., 2014). Specifically, we created multiple records for each

Table 1
Numbers of mountain lions included in survival and mortality models by sex, age-class, and study location in greater Los Angeles, CA. All animals were tracked between 2002–2019. Total number of individuals was 58 but columns sum to more than this because some animals were tracked in multiple age-classes and study locations.

	SMMs[a]		Outside of SMMs[b]	
	Males	Females	Males	Females
Kittens	13	9	–	–
Subadults	16	14	6	1
Adults	9	8	7	5

[a] Santa Monica Mountains.
[b] Simi Hills, Santa Susana Mountains, Griffith Park, Verdugo Mountains.

individual (one record for each cause of death: human, natural, or unknown) with an associated stratum variable indicating the specific cause of death. Then we fit models with this stratum variable in the model statement to allow for separate hazard functions for each cause of death. Within these models, we included an interaction between our dummy-coded variable for adult and the cause of death variable with its associated stratum identifier to test the prediction that adults and subadults varied with respect to vulnerability to human and natural mortality causes.

We examined parameter estimates for strongly supported models (ΔAICc < 2) and present exponentiated beta coefficients (hazard ratios), robust standard errors, 95% confidence intervals, and robust *P*-values. We considered hazard ratios with 95% confidence intervals that did not overlap 1 and variables for which $P < 0.05$ to indicate significantly increased or decreased mortality risk. We conducted all survival and mortality analyses using the 'survival', 'MASS', and 'AICcmodavg' packages in R version 3.3.1 (R Development Core Team, 2016). We verified the proportional hazards assumption of all Cox models by examining the distribution of Schoenfeld residuals with a chi-square test using the cox.zph function in the 'survival' package (Therneau and Grambsch, 2000).

3. Results

3.1. Survival and cause-specific mortality rates

We captured and radio-tracked 58 individual mountain lions for a total of 41, 263 tracking days across our study area (Table 1). The estimated annual adult survival rate was 0.808 (SE = 0.044, 95% CI [0.726, 0.990], n = 29 animals, n = 15 deaths; Fig. 2). Estimated annual subadult survival was 0.681 (SE = 0.079, 95% CI [0.542, 0.855], n = 34 animals, n = 11 deaths; Fig. 3). Kitten survival to independence was 0.632 (SE = 0.134, 95% CI [0.417, 0.957], n = 22 animals from 10 litters, n = 7 deaths; Fig. 4). Of the 10 litters for which we tracked kittens, we documented 2 mortalities in 2 litters, 1 mortality in 3 litters, and 0 mortalities in 5 litters.

For independent-aged mountain lions, the annual cause-specific mortality rates were 0.13 (SE = 0.03, 95% CI [0.07, 0.18], n = 14 deaths) for human causes, 0.05 for natural causes (SE = 0.02, 95% CI [0.02, 0.09], n = 6 deaths), and 0.05 for unknown causes (SE = 0.02, 95% CI [0.01, 0.09], n = 6). Human-caused mortality included vehicle collisions (n = 6), rodenticide poisoning (n = 5), poaching (n = 2), and starvation after sustaining severe burns in a wildfire ignited by humans (n = 1). All natural mortality was due to intraspecific strife (n = 6). Most mortality of radio-instrumented kittens prior to independence was due to natural causes including starvation following abandonment (n = 5) and predation (n = 1). Additionally, 1 kitten was killed by a wildfire ignited by humans.

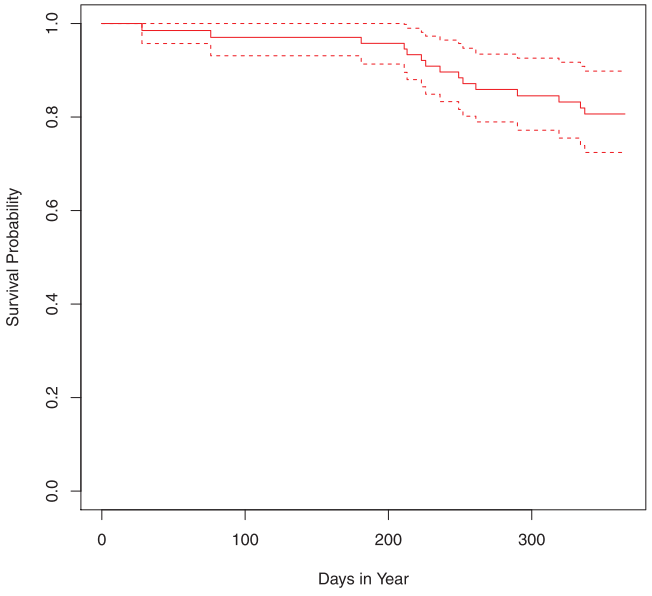

Fig. 2. Estimated annual survival probability and 95% confidence interval for adult mountain lions (n = 29) in greater Los Angeles.2002–2019.

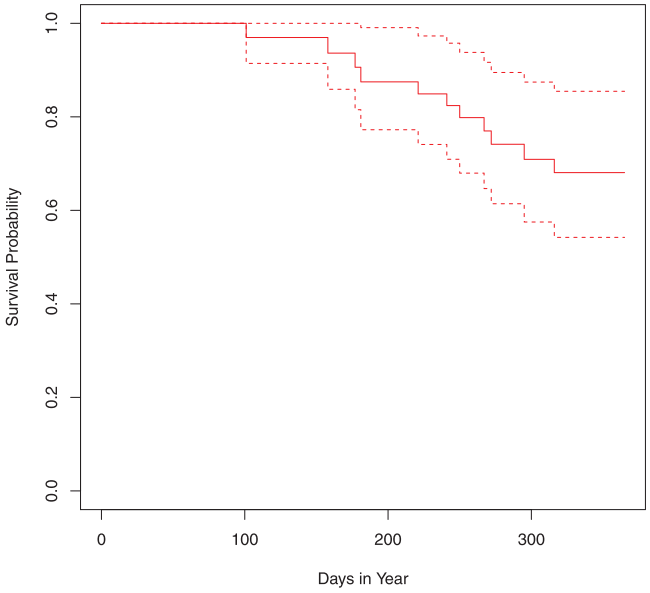

Fig. 3. Estimated annual survival probability and 95% confidence interval for subadult mountain lions (n = 34) in greater Los Angeles.2003–2019.

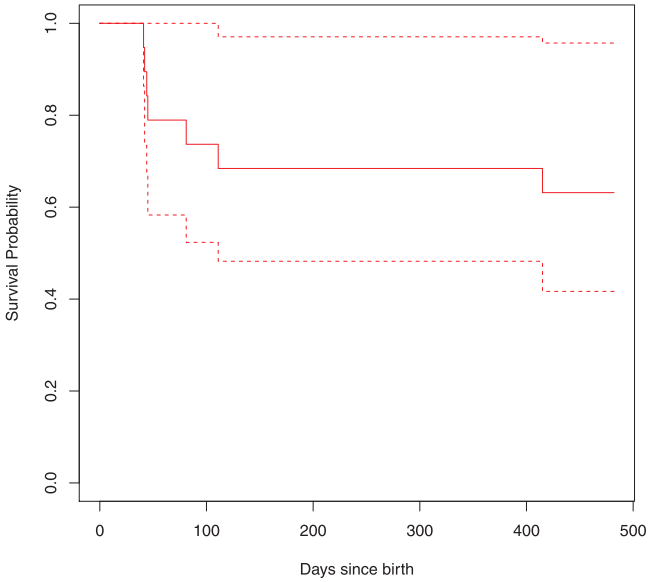

Fig. 4. Estimated survival probability to independence and 95% confidence interval for mountain lion kittens (n = 22 kittens from 10 litters) in greater Los Angeles.2004–2018.

3.2. Mortality risk and competing risks models

For independent-aged mountain lions, the model with the strongest support retained only the dummy-coded age-class variable for adult (ΔAICc = 0). However, mortality risk did not differ significantly between adults and subadults (hazard ratio = 0.55, SE = 0.4, 95% CI [0.25, 1.20], P = 0.135, n = 26 deaths). The null model was a closely competing model (ΔAICc = 0.10), further suggesting weak support for

a statistical difference between adults and subadults. Other models with ΔAICc < 2 retained the dummy-coded variables of adults and males (ΔAICc = 1.26) and the dummy-coded variable of males (ΔAICc = 1.10), but there was no statistical difference in mortality risk between sexes, age-classes, or locations in these models (all $P > 0.170$). In terms of competing risks, mortality risk from natural causes was greater for subadults relative to other causes of death (hazard = 11.6, SE = 1.1, $P = 0.025$). Mortality risk from human-causes was greater for adults relative to natural causes of death (hazard = 17.1, SE = 1.3, $P = 0.026$, $n = 26$ deaths).

4. Discussion

The risk from different causes of mortality differed strongly between age-classes, as adults were more likely to die from human sources, whereas subadults were more likely to be killed by male mountain lions. The greater mortality risk for subadults from intraspecific killing within the SMMs appears to be a function of the difficulty of dispersal associated with anthropogenic barriers, which makes it difficult for subadults to avoid dangerous adult males (Riley et al., 2014). Mortality due to intraspecific aggression is certainly not unique to the SMMs as studies of other populations of mountain lions have shown this to be an important source of mortality (e.g., Logan and Sweanor, 2001; Benson et al., 2011). However, the prevalence of intraspecific killing within the SMMs may be exacerbated by the lack of landscape connectivity that mostly prevents subadults from dispersing out of this isolated mountain range (Riley et al., 2014).

Vickers et al. (2015) found no difference in mortality risk between adult and subadult mountain lions in the Santa Ana Mountains and eastern Peninsular Ranges south of Los Angeles where annual survival rate for all independent age mountain lions was 0.56 (95% CI: 0.46-0.66). Most mortality in these populations was from vehicle strikes, depredation killings, and poaching (Vickers et al., 2015). The stronger annual survival of adults we documented has clearly contributed to the persistence of the small, isolated population within the SMMs (Vickers et al., 2015; Benson et al., 2016a, 2019).

Kittens mostly died during the first four months of life (Fig. 3) similar to findings of other studies tracking kittens tagged at dens (Ruth et al., 2011; Clark et al., 2015). Our point estimate of kitten survival (0.63) was similar to several studies across the western United States (0.59, Logan and Sweanor, 2001; 0.57, Lambert et al., 2006; 0.66, Clark et al., 2015). Robinson et al. (2014) reported a slightly higher estimate of 0.79, whereas Ruth et al. (2011) reported slightly lower kitten survival (0.46-0.58). Elbroch et al. (2018) reported even lower estimates for kittens (approximately 0.25-0.30; rates inferred from figure); however, the uncertainty associated with all previously reported kitten survival rates and our own made it unclear whether these rates differed statistically. Another point estimate for kitten survival that was lower than ours came from Florida panthers (an endangered subspecies of mountain lion (Puma concolor coryi), 0.323, SE = 0.065; Hostetler et al., 2010). However, the estimate for panthers included many kittens from the period when panther fitness was reduced by inbreeding depression (Hostetler et al., 2010). Survival rates for non-inbred panther kittens with greater genetic diversity appeared to range from approximately 0.40 to over 0.50 with wide confidence intervals (rates inferred from figures; Hostetler et al., 2010) that overlapped with the confidence intervals of our estimates. High rates of inbreeding and low genetic diversity have been documented in the SMMs and there is concern about potential demographic consequences of inbreeding (Riley et al., 2014; Benson et al., 2016a, 2019). That our kitten survival estimates were comparable to many studies of genetically diverse populations, and greater than those of inbred Florida panthers, may suggest that inbreeding depression is not severely compromising survival of mountain lions in the SMMs at this time.

We acknowledge that our sample sizes within age-classes were numerically small and that this limited statistical power in our models. However, our telemetry dataset was strengthened by two aspects which improved our ability to model mortality risk and estimate useful survival and cause-specific mortality rates. First, our main study population in the SMMs is very small (estimated maximum of 15 individuals; Benson et al., 2016a) and we tracked a mean of 6 (range 1–12) independent-aged mountain lions each year from 2002 to 2019 (Table 1), which represented a substantial proportion of the population. Second, we tracked many mountain lions for multiple years (mean = 695 days, range 15–2990 days) which added power to our analyses and improved our ability to detect mortality events for this long-lived top predator. We also acknowledge that some kittens in the litters we tagged could have died prior to our visits at 3–5 weeks which might mean that our survival estimate is higher than reality (Logan and Sweanor, 2001). However, we are unaware of a safe and feasible method for radio-tracking kittens < 3 weeks old. Most kitten mortality in our study occurred following abandonment, but we do not think this was related to capture and handling of kittens for multiple reasons. First, in these cases the females returned to the dens after handling and continued raising all or some of the offspring. In two of the three litters from which kittens were abandoned, the female continued to raise other (1–2) kittens that were also handled to independence. Finally, handling kittens at dens is relatively common in mountain lion research and we are unaware of previous studies reporting abandonment due to handling (e.g., Logan and Sweanor, 2001; Hostetler et al., 2010; Ruth et al., 2011; Clark et al., 2015; Elbroch et al., 2018).

Previous population viability analyses indicated that demographic and environmental stochasticity in survival, as well as simulating higher mortality rates both increase the probability of local extinction for mountain lions in the SMMs, highlighting the importance of reducing mortality (Benson et al., 2016a, 2019). Thus, our current finding that adults are more likely to die of human-caused mortality has important management implications. Adult female survival is the most influential demographic parameter influencing population growth potential in the SMMs (Benson et al., 2016a,[Benson et al.,2016b], 2019). Additionally, the small size of this population and the skewed (female-biased) sex ratio of adults means that only an estimated 1–2 breeding adult males generally occupy the SMMs at any one time (Benson et al., 2016a, 2019). Thus, human-caused mortality of adult males has the potential to lead to temporary cessation of reproduction in the SMMs (Benson et al., 2016a, 2019), which has been documented in the small, isolated population in the Santa Ana Mountains south of Los Angeles (Beier et al., 2010).

Given the importance of adult survival, reducing human-caused mortality through management and education is an important conservation objective. For instance, there are efforts underway to fund the construction of a structure to allow mountain lions and other animals to cross the 101 Freeway to facilitate movement and gene flow between the SMMs and adjacent areas. Highway crossing structures could also reduce mortality from vehicle collisions, which was the most frequent source of human-caused mortality in our study. Increased connectivity via highway crossing structures between the SMMs and habitat in adjacent areas should also improve the likelihood of subadults successfully dispersing out of the SMMs, which may reduce mortality due to intraspecific strife (Riley et al., 2014).

A well-documented example from our study highlights apparent links between anthropogenic pressures and mortality risk from seemingly natural sources (i.e. strife) in this population persisting in a major metropolitan area. In July 2019, a radio-collared adult male crossed the 405 freeway leaving the SMMs and entering the canyons surrounding the Los Angeles neighborhood of Bel-Air east of the freeway. The 10-lane 405 Freeway has been documented to be a major impediment to movement and gene flow for mountain lions (Riley et al., 2014), and this was the first time that a radio-collared animal had crossed it in the 18 years of the study. In September 2019, this male was killed by a vehicle as it attempted to again cross the 405, presumably returning to the SMMs. Video footage from multiple surveillance

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cameras provided by a local home-owners association showed the radio-collared male being chased by a large uncollared mountain lion just east of the 405 fewer than 25 min before being struck on the freeway. Thus, aspects of mountain lion social ecology (territoriality and intraspecific strife) appear to interact with space limitation and anthropogenic barriers to increase mortality risk in this urban landscape.

The second most frequent form of human-caused mortality was rodenticide poisoning. Anticoagulant rodenticides have also caused mortality of other wildlife species, such as bobcats, coyotes in greater Los Angeles and other metropolitan areas in the US (e.g., Riley et al., 2007; Poessel et al., 2015). Furthermore, exposure to rodenticide has been implicated in the onset of notoedric mange in bobcats and mountain lions in greater Los Angeles (Riley et al., 2007; Serieys et al., 2018). Thus, discouraging the use of rodenticides, could help reduce mortality for mountain lions and other wildlife. Reducing mortality of mountain lions in the SMMs and adjacent areas in greater Los Angeles will require continued collaboration with local governments and agencies involved in road management, as well as outreach efforts with local landowners and businesses to mitigate potential human-wildlife conflicts and associated mortality. Given the potential for local extirpation in the SMMs and other isolated populations in the Los Angeles area, efforts to reduce mortality from human causes as well as restoring landscape connectivity are critical for the persistence of this top predator in the human-dominated landscape of southern California (Benson et al., 2016a, 2019).

Declaration of Competing Interest

The authors have no conflict of interest to declare.

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Letter to the Editor (Response)

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Conserving ecological roles of top predators in isolated mountains

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Recently, Bleich (2019) wrote a letter to the editor about a paper in which we modeled the population viability of mountain lions (*Puma concolor*) in isolated mountain ranges in southern California (Benson et al. 2019). Bleich (2019) expressed concern that some might misinterpret several statements made in our discussion about the role of mountain lions in these isolated mountain ranges. We appreciated the positive statements about our work in the letter and did not disagree with much of what he said. However, we were confused as to why he felt this "cautionary note" was needed and by some of the statements in the letter. Regardless, we stand by our statements regarding the value of conserving mountain lions in these mountain ranges.

Bleich (2019) began by providing two quotes from our paper that he felt could be misinterpreted. With the first, we stated that conserving mountain lions in these mountain ranges would be an important step toward maintaining intact, functioning ecosystems within one of the most human-impacted landscapes in the world. With the second, we noted the value of conserving a native top predator to maintain stable predator–prey dynamics. We used measured language and specified the ecosystem process (predation) that we believe mountain lions influence. To ensure that there is no misinterpretation, we want to make it clear that we believe (1) having viable populations of mountain lions in the Santa Ana and Santa Monica Mountains results in more intact ecosystems than if they were to go locally extinct, and (2) having a top predator in these mountain ranges whose main prey are the largest herbivores in the system contributes positively to the goal of maintaining stable predator–prey dynamics. We also wish to point out that these statements come from two to three sentences in our discussion and the focus of our original paper was population viability rather than ecosystem processes.

Bleich (2019) states that "in the absence of some components, the system cannot be considered intact" and then points out that grizzly bears (*Ursus arctos*) and California condors (*Gymnogyps californianus*) are no longer present in these mountain ranges. The confusion may stem from different understandings of what constitutes an intact, functioning ecosystem. We believe that ecosystems are probably best viewed in terms of processes rather than as a checklist of species. Indeed, scientists often refer to the degree to which a given ecosystem is intact and functioning, because ecosystems can lose species, but maintain important processes (Yachi and Loreau 1999, Hooper et al. 2005). When a species plays a role that appears to be unlike that of any other species in the system, the loss of that species may result in loss of the process (Lawton 1994, Tilman et al. 1997, Ritchie et al. 2012). Conversely, when there is redundancy in ecological function across species, some species may be lost without substantial loss of ecosystem processes (Ehrlich and Walker 1998, Hooper et al. 2005). We were careful in our use of the term "intact, functioning ecosystem" to specify the component process that we believe would be disrupted by the loss of the only remaining large carnivore in our study systems. We believe it is safe to assume that predator–prey dynamics between mountain lions and mule deer (*Odocoileus hemionus*) would be compromised without viable populations of mountain lions.

Bleich (2019) cites several studies as evidence that the role of mountain lions as predators has been altered in human-dominated landscapes (e.g., Smith et al. 2015, Robins et al. 2019). Robins et al. (2019) found that mountain lion predation remained relatively consistent across a gradient of human presence and concluded that mountain-lion–ungulate predator–prey systems can persist in human-dominated landscapes. Thus, the findings of Robins et al. (2019) actually seem very consistent with our statements. Bleich (2019) also cites several studies documenting aversion of mountain lions to playback of human voices over loudspeakers (Smith et al. 2017, Suraci et al. 2019). These studies were well done, interesting, and provocative. However, they do not provide evidence that mountain lions cannot play important roles as top predators in landscapes adjacent to urban areas.

The absence of grizzly bears or condors does not negate the ecological value of mountain lions. Bleich (2019) suggests that the absence of these scavengers has resulted in lower predation rates of mountain lions. Speculating on historical or contemporary predation rates by mountain lions in our study systems is beyond the scope of our population viability analyses and existing data. However, it caught our attention that Bleich (2019) suggested that predation rates have decreased with the absence of grizzly bears and then cites the work of Smith et al. (2015), suggesting that kill rates of mountain lions on deer can increase in anthropogenic

landscapes due to disturbance at kill sites. Could these community-level changes (loss of bears, increase of humans) potentially offset such that human disturbance compensates for the loss of native scavengers in human-dominated landscapes in coastal California? An interesting, but admittedly speculative idea. However, it is relevant to our point above that ecosystem processes can continue even with changes in species assemblages. There have been other changes in these mountain ranges between historical and contemporary periods beyond the loss of bears and condors. Have other species of scavengers present in these mountains (e.g., coyotes [*Canis latrans*], Turkey Vultures [*Cathartes aura*], Common Ravens [*Corvus corax*], American Crows [*Corvus brachyrhynchos*]) increased or decreased since the loss of grizzly bears and condors? Are they more likely to visit or stay longer at mountain lion kills in the absence of larger mammalian and avian scavengers? There is evidence that black bears limit the presence and feeding time of other scavengers at carcasses in northern California (Allen et al. 2015). Thus, subordinate scavengers could have been released from similar limitation with the extirpation of grizzly bears from our study systems.

Our point is that caution is warranted when drawing conclusions about the nature and strength of predator–prey interactions between mountain lions and mule deer in these mountain ranges, and how they may have changed relative to changes in human disturbance and the scavenger community without data. The influence of predation by mountain lions on mule deer populations may be stronger or weaker than it was historically for a variety of reasons. Indeed, there is evidence that human presence may decrease (Hebblewhite et al. 2005, Muhly et al. 2011), increase (Smith et al. 2015), or fail to appreciably influence (Robins et al. 2019) the impact of large carnivores on ungulate prey (reviewed by Kuijper et al. 2016). As noted in our original paper, it would be beneficial to evaluate mule deer population dynamics in our study systems to provide a better understanding of predator–prey interactions between mountain lions and mule deer (Benson et al. 2019). It seems unlikely that mountain lion predation on mule deer in the Santa Monica and Santa Ana Mountains is exactly the same as it was over 100 yr ago when grizzly bears were present. However, this should not be a prerequisite for justifying the conservation of mountain lions or their predator–prey interactions.

We suggested that long-term persistence of mountain lions in greater Los Angeles would provide evidence that large carnivores and abundant human populations are compatible (Benson et al. 2019). Bleich (2019) was concerned that this statement "could be seized upon to support other agendas that are neither fiscally prudent nor socially acceptable, or even logistically possible." We are unsure how to respond to this because Bleich (2019) did not identify these "other" agendas. Our point was to highlight that the conservation of large carnivores has been an extremely challenging task for conservation biology around the globe. Thus, conserving viable populations of top predators within the second-largest metropolitan area in the United States with some of the busiest freeways in the world suggests to us that large carnivores and humans can share landscapes if we can maintain and restore connectivity. Bleich (2019) also states that "Inaccurate information in the context of risks to human safety or in the current context of conservation, can be especially problematic because it engenders public distrust and suspicion of management agencies, their scientists, and the conservation programs for which they are responsible." We completely agree, but the relevance of this statement to our paper is not clear.

Bleich (2019) goes on to say that "much of the general public, a substantial portion of elected officials, and a variety of special interest groups view large carnivores with reverence or awe," and suggests that many from these groups have made false claims to further their agendas. The same could probably be said about those among the same segments of society who feel negatively about large carnivores. Large carnivores are controversial and tend to elicit strong positive and negative responses from humans (Primm and Clark 1996). As scientists, we have an obligation to objectively evaluate evidence, present reliable information, and make statements that are defensible when considered in the proper context. However, it is not always possible to prevent those seeking to promote false agendas on either side of an issue to "seize upon" statements taken out of context for political purposes.

Bleich (2019) ends by saying the appropriate rationale for the conservation of mountain lions in these isolated mountain ranges "is that of maintaining the ecosystem services provided by mountain lions, and the role of those services in ecosystem function (sensu Bleich 2018)." We are unsure as to what this means. Bleich (2019) does not identify what ecosystem services (i.e., benefits humans obtain from ecosystems) he is attributing to mountain lions and we found no mention of ecosystem services in Bleich (2018). Bleich (2018) described two large mortality events for mule deer in a year following heavy snowfall in the Sierra Nevada Mountains and speculated on the potential influence of such events for ecosystem function and mule deer management. Thus, it is unclear to us how Bleich (2018, 2019) provides the appropriate rationale for mountain lion conservation in the Santa Monica and Santa Ana Mountains. We did not study or document benefits derived by humans from mountain lions and felt it was more appropriate to briefly note the value of mountain lion viability with respect to maintaining predator–prey interactions as an important ecosystem process.

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ESTIMATING BIOMASS IN CALIFORNIA'S CHAPARRAL AND COASTAL SAGE SCRUB SHRUBLANDS

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ABSTRACT

Despite being one of the most extensive vegetation types in the North American Mediterranean Climate Zone, information on the amount of biomass and carbon stock associated with shrubland vegetation is still largely unknown. Efforts to quantify shrubland biomass through fieldwork consist of either direct measurement using destructive vegetation sampling or indirect measurement through the combined use of stem measurements and allometric equations. Both methods have their own benefits and shortcomings, resulting in substantial variation in how shrubland biomass is reported. Here we aim to provide a comprehensive review and synthesis of available shrubland biomass data from studies based in California to provide a concise and reliable source for natural resource managers. We conducted a literature review of 37 studies published over a span of 72 yrs to compile estimates of aboveground biomass (live, dead, and total), leaf biomass, stem biomass (live, dead, and total), litter biomass, and belowground biomass for three prominent shrubland communities and four shrubland species in the California Floristic Province. Overall aboveground biomass in shrub communities was greatest in mixed chaparral (3461 g/m^2), followed by chamise chaparral (2114 g/m^2), and coastal sage scrub (1583 g/m^2). In each community total aboveground biomass increased with the age of the stand. Leaf, stem, and litter biomass estimates were also highest for mixed chaparral compared to the other communities. Of the four shrub species we summarized biomass data for, *Ceanothus greggii* A. Gray (Rhamnaceae) had the highest average aboveground biomass, followed by *Adenostoma fasciculatum* Hook. & Arn. (Rosaceae), *Quercus berberidifolia* Liebm. (Fagaceae), and *C. cuneatus* (Hook.) Nutt. By compiling these studies and summarizing the biomass data reported in them, we provide a single resource to characterize the amount of biomass of three different shrublands and four species over their life cycle. This is an essential resource for land managers and practitioners who need field-based biomass and carbon stock figures for monitoring and reporting purposes.

Key Words: Aboveground biomass, *Adenostoma fasciculatum* Hook. & Arn., belowground biomass, California, carbon storage, *Ceanothus* sp., chaparral, coastal sage scrub, North American Mediterranean Climate Zone, *Quercus berberidifolia* Liebm.

Shrublands cover extensive areas of the North American Mediterranean Climate Zone (also known as the California Floristic Province), which includes most of California, southwestern Oregon, northwestern Baja California, Mexico, and a sliver of western Nevada. However, despite their large spatial extent there is little appreciation of the contribution shrublands make to carbon storage and carbon sequestration (Di Castri et al. 1981, Luo et al. 2007). Chaparral and coastal sage scrub are two highly characteristic shrubland types of the lowland and middle elevation of this Mediterranean Climate Zone, especially in the southern portions of California and northwest Baja California. These ecosystems support high levels of plant species richness and endemism (Burge et al. 2016), as do their analogues in other Mediterranean-type ecosystems globally (Cowling et al. 1996, Myers et al. 2000). However, very little is known of their contributions to carbon storage or cycling other than the fact that many species have extensive and deep root systems that can provide substantial belowground carbon storage (Kummerow et al. 1977, Luo et al. 2007).

Studies and data for estimating biomass and carbon storage for major habitat types dominated by forest, such as tropical rainforests, are routinely conducted and reported. For example, some early studies providing image-derived biomass estimates for tropical rainforests were instrumental in highlighting their critical role in the global carbon cycle

(e.g., Foody et al. 2001, Saatchi et al. 2007, Propastin 2013).Within the North American Mediterranean Climate Zone, studies estimating biomass for forested portions of the landscape have been conducted, for example, for the Sierra Nevada of California (McGinnis et al. 2010, Zhang et al. 2014) and forests of northern California and southwestern Oregon (Hudiburg et al. 2009). However, studies estimating biomass of shrublands in Mediterranean climates, either in North America or in the four other regions of the world where this climate occurs, are comparatively rare (e.g., Cerrillo and Oyonarte 2006).

At the continental scale in the USA, shrubland mapping efforts generally underestimate the amount of biomass in shrublands. National scale datasets such as the National Biomass and Carbon Dataset (http://www.whrc.org/mapping/nbcd/) and LandCarbon (http://landcarbon.org/) use USDA Forest Service Forest Inventory and Analysis (FIA) plot data alongside Landsat imagery and occasionally radar remote sensing imagery. The FIA database includes shrubland plots but unlike in forest plots, aboveground biomass is not measured in shrub plots, thus carbon mapping relying on the FIA dataset shows shrubland carbon storage as zero. At the California state scale, efforts to map carbon include the California Department of Forestry and Fire Protection's biomass assessment of forests and shrublands (FRAP 2005). Estimates are based on integrating data from land cover datasets, fuel models, as well as other spatial data on slope, land cover, ownership and fire threat (Anderson 1982, FRAP 2002, 2003, 2005).

Alternatively, the California Forest and Rangeland Greenhouse Gas Inventory assessment (Battles et al. 2014) used USGS Landfire data (30m) on Existing Vegetation Type (EVT) and the associated information on vegetation height and cover, and generated biomass densities by shrub-height classes based on the literature. Note that none of the mapping efforts described above address biomass stored belowground, which can be substantial, accounting for up to 41% of the species biomass in *Adenostoma fasciculatum* Hook. & Arn. (Kummerow et al. 1977) and 47% in *Arctostaphylos glauca* Lindl. (Miller and Ng 1977). At finer spatial scales, studies reporting field measurements of biomass in shrublands are characterized by a lack of consistency in the data collection methods and reporting. These inconsistencies are largely due to the variation in the focus of different studies and the research questions they aim to answer. Field studies vary in plot and sample size and biomass is reported using a variety of different metrics making extrapolations over larger shrubland areas challenging, given the variation in elevation (300–3000 m), soils, topography, aspect, coastal or desert exposure, and disturbance history.

Site specific influences on biomass make generalizations over large landscapes difficult. Plant community composition and structure are largely a direct reflection of the environment. At the regional scale, precipitation drives the distribution of mixed chaparral, chamise, and sage scrub, with mixed chaparral found in comparably wetter areas than both chamise and sage scrub (Conrad et al. 1986). In more productive sites, for example, with higher annual precipitation, higher annual production drives higher biomass accumulation (Gray 1982, Keeley and Keeley 1988, Schlesinger and Gill 1980, Uyeda et al. 2016). At a local scale, these differences in productivity can be due to slope, aspect, elevation, and soil characteristics (Hellmers 1955, Keeley and Keeley 1988, Regelbrugge and Conard 1996, Riggan and Dunn 1982, Schlesinger et al. 1982).

One reason for the lack of comprehensive data on shrubland biomass is the physical difficulty of conducting fieldwork in these systems. Dense stands of shrublands, particularly chaparral, are often described as 'impenetrable' and slopes are often steep, consequently undertaking systematic fieldwork requires substantial resources and effort (Uresk and Menke 1977). Executing full shrub harvests to directly measure above- and belowground biomass requires excessive time and resources and is not feasible to do at a large scale. A more common field method for assessing biomass combines destructive and non-destructive sampling. First, shrubs representative of the stand are selected and all aboveground biomass is collected. Plant material is then dried and weighed, occasionally being broken down into different stem size classes, plant parts and/or live and dead material. These shrub samples are then used to build species-specific regression equations that relate more easily measured variables (e.g., stem diameter, cover) to overall biomass. Ideally the roots are also excavated, however in most cases belowground biomass is either ignored or calculated based on pre-determined root:shoot ratios (Mooney and Rundel 1979).

The variation in the locations and site specific characteristics of field studies combined with the lack of accurate image-derived maps at a useful scale, create a need for the available biomass data to be synthesized in a concise and comprehensive way. From a resource management perspective, there is an increasing need to be able to accurately quantify biomass in shrubland landscapes and understand how it is impacted by management actions or by disturbance events such as wildfire. Similarly, information on the projected recovery of biomass post disturbance allows resource managers to anticipate the return of carbon storage ecosystem services and also the return of other services associated with vegetation and biomass, such as wildlife habitat or an established root system for retaining sediment, which is otherwise eroded from denuded slopes (Wohlgemuth et al. 1999). If disturbances become too frequent in shrubland communities (e.g., extremely short fire-return intervals) they can result in vegetation type-conversions, changing the nature of carbon storage and sequestration on the landscape as biomass values differ substantially between shrub-

lands and non-native annual grasses (Keeley et al. 2005, Lippitt et al. 2013).

From a policy perspective, federal agencies such as the USDA Forest Service are now required to record and report information on carbon stocks. The Climate Change Scorecard for example, requires the quantity of carbon stocks under Forest Service management to be reported as well as the estimated impact of disturbance and management activities on these carbon stocks (http://www.fs.fed.us/climatechange/advisor/scorecard/carbon-assessment-stewardship.html). There is also increasing interest in mapping and quantifying the ecosystem services that natural landscapes provide, which can – among other things – provide the basis for developing market based approaches such as Payment for Ecosystem Services (Chan et al. 2006). In this paper we review and summarize the available literature on above- and belowground biomass of shrublands from studies based in California with the intention of providing a concise and reliable resource for natural resource managers.

METHODS

To compile the available data on biomass we carried out an extensive literature search online. We used the Web of Science and Google Scholar search engines specifying key words that included 'chaparral', 'shrubland', 'biomass', 'chamise', 'sage scrub', and 'California'. In addition, more general web searches were conducted to locate government documents or conference and symposium proceedings. From the relevant literature we extracted all reported biomass values and associated details including location (general and specific coordinates), sample size, parent material, elevation, aspect, age, stand height, unit of measurements, and species mix (when specified). In some cases biomass values were presented in graphical form rather than tables in which case it was necessary to approximate the actual values. We also recorded specific details of the biomass measurements, for example, whether reported values were calculated using destructive sampling, allometric equations, and/or whether dead material was included in the total biomass values. Studies that reported biomass values in a format that did not allow for comparisons with other studies were excluded (e.g., biomass per plant versus biomass per area).

To synthesize the array of different datasets we made the following assumptions. When only certain biomass components were reported we calculated the missing components when feasible. For example, if live and dead biomass values were reported without reporting a total aboveground biomass, we summed live and dead to report total aboveground biomass. Alternately, if a total aboveground biomass value and a live aboveground biomass value were reported without a value for dead biomass, we subtracted live from the total to provide a value for dead biomass. Finally, if aboveground biomass was reported without specifying live or dead, we assumed both were included. This last assumption may lead to an underestimate of total aboveground biomass, with combined live and dead averages occasionally exceeding total aboveground averages. Similarly for species-level data, when only live aboveground biomass was reported, we included it when averaging total aboveground biomass which may cause minor underestimates of species-level total aboveground biomass due to the missing dead biomass component. Consequently, in using these data we caution that some interpretation was necessary where the published material was unclear.

Once collected, we summarized the studies based on community type, age of shrubland and species. Community type was determined based on either the designation provided by the authors of the given study or assigned based on the shrub species reported for the given stand. Mixed chaparral stands varied in the number of species present and at times were largely dominated by one or two chaparral species such as *Ceanothus greggii* A. Gray or *Quercus berberidifolia* Liebm. Only pure stands of *Adenostoma fasciculatum* or stands that were explicitly dominated by *A. fasciculatum* were classified as chamise chaparral. In some cases, biomass averages of monospecific shrub communities were included in the species breakdown. It was assumed that the stand level biomass per unit area was the same as the shrub level biomass per unit area when there was only one species present in the stand. For example, a pure stand of *A. fasciculatum* included in the chamise chaparral summaries, was also included in the species summary for *A. fasciculatum*.

We summarized data for shrub communities and species that were sufficiently documented in the literature. Shrub communities with less than three studies reporting overall biomass, such as desert shrubland, are not reported. Data were grouped into different age classes (e.g., 1–10, 11–20, 21–30, >30 yr) and summarized accordingly. When shrubland age was not provided, effort was made to determine the general age of the stand through descriptions in the text. For instance, if a stand was described as "mature" but not assigned a specific age, it was placed in the oldest age class. If no age was provided nor was there sufficient information to assign an age class, the associated data were included in the overall averages but not in a specific age class. It is important to note that in most studies, the age of shrubland was determined by the time of last fire. Furthermore, biomass metrics reported in different studies varied widely with little consistency in the units of measurement used, which included tons/acre, lbs/acre, g/m^2, kg/m^2, Mg/ha, kg/ha, and tonnes/ha. We standardized all biomass units to g/m^2.

We report the available biomass studies at two spatial scales. First by community type: mixed chaparral, chamise chaparral, and coastal sage scrub; and second, at a higher resolution using four

dominant shrubland species: *Adenostoma fasciculatum*, *Ceanothus greggii, Quercus berberidifolia,* and *C. cuneatus*. Subdividing the data by stand age, we summarize total aboveground biomass and range and the live and dead aboveground biomass and range (for the community level only).These were the most commonly reported variables in the studies reviewed. Other data we present include annual aboveground biomass increment, a breakdown of live and dead stem biomass, leaf biomass, litter biomass, and root-to-shoot ratios.

Finally, as a case study, we examined the relationship between aboveground biomass and one of the key drivers in productivity – precipitation. We mapped a subset of study locations (n = 36) and display these with annual mean precipitation from the Basin Characterization Model (BCM) dataset (1981–2010, Flint et al. 2013). Where a single location had multiple biomass measurements for different age classes of chaparral, we averaged measurements of stands >10 yr old (this allowed us to keep most of the plots except for the very young ones). For these 36 plots we identified mean annual precipitation values and assessed the correlation with mean aboveground biomass.

Results

We reviewed 37 studies published between 1944 and 2016 with the majority published in the 1970s and 1980s. While we did our best to capture as much of the relevant literature as possible using the keyword searches described, it is inevitable that some studies might have been missed owing to time and resource constraints. Just over half of these documents (51%) were published in peer-reviewed journals and sources for the remaining documents included conferences and/or symposium proceedings (14%), government documents (14%), dissertations (11%), book chapters (8%), and university reports (3%). The most common shrub community types reported in the literature were mixed chaparral and chamise chaparral, followed by coastal sage scrub and desert shrublands. Many studies also reported biomass at the species level, with 75% of these sudies reporting biomass values for *A. fasciculatum*. Other species such as *Q. berberidifolia*, *C. greggii*, and *C. cuneatus* were less prevalent in the literature, each reported in 15% of the studies. There were 21 additonal species reported on but much less frequently.

Of the biomass metrics reported in the 37 studies, total aboveground biomass was reported most frequently (almost 90% of the studies), followed by live aboveground biomass, and dead aboveground biomass. Litter biomass, leaf biomass, live and dead stem biomass, and aboveground annual increment of biomass (i.e., accumulated biomass per yr) were less commonly reported (< 33% of the studies). Belowground biomass was the least common biomass metric, reported in only 16% of the studies.

Aboveground Biomass Estimates

Biomass at the community level. Mixed chaparral was the most widely reported shrub community in the literature. Summaries show that average total, live, and dead aboveground biomass were all lowest in 1–10 yr old stands (Table 1, Fig. 1). In these young stands total aboveground biomass on average was 861 g/m^2 with an average of 792 g/m^2 of live aboveground biomass and 300 g/m^2 of dead aboveground biomass. Total and dead aboveground biomass was the highest on average in stands >30 yr old with 4931 g/m^2 and 1575 g/m^2 respectively. Live aboveground biomass was the highest on average in 21–30 yr old stands with 4674 g/m^2 (Table 1, Fig. 1). The highest aboveground biomass reported among studies focusing on mixed chaparral was 11,800 g/m^2 in a 55 yr old *Ceanothus*-dominated stand (Regelbrugge and Conard 1996). Average annual aboveground biomass increment was highest in 21–30 year old stands at 952 g/m^2, however annual increment data reported for older stands (>30 yr old) were limited to only one study (Riggan and Lopez 1982; average biomass increment 67 g/m^2), so this value is unlikely to be representative of older mixed chaparral stands as a whole.

Chamise chaparral was the second most commonly reported shrub community in the literature (Table 2). There were no studies that report comparable biomass values for chamise chaparral in the 21–30 yr age class. Due to the lack of data for this age class, it was necessary to combine the 11–20 and 21–30 age classes. The lowest values for average aboveground total, live and dead biomass were found in the youngest stands (1–10 yr; Fig 2). Average total aboveground biomass in this age class was very similar to that of the young mixed chaparral stands with a value of 923 g/m^2. On average, total, live and dead aboveground biomass were all highest in >30 yr old stands. The highest reported total aboveground biomass was 4909 g/m^2 in a 37 yr old *A. fasciculatum* stand with a small component of *Ceanothus crassifolius* Torr. present (Specht 1969). Average biomass in >30 yr old chamise chaparral stands was about half that reported in equivalent stands of mixed chaparral (2787 g/m^2 and 4931 g/m^2 respectively).

In contrast, biomass data from coastal sage scrub stands were relatively limited and data only supported a breakdown into two age classes, 1–10 yr and >10 yr (Table 3). Average total and live aboveground biomass were both lowest in 1–10 yr old stands with 598 g/m^2 and 409 g/m^2 respectively (Fig. 3). Dead aboveground biomass for this age group was not reported in the literature. Average total and live aboveground biomass were highest in stands >10 yr old (the oldest stand reported on was 40 yr). Total aboveground biomass for older stands averaged 1901 g/m^2, with average live of 995 g/m^2 and average dead of 555 g/m^2.

Data on leaf, stem, and litter biomass were less commonly reported in the studies reviewed. Leaf

TABLE 1. SUMMARY OF CALIFORNIA MIXED CHAPARRAL BIOMASS DATA BASED ON 25 STUDIES WITH BIOMASS MEASUREMENTS FROM 1944–2016 IN THE AVAILABLE LITERATURE [REFERENCES 1–7, 9–12, 17, 20–25, 27, 28, AND 32–36 IN APPENDIX 1]. Note: average total aboveground biomass does not equate to live plus dead because not all studies report all three variables. Total includes all age classes as well as studies that did not provide a shrubland age. [i]Values averaged from ≤ 2 studies.

Age class (yrs.)	Total aboveground biomass (g/m^2)		Live aboveground biomass (g/m^2)		Dead aboveground biomass (g/m^2)		Avg biomass increment ($g/m^2/yr.$)	Avg leaf biomass (g/m^2)	Avg live stem biomass (g/m^2)	Avg dead stem biomass (g/m^2)	Avg total stem biomass (g/m^2)	Avg litter biomass (g/m^2)	Avg belowground biomass (g/m^2)
	Avg	Min-Max	Avg	Min-Max	Avg	Min-Max							
1–10	861.4	120–1814	791.5	200–2055	300.0	40–700	201.9	197.0	998.5[i]	–	1205.0[i]	–	–
11–20	3473.8	411–8740	3417.9	1000–7644	422.4	0–1520	850.0[i]	336.0[i]	2896.0[i]	–	–	–	–
21–30	4352.5	1912–8290	4673.5	2012–6680	955.3	400–1610	951.9	388.2	5167.5[i]	1304.0[i]	5244.1	2108.0	–
>30	4931.0	1730–11800	3999.7	1850–10000	1574.9	0–4500	66.5[i]	200.0[i]	1580.0[i]	1165.7[i]	2870.0[i]	5300.0[i]	1330.0[i]
Total	3460.5	120–11800	3166.3	200–10000	688.8	0–4500	427.0	303.0	2801.3	1257.9	4198.8	2541.3	1330.0[i]

TABLE 2. SUMMARY OF CHAMISE CHAPARRAL BIOMASS DATA BASED ON 13 STUDIES WITH BIOMASS MEASUREMENTS FROM 1944–2012 IN THE AVAILABLE LITERATURE [REFERENCES 1–3, 5, 10, 12, 17, 21, 23, 27, 30, 31, AND 35 IN APPENDIX 1]. Note: average total aboveground biomass does not equate to live plus dead because not all studies report all three variables. Total includes all age classes as well as studies that did not provide a shrubland age. [i]Values averaged from ≤ 2 studies.

Age class (yrs.)	Total aboveground biomass (g/m^2)		Live Aboveground Biomass (g/m^2)		Dead aboveground biomass (g/m^2)		Avg biomass increment ($g/m^2/yr.$)	Avg leaf biomass (g/m^2)	Avg live stem biomass (g/m^2)	Avg dead stem biomass (g/m^2)	Avg total stem biomass (g/m^2)	Avg litter biomass (g/m^2)	Avg belowground biomass (g/m^2)
	Avg	Min-Max	Avg	Min-Max	Avg	Min-Max							
1–10	922.6	175–1636	670.4	115–1054	451.7[i]	158–583[i]	110.0[i]	–	–	762.2[i]	–	–	–
11–30	2536.7	1440–3050	1921.1	1400–2530	583.4	40–920	–	–	–	–	–	–	–
> 30	2787.2	1510–4909	2129.9	1400–3049	711.0	200–2184	–	–	–	560.4[i]	–	–	–
Total	2114.4	175–4909	1687.5	115–5600	642.4	25–2184	110.0[i]	–	–	661.3[i]	–	1277.8[i]	–

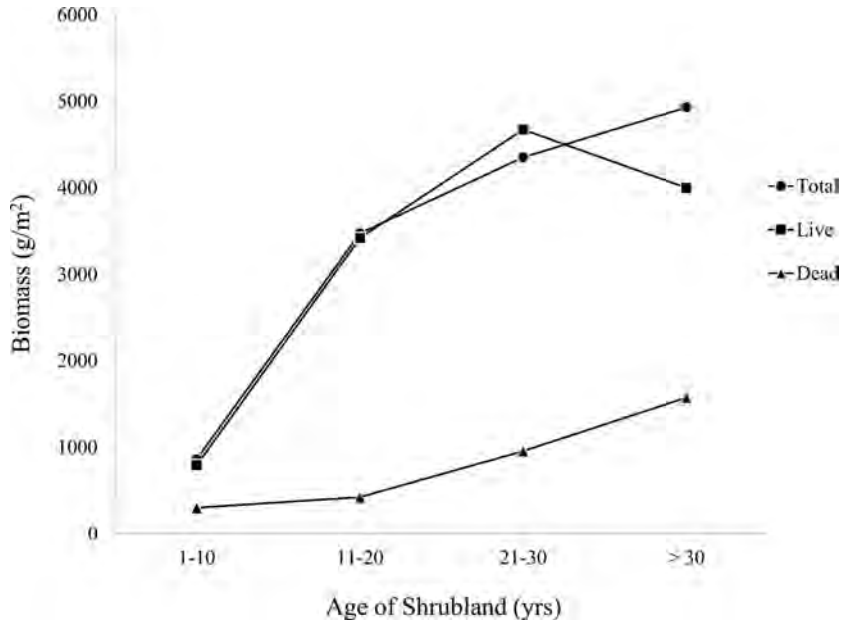

FIG. 1. Estimates of aboveground biomass (g/m^2) for mixed chaparral by age class based on 25 studies with biomass measurements from 1944–2016. Note: average total aboveground biomass does not equate to live plus dead because not all studies reported all three variables.

biomass in mixed chaparral was approximately twice that of coastal sage scrub communities (303 g/m^2 compared to 141 g/m^2; Tables 1 and 3). Similarly, total stem biomass was about four times greater in mixed chaparral compared to coastal sage scrub (4199 g/m^2 compared to 1120 g/m^2). The amount of litter across all age classes was highest in mixed chaparral followed by coastal sage scrub and then chamise chaparral communities (2541 g/m^2, 1392 g/m^2, and 1278 g/m^2 respectively).

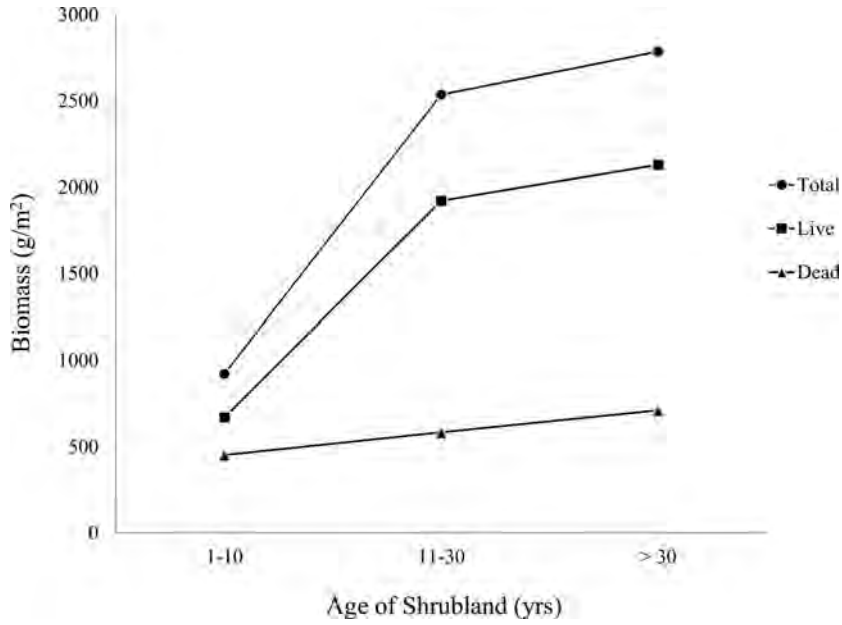

FIG. 2. Estimates of aboveground biomass (g/m^2) for chamise chaparral by age class based on 13 studies with biomass measurements from 1944–2012. Note: average total aboveground biomass does not equate to live plus dead because not all studies reported all three variables.

TABLE 3. SUMMARY OF COASTAL SAGE SCRUB BIOMASS DATA BASED ON 10 STUDIES WITH BIOMASS MEASUREMENTS FROM 1981–2012 IN THE AVAILABLE LITERATURE [REFERENCES 2, 3, 5, 7, 8, 10, 14, 21, 35, AND 37 IN APPENDIX 1]. Note: average total aboveground biomass does not equate to live plus dead because not all studies report all three variables. Total includes all age classes as well as studies that did not provide a shrubland age. [i]Values averaged from ≤ 2 studies.

Age class (yrs.)	Total aboveground biomass (g/m^2)		Live aboveground biomass (g/m^2)		Dead aboveground biomass (g/m^2)		Avg biomass increment ($g/m^2/yr.$)	Avg leaf biomass (g/m^2)	Avg live stem biomass (g/m^2)	Avg dead stem biomass (g/m^2)	Avg total stem biomass (g/m^2)	Avg litter biomass (g/m^2)	Avg belowground biomass (g/m^2)
	Avg	Min-Max	Avg	Min-Max	Avg	Min-Max							
1–10	597.8[i]	255–958[i]	409.4[i]	200–630[i]	–	–	306.9[i]	–	–	–	–	–	–
> 10	1901.1	1172–2800	995.0	400–1300	555.4	247–852	305.1[i]	140.8[i]	867.3[i]	253.1[i]	1120.4[i]	1370.9[i]	–
Total	1582.7	255–3094	660.3	200–2200	617.7	247–919	306.5	140.8[i]	867.3[i]	253.1[i]	1120.4[i]	1392.2[i]	–

TABLE 4. SUMMARY OF BIOMASS MEASUREMENTS FOR 4 DOMINANT CHAPARRAL SPECIES BASED ON 20 STUDIES WITH BIOMASS MEASUREMENTS FROM 1944–2012 IN THE AVAILABLE LITERATURE [REFERENCES 4, 7, 9, 12, 13, 15, 16, 18–20, 22, 25–32, AND 35 IN APPENDIX 1]. Note: some ages inferred based on stand age or age of surrounding shrubs. [i]Values averaged from ≤ 2 studies.

Species	Age range of shrubs included (yrs)	Total aboveground biomass (g/m^2)		Avg annual biomass increment ($g/m^2/yr.$)	Avg leaf biomass (g/m^2)	Avg total stem biomass (g/m^2)	Avg litter biomass (g/m^2)	Total belowground biomass (g/m^2)		Avg root:shoot ratio
		Avg	Min-Max					Avg	Min-Max	
Adenostoma fasciculatum	1–60+	1957.6	198–6818	252.8	246.7	1136.3	–	1632.7	90.3– 4789	0.6[i]
Ceanothus greggii	21–24	4876.8[i]	1109–10139[i]	595.5[i]	–	1275.3[i]	2217.3[i]	798.4[i]	154.8–1442[i]	0.3[i]
Quercus berberidifolia	23–35+	1709.5	1233–2046	238.2[i]	310.0[i]	1695.7[i]	5300.0[i]	1330.0[i]	–	–
Ceanothus cuneatus	15–25	880.6	814–990	–	46.9[i]	767.0[i]	–	–	–	–

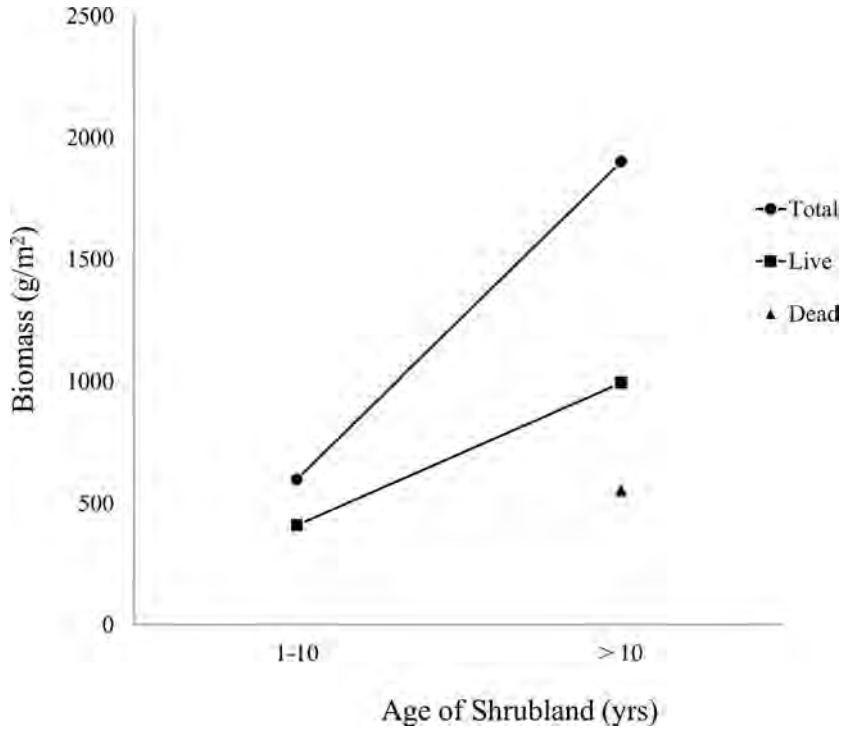

FIG. 3. Estimates of aboveground biomass (g/m^2) for coastal sage scrub based on 10 studies with biomass measurements from 1981–2016. Note: average total aboveground biomass does not equate to live plus dead because not all studies reported all three variables.

Biomass at the species level. At a finer species-level scale, we report on four dominant chaparral species based on their prevalence in the literature (Table 4). We only report total aboveground biomass, excluding a breakdown of live and dead aboveground biomass due to insufficient data. The most frequent shrub species measured was *A. fasciculatum*. Average total aboveground biomass for *A. fasciculatum* was 1958 g/m^2 (Table 4). The lowest reported biomass in the literature was 198 g/m^2 for a 1 yr old individual (Sparks and Oechel 1993) and the highest was 6818 g/m^2 reported by Kummerow et al. (1977) for a 2 yr old individual. Kummerow et al. (1977) note that this individual was resprouting and had numerous dead stems resulting in a root:shoot ratio of 0.7. The next highest biomass reported in the literature for *A. fasciculatum* was for a mature individual with a biomass of 4260 g/m^2 (3,363 g/m^2 of which was live; Green 1970). Average total aboveground biomass was the highest for *C. greggii*, which also had the maximum biomass reported at 10,139 g/m^2 for one individual (no age provided), although 20–30% of this biomass was from dead stems (Kummerow et al. 1977). Biomass reported for *Q. berberidifolia* was lowest in a mature shrub at 1233 g/m^2 (Green 1970) and highest in a 23 yr old shrub at 2046 g/m^2 (Mooney et al. 1977). *C. cuneatus* had the lowest average total aboveground biomass as well as the smallest range of biomass values reported with 814 g/m^2 as the minimum reported biomass (Parsons and Stohlgren 1986) and 990 g/m^2 as the maximum reported biomass (Stohlgren et al. 1989). Of the species reported, *Q. berberidifolia* had slightly higher leaf biomass compared to *A. fasciculatum* (310 g/m^2 compared to 247 g/m^2), and *C. cuneatus* the least (47 g/m^2). *Q. berberidifolia* also had the highest stem biomass and litter biomass, although litter biomass at the species level was only available for *Q. berberidifolia* and *C. greggii* (Table 4).

Patterns of aboveground biomass with precipitation. The 36 plots we mapped ranged from coastal locations in Ventura County to higher elevation areas in the Angeles National Forest. It is these higher elevation areas where mean annual precipitation is also highest (Fig. 4). The correlation of mean aboveground biomass with mean annual precipitation showed a positive relationship with biomass increasing with greater mean precipitation ($R^2 = 0.23$, Fig. 5).

Belowground Biomass Estimates

Belowground biomass was by far the least reported metric in the literature. Only four studies reported belowground biomass values determined via direct measurements. Two were published in the late 1970's, one in the early 1980's and one in 2004, all in southern California. The most detailed studies were

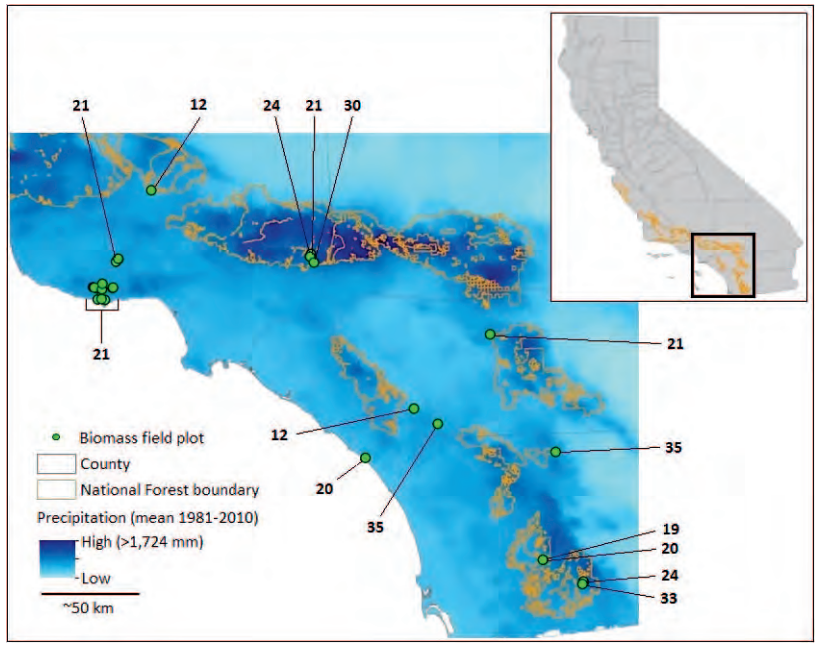

FIG. 4. Location of 36 field plots mapped with mean annual precipitation. Inset map shows enlarged area outlined in black. Numbered plot locations correspond to references listed in Appendix 1. Note: (a) a number of plots in the map overlap making them difficult to distinguish and (b) plots with multiple stand values were averaged where stands were >10 yr olds.

undertaken by Kummerow et al. (1977) and Miller and Ng (1977). In a 70 m^2 mixed chaparral stand dominated by *A. fasciculatum*, Kummerow et al. (1977) wired shrubs into place and hydraulically excavated the roots. Biomass as well as root:shoot ratios were determined for each individual shrub excavated and belowground biomass values ranged from about 1402 g/m^2 to 4789 g/m^2 for *A. fasciculatum*, 2028 g/m^2 for *Arctostaphylos pungens*, and 1442 g/m^2 for *Ceanothus greggii*. An average

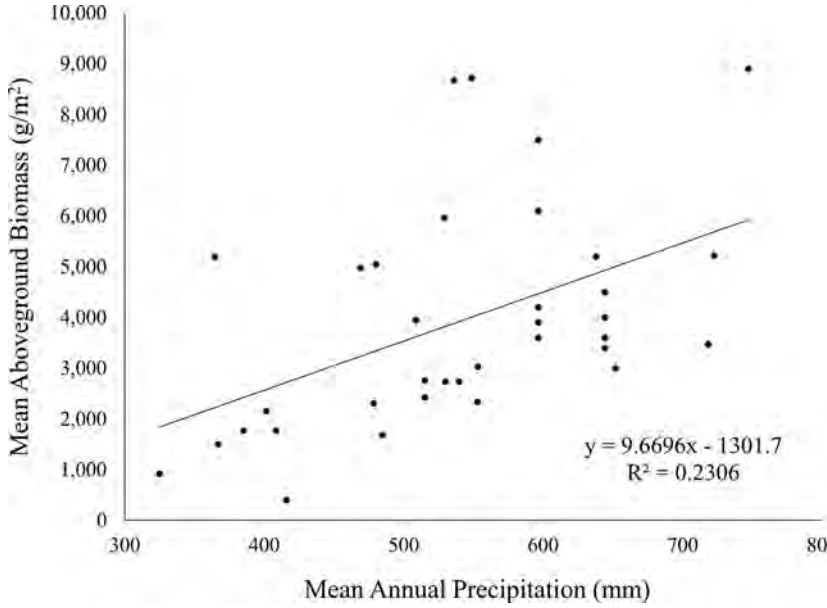

FIG. 5. Correlation between mean aboveground biomass and mean annual precipitation (1981–2010) for 36 field plots with precise coordinates.

overall root:shoot ratio of 0.6 was determined for all species included in the study. Species-specific root:-shoot ratios included 0.44 for an *Arctostaphylos pungens* individual and 0.7 for an *A. fasciculatum* individual (Kummerow et al. 1977). Similarly, Miller and Ng (1977) hydraulically excavated individual shrubs in a 21 yr old mixed chaparral stand. Biomass values reported were per shrub only, however, and varied greatly depending on shrub size. *A. fasciculatum* was the main shrub analyzed in the study (4 individuals total) and had a root:shoot ratio ranging from 0.49 to 0.69.

Lipson et al. (2004) undertook a study of the effects of long-term elevated atmospheric CO_2 on root growth among other variables in an 11 yr old *A. fasciculatum* dominated stand. Samples were collected for root biomass measurements using a 10 cm diameter metal soil coring device to a depth of 30 cm, and reported a root biomass of 250 m/g^2 in the control, which is likely an underestimate of the total belowground biomass due to sampling methods. Riggan and Lopez (1982) assessed nitrogen relations in a 35 yr old *Q. berberidifolia* dominated chaparral stand and report the pre-fire burl biomass of *Q. berberidifolia* as 1330 g/m^2 but did not assess the biomass of the entire root system.

There were also several studies that looked at root:shoot ratios of shrub seedlings (<12 months old) to assess nitrogen fertilization and allocation tradeoffs among life history traits, among other things. Padgett and Aleen (1999), for example, assessed biomass accumulation in coastal sage scrub species after growing for three months in pots and found that *Artemisia californica* root:shoot ratios range from 0.12 to 0.48 depending on the amount and type of nitrogen added. In a study comparing biomass allocation in shrubs exhibiting three different life history traits, Pratt et al. (2012) found that non-sprouting shrubs (e.g., *Ceanothus megacarpus*, *C. cuneatus*) had an average root:shoot ratio of 0.77 when grown in the sun and 0.44 when grown in the shade. Facultative sprouters (e.g., *C. spinosus*, *C. leucodermis*) had an average root:shoot ratio of 0.84 in the sun and 0.31 in the shade and lastly, obligate seeders (e.g., *Rhamnus ilicifolia, R. californica*) had an average root:shoot ratio of 1.7 in the sun and 0.89 in the shade (Pratt et al. 2012).

Discussion

Our review included 37 studies over 72 yrs from which we compiled summary estimates on total, live and dead biomass by age class, as well as information on leaf biomass, live and dead stem biomass, and belowground biomass from a subset of these studies. Key findings were that overall total aboveground biomass in the shrub communities reported was greatest in mixed chaparral (3461 g/m^2), followed by chamise chaparral (2114 g/m^2), and coastal sage scrub with a total aboveground biomass less than half that of mixed chaparral (1583 g/m^2). In each community total average aboveground biomass generally increased with the age of the stand. Other variables measured included leaf biomass, stem biomass and litter biomass which were also all highest in mixed chaparral compared to chamise chaparral or coastal sage scrub communities. By species, *C. greggii* had the highest average aboveground biomass (4877 g/m^2) and *C. cuneatus* had the least biomass with 881 g/m^2. *Q. berberidifolia* had the highest leaf, total stem, and litter biomass of the four species reported and *A. fasciculatum* had the highest belowground biomass of the two species where reporting was possible, with an average root:shoot ratio of 0.6.

Although we summarized available data on the annual net growth of shrubland communities and individual species, we did not include biomass estimates for annual flower and fruit production in our summaries due to the lack of information on this biomass component in the literature as well as the ephemeral nature of reproductive structures. Reproductive output, however, can be quite substantial, especially for non-sprouting shrub species (e.g., over 150 g/m^2 for *Arctostaphylos glauca*; Keeley and Keeley 1977). While this biomass does not remain as standing biomass on individual shrubs over time, it is likely accounted for indirectly through estimates of biomass present in the litter layer. Annual reproductive output is important to take into consideration but it may not be relevant when estimating long-term carbon storage.

This review provides a summary of biomass at the community and species level, however, levels of biomass vary considerably acoss the landscape, most notably with water availability and associated plant water stress during the summer drought (Mooney 1977a). Areas with higher annual precipitation and at higher elevations, e.g., mesic north-facing slopes, and slopes with deeper soils, have sustained high rates of production (Riggan and Dunn 1982). The example we provide using the 36 plots which had precise coordinates supports this point, and shows that mean aboveground biomass has a positive correlation with mean annual precipitation in southern California. Miller (1947) estimated that north facing slopes have roughly 30% more water available in the soil, and consequently chaparral communities on these aspects develop a larger leaf area and higher rates of production than those on south facing slopes (Krause and Kummerow 1977).

A noteable point from these summaries is the amount of dead aboveground biomass reported. Dead biomass accounts for approximately one-half the total biomass in coastal sage shrub, one-third in chamise chaparral, and one-fifth in mixed chaparral. The ratio of live to dead biomass in a stand is often related to the stand's fire history. Chaparral species typically have one of three life history strategies: obligate seeder, obligate resprouter, or faculative seeder. Of these three strategies, obligate resprouters and facultative seeders are capable of regenerating

vegetatively after fire (Keeley and Keeley 1988). Shrubs that resprout typically have belowground lignotubers, also called burls, that store carbohydrates and send out sprouts when burned. The biomass of these burls can make up a significant portion of the overall biomass of an individual shrub (Kummerow et al. 1977, Miller and Ng 1977). Additionally, recently burned stands tend to have a higher ratio of dead to live aboveground biomass due to the original stems not being fully consumed by the fire. Alternatively, during long fire-free periods, slow decomposition rates can lead to dead material accumulating in these stands and if fire has not entered into a stand for long enough, it is possible for more competitive, disturbance-free taxa to replace disturbance-dependant taxa, altering the type and amount of biomass in the system (Keeley and Keeley 1988, Hilbert and Larigauderie 1990).

Using simulation modeling, Hilbert and Larigauderie (1990) investigated the mechanisms behind stand senescence in Mediterranean-climate shrublands using available data in the literature. The authors developed two versions of a general model based on dynamics observed in pure stands of *Adenostoma fasciculatum*: one that accounts for individual shrub senescence (e.g., accelerated mortality of mature plants) and one that does not. According to the model results, live biomass and cover tends to peak at about 25–30 yr and litter biomass peaks at about 40 yr after fire, while standing dead biomass shows a slow increase over a 100 yr period. With the incorporation of shrub senescence in the model these trends were accelerated. The authors concluded that the two main factors leading to a decline in biomass and cover over time in shrubland stands are the absence of recruitment and the limit of individual shrub growth (Hilbert and Larigauderie 1990).

Studies varied in how biomass values were generated. The majority of studies utilized allometric equations to estimate biomass across a certain area. This method typically involves select whole shrub harvesting to create linear equations which are then used to calculate plot level biomass using stem diameter measurements. Very few of the studies included in this review carried out full plant harvests that included the root system. In general, the use of allometric equations and pre-determined root:shoot ratios appear to be the most popular methods for generating stand-level biomass. Species-level biomass studies, on the other hand, typically select several shrubs rather than a plot area, allowing a more thorough measurement of biomass for each individual. However, these studies are also extremely limited in the number extracting belowground biomass for direct measurements. Sample size and plot size varied widely in the identified literature, depending on the focus of a given study as well as the resources available to undertake it, sample size varied from n=1 to n=100 and the size of plots varied from 1 m^2 (Guo 2001) to 120 m^2 (Riggan et al. 1988). This is important to recognize as both the number of samples and the size of plots influence the amount of variation captured within a shrubland community. A larger plot (especially one that captures different slopes and aspects), for example, will likely capture openings within the shrubland as well as both live and dead shrubs, providing biomass values that are more representative across the landscape.

Of particular note in undertaking this review is the comparative lack of studies published in the last 10 yr. The majority of the field studies (60%) were carried out in the 1970's and 1980's, a time at which there was funding and great academic and practical interest in comparing the five Mediterranean-type climate regions of the world. For example, the United Nations Man and the Biosphere Programme (MAB) was launched in the early 1970's as an intergovernmental scientific program aiming to promote planning and implementation of research and training programs (http://www.unesco.org/new/en/natural-sciences/environment/ecological-sciences/man-and-biosphere-programme/). As part of this program, in 1976 the San Dimas Experimental Forest (designated in 1933) in the San Gabriel Mountains of southern California was established as a biosphere reserve, which resulted in numerous experimental studies in chaparral landscapes. In the 1970s the US also joined the International Biological Program (IBP) which focused on documenting the productive capacity of different regions of the world. More specifically, as part of the IBP, a Convergent Evolution program was created to compare the productive structure of vegetation that evolved to meet the challenges of dry summer climates, for example between California and Chile (Mooney and Dunn 1970, Mooney 1977b). Additionally, the relative lack of more recent field studies, especially those that assess belowground biomass, may be due to a shifting focus towards using remote sensing tools to estimate biomass at much larger scales. These studies typically rely on previously established field-based biomass estimates and are often focused on making repeatable regional biomass estimates, often disregarding the importance of belowground biomass (e.g., Schmidt et al. 2016, Uyeda et al. 2017). While it is important to continue developing the most accurate and efficient methods for determining biomass at a landscape level, further work quantifying belowground biomass would strengthen our understanding of biomass accumulation in shrublands.

In this review, by parsing out biomass at the stand and species level and reporting on above- and belowground biomass, live and dead biomass, and leaf, litter and stem biomass, we provide a valuable resource for land managers and conservation practitioners who need estimates of shrubland biomass at different life stages. Understanding these biomass values is foundational information for mapping biomass and monitoring changes,and ultimately quantifying carbon storage ecosystem services (it is generally assumed that carbon makes up 45–50% of

plant biomass; Kort and Turnock 2003, Schlesinger and Bernhardt 2013).

While much attention has focused on the role of forested landscapes as a sink of atmospheric CO_2, the contribution of Mediterranean climate shrublands to the global carbon cycle has received little attention (Evrendilek et al. 2006). Despite shrublands historically being considered overmature after reaching 60 yrs of age (Hanes 1971), shrublands over 100 yrs old have been reported as vigorous (Keeley 1992). Indeed, Luo et al. (2007) recorded a 100 yr old chamise-dominated chaparral stand to be a significant carbon sink (-155 g $C/m^2/yr$). In another study of Mediterranean climate shrublands in Italy, shrublands were reported to remove significant quantities of C from the atmosphere (2200 g $C/m^2/yr$; Gratani et al. 2013). Future changes in climate are likely to impact the capability of shrublands to store and sequester carbon, however there is considerable uncertainty surrounding this. For example, some studies predict that changes in temperature and precipitation may decrease the area of shrublands in the North American Mediterranean Climate Zone owing to expansion of grasslands (Hayhoe et al. 2004) while other studies predict an increase as shrublands encroach into areas currently dominated by conifers in California (Lenihan et al. 2008). In addition, climate changes may lead to variations of shrubland structure and productivity (Haase et al. 2000) and conseqently effect carbon sequestration and storage capabilities (Evrendilek et al. 2006). Luo et al. (2007), for example, recorded that after a period of severe drought the ability of the chaparral stand to sequester carbon was limited. Through increasing our knowledge surrounding biomass accumulation and associated carbon sequestration in shrublands, land managers will be better able to understand the potential for these stands to sequester carbon in the future and also provide the information necessary for embarking on Payment for Ecosystem Services schemes for carbon.

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APPENDIX 2. REPORTED ABOVEGROUND BIOMASS VALUES ORGANIZED BY COMMUNITY TYPE, GENERAL LOCATION, AND AGE OF STAND. Studies that did not report on total, live or dead aboveground biomass are excluded from this table. When a study provided multiple biomass values for the same age and location, we report the average of those values. [a]General locations are based on descriptions provided in the reference text, for more detailed information please refer to the original source; [b]References are listed in Appendix 1.

Community type	General location[a]	Age (yrs)	Aboveground biomass (g/m^2)			Reference[b]
			Total	Live	Dead	
Mixed chaparral	Los Padres NF	5	–	2055	–	28
Mixed chaparral	Los Padres NF	12	–	3232	–	28
Mixed chaparral	Los Padres NF	21	6337	4871	1466	28
Mixed chaparral	Los Padres NF	25	3039	2012	1028	4
Mixed chaparral	San Dimas Experimental Forest, Angeles NF	6	1430	1330	100	24
Mixed chaparral	San Dimas Experimental Forest, Angeles NF	11	2817	2638	179	34
Mixed chaparral	San Dimas Experimental Forest, Angeles NF	21	5575	4838	743	24
Mixed chaparral	Angeles NF	33	8900	6008	2892	21
Mixed chaparral	Sky Oaks Biological Field Sta., San Diego Co.	1	–	200	–	35
Mixed chaparral	Sky Oaks Biological Field Sta., San Diego Co.	2	–	475	–	35
Mixed chaparral	Sky Oaks Biological Field Sta., San Diego Co.	3	–	660	–	35
Mixed chaparral	Sky Oaks Biological Field Sta., San Diego Co.	4	–	600	–	35
Mixed chaparral	Sky Oaks Biological Field Sta., San Diego Co.	5	–	500	–	35
Mixed chaparral	Sky Oaks Biological Field Sta., San Diego Co.	6	–	560	–	35
Mixed chaparral	Sky Oaks Biological Field Sta., San Diego Co.	7	–	700	–	35
Mixed chaparral	Sky Oaks Biological Field Sta., San Diego Co.	8	–	800	–	35
Mixed chaparral	Sky Oaks Biological Field Sta., San Diego Co.	54	3005	–	–	17
Mixed chaparral	Sky Oaks Biological Field Sta., San Diego Co.	85	3085	–	–	17
Mixed chaparral	Cleveland NF; Sky Oaks Biological Sta.; West of Anza-Borrego Desert	4	1500	800	700	1
Mixed chaparral	Cleveland NF; Sky Oaks Biological Sta.; West of Anza-Borrego Desert	11	2600	2400	200	1
Mixed chaparral	Cleveland NF; Sky Oaks Biological Sta.; West of Anza-Borrego Desert	54	5000	3700	1300	1
Mixed chaparral	Cleveland NF; Sky Oaks Biological Sta.; West of Anza-Borrego Desert	80	4500	3500	1000	1
Mixed chaparral	Cleveland NF; Sky Oaks Biological Sta.; West of Anza-Borrego Desert	85	4500	3700	800	1
Mixed chaparral	Descanso Ranger District, Cleveland NF	2	1813	–	–	36
Mixed chaparral	Descanso Ranger District, Cleveland NF	3	199	–	–	36
Mixed chaparral	Descanso Ranger District, Cleveland NF	5	540	–	–	36
Mixed chaparral	Descanso Ranger District, Cleveland NF	10	1489	–	–	36
Mixed chaparral	Descanso Ranger District, Cleveland NF	11	411	–	–	36
Mixed chaparral	Descanso Ranger District, Cleveland NF	13	1639	–	–	36
Mixed chaparral	Descanso Ranger District, Cleveland NF	18	1839	–	–	36
Mixed chaparral	Descanso Ranger District, Cleveland NF	20	1418	–	–	36
Mixed chaparral	Descanso Ranger District, Cleveland NF	22	2813	–	–	36
Mixed chaparral	Kitchen Creek, Cleveland NF	1	–	280	–	24
Mixed chaparral	Kitchen Creek, Cleveland NF	7	1320	–	–	33
Mixed chaparral	Kitchen Creek, Cleveland NF	28	4140	–	–	33
Mixed chaparral	Kitchen Creek, Cleveland NF	35	–	2325	–	25
Mixed chaparral	Kitchen Creek, Cleveland NF	35	3000	3000	0	24
Mixed chaparral	Kitchen Creek, Cleveland NF	68	5060	–	–	33
Mixed chaparral	Camp Pendleton, San Diego Co.	–	6236	3853	890	2
Mixed chaparral	Camp Pendleton, San Diego Co.	–	9774	–	–	3
Mixed chaparral	Camp Pendleton, San Diego Co.	"mature"	9000	4500	4500	6
Mixed chaparral	Puerta La Cruz Rd, Warner Springs, San Diego Co.	4	840	–	–	17
Mixed chaparral	Puerta La Cruz Rd, Warner Springs, San Diego Co.	11	1873	–	–	17
Mixed chaparral	Puerta La Cruz Rd, Warner Springs, San Diego Co.	54	2535	–	–	17
Mixed chaparral	Puerta La Cruz Rd, Warner Springs, San Diego Co.	80	3500	–	–	17
Mixed chaparral	Echo Valley International Biological Program	23	2308	–	–	20
Mixed chaparral	Leo Carrillo State Park, Santa Monica Mountains, Los Angeles Co.	22	7705	6482	1223	7
Mixed chaparral	Stunt Ranch Santa Monica Mountains UC Reserve, Los Angeles Co.	1	130	–	–	11
Mixed chaparral	Stunt Ranch Santa Monica Mountains UC Reserve, Los Angeles Co.	2	410	–	–	11

APPENDIX 2. CONTINUED

Community type	General location[a]	Age (yrs)	Aboveground biomass (g/m^2)			Reference[b]
			Total	Live	Dead	
Mixed chaparral	Stunt Ranch Santa Monica Mountains UC Reserve, Los Angeles Co.	3	590	–	–	11
Mixed chaparral	Stunt Ranch Santa Monica Mountains UC Reserve, Los Angeles Co.	4	855	–	–	11
Mixed chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	14	5010	3945	1065	21
Mixed chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	17	8730	7420	1310	5
Mixed chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	17	8698	7420	1255	21
Mixed chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	18	5920	4840	1080	5
Mixed chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	18	5963	4864	1098	21
Mixed chaparral	North Mountain Experimental Area, Riverside Co.	"mature"	7846	6165	1681	9
Mixed chaparral	Bear Creek, Riverside Co.	30-50	5201	4775	426	12
Mixed chaparral	Sequoia National Park, Tulare Co.	3	540	–	–	32
Mixed chaparral	Sequoia National Park, Tulare Co.	15	3020	–	–	32
Mixed chaparral	Sequoia National Park, Tulare Co.	24	3165	–	–	22
Mixed chaparral	Southern California	14	4900	–	–	23
Mixed chaparral	Southern California	19	7300	–	–	23
Mixed chaparral	Southern California	33	8200	–	–	23
Mixed chaparral	Southern California	50	5100	–	–	23
Mixed chaparral	Southern California	55	11800	–	–	23
Mixed chaparral	Mendocino Co.; Lake Co.; Shasta Co.	1	127	–	–	27
Mixed chaparral	Mendocino Co.; Lake Co.; Shasta Co.	2	204	–	–	27
Mixed chaparral	Mendocino Co.; Lake Co.; Shasta Co.	3	433	–	–	27
Mixed chaparral	Mendocino Co.; Lake Co.; Shasta Co.	4	629	–	–	27
Mixed chaparral	Mendocino Co.; Lake Co.; Shasta Co.	5	1011	–	–	27
Mixed chaparral	Mendocino Co.; Lake Co.; Shasta Co.	6	1088	–	–	27
Mixed chaparral	Mendocino Co.; Lake Co.; Shasta Co.	7	1134	–	–	27
Mixed chaparral	Mendocino Co.; Lake Co.; Shasta Co.	8	1186	–	–	27
Mixed chaparral	Mendocino Co.; Lake Co.; Shasta Co.	"Old stand"	3100	–	–	27
Chamise chaparral	San Dimas Experimental Forest, Angeles NF	1	273	115	158	30
Chamise chaparral	San Dimas Experimental Forest, Angeles NF	3	1087	521	566	30
Chamise chaparral	San Dimas Experimental Forest, Angeles NF	9	–	863	–	30
Chamise chaparral	San Dimas Experimental Forest, Angeles NF	18	2039	1659	380	30
Chamise chaparral	San Dimas Experimental Forest, Angeles NF	37	4909	2726	2184	30
Chamise chaparral	Sky Oaks Biological Field Sta., San Diego Co.	"pre-fire"	–	1686	–	35
Chamise chaparral	Cleveland NF; Sky Oaks Biological Sta.; West of Anza-Borrego Desert	4	1300	800	500	1
Chamise chaparral	Cleveland NF; Sky Oaks Biological Sta.; West of Anza-Borrego Desert	11	1440	1400	40	1
Chamise chaparral	Cleveland NF; Sky Oaks Biological Sta.; West of Anza-Borrego Desert	54	2050	1800	250	1
Chamise chaparral	Cleveland NF; Sky Oaks Biological Sta.; West of Anza-Borrego Desert	80	1600	1400	200	1
Chamise chaparral	Cleveland NF; Sky Oaks Biological Sta.; West of Anza-Borrego Desert	85	3400	2500	900	1
Chamise chaparral	Camp Pendleton, San Diego Co.	–	2843	1189	1015	2
Chamise chaparral	Camp Pendleton, San Diego Co.	–	3755	–	–	3
Chamise chaparral	Puerta La Cruz Rd, Warner Springs, San Diego Co.	4	770	–	–	17
Chamise chaparral	Puerta La Cruz Rd, Warner Springs, San Diego Co.	80	1510	–	–	17
Chamise chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	13	2805	2085	720	5
Chamise chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	13	2679	2074	605	21
Chamise chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	14	2309	1547	762	21
Chamise chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	17	3050	2170	880	5

APPENDIX 2. CONTINUED

Community type	General location[a]	Age (yrs)	Aboveground biomass (g/m^2)			Reference[b]
			Total	Live	Dead	
Chamise chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	17	2735	2197	538	21
Chamise chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	40	2760	2220	540	5
Chamise chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	40	2735	2219	516	21
Chamise chaparral	Newhall, Los Angeles Co.	35-50	1771	1569	202	12
Chamise chaparral	San Bernardino NF	55	3945	3049	897	21
Chamise chaparral	Santa Rosa Plateau Preserve, Riverside Co.	10	1636	1054	583	12
Chamise chaparral	Sequoia National Park, Tulare Co.	>60	3066	–	–	31
Chamise chaparral	Southern California	10	1600	–	–	23
Chamise chaparral	Southern California	14	2300	–	–	23
Chamise chaparral	Southern California	19	2800	–	–	23
Chamise chaparral	Southern California	50	1700	–	–	23
Chamise chaparral	Southern California	55	4000	–	–	23
Chamise chaparral	Mendocino Co.; Lake Co.; Shasta Co.	1	175	–	–	27
Chamise chaparral	Mendocino Co.; Lake Co.; Shasta Co.	2	309	–	–	27
Chamise chaparral	Mendocino Co.; Lake Co.; Shasta Co.	3	465	–	–	27
Chamise chaparral	Mendocino Co.; Lake Co.; Shasta Co.	4	740	–	–	27
Chamise chaparral	Mendocino Co.; Lake Co.; Shasta Co.	5	1000	–	–	27
Chamise chaparral	Mendocino Co.; Lake Co.; Shasta Co.	6	1130	–	–	27
Chamise chaparral	Mendocino Co.; Lake Co.; Shasta Co.	7	1215	–	–	27
Chamise chaparral	Mendocino Co.; Lake Co.; Shasta Co.	8	1276	–	–	27
Coastal sage scrub	Camp Pendleton, San Diego Co.	–	2869	661	773	2
Coastal sage scrub	Camp Pendleton, San Diego Co.	–	2959	–	–	3
Coastal sage scrub	Santa Margarita Ecological Reserve, San Diego Co.	1	–	575	–	35
Coastal sage scrub	Santa Margarita Ecological Reserve, San Diego Co.	2	–	395	–	35
Coastal sage scrub	Santa Margarita Ecological Reserve, San Diego Co.	3	–	630	–	35
Coastal sage scrub	Santa Margarita Ecological Reserve, San Diego Co.	4	–	520	–	35
Coastal sage scrub	Santa Margarita Ecological Reserve, San Diego Co.	5	–	200	–	35
Coastal sage scrub	Santa Margarita Ecological Reserve, San Diego Co.	6	–	210	–	35
Coastal sage scrub	Santa Margarita Ecological Reserve, San Diego Co.	7	–	325	–	35
Coastal sage scrub	Santa Margarita Ecological Reserve, San Diego Co.	8	–	420	–	35
Coastal sage scrub	Santa Margarita Ecological Reserve, San Diego Co.	35	–	400	–	35
Coastal sage scrub	Santa Monica Mountains National Recreation Area, Los Angeles Co.	14	1750	1170	580	5
Coastal sage scrub	Santa Monica Mountains National Recreation Area, Los Angeles Co.	14	1771	1188	583	21
Coastal sage scrub	Santa Monica Mountains National Recreation Area, Los Angeles Co.	18	2152	1300	852	21
Coastal sage scrub	Santa Monica Mountains National Recreation Area, Los Angeles Co.	30	1502	986	516	21
Coastal sage scrub	Santa Monica Mountains, Los Angeles Co.	1	598	–	–	14
Coastal sage scrub	Leo Carrillo State Park, Santa Monica Mountains	22	1172	925	247	7
Coastal sage scrub	Leo Carrillo State Park, Santa Monica Mountains	22	1418	–	–	8
Coastal sage scrub	Robert J. Bernard Biological Field Sta., Los Angeles Co.	40	2725	–	–	37

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RESEARCH ARTICLE

An objective road risk assessment method for multiple species: ranking 166 reptiles and amphibians in California

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Abstract
Context Transportation and wildlife agencies may consider the need for barrier structures and safe wildlife road-crossings to maintain the long-term viability of wildlife populations. In order to prioritize these efforts, it is important to identify species that are most at risk of extirpation from road-related impacts.
Purpose Our goal was to identify reptiles and amphibians in California most susceptible to road mortality and fragmentation. With over 160 species and a lack of species-specific research data, we developed an objective risk assessment method based upon road ecology science.
Methods Risk scoring was based upon a suite of life history and space-use characteristics associated with negative road effects applied in a hierarchical manner from individuals to species. We evaluated risk to both aquatic and terrestrial connectivity and calculated buffer distances to encompass 95% of population-level movements. We ranked species into five relative categories of road-related risk (very-high to very-low) based upon 20% increments of all species scores.
Results All chelonids, 72% of snakes, 50% of anurans, 18% of lizards and 17% of salamander species in California were ranked at high or very-high risk from negative road impacts. Results were largely consistent with local and global scientific literature in identifying high risk species and groups.
Conclusions This comparative risk assessment method provides a science-based framework to identify species most susceptible to negative road impacts. The results can inform regional-scale road mitigation planning and prioritization efforts and threat assessments for special-status species. We believe this approach is applicable to numerous landscapes and taxonomic groups.

Keywords Reptile · Amphibian · Road mortality · Habitat fragmentation · Road ecology · Risk assessment · Road

Introduction

There have been many attempts to better characterize and quantify threat criteria in order to classify species at higher risk of extinction at state, national, and global levels (Congress 1973 (U.S. Endangered Species Act); Mace et al. 2008; Hobday et al. 2011; Thomson et al. 2016; IUCN 2017). Roads are a significant threat to wildlife populations (e.g., Forman et al. 2003;

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Andrews et al. 2015a; van der Ree et al. 2015), causing both barrier (habitat fragmentation) and depletion (road mortality) effects. Barrier effects occur when animals avoid crossing roads, in which case roads essentially fragment species habitat. Barrier effects include reduced size and quality of available habitat, reduced effective population size, reduced ability to find mates and resources, increased genetic structuring, and increased probability of local extirpation (e.g., Forman et al. 2003; Fahrig and Rytwinski 2009; D'Amico et al. 2016). Depletion effects occur when animals attempt to cross roads and are killed by vehicles. Depletion effects include all of the risks from barrier effects as well as reduced survivorship, making high road mortality an even greater concern (Jackson and Fahrig 2011). Among other stressors, such as habitat loss and fragmentation, invasive species, pesticide use, changing climate, and disease, the negative impacts from roads may independently or cumulatively threaten the persistence of populations and even species.

Amphibians and reptiles have been identified as being particularly susceptible to the negative effects of roads within their habitat (e.g., Klauber 1931; Forman et al. 2003; Rytwinski and Fahrig 2012; Andrews et al. 2015a, b; D'Amico et al. 2015). Many are slow moving, do not avoid roads, and are simply too small for drivers to see and avoid. During rains many amphibians make long linear terrestrial movements regardless of the presence of intersecting roadways (Glista et al. 2008), and because paved roads typically absorb and retain more heat than the surrounding habitat, snakes and lizards are often attracted to roads for thermoregulation (Case and Fisher 2001; Jochimsen et al. 2004). In fact, road surveys are one of the most common methods for surveying these reptiles (e.g., Sullivan 2012). Many herpetofauna species utilize both aquatic and terrestrial habitat for breeding, development, foraging, and overwintering and therefore require connectivity within and between both aquatic and terrestrial habitats to support basic life history requirements.

The primary goal of this study was to provide information to transportation and other planning agencies in California to assist them in prioritizing road mitigation efforts for amphibian and reptile species. Although there is still a lot to learn about the effectiveness of different designs of road mitigation systems, the use of barrier systems, underpasses, and overpasses can reduce road mortality and help to maintain connectivity and safe passage across roads for herpetofauna and other wildlife (Jochimsen et al. 2004; Colino-Rabanal and Lizana 2012; Langton 2015; Langen et al. 2015b). Because it is currently unrealistic and cost prohibitive to mitigate all roadways for all species, it is vital to identify species most susceptible to road-related impacts. Within species ranges, risks to populations and need for mitigation can then be evaluated based upon local road densities and matrix, road-types, traffic, and road locations in relation to species habitat and movement corridors (e.g., Jaeger 2000; Litvaitis and Tash 2008; Langen et al. 2015b; Zimmermann Teixeira et al. 2017).

Here we describe a road risk assessment methodology applied to native amphibian and reptile species in California, a global biodiversity hotspot (Myers et al. 2000). We also included analysis of subspecies if they had special federal or state protection status. This includes 166 species and subspecies of frogs, toads, salamanders, snakes, lizards, turtles, and tortoise. Rankings and prioritizations such as these can be very subjective. In order to avoid including low risk species that may be favored by the assessors or to unintentionally overlook species that are at high risk, it was important for this be done in an objective manner informed by current road ecology literature.

Very few quantitative data are available on the impact of roads on population persistence. Jaeger et al. (2005) were the first to develop a relative ranking system to compare the impact of roads on wildlife populations. Their ranking system was largely based upon behavioral responses of animal species to the road surface, road size, traffic noise, and vehicles with varying road sizes and traffic volumes. However, knowledge of these detailed behavioral responses to ranges in road and traffic characteristics is rarely found in literature and the link between individual behavior and population-level effects has not been clearly established (Rytwinski and Fahrig 2012, 2013).

Rytwinski and Fahrig (2012) performed a meta-analysis of wildlife groups to test whether certain life history characteristics were related to negative responses to roads. High reproductive rate (fecundity) was negatively associated with the magnitude of population-level effects for amphibians. No associations were significant in reptiles, although there were

few studies to inform this analysis. However, a strong link was shown between body size, greater mobility, lower reproductive rates and the magnitude of negative road effects in mammals, the most studied wildlife group. Conversely, simulations predicted populations of species with small home ranges and high reproductive rates were the least likely to be affected by roads (Rytwinski and Fahrig 2013).

We used these findings as a basis for creating a multi-tiered system to rank and identify reptile and amphibian species that may be most susceptible to road impacts. We based our ranking upon a suite of species life history and space-use characteristics associated with negative road effects, as well as including species distribution and conservation status. We evaluated risk to both aquatic and terrestrial connectivity and include buffer distances that were calculated to encompass 95% of population movements. Relative confidence in these distances is given for each species based upon the amount of support from scientific studies. We solely focused on the direct effects of roads as barriers and sources of road mortality and not impacts from road construction and maintenance or indirect effects from increased human use of the landscape once a road is in place (see review by Langen et al. 2015a).

Because we based the risk assessment solely upon space-use and life history characteristics, this represents a species relative susceptibility to road impacts. It is understood that circumstances associated with particular populations (e.g., local road types, locations, densities) may elevate or reduce the risk for certain populations and species.

Methods

Road risk assessment (overview)

We assessed the relative risk of California herpetofauna species to negative road-related impacts at three scales in a hierarchical fashion. We first assessed risk at the scale of an individual animal and then expanded the risk to the population and then to species (Fig. 1).

At the individual-level, we based road risk primarily upon the likelihood that an individual would encounter one or more roads. We considered this a product of movement distance (home range, seasonal migrations) and movement frequency (e.g., active foragers, seasonal migrants, sit-and-wait predators vs. sedentary species) (e.g., Bonnet et al. 1999; Carr and Fahrig 2001). Because many species are semi-aquatic, movement distance and frequency were scored separately for both aquatic and terrestrial habitats.

There is a theorized higher risk associated with depletion effects (i.e., road mortality) in comparison to barrier effects (Fahrig and Rytwinski 2009; Jackson and Fahrig 2011). Therefore, we gave additional weight to those species more likely to go out onto a road surface and be killed by vehicular traffic. For this we considered factors of habitat preference (e.g., open vs. closed), roads as potential attractants (e.g., for basking), and movement speed (e.g., slow vs. fast). However, individuals within and among species may respond differently to roads (attraction vs. avoidance) based upon local landscape features, road width, traffic volume, and perceived danger (Forman et al. 2003; Andrews 2005; Brehme et al. 2013; Jacobson et al. 2016). Because a state-wide analysis encompasses extreme variation in landscape and road characteristics, the extent to which roads act as barriers or sources of direct mortality within a species range is unknown. The risk disparity between depletion and barrier effects could also be highly variable. Therefore, we limited the additional weight for potential depletion effects to twenty percent of the individual risk score.

We assessed population-level road risk by multiplying individual risk with scores representing: (1) the relative proportion of the population at risk; and (2) the species ability to sustain higher rates of mortality. For instance, the proportion of the population at risk was expected to be higher for migratory species than for territorial species. Highly fecund species were expected to better withstand (or more quickly recover from) higher mortality in comparison to those with few annual offspring.

Finally, we assessed species-level road risk by multiplying population road risk with scores for range size (both within and outside of California) and conservation status according to the U.S. Fish and Wildlife Service (USFWS 2016) and the California Department of Fish and Wildlife (CDFW 2016a; Thomson et al. 2016). Species with smaller ranges typically have fewer populations and are thus less resilient to population-level stressors. Endangered, threatened, and special concern species have already been designated at risk of extirpation, often due to

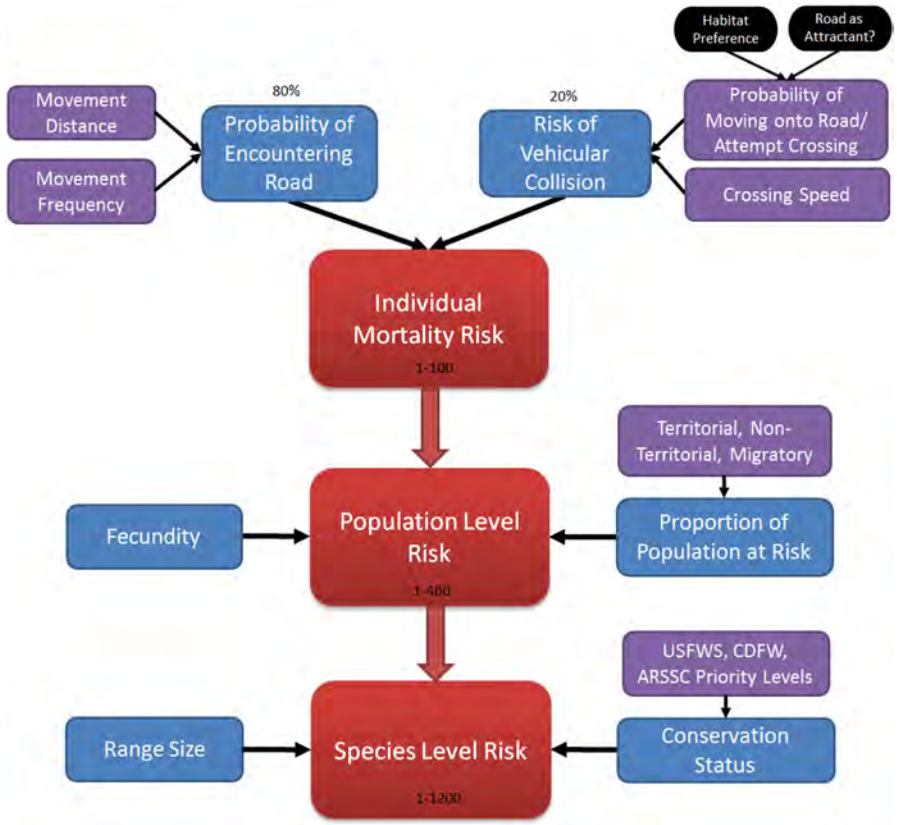

Fig. 1 California reptile and amphibian road risk assessment conceptual model (*ARSSC* Amphibian and Reptile Species of Special Concern (Thomson et al. 2016))

multiple stressors, and are thus thought to be less likely to be resilient to additional road impacts.

Although we present both aquatic and terrestrial risk scores for semi-aquatic species, we used the higher of the two scores for the overall risk ranking.

Literature review

Species life history data were primarily taken from and cross-checked among the following species account review sources;

1. U.S. Fish and Wildlife Service (USFWS) Recovery Plans and 5-year Reviews https://www.fws.gov/endangered/.
2. California Amphibian and Reptile Species of Special Concern (ARSSC; Thomson et al. 2016).
3. A Field Guide to Amphibians and Reptiles of California (Stebbins and McGinnis 2012)
4. Amphibian declines: the conservation status of United States species (Lannoo 2005).
5. Conservation Status of Amphibians and Reptiles on USDA National Forests, Pacific Southwest Region, 2012 (Evelyn and Sweet 2012).
6. Natureserve Explorer (natureserve.org): Species Accounts largely authored by G. Hammerson (2003–2016).

When these reviews were lacking life history information needed for the road risk assessment, we then searched for supplementary peer-reviewed literature using the Google Scholar search engine. Because movement distances (terrestrial, aquatic, home range, migratory) were so important for the risk assessment, we acquired referenced articles from the species accounts and independently searched the literature to acquire these data. Search terms included the species common name, scientific name, or genus and terms such as “movement”, “home-range”, “spatial”, and “telemetry”. We also reviewed articles for citations of other studies to find more recent information on movement. This literature included published articles,

book chapters, M.S. Theses, Ph.D. dissertations, agency reports, and consultant reports. In the case that specific life history or movement information was not found for a species, we chose a surrogate species based upon phylogeny, habitat, and body size. We first looked for the closest related species within the genus or family and chose a closely related surrogate based upon similar habitat and body size. If surrogates were used, these are clearly reported.

Road risk metrics

The following section describes in detail the rank scoring used for Individual-level Road Risk, Population-level Road Risk, and Species-level Road Risk. All rank values are meant to represent the relative contribution of each attribute to either additive or multiplicative road risk.

Individual-level risk (100 points possible)

Out of a total of 100 points for individual road mortality risk, we attributed up to 80 points (80%) to the risk of encountering a road and up to 20 points (20%) for the risk of an individual moving onto a road and being killed by a motor vehicle.

The risk of encountering a road was based on a combination of movement distance and general movement frequency. Movement distance was ranked 1–40 based upon home range movement distances (diameter) for non-migrants or migration distances for seasonal migrants that spanned from 0 to > 1200 m (Table 1). The scores are linearly correlated with increasing movement distance.

For species that use both terrestrial and wetland/stream/riverine habitats, such as frogs, toads, aquatic snakes and turtles, we scored aquatic and terrestrial movement distances and frequencies separately. This was necessary as some species move much larger distances and at different frequencies in one habitat versus the other. This also informs the type(s) of mitigation structures that may be warranted based upon habitat type, buffer distances and risk scores for each species. Aquatic movement distances were not calculated for pond-breeding amphibians. Ponds are typically small ephemeral bodies of water and terrestrial movements of amphibians to and among ponds account for the majority of movement for these species.

Table 1 Individual-level Road Risk (IRR): Score criteria for risk of individuals encountering a road

Risk of individuals encountering a road = Movement distance × frequency			
Movement distance (m)	Score	Frequency	Score
> 1200	40	Active throughout home range	2
901–1200	32	Migratory (2–4 × per year)/ non-migratory sit and wait foragers	1.5
601–900	24	Sedentary, confined to specialized habitat	1
451–600	16		
301–450	12		
201–300	8		
101–200	5		
51–100	3		
0–50	1		

The calculations and rankings for movement distances were well considered and deserve further explanation. Our original thinking was that maximum distances should reflect relative movement distances across species and these data were commonly reported in species accounts. However, it became increasingly difficult to determine whether maximum distances reported were seasonal migration movements, home range movements or rarer dispersal events. We believed this assessment should reflect annual movement distances and not rare dispersal events. We considered using average/median movement distances; however, these often underestimate the movement of seasonal migrants because in many cases a sizeable portion of the population may remain close to a breeding site, while another sizable portion make longer distance migrations causing an average or median to be uninformative. Therefore, we decided to use a buffer distance that incorporates the movement distances of 95% of the population studied. A 95% population movement distance is commonly accepted for the delineation of terrestrial buffer zones for amphibians (i.e., Semlitsch 1998; Semlitsch and Bodie 2003) and we believe it was the most biologically

meaningful and useful measure for this study. This measure, which we will refer to as Maximum Population Movement Distance (MPMD), should include almost all population movements, such as seasonal migration distances and annual home ranges (diameter), but not rare dispersal events. The MPMD should also be useful for local risk assessments as these distances can be used to aide in mapping and mitigation decisions.

The calculation we used for MPMD is commonly known as the 95% upper tolerance interval (Vangel 2015). A tolerance interval is an interval that is meant to contain a specified percentage of individual population measurements. This should not be confused with a confidence interval, which is an interval that is meant to contain the population mean. We chose a 50% confidence level for the upper 95% confidence limit of movement distances which is equal to the 95% prediction interval for future observations and is the mean + 1.645 × standard deviation. In cases where a standard deviation was not reported, we back calculated standard deviation from the standard error and sample size, calculated it from the individual data, or estimated it based on the methods recommended by Hozo et al. (2005). Although non-parametric tolerance intervals would be more appropriate for non-normally distributed movement data, the data required to calculate these is rarely reported in the published literature. In the case of non-normally distributed data where medians, sample sizes and ranges are reported, Hozo et al. (2005) methods allow for approximation of means and standard deviations with no assumption of the underlying data distribution. We found the resulting MPMDs to be reasonable in excluding large outliers but including multiple long distance movements below the maximum movement distance.

We recognize that for any species there can be substantial variability in movement distances that depend upon varying local, landscape, and climatic factors. This was often reflected in studies with sometimes widely varying estimates of home range and migration distances. We attempted to be conservative by using the study data for calculation of MPMD in which the largest population movement distances were observed. For studies where movement distance significantly varied between females and males, we used the information from the wider ranging sex. For migratory distances, we did not use distances from extreme environments, such as Canada, where suitable overwintering sites are typically much farther away from breeding and summer activity areas than in milder California climates (e.g., Gregory 1984). We did use study data from adjacent states or lower estimates of migration distances from those reported in Midwestern states. In some cases where little information was available, we made an educated guess based upon limited study data and/or closely related species and noted these in the tables. For all MPMDs, we report a relative confidence level based upon the number and quality of studies, sample sizes, and locations in or adjacent to California. It is intended that the scores be adjusted as new information becomes available.

To compute the risk of encountering a road, the MPMD was multiplied by a relative index of the expected frequency of longer distance movements (1–2 points; Table 1). We defined three frequency categories largely based upon annual migratory movements or foraging strategies for non-migratory species. The highest category included actively foraging predators which are characterized by frequent wandering movements throughout their home range (Pianka 1966). Less frequent movers included seasonal migrants traveling among breeding, summer foraging, and/or overwintering sites and non-migratory 'sit-and-wait' predators that remain still for long periods of time to ambush prey (Pianka 1966). Finally, low frequency included highly sedentary species with high site fidelity, particularly specialized rock, crevice, soil, or tree dwellers that may rarely traverse terrestrial or aquatic habitats.

The risk of an individual moving onto a road and being killed by a moving vehicle was ranked by attributes of habitat preference, road use, and movement speed (Table 2). Habitat preference represents the degree to which an individual is expected to go out onto or avoid an open road as predicted from their habitat and microhabitat preferences. Open habitat specialists and generalists were expected to more readily move onto a road than species that prefer cover (e.g., Forman et al. 2003; Brehme et al. 2013). Although many amphibians are closed habitat specialists, most readily move through open habitats during rain events, when most overland migratory movements tend to occur (Glista et al. 2008). Therefore, amphibians were considered open habitat specialists for this ranking. An additional factor that may increase road use is for thermoregulation for lizards

Table 2 Individual-level Road Risk (IRR): Score criteria for risk of road mortality

Risk of road mortality = Habitat preference + road use + movement speed					
Habitat preference	Score	Road use	Score	Movement speed	Score
Open habitat specialist/amphibians	10	Thermoregulation (snakes/lizards)	4	Slow (< 0.6 m/s)	6
Generalist	8	Other	0	Medium (0.6–2.0 m/s)	3
Edge specialist	4			Fast (> 2.0 m/s)	0
Closed habitat or aquatic specialist	0				

Table 3 Population-level Road Risk (PRR): Score criteria for population level road risk

PRR = IRR × (Fecundity + Proportion of population at risk)				
Fecundity	Ave. potential offspring/year	Score	Proportion of population at risk	Score
Low	0–10	2	Seasonal migrants (Migratory)	2
Med	11–25	1.5	Wandering	1.5
High	26–100	1	Territorial	1
Very high	> 100	0		

and snakes, as roads often retain more heat than the surrounding environment (Colino-Rabanal and Lizana 2012; Mccardle and Fontenot 2016). Finally, there is an increased risk of road mortality for slow versus fast moving species (see Andrews and Gibbons 2005; Mazerolle et al. 2005; Andrews et al. 2015b).

Population-level Road Risk (400 points possible)

To assess the risk of negative road impacts on the persistence of a population we incorporated scores for population-level movement behavior and fecundity (Table 3). For the proportion of a population expected to encounter a road, we scored the greatest risk to species that seasonally migrate to overwintering and breeding areas (Jackson et al. 2015). For those that do not migrate, we expected higher proportions of non-territorial or loosely territorial species ("wandering") to encounter roads than species that defend distinct territories.

Species with low fecundity are less resilient to road mortality impacts than highly fecund species (Rytwinski and Fahrig 2013). Relative fecundity was simply calculated from the average number of potential offspring per year whether the animals were oviparous or live-bearing. For egg-laying species, the number of potential offspring was calculated by multiplying the average clutch size by the average number of clutches per year.

Individual mortality risk (1–100 points) was multiplied by the sum of these population-level factors (1–4 points) to calculate population-level road risk.

Species-level road risk (1200 points possible)

In comparison to population-level risk, we considered the overall risk of roads to species to be negatively associated with species range and conservation status. Although some populations may be at high risk, species with a wide distribution and many populations should be more resilient to localized declines and extirpations. Therefore, we assigned a range isolation score ranging from 0 to 1 that considered species distributions range-wide (North America) and within California (CA) (Table 4). Range-wide distribution varied from "CA only" to "widespread" (> 4 states). If the species range extended into Mexico and/or Canada, these countries were counted as another state for calculation of the index. California-wide distribution was calculated based upon the number of CA geographic regions occupied out of twelve regions defined by Hickman (1993) and used in Stebbins and

Table 4 Species-level Road Risk (SRR): Score criteria for species-level road risk

SRR[a] = PRR × ((Range isolation score + Conservation status score)/2)	
(a) Range isolation score = (North America range + CA range)/2	
North America range	Rank/score
CA only	1.00
2 states (very restricted distribution)	1.00
2 states (restricted)	0.67
2–3 states	0.33
Widespread (4 + states)	0.00
California range (No. of geographic regions occupied)	Rank/score
1	0.92
2	0.83
3	0.75
4	0.67
5	0.58
6	0.50
7	0.42
8	0.33
9	0.25
10	0.17
11	0.08
12	0.00
(b) Conservation status score	
Conservation status	Rank/score[a]
CA or federal threatened/endangered	1.00
SSC priority 1	0.75
SSC priority 2	0.50
SSC priority 3	0.25
None	0.00

[a]Population-level risk > 80 only

McGinnis (2012). These two scores (Range-wide isolation, CA isolation) were summed and divided by two in order to normalize the overall range isolation score to a 0 to 1 scale.

At the species-level, we also incorporated conservation status (Table 4). Some species are declining and are at higher risk of extinction often due to multiple stressors. Federal and State Threatened and Endangered Species were given the highest score (1.0). In California, forty-five species are designated "Species of Special Concern (SSC)" with a ranking of 1, 2, or 3 based upon severity and immediacy of threats affecting each taxon (Thomson et al. 2016). SSC species were given a conservation status score ranging from 0.25 to 0.75 based upon their SSC ranking. Population-level Road Risk (score range 1–400) was multiplied by (1 + Range Isolation Score + Conservation Status Score; score range 1–3) to calculate the final Species-level Road Risk.

Range and conservation status were only used as a multiplier for species-level road risk if the population-level road risk was greater than 80 (20% of possible population score). This helped to prevent false inflation of the road risk metrics for low road susceptible species.

Because all members of the genus *Batrachoseps* (slender salamanders) are similar in body size, range size and general life history characteristics, we scored

Table 5 Species-level frequency distributions and road risk rankings

Percentile	Scores	Relative ranks
81–100	322–710	Very high
61–80	213–321	High
41–60	63–212	Medium
21–40	53–62	Low
1–20	0–52	Very Low

the genus as whole with the most conservative estimates and conservation status but included all 20 species in the final count and calculations.

Once all 166 species (including subspecies with conservation status) were scored for species-level road risk within both terrestrial and aquatic habitats, we took the maximum score for each species and sorted them from the highest to lowest scores. We grouped species into categories of risk (Very high, high, medium, low, and very low) based upon ranges of values that represented frequency distributions in 20% increments of all species scores (Table 5, Fig. 2).

As a way to support the results of our ranking model with species literature, we focused on special status species. We reviewed recovery plans and 5-year reviews for federally listed species and state species accounts for California listed species and species of special concern (collectively referred to as special status species). For each rank group (i.e., "very low" to "very high"), we calculated the percentage of special status species where roads were specifically listed as a threat. Similarly, we tallied the number of species identified in a recent California preliminary road risk assessment (Levine 2013, Amy Golden pers. comm.) and compared the number of species that fell within each of our road risk categories.

Results

All chelonids, 72% of snakes, 50% of anurans, 18% of lizards and 17% of salamander species were ranked as high or very high risk from negative road impacts. (Table 6, Fig. 3).

Review of species accounts, recovery plans, and 5-year reviews for all special status species showed

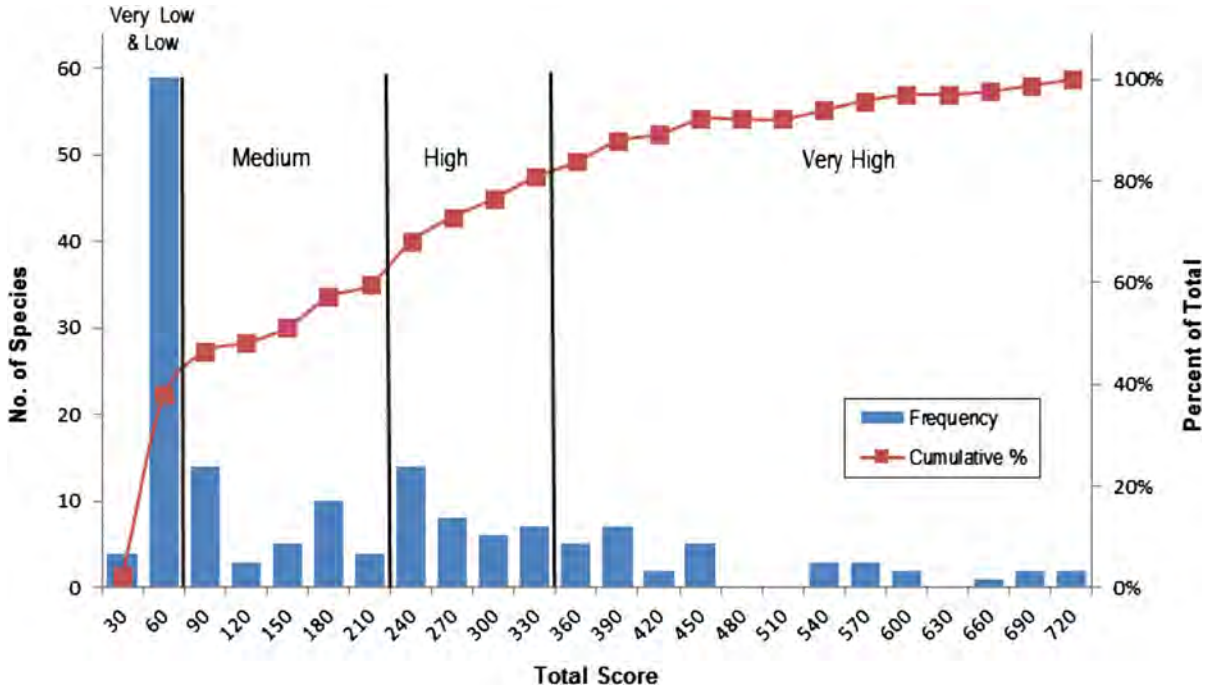

Fig. 2 Histogram of species-level scores and approximate 20 percentile road risk categories

Table 6 Numbers of species by taxa within each risk category

Species group	Species-level rankings				
	Very high	High	Med	Low	Very low
Salamander	4	4	3	26	9
Lizard	5	3	8	7	21
Anuran	5	6	6	4	1
Snake	15	21	13	0	1
Tortoise	1	0	0	0	0
Turtle	3	0	0	0	0

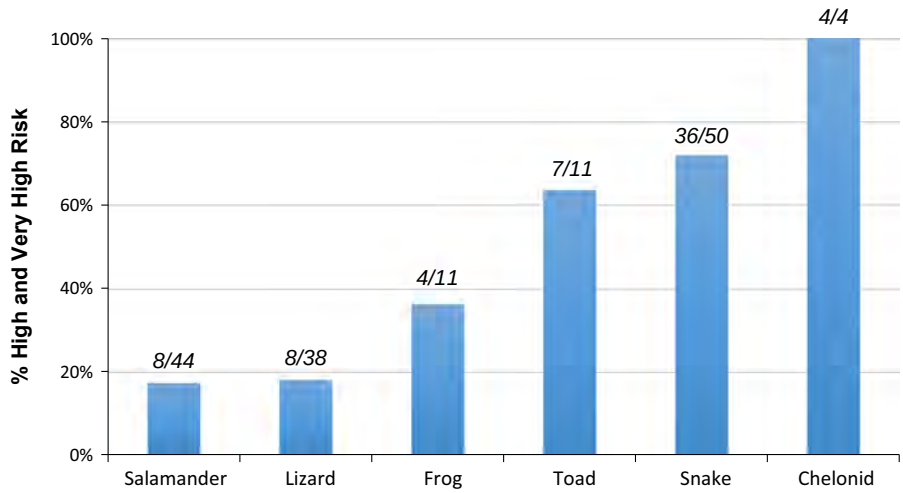

Fig. 3 Percentages of species by taxa in high and very high road risk categories

that 94% (17/18) of species accounts that referenced roads as a threat to the species were ranked as "high" or "very high" in our risk assessment (Table 7). Of the special status species that ranked 'high' and 'very high', close to fifty percent (17/35) had road-related threats referenced in their listing literature. In comparison, only 4% (1/27) of 'medium' to 'very low' risk special status species accounts mentioned roads as a potential threat. In addition, 79% (15/19) of species of concern recommended in a recent Caltrans preliminary road risk assessment scored as 'high' or 'very high' risk in our analysis (Levine 2013, Amy Golden pers. comm.).

Table 7 Comparison of road risk results and number of special status species with roads listed as threat

Road risk level	Special status species			Caltrans PI[a]
	No. species in road risk level	No. species with roads listed as threat	% of Total	No. Spp in road risk level
Very high	25	14	56	11
High	11	3	27	4
Medium	5	1	20	3
Low	10	0	0	1
Very low	7	0	0	0

[a]Caltrans PI are Caltrans identified sensitive species

Table 8 Amphibian and reptile road risk assessment: very high risk species (80–100% percentile), high risk species (60–80% percentile), medium risk species (40–60% percentile range), low risk species (20–40% percentile) and very low risk species (0–20% percentile)

	Species			Road Risk Scores			Status		
Risk Level-Species	Group	Common Name	Scientific name	Maximum (Aquatic & Terrestrial)[a]	Terrestrial	Aquatic (Wetlands/ Rivers/ Streams, Perennial to Intermittent)	Federal or State Listing/ ARSSC Priority Rank (1-3)[b]	Roads Listed as Potential Threat in Listing?[c]	Caltrans Identified Sensitive Species?[d]
Very High	Snake	Giant Gartersnake	*Thamnophis gigas*	710	44	710	THR	Yes	Yes
	Turtle	Southern Western Pond Turtle	*Actinemys pallida*	707	283	707	1		Yes
	Snake	San Joaquin Coachwhip	*Masticophis flagellum ruddocki*	689	689	-	2	Yes	
	Snake	San Francisco Gartersnake	*Thamnophis sirtalis tetrataenia*	663	238	663	END		Yes
	Snake	Alameda Striped Racer	*Masticophis lateralis euryxanthus*	652	652	-	THR	Yes	
	Snake	California Red-sided Gartersnake	*Thamnophis sirtalis infernalis*	588	211	588	1		
	Tortoise	Mohave Desert Tortoise	*Gopherus agassizii*	580	580	-	THR	Yes	Yes
	Salamander	Red-bellied Newt	*Taricha rivularis*	561	561	72	2	Yes	Yes
	Turtle	Northern Western Pond Turtle	*Actinemys marmorata*	547	219	547	3		Yes
	Snake	Two-striped Gartersnake	*Thamnophis hammondii*	541	195	541	2		
	Snake	Baja California Coachwhip	*Masticophis fuliginosus*	534	534	-	3	Yes	
	Snake	Coast Patch-nosed Snake	*Salvadora hexalepis virgultea*	533	533	-	2	Yes	
	Salamander	California Newt	*Taricha torosa*	532	532	72	2	Yes	Yes
	Lizard	Banded Gila Monster	*Heloderma suspectum cinctum*	446	446	-			
	Salamander	California Tiger Salamander	*Ambystoma californiense*	437	437	-	THR	Yes	Yes
	Salamander	Sierra Newt	*Taricha sierrae*	437	437	72			
	Snake	Striped Whipsnake	*Masticophis taeniatus*	425	425	-			
	Lizard	Flat-tail Horned Lizard	*Phrynosoma mcallii*	425	425	-	2	Yes	
	Turtle	Sonoran Mud Turtle	*Kinosternon sonoriense*	399	37	399	1		
	Lizard	Blunt-nosed Leopard Lizard	*Gambelia sila*	393	393	-	END	Yes	Yes
	Snake	Baja California Ratsnake	*Bogertophis rosaliae*	387	387	-			
	Snake	Panamint Rattlesnake	*Crotalus stephensi*	387	387	-			
	Frog	California Red-legged Frog	*Rana draytonii*	380	380	300	THR	Yes	Yes
	Toad	Yosemite Toad	*Anaxyrus canorus*	379	379	284	THR	Yes	
	Toad	Black Toad	*Anaxyrus exsul*	379	379	284	THR		
	Lizard	Cope's Leopard Lizard	*Gambelia copeii*	372	372	-	2		
	Toad	Sonoran Desert Toad	*Incilius alvarius (Possibly extinct in CA)*	361	361	285	1		
	Lizard	Desert Horned Lizard	*Phrynosoma platyrhinos*	356	356	-			
	Snake	California Glossy Snake	*Arizona elegans occidentalis*	340	340	-	1		
	Snake	North American Racer	*Coluber constrictor*	334	334	-			
	Snake	Coachwhip	*Masticophis flagellum*	333	333	-			
	Toad	Arroyo Toad	*Anaxyrus californicus*	331	331	248	END	Yes	Yes
	Snake	Striped Racer	*Masticophis lateralis*	322	322	-			

[a] Maximum scores color-coded for toad risk type; terrestrial (gray), aquatic (blue), or both (gray/blue)
[b] END=Endangered, THR= Threatened, 1-3= ARSSC Priority Ranking
[c] Federal Recovery plans, 5-year reviews, California species accounts for special status species
[d] California Amphibian and Reptile Crossing Preliminary Investigation

Risk scores and relative rankings for California reptile and amphibian species in both terrestrial and aquatic habitats are presented in Tables 8. Terrestrial and Aquatic rankings are provided separately in Tables 9 and 10 and also include population-level risk scores, 95% population buffer distances, confidence levels, and identification of any surrogate species used for the distance calculations. Species scores for all ranking criteria and life history and movement references are provided in Appendices 1 and 2.

Discussion

To our knowledge, this is the first attempt to objectively assess the relative risk of roads at a species level using a logical and scientifically based framework and apply it across a large array of species and habitats. We believe this approach could be useful for assessing and comparing susceptibility of species to negative road impacts within and among all taxonomic groups. To date, such risk assessments have been based largely upon expert opinion, limited information available on

Table 8 continued

	Species			Road Risk Scores			Status		
Risk Level-Species	Group	Common Name	Scientific name	Maximum (Aquatic & Terrestrial)[a]	Terrestrial	Aquatic (Wetlands/ Rivers/ Streams, Perennial to Intermittent)	Federal or State Listing/ ARSSC Priority Rank (1-3)[b]	Roads Listed as Potential Threat in Listing?[c]	Caltrans Identified Sensitive Species?[d]
High	Snake	Red Diamond Rattlesnake	*Crotalus ruber*	321	321	-	3	Yes	
	Snake	Speckled Rattlesnake	*Crotalus mitchellii*	317	317	-			
	Frog	Oregon Spotted Frog	*Rana pretiosa (Possibly extinct in CA)*	315	41	315	THR		
	Salamander	Santa Cruz Long-toed Salamander	*Ambystoma macrodactylum croceum*	308	308	-	END	Yes	Yes
	Salamander	Rough-skinned Newt	*Taricha granulosa*	304	304	72			
	Snake	Sierra Gartersnake	*Thamnophis couchii*	304	44	304			
	Snake	Regal Ring-necked Snake	*Diadophis punctatus regalis*	298	298	-	2		Yes
	Snake	California Lyresnake	*Trimorphodon lyrophanes*	293	293	-			
	Frog	Northern Red-legged Frog	*Rana aurora*	291	291	230	2		Yes
	Snake	Mojave Rattlesnake	*Crotalus scutulatus*	276	276	-			
	Snake	Western Patch-nosed Snake	*Salvadora hexalepis*	276	276	-			
	Snake	Common Gartersnake	*Thamnophis sirtalis*	271	165	271			
	Snake	Aquatic Gartersnake	*Thamnophis atratus*	266	40	266	0		
	Snake	Sidewinder	*Crotalus cerastes*	263	263	-			
	Salamander	California Giant Salamander	*Dicamptodon ensatus*	260	260	72	3	Yes	
	Snake	Sonoran Lyresnake	*Trimorphodon lambda*	260	260	-			
	Snake	Western Rattlesnake	*Crotalus oreganus*	250	250	-			
	Snake	Northwestern Gartersnake	*Thamnophis ordinoides*	245	138	245			
	Snake	Desert Nightsnake	*Hypsiglena chlorophaea*	241	241	-			
	Snake	Western Terrestrial Gartersnake	*Thamnophis elegans*	240	75	240			
	Lizard	Switak's Banded Gecko	*Coleonyx switaki*	236	236	-	THR		
	Toad	Western Spadefoot	*Spea hammondii*	234	234	-	1		Yes
	Snake	Coast Nightsnake	*Hypsiglena ochrorhyncha*	233	233	-			
	Lizard	Long-nosed Leopard Lizard	*Gambelia wislizenii*	226	226	-			
	Toad	Great Plains Toad	*Anaxyrus cognatus*	222	222	175			
	Toad	Woodhouse's Toad	*Anaxyrus woodhousii*	222	222	175			
	Lizard	Coastal Whiptail	*Aspidoscelis tigris stejnegeri*	219	219	-	2		
	Snake	Western Shovel-nosed Snake	*Chionactis occipitalis*	218	218	-			
	Snake	Spotted Leaf-nosed Snake	*Phyllorhynchus decurtatus*	218	218	-			
	Salamander	Southern Long-toed Salamander	*Ambystoma macrodactylum sigillatum*	217	217	-	2		
	Frog	Cascades Frog	*Rana cascadae*	217	217	72	2		
	Snake	Western Diamond-backed Rattlesnake	*Crotalus atrox*	214	214	-			
	Snake	Western Groundsnake	*Sonora semiannulata*	212	212	-			

[a] Maximum scores color-coded for toad risk type; terrestrial (gray), aquatic (blue), or both (gray/blue)

[b] END=Endangered, THR= Threatened, 1-3= ARSSC Priority Ranking

[c] Federal Recovery plans, 5-year reviews, California species accounts for special status species

[d] California Amphibian and Reptile Crossing Preliminary Investigation

road mortality, and even less information available on population or species-level road effects (Levine 2013; Rytwinski and Fahrig 2015).

Overall, this is meant to be a first step in highlighting reptile and amphibian species that may be at highest risk from roads transecting their habitat. These species may deserve consideration for further study and for implementing mitigation solutions to reduce mortality and to maintain or enhance connectivity. The risk assessment was done for both terrestrial and aquatic habitats to further inform mitigation. Some aquatic species may greatly benefit from fish passages while others may better benefit from terrestrial barriers and wildlife crossings or both.

Although data are currently lacking to validate completely the scoring and results of the risk assessment, our review of species accounts, recovery plans, 5-year reviews for federal and state-listed species and California species of special concern show a strong association between elevated road risk from our

Table 8 continued

	Species			Road Risk Scores			Status		
Risk Level-Species	Group	Common Name	Scientific name	Maximum (Aquatic & Terrestrial)[a]	Terrestrial	Aquatic (Wetlands/ Rivers/ Streams, Perennial to Intermittent)	Federal or State Listing/ ARSSC Priority Rank (1-3)[b]	Roads Listed as Potential Threat in Listing?[c]	Caltrans Identified Sensitive Species?[d]
Medium	Snake	Checkered Gartersnake	*Thamnophis marcianus*	210	69	210			
	Lizard	Blainville's Horned Lizard	*Phrynosoma blainvillii*	209	209	-	2		Yes
	Frog	Foothill Yellow-legged Frog	*Rana boylii*	199	26	199	1		
	Snake	Gopher Snake	*Pituophis catenifer*	189	189	-			
	Snake	California Mountain Kingsnake	*Lampropeltis zonata*	184	184	-			Yes
	Snake	Glossy Snake	*Arizona elegans*	180	180	-			
	Lizard	Pygmy Short-horned Lizard	*Phrynosoma douglasii*	179	179	-			
	Toad	Couch's Spadefoot	*Scaphiopus couchii*	178	178	-	3		
	Snake	California Kingsnake	*Lampropeltis californiae*	175	175	-			
	Snake	Long-nosed Snake	*Rhinocheilus lecontei*	165	165	-			
	Toad	Western Toad	*Anaxyrus boreas*	165	165	130			
	Snake	Ring-necked Snake	*Diadophis punctatus*	164	164	-			Yes
	Lizard	San Diego Banded Gecko	*Coleonyx variegatus abbotti*	158	158	-	3	Yes	
	Salamander	Northwestern Salamander	*Ambystoma gracile*	152	152	-			
	Toad	Great Basin Spadefoot	*Spea intermontana*	152	152	-			
	Toad	Red-spotted Toad	*Anaxyrus punctatus*	147	147	72			
	Salamander	Long-toed Salamander	*Ambystoma macrodactylum*	143	143	-			
	Lizard	Orange-throated Whiptail	*Aspidoscelis hyperythra*	137	137	-			
	Snake	Smith's Black-headed Snake	*Tantilla hobartsmithi*	136	136	-			
	Snake	California Black-headed Snake	*Tantilla planiceps*	133	133	-			
	Lizard	Western Whiptail	*Aspidoscelis tigris*	118	118	-			
	Salamander	Coastal Giant Salamander	*Dicamptodon tenebrosus*	117	117	48			
	Lizard	Western Banded Gecko	*Coleonyx variegatus*	105	105	-			
	Lizard	Common Chuckwalla	*Sauromalus ater*	78	78	-			
	Snake	Northern Rubber Boa	*Charina bottae*	77	77	-			
	Snake	Southern Rubber Boa	*Charina umbratica*	77	77	-	THR		
	Snake	Northern Three-lined Boa	*Lichanura orcutti*	77	77	-			
	Lizard	Desert Iguana	*Dipsosaurus dorsalis*	72	72	-			
	Snake	Forest Sharp-tailed Snake	*Contia longicauda*	70	70	-			
	Snake	Common Sharp-tailed Snake	*Contia tenuis*	70	70	-			
	Frog	Pacific Treefrog	*Pseudacris regilla*	68	68	36			

[a] Maximum scores color-coded for toad risk type; terrestrial (gray), aquatic (blue), or both (gray/blue)

[b] END=Endangered, THR= Threatened, 1-3= ARSSC Priority Ranking

[c] Federal Recovery plans, 5-year reviews, California species accounts for special status species

[d] California Amphibian and Reptile Crossing Preliminary Investigation

objective analysis and the probability that roads are listed as a potential threat to the species in the species listing literature.

Although more than 40% of special status species are semi-aquatic, roads were rarely considered a threat to aquatic connectivity in the species literature. This may be accurate if bridges or large culverts currently exist for water flow that also provide permeability to aquatic movement. Bridges are generally considered to be completely passable by all aquatic species. Bridges are more likely to be constructed adjacent to or over large water bodies and rivers, presumably resulting in less risk to aquatic movement of populations that inhabit lake and river systems. However, culverts that are more commonly constructed under roads in streams and wetlands vary in passability depending on factors such as diameter, length, slope, outlet configuration, and other characteristics (Furniss et al. 1991; Clarkin et al. 2005; Kemp and O'Hanley 2010). In fact, Januchowski-Hartley et al. (2013) found that only 36% of road crossings were fully passable to fish in the Great Lakes basin. In addition, many low water crossings in arid regions of the state are simply a dip in the road that allows water to flow

Table 8 continued

	Species			Road Risk Scores			Status		
Risk Level-Species	Group	Common Name	Scientific name	Maximum (Aquatic & Terrestrial)[a]	Terrestrial	Aquatic (Wetlands/ Rivers/ Streams, Perennial to Intermittent)	Federal or State Listing/ ARSSC Priority Rank (1-3)[b]	Roads Listed as Potential Threat in Listing?[c]	Caltrans Identified Sensitive Species?[d]
Low	Salamander	Scott Bar Salamander	*Plethodon asupak*	62	62	-	THR		
	Salamander	Dunn's Salamander	*Plethodon dunni*	62	62	-			
	Salamander	Del Norte Salamander	*Plethodon elongatus*	62	62	-			
	Salamander	Siskiyou Mountains Salamander	*Plethodon stormi*	62	62	-	THR		
	Frog	California Treefrog	*Pseudacris cadaverina*	61	61	26			
	Salamander	Southern Torrent Salamander	*Rhyacotriton variegatus*	61	61	5	1		
	Lizard	Peninsula Leaf-toed Gecko	*Phyllodactylus nocticolus*	60	60	-			
	Lizard	Northern Alligator Lizard	*Elgaria coerulea*	60	60	-			
	Frog	Coastal Tailed Frog	*Ascaphus truei*	59	59	30	2		Yes
	Lizard	Common Side-blotched Lizard	*Uta stansburiana*	59	59	-			
	Lizard	Coachella Fringe-toed Lizard	*Uma inornata*	56	56	-	THR		
	Lizard	Colorado Desert Fringe-toed Lizard	*Uma notata*	56	56	-	2		
	Lizard	Mohave Fringe-toed Lizard	*Uma scoparia*	56	56	-	3		
	Frog	Lowland Leopard Frog	*Lithobates yavapaiensis (Possibly extinct in CA)*	54	31	54	1		
	Frog	Southern Mountain Yellow-legged Frog	*Rana muscosa*	54	26	54	END		
	Lizard	Zebra-tailed Lizard	*Callisaurus draconoides*	54	54	-			
	Salamander	Wandering Salamander	*Aneides vagrans*	53	53	-			
	Salamander	Slender Salamanders	*Batrachoseps (genus: 20 spp.)*	53	53	-	END[e]		
Very Low	Salamander	Ensatina	*Ensatina eschscholtzii*	51	51	-			
	Salamander	Yellow-blotched Ensatina	*Ensatina eschscholtzii croceater*	51	51	-			
	Salamander	Large-blotched Ensatina	*Ensatina eschscholtzii klauberi*	51	51	-			
	Lizard	Southern Alligator Lizard	*Elgaria multicarinata*	51	51	-			
	Lizard	Panamint Alligator Lizard	*Elgaria panamintina*	51	51	-	3		
	Frog	Sierra Nevada Yellow-legged Frog	*Rana sierrae*	51	51	36	THR		
	Lizard	Western Fence Lizard	*Sceloporus occidentalis*	49	49	-			
	Salamander	Limestone Salamander	*Hydromantes brunus*	48	48	-	THR		
	Salamander	Mount Lyell Salamander	*Hydromantes platycephalus*	48	48	-			
	Salamander	Clouded Salamander	*Aneides ferreus*	44	44	-			
	Salamander	Arboreal Salamander	*Aneides lugubris*	44	44	-			
	Lizard	Granite Spiny Lizard	*Sceloporus orcutti*	43	43	-			
	Snake	Western Blind Snake	*Rena humilis*	42	42	-			
	Lizard	Desert Spiny Lizard	*Sceloporus magister*	41	41	-			
	Lizard	Common Sagebrush Lizard	*Sceloporus graciosus*	39	41	-			
	Lizard	Gilbert's Skink	*Plestiodon gilberti*	39	39	-			
	Lizard	Western Skink	*Plestiodon skiltonianus*	39	39	-			
	Lizard	California Legless Lizard	*Anniella pulchra*	35	39	-	2		
	Salamander	Black Salamander	*Aneides flavipunctatus*	35	35	-			
	Salamander	Santa Cruz Black Salamander	*Aneides flavipunctatus niger*	35	35	-			
	Lizard	Baja California Collared Lizard	*Crotaphytus vestigium*	35	35	-			
	Lizard	Sandstone Night Lizard	*Xantusia gracilis*	33	33	-	3		
	Lizard	Granite Night Lizard	*Xantusia henshawi*	33	33	-			
	Lizard	Island Night Lizard	*Xantusia riversiana*	33	33	-	THR		
	Lizard	Sierra Night Lizard	*Xantusia sierrae*	33	33	-	1		
	Lizard	Desert Night Lizard	*Xantusia vigilis*	33	33	-			
	Lizard	Wiggins' Night Lizard	*Xantusia wigginsi*	33	33	-			
	Lizard	Long-tailed Brush Lizard	*Urosaurus graciosus*	27	27	-			
	Lizard	Baja California Brush Lizard	*Urosaurus nigricaudus*	27	27	-			
	Lizard	Ornate Tree Lizard	*Urosaurus ornatus*	27	27	-			
	Lizard	Mearns' Rock Lizard	*Petrosaurus mearnsi*	21	21	-			

[a] Maximum scores color-coded for toad risk type; terrestrial (gray), aquatic (blue), or both (gray/blue)
[b] END=Endangered, THR= Threatened, 1-3= ARSSC Priority Ranking
[c] Federal Recovery plans, 5-year reviews, California species accounts for special status species
[d] California Amphibian and Reptile Crossing Preliminary Investigation
[e] 4 Batrachoseps species with conservation status

Table 9 Terrestrial risk ranking and population buffer distances

Risk Level (Terrestrial)		Species			Risk Scores (Terrestrial)		Movement Distances (Terrestrial)		
Species	Population	Group	Common Name	Scientific name	Road Risk: Species- Level	Road Risk: Population-Level	95% Population Movement Distance (m)	Confidence in Distance Estimate	Surrogate Used
Very High	Very High	Snake	San Joaquin Coachwhip	*Masticophis flagellum ruddocki*	689	285	1618	High	*M. fulginosus*
	Very High	Snake	Alameda Striped Racer	*Masticophis lateralis euryxanthus*	652	221	631	Med/High	
	Very High	Tortoise	Mohave Desert Tortoise	*Gopherus agassizii*	580	240	1155	High	
	Very High	Salamander	Red-bellied Newt	*Taricha rivularis*	561	228	1600	High	
	Very High	Snake	Baja California Coachwhip	*Masticophis fuliginosus*	534	285	1904	High	
	Very High	Snake	Coast Patch-nosed Snake	*Salvadora hexalepis virgultea*	533	221	631	Low	*M. lateralis*
	Very High	Salamander	California Newt	*Taricha torosa*	532	228	2500	Med/High	
	Very High	Lizard	Banded Gila Monster	*Heloderma suspectum cinctum*	446	210	1250	High	
	High	Salamander	California Tiger Salamander	*Ambystoma californiense*	437	152	1849	Med/High	
	Very High	Salamander	Sierra Newt	*Taricha sierrae*	437	228	2050	Med	*T. torosa, T. rivularis*
	Very High	Snake	Striped Whipsnake	*Masticophis taeniatus*	425	300	2380	Med	
	Very High	Lizard	Flat-tail Horned Lizard	*Phrynosoma mcallii*	425	217	788	Med/High	
	High	Lizard	Blunt-nosed Leopard Lizard	*Gambelia sila*	393	133	510	High	
	Very High	Snake	Baja California Ratsnake	*Bogertophis rosaliae*	387	238	780	Low	*Elaphe obsoleta*
	Very High	Snake	Panamint Rattlesnake	*Crotalus stephensi*	387	238	938	Med	*C. mitchelli*
	High	Frog	California Red-legged Frog	*Rana draytonii*	380	152	2360	High	
	High	Toad	Yosemite Toad	*Anaxyrus canorus*	379	128	1152	Med/High	
	High	Toad	Black Toad	*Anaxyrus exsul*	379	128	951	Low	*A. canorus, A. punctatus*
	High	Lizard	Cope's Leopard Lizard	*Gambelia copeii*	372	175	643	Low/Med	*G. wislenzii*
	High	Toad	Sonoran Desert Toad	*Incilius alvarius (Possibly extinct in CA)*	361	152	1400	Low/Med	*A. cognatus*
	Very High	Lizard	Desert Horned Lizard	*Phrynosoma platyrhinos*	356	259	1308	Med/High	
	High	Snake	California Glossy Snake	*Arizona elegans occidentalis*	340	154	316	Low	*R. leconti*
	Very High	Snake	North American Racer	*Coluber constrictor*	334	308	1800	Med	
	Very High	Snake	Coachwhip	*Masticophis flagellum*	333	285	1618	High	*M. fulginosus*
	High	Toad	Arroyo Toad	*Anaxyrus californicus*	331	128	1082	Med/High	
	Very High	Snake	Striped Racer	*Masticophis lateralis*	322	221	631	Med	
High	High	Snake	Red Diamond Rattlesnake	*Crotalus ruber*	321	175	853	High	
	Very High	Snake	Speckled Rattlesnake	*Crotalus mitchellii*	317	238	938	High	
	Med	Salamander	Santa Cruz Long-toed Salamander	*Ambystoma macrodactylum croceum*	308	104	700	High	
	Very High	Salamander	Rough-skinned Newt	*Taricha granulosa*	304	228	2050	Med	*T. torosa, T. rivularis*
	High	Snake	Regal Ring-necked Snake	*Diadophis punctatus regalis*	298	152	566	Low/Med	
	Very High	Snake	California Lyresnake	*Trimorphodon lyrophanes*	293	195	800	Low	
	High	Frog	Northern Red-legged Frog	*Rana aurora*	291	152	2360	Med	*R. draytonii*
	High	Turtle	Southern Western Pond Turtle	*Actinemys pallida*	283	128	309	Med-High	
	High	Snake	Mojave Rattlesnake	*Crotalus scutulatus*	276	189	815	Med/High	
	Very High	Snake	Western Patch-nosed Snake	*Salvadora hexalepis*	276	221	631	Low	*M. lateralis*
	High	Snake	Sidewinder	*Crotalus cerastes*	263	186	767	High	
	Med	Salamander	California Giant Salamander	*Dicamptodon ensatus*	260	120	600	Low	*D. tenebrosus*
	Very High	Snake	Sonoran Lyresnake	*Trimorphodon lambda*	260	195	800	Low	
	Very High	Snake	Western Rattlesnake	*Crotalus oreganus*	250	231	1096	Med/High	
	High	Snake	Desert Nightsnake	*Hypsiglena chlorophaea*	241	175	566	Low	*D. punctatus*
	Med	Snake	San Francisco Gartersnake	*Thamnophis sirtalis tetrataenia*	238	81	300	Med	
	Med	Lizard	Switak's Banded Gecko	*Coleonyx switaki*	236	90	200	Low	*C. variegatus (AZ)*
	Med	Toad	Western Spadefoot	*Spea hammondii*	234	104	670	Med	
	High	Snake	Coast Nightsnake	*Hypsiglena ochrorhyncha*	233	175	566	Low	*D. punctatus*
	High	Lizard	Long-nosed Leopard Lizard	*Gambelia wislizenii*	226	175	643	Med/High	
	High	Toad	Great Plains Toad	*Anaxyrus cognatus*	222	152	1400	Med/High	
	High	Toad	Woodhouse's Toad	*Anaxyrus woodhousii*	222	152	1400	Low	*A. cognatus*
	Med	Lizard	Coastal Whiptail	*Aspidoscelis tigris stejnegeri*	219	105	300	Low	*A. hyperythra (multiplied by 2 for body size)*
	High	Turtle	Northern Western Pond Turtle	*Actinemys marmorata*	219	128	448	Med	
	High	Snake	Western Shovel-nosed Snake	*Chionactis occipitalis*	218	154	400	Low	
	High	Snake	Spotted Leaf-nosed Snake	*Phyllorhynchus decurtatus*	218	154	400	Low	*C. occipitalis, M. taeniatus*
	Med	Salamander	Southern Long-toed Salamander	*Ambystoma macrodactylum sigillatum*	217	104	700	Med	
	Med	Frog	Cascades Frog	*Rana cascadae*	217	104	759	High	
	High	Snake	Western Diamond-backed Rattlesnake	*Crotalus atrox*	214	147	484	Med	
	High	Snake	Western Groundsnake	*Sonora semiannulata*	212	154	400	Low	*C. occipitalis*
	Med	Snake	California Red-sided Gartersnake	*Thamnophis sirtalis infernalis*	211	81	300	Low/Med	*T.s. tetrataenia*

Table 9 continued

Risk Level (Terrestrial)		Species			Risk Scores (Terrestrial)		Movement Distances (Terrestrial)		
Species	Population	Group	Common Name	Scientific name	Road Risk: Species- Level	Road Risk: Population-Level	95% Population Movement Distance (m)	Confidence in Distance Estimate	Surrogate Used
Medium	Med	Lizard	Blainville's Horned Lizard	*Phrynosoma blainvillii*	209	114	495	Med	
	Med	Snake	Two-striped Gartersnake	*Thamnophis hammondii*	195	81	239	Low/Med	
	High	Snake	Gopher Snake	*Pituophis catenifer*	189	189	820	Med/High	
	High	Snake	California Mountain Kingsnake	*Lampropeltis zonata*	184	147	501	Low/Med	*L. getula, L. triangulum*
	High	Snake	Glossy Snake	*Arizona elegans*	180	154	316	Low	*R. lecontii*
	Med	Lizard	Pygmy Short-horned Lizard	*Phrynosoma douglasii*	179	123	400	Low	*P. mccallii (reduced 0.5 for body size)*
	Med	Toad	Couch's Spadefoot	*Scaphiopus couchii*	178	104	670	Med	
	High	Snake	California Kingsnake	*Lampropeltis californiae*	175	175	501	Med/High	
	High	Snake	Long-nosed Snake	*Rhinocheilus lecontei*	165	132	337	Low/Med	
	High	Snake	Common Gartersnake	*Thamnophis sirtalis*	165	137	532	Low/Med	
	High	Toad	Western Toad	*Anaxyrus boreas*	165	152	2144	Med/High	
	High	Snake	Ring-necked Snake	*Diadophis punctatus*	164	136	566	Low/Med	
	Med	Lizard	San Diego Banded Gecko	*Coleonyx variegatus abbotti*	158	84	200	Low/Med	*C. variegatus (AZ)*
	Med	Salamander	Northwestern Salamander	*Ambystoma gracile*	152	104	700	Low	*A. macrodactylum croceum*
	Med	Toad	Great Basin Spadefoot	*Spea intermontana*	152	104	670	Med	
	Med	Toad	Red-spotted Toad	*Anaxyrus punctatus*	147	104	750	Low	
	Med	Salamander	Long-toed Salamander	*Ambystoma macrodactylum*	143	104	700	Med	
	Med	Snake	Northwestern Gartersnake	*Thamnophis ordinoides*	138	95	239	Low	*T. hammondii*
	Med	Lizard	Orange-throated Whiptail	*Aspidoscelis hyperythra*	137	84	150	Low/Med	
	Med	Snake	Smith's Black-headed Snake	*Tantilla hobartsmithi*	136	105	150	Low	
	Med	Snake	California Black-headed Snake	*Tantilla planiceps*	133	84	150	Low	
	Med	Lizard	Western Whiptail	*Aspidoscelis tigris*	118	105	300	Low	*A. hyperythra (multiplied by 2 for body size)*
	Med	Salamander	Coastal Giant Salamander	*Dicamptodon tenebrosus*	117	80	600	Low/Med	
	Med	Lizard	Western Banded Gecko	*Coleonyx variegatus*	105	84	200	Low/Med	*C. variegatus (AZ)*
	Med	Lizard	Common Chuckwalla	*Sauromalus ater*	78	78	296	Med	
	Med	Snake	Northern Rubber Boa	*Charina bottae*	77	77	230	Low/Med	*L. trivirgata*
	Med	Snake	Southern Rubber Boa	*Charina umbratica*	77	77	230	Low/Med	*L. trivirgata*
	Med	Snake	Northern Three-lined Boa	*Lichanura orcutti*	77	77	230	Med/High	
	Med	Snake	Western Terrestrial Gartersnake	*Thamnophis elegans*	75	75	104	Low/Med	*T.gigas (-40% for size diff)*
	Med	Lizard	Desert Iguana	*Dipsosaurus dorsalis*	72	72	150	Low/Med	
	Med	Snake	Forest Sharp-tailed Snake	*Contia longicauda*	70	70	150	Low	
	Med	Snake	Common Sharp-tailed Snake	*Contia tenuis*	70	70	150	Low	
	Med	Snake	Checkered Gartersnake	*Thamnophis marcianus*	69	69	239	Low	*T. hammondii*
	Med	Frog	Pacific Treefrog	*Pseudacris regilla*	68	68	400	Low/Med	
Low	Low	Salamander	Scott Bar Salamander	*Plethodon asupak*	62	62	92	Low	*P. glutinosus*
	Low	Salamander	Dunn's Salamander	*Plethodon dunni*	62	62	92	Low	*P. glutinosus*
	Low	Salamander	Del Norte Salamander	*Plethodon elongatus*	62	62	92	Low	*P. glutinosus*
	Low	Salamander	Siskiyou Mountains Salamander	*Plethodon stormi*	62	62	92	Low	*P. glutinosus*
	Low	Frog	California Treefrog	*Pseudacris cadaverina*	61	61	50	Low/Med	
	Low	Salamander	Southern Torrent Salamander	*Rhyacotriton variegatus*	61	61	50	Low	*R. cascadae*
	Low	Lizard	Peninsula Leaf-toed Gecko	*Phyllodactylus nocticolus*	60	60	200	Low	*C. variegatus (AZ)*
	Low	Lizard	Northern Alligator Lizard	*Elgaria coerulea*	60	60	106	Med	
	Low	Frog	Coastal Tailed Frog	*Ascaphus truei*	59	59	150	Med/High	
	Low	Lizard	Common Side-blotched Lizard	*Uta stansburiana*	59	59	152	Med/High	
	Low	Lizard	Coachella Fringe-toed Lizard	*Uma inornata*	56	56	52	Med/High	
	Low	Lizard	Colorado Desert Fringe-toed Lizard	*Uma notata*	56	56	75	Med/High	
	Low	Lizard	Mohave Fringe-toed Lizard	*Uma scoparia*	56	56	64	Med	*U. notata, U. inornata*
	Low	Lizard	Zebra-tailed Lizard	*Callisaurus draconoides*	54	54	150	Med	
	Low	Salamander	Wandering Salamander	*Aneides vagrans*	53	53	39	Med/High	
	Low	Salamander	Slender Salamanders (20 species)	*Batrachoseps (genus)*	53	53	50	Low/Med	*B. pacificus*

Table 9 continued

Risk Level (Terrestrial)		Species			Risk Scores (Terrestrial)		Movement Distances (Terrestrial)		
Species	Population	Group	Common Name	Scientific name	Road Risk: Species- Level	Road Risk: Population-Level	95% Population Movement Distance (m)	Confidence in Distance Estimate	Surrogate Used
Very Low	Very Low	Salamander	Ensatina	*Ensatina eschscholtzii*	51	51	75	Med	
	Very Low	Salamander	Yellow-blotched Ensatina	*Ensatina eschscholtzii croceater*	51	51	75	Med	
	Very Low	Salamander	Large-blotched Ensatina	*Ensatina eschscholtzii klauberi*	51	51	75	Med	*E. eschscholtzii croceater*
	Very Low	Lizard	Southern Alligator Lizard	*Elgaria multicarinata*	51	51	106	Low/Med	*E. coerulea*
	Very Low	Lizard	Panamint Alligator Lizard	*Elgaria panamintina*	51	51	106	Low/Med	*E. coerulea*
	Very Low	Frog	Sierra Nevada Yellow-legged Frog	*Rana sierrae*	51	51	420	Med	
	Very Low	Lizard	Western Fence Lizard	*Sceloporus occidentalis*	49	49	160	Med	
	Very Low	Salamander	Limestone Salamander	*Hydromantes brunus*	48	48	80	Low	
	Very Low	Salamander	Mount Lyell Salamander	*Hydromantes platycephalus*	48	48	80	Low	
	Very Low	Salamander	Clouded Salamander	*Aneides ferreus*	44	44	39	Med	*A. vagrans*
	Very Low	Salamander	Arboreal Salamander	*Aneides lugubris*	44	44	39	Med	*A. vagrans*
	Very Low	Snake	Giant Gartersnake	*Thamnophis gigas*	44	44	174	High	
	Very Low	Snake	Sierra Gartersnake	*Thamnophis couchii*	44	44	115	Low/Med	*T.gigas (-34% for size diff)*
	Very Low	Lizard	Granite Spiny Lizard	*Sceloporus orcutti*	43	43	91	Low/Med	
	Very Low	Snake	Western Blind Snake	*Rena humilis*	42	42	50	Low	
	Very Low	Lizard	Desert Spiny Lizard	*Sceloporus magister*	41	41	91	Low	
	Very Low	Frog	Oregon Spotted Frog	*Rana pretiosa (Possibly extinct in CA)*	41	41	100	Low	
	Very Low	Lizard	Common Sagebrush Lizard	*Sceloporus graciosus*	41	41	41	Med/High	
	Very Low	Snake	Aquatic Gartersnake	*Thamnophis atratus*	40	40	99	Low/Med	*T.gigas (-43% for size diff)*
	Very Low	Lizard	Gilbert's Skink	*Plestiodon gilberti*	39	39	93	Low/Med	*P. skiltonianus; P. fasciatus, S. laterale*
	Very Low	Lizard	Western Skink	*Plestiodon skiltonianus*	39	39	93	Low/Med	
	Very Low	Lizard	California Legless Lizard	*Anniella pulchra*	39	39	15	High	
	Very Low	Turtle	Sonoran Mud Turtle	*Kinosternon sonoriense*	37	37	60	Med	
	Very Low	Salamander	Black Salamander	*Aneides flavipunctatus*	35	35	39	Med	*A. vagrans*
	Very Low	Salamander	Santa Cruz Black Salamander	*Aneides flavipunctatus niger*	35	35	39	Med	*A. vagrans*
	Very Low	Lizard	Great Basin Collared Lizard	*Crotaphytus bicinctores*	35	35	150	Low/Med	*C. collaris*
	Very Low	Lizard	Baja California Collared Lizard	*Crotaphytus vestigium*	35	35	150	Low/Med	*C. collaris*
	Very Low	Lizard	Sandstone Night Lizard	*Xantusia gracilis*	33	33	14	Med/High	*X. riversiana*
	Very Low	Lizard	Granite Night Lizard	*Xantusia henshawi*	33	33	14	Med/High	*X. riversiana*
	Very Low	Lizard	Island Night Lizard	*Xantusia riversiana*	33	33	14	High	
	Very Low	Lizard	Sierra Night Lizard	*Xantusia sierrae*	33	33	14	Med/High	*X. riversiana*
	Very Low	Lizard	Desert Night Lizard	*Xantusia vigilis*	33	33	14	Med/High	*X. riversiana*
	Very Low	Lizard	Wiggins' Night Lizard	*Xantusia wigginsi*	33	33	14	Med/High	*X. riversiana*
	Very Low	Frog	Lowland Leopard Frog	*Lithobates yavapaiensis (Possibly extinct in CA)*	31	31	100	Low	
	Very Low	Lizard	Long-tailed Brush Lizard	*Urosaurus graciosus*	27	27	130	Low/Med	*S. occidentalis, S. graciosus*
	Very Low	Lizard	Baja California Brush Lizard	*Urosaurus nigricaudus*	27	27	130	Low/Med	*S. occidentalis, S. graciosus*
	Very Low	Lizard	Ornate Tree Lizard	*Urosaurus ornatus*	27	27	130	Low/Med	*S. occidentalis, S. graciosus*
	Very Low	Frog	Foothill Yellow-legged Frog	*Rana boylii*	26	26	40	Med/High	
	Very Low	Frog	Southern Mountain Yellow-legged Frog	*Rana muscosa*	26	26	40	Med	*R. boylii*
	Very Low	Lizard	Mearns' Rock Lizard	*Petrosaurus mearnsi*	21	21	80	Low/Med	
	Very Low	Lizard	Mearns' Rock Lizard	*Petrosaurus mearnsi*	21	21	80	Low/Med	

over the surface during high flow events. These may be used as road crossings by species traveling along ephemeral stream corridors with or without water flow. Given these potential vulnerabilities, we believe that road impacts to aquatic connectivity of herpetofauna deserve greater consideration.

Across broad taxonomic groups, chelonids (tortoises/turtles) and snakes had the greatest percentages of species at 'high' or 'very high' risk from roads. They are similar in that many move long distances (home range and/or migratory), tend not to avoid roads (or are attracted to them for thermoregulation), are long lived, and have relatively low fecundity in comparison to other herpetofaunal groups. Because of these traits, chelonids and snakes have been identified elsewhere as being particularly susceptible to negative population effects from roads (Gibbs and Shriver 2002; Andrews et al. 2015b; Jackson et al. 2015).

There are only four species of chelonids in California, (desert tortoise (*Gopherus agazzii*),

Northwestern pond turtle (*Actinemys marmorata*), Southwestern pond turtle (*Actinemys pallida*), and the Sonoran mud turtle (*Kinosternon sonoriense*)). There has been a high level of attention to road impacts on the desert tortoise (*Gopherus agazzii*) as numerous studies have documented not only high road mortality, but measurable road effect zones, and mostly positive responses to barriers and underpasses (e.g., Boarman and Sazaki 1996, 2006; Peaden et al. 2016; but see Peadon et al. 2017). Although not listed as a primary threat to pond turtle populations in California (Thomson et al. 2016), road mortality is a major concern for western pond turtle populations in Oregon (Rosenberg et al. 2009). Pond turtles travel kilometers within perennial waters and from pool to pool in intermittent aquatic habitats to forage and find mates (Goodman and Stewart 2000). In addition, females nest and lay eggs in terrestrial habitats up to 0.5 km away from water which make roads that parallel aquatic habitat a threat to both females and hatchlings (Reese and Welsh 1997; Rathbun et al. 2002; Pilliod et al. 2013). In fact, road mortality of females has been identified as a cause for male-biased sex ratios in some populations of pond turtles and other freshwater turtle species (Steen et al. 2006; Rosenberg et al. 2009; Reid and Peery 2014). Therefore, this species requires consideration of both aquatic and terrestrial connectivity to satisfy their annual resource requirements. Sonoran mud turtles also travel long distances within intermittent streams and thus may be at risk of roads that transect their aquatic habitat (Hensley et al. 2010).

Larger colubrid snakes (Family Colubridae; many genera) and rattlesnakes (genus *Crotalus*) were ranked among the highest risk from negative road effects. In addition to being attracted to paved road surfaces for thermoregulation, many large snakes have wide home-ranges or may move large distances between winter hibernacula and summer foraging areas. In contrast to smaller species, larger snakes are also less likely to avoid roads (Rosen and Lowe 1994; Andrews and Gibbons 2005; Andrews et al. 2008; Siers et al. 2016). High road mortality (e.g., Klauber 1931; Rosen and Lowe 1994; Jones et al. 2011), reduced abundance near roads (Rudolph et al. 1999; Jones et al. 2011), increased extinction risk (Row et al. 2007), and decreased genetic diversity (Clark et al. 2010; Hermann et al. 2017) have been documented for numerous snake species; as have positive responses to barriers and underpasses (Dodd et al. 2004; Colley et al. 2017). In our statewide risk analysis, coachwhips (genus *Masticophis/Coluber*) were amongst the highest risk groups at both the population and species-levels. These are particularly wide-ranging and very active foragers in comparison to other snake genera (Stebbins and McGinnis 2012). The coachwhip (*Masticophis flagellum)* was found to be ninefold more likely to be extirpated from habitats that were fragmented by roads and urbanization, contributing to their decline throughout California (Case and Fisher 2001; Mitrovich 2006). Similarly, habitat fragmentation from roads and urbanization were identified as primary threats to the Alameda whipsnake (*Masticophis lateralis euryxanthus* USFWS 2011). Although road use and mortality have been documented for many other terrestrial California snake species on road-riding surveys (e.g., Klauber 1931; Jones et al. 2011; Shilling and Waetjen 2017), there is a paucity of studies examining population-level effects of roads on California snake species. We could find only one such study, where presence of a highway was shown to reduce gene flow in the Western diamond-backed rattlesnake (*Crotalus atrox)* in the Sonoran Desert, AZ (Hermann et al. 2017).

Long foraging movements within aquatic habitats also contributed to the majority of garter snakes (genus: *Thamnophis*) falling within the highest road risk categories. Maintaining aquatic and wetland connectivity is of primary concern for these species. Garter snakes also use terrestrial habitats for overwintering, reproduction, and for moving among wetland or aquatic patches. Some migrate long distances to winter hibernacula, making them also susceptible to roads within adjacent terrestrial habitats (Roe et al. 2006; Jackson et al. 2015). The highly aquatic giant garter snake (*Thamnophis gigas*) had the highest aquatic road risk score. Because it moves only short distances on land (Halstead et al. 2015), mitigation may best focus on functional aquatic passages with lengths of adjacent road barriers based upon their terrestrial movement distances.

Toads were the third highest ranking group with 64% ranked in the highest risk categories. In particular, Bufonid toads (family Bufonidae) may move large distances ($>$ 1 km) in both aquatic and terrestrial habitats to satisfy their annual resource requirements; thus 5 of 7 bufonid species ranked high or very high risk from roads. Consistent with our risk assessment

Table 10 Aquatic risk ranking and population buffer distances

Risk Level (Aquatic)		Species			Risk Scores (Aquatic)		Movement Distances (Aquatic)		
Species	Population	Group	Common Name	Scientific name	Road Risk: Species- Level	Road Risk: Population-Level	95% Population Movement Distance (m)	Confidence in Distance Estimate	Surrogate Used
Very High	Very High	Snake	Giant Gartersnake	*Thamnophis gigas*	710	240	1556	Med/High	
	Very High	Turtle	Southern Western Pond Turtle	*Actinemys pallida*	707	320	3145	High	
	Very High	Snake	San Francisco Gartersnake	*Thamnophis sirtalis tetrataenia*	663	224	1146	Med	*T. sirtalis*
	Very High	Snake	California Red-sided Gartersnake	*Thamnophis sirtalis infernalis*	588	224	1146	Med	*T. sirtalis*
	Very High	Turtle	Northern Western Pond Turtle	*Actinemys marmorata*	547	320	3145	High	*A. pallida*
	Very High	Snake	Two-striped Gartersnake	*Thamnophis hammondii*	541	224	979	Low	*T.gigas (-37% for size diff)*
	High	Turtle	Sonoran Mud Turtle	*Kinosternon sonoriense*	399	168	1000	Med	
High	Med	Frog	Oregon Spotted Frog	*Rana pretiosa (Possibly extinct in CA)*	315	120	1300	Low	
	Very High	Snake	Sierra Gartersnake	*Thamnophis couchii*	304	192	1021	Low	*T.gigas (-34% for size diff)*
	Med	Frog	California Red-legged Frog	*Rana draytonii*	300	120	1864	High	
	Med	Toad	Sonoran Desert Toad	*Incilius alvariüs (Possibly extinct in CA)*	285	120	1400	Low/Med	*A. cognatus*
	Med	Toad	Yosemite Toad	*Anaxyrus canorus*	284	96	1152	Med/High	
	Med	Toad	Black Toad	*Anaxyrus exsul*	284	96	951	Low/Med	*A. canorus, A. punctatus*
	Very High	Snake	Common Gartersnake	*Thamnophis sirtalis*	271	224	1146	Med	
	High	Snake	Aquatic Gartersnake	*Thamnophis atratus*	266	168	889	Low	*T.gigas (-43% for size diff)*
	Med	Toad	Arroyo Toad	*Anaxyrus californicus*	248	96	1000	Med/High	
	High	Snake	Northwestern Gartersnake	*Thamnophis ordinoides*	245	168	775	Low	*T.gigas (-50% for size diff)*
	Very High	Snake	Western Terrestrial Gartersnake	*Thamnophis elegans*	240	192	931	Low	*T.gigas (-40% for size diff)*
	Med	Frog	Northern Red-legged Frog	*Rana aurora*	230	120	1864	Med	*R. draytonii*
Medium	High	Snake	Checkered Gartersnake	*Thamnophis marcianus*	210	144	835	Low	*T.gigas (-46% for size diff)*
	Med	Frog	Foothill Yellow-legged Frog	*Rana boylii*	199	90	2420	Med/High	
	Med	Toad	Great Plains Toad	*Anaxyrus cognatus*	175	120	1400	Med/High	
	Med	Toad	Woodhouse's Toad	*Anaxyrus woodhousii*	175	120	1400	Low/Med	*A. cognatus*
	Med	Toad	Western Toad	*Anaxyrus boreas*	130	120	1274	Low/Med	
	Med	Salamander	Red-bellied Newt	*Taricha rivularis*	72	72	600	High	
	Med	Salamander	California Newt	*Taricha torosa*	72	72	600	Med/High	*T. rivularis*
	Med	Salamander	Sierra Newt	*Taricha sierrae*	72	72	600	Med	*T. rivularis*
	Med	Salamander	Rough-skinned Newt	*Taricha granulosa*	72	72	600	Med	*T. rivularis*
	Med	Salamander	California Giant Salamander	*Dicamptodon ensatus*	72	72	600	Low	*Educated guess*
	Med	Frog	Cascades Frog	*Rana cascadae*	72	72	759	High	
	Med	Toad	Red-spotted Toad	*Anaxyrus punctatus*	72	72	750	Med	
Low	Low	Frog	Lowland Leopard Frog	*Lithobates yavapaiensis (Possibly extinct in CA)*	54	54	900	Low	
	Low	Frog	Southern Mountain Yellow-legged Frog	*Rana muscosa*	54	54	665	Med	
Very Low	Very Low	Salamander	Coastal Giant Salamander	*Dicamptodon tenebrosus*	48	48	600	Low	*Educated guess*
	Very Low	Frog	Pacific Treefrog	*Pseudacris regilla*	36	36	400	Low	*Educated guess*
	Very Low	Frog	Sierra Nevada Yellow-legged Frog	*Rana sierrae*	36	36	525	Med/High	
	Very Low	Frog	Coastal Tailed Frog	*Ascaphus truei*	30	30	266	Med/High	
	Very Low	Frog	California Treefrog	*Pseudacris cadaverina*	26	26	200	Low/Med	
	Very Low	Salamander	Southern Torrent Salamander	*Rhyacotriton variegatus*	5	5	50	Low/Med	*R. cascadae*

results, there is evidence that bufonid toads are particularly susceptible to negative impacts from roads elsewhere (Trenham et al. 2003; Orłowski 2007; Eigenbrod et al. 2008).

Roads and traffic have been associated with reduced abundance and species richness of frog populations (e.g., Fahrig et al. 1995; Houlahan and Findlay 2003). However, approximately half of California species are small, primarily aquatic, highly fecund, with relatively limited movements and thus ranked low for road impacts. Four of 11 species ranked within the highest risk groupings; California red-legged frog (*Rana draytonii*), Oregon spotted frog (*R. pretiosa*), Northern red-legged frog (*R. aurora*), and Cascades frog (*R. cascadae*). The Oregon spotted frog (*R. pretiosa*) is known to move large distances within aquatic habitats (Bourque 2008; USFWS 2009). Construction of a highway that bisected the

Yellowstone population of Oregon spotted frogs was one important factor that reduced the population dramatically in the 1950s (see discussion in Watson et al. 2003). Although portions of the populations show high site fidelity, California red-legged frog and Northern red-legged frog migrants can move large distances (> 1 km) across both aquatic and terrestrial habitats (Bulger et al. 2003; Fellers and Kleeman 2007; Hayes et al. 2007). Road mortality or habitat fragmentation from roads and urbanization were listed as primary threats to these species elsewhere (USFWS 2002; COSEWIC 2015).

Lizards had relatively low percentages of species in the high risk groupings. Many lizard species are small, non-migratory, territorial, have small home ranges and are thus at low risk of negative road effects. Similar to snakes, lizards can also be attracted to road surfaces for thermoregulation. A few wide ranging species scored in the highest risk categories including the Gila monster (*Heloderma suspectum*), leopard lizards (genus *Gambelia*) and two horned lizard species (genus *Phrynosoma*). The Gila monster has been negatively associated with urbanization, where larger home ranges and greater movement rates result in higher mortality for males (Kwiatkowski et al. 2008). Sensitive to habitat fragmentation, the blunt-nosed leopard lizard (*Gambelia sila*) was found to be largely absent from habitat patches less than 250 ha (Bailey and Germano 2015). Flat-tailed horned lizards (*Phrynosoma mccallii*) are also susceptible to habitat fragmentation with very large home ranges for their size, particularly in wet years (Young and Young 2000). In fact, road mortality is a well-known threat for this species (see review by CDFW 2016b). Horned lizards are also particularly vulnerable to being killed on roads due to their tendency to flatten and remain motionless while being approached (Young and Young 2000).

Salamanders also had relatively low percentages of species in the high risk grouping. Over 75% (35/46) of the California salamanders are lungless salamanders (Plethodontidae) and Torrent salamanders (Rhyacotritonidae). These species are mostly small, sedentary, non-migratory, closed habitat specialists with limited movement distances and these traits have resulted in a high level of speciation. This is exemplified by there being at least 20 species of slender salamanders (genus *Batrachoseps*) in California alone (Martinez-Solano et al. 2007; Vences and Wake 2007). However, within the salamander group, newts and several other migratory salamander species were ranked within the highest risk categories from negative road effects. There is substantial evidence that habitat fragmentation and mortality due to roads negatively affect many of these species. For instance, newts regularly migrate long distances over land from and to breeding ponds, and to terrestrial foraging habitats (> 2 km; Trenham 1998). Large numbers are found dead on roads during dispersal periods and newt species are often the first to disappear in fragmented landscapes (Gibbs 1998; Trenham 1998, Shields pers. comm.). Similarly, road mortality and habitat fragmentation are primary threats to the California tiger salamander and other Ambystomid salamanders because terrestrial habitat is used for interpond migration and overwintering (Semlitsch 1998; Trenham et al. 2001; Bolster 2010).

Because this assessment covers a wide array of species and habitats, the risk to particular species populations must be re-assessed on a local level. This includes consideration of the locations, types, and densities of roads in relation to population and species ranges along with goals for functional, meta-population, and genetic connectivity (e.g., Marsh and Jaeger 2015). Due to very low road densities in their limited ranges, some species and populations may be at lower risk. For instance the Gila monster, Oregon spotted frog, Sonoran mud turtle, Sonoran desert toad (*Incilius alvarius*) and Yosemite toad (*Anaxyrus canorus*) scored high due to life history and space-use characteristics, however their limited ranges are largely in protected or low road density areas in the state. Thus roads may not be a significant threat to these species in California. In contrast, high road densities may increase the risk for species within coastal regions such as remaining populations of Santa Cruz long-toed salamander (*Ambystoma macrodactylum croceum*), Alameda striped racer (*Masticophis lateralis euryxanthus*), and San Francisco garter snake (*Thamnophis sirtalis tetrataenia*). However, most species consist of numerous populations with a myriad of differing road-related threat levels. Although detailed species ranges and occupancy within ranges are well known for some species with very limited ranges, for most species range-wide surveys have not been conducted. Therefore, only general range boundaries are available that encompass large portions of the state and availability of species distribution models of habitat suitability and occupancy within their ranges is rare. This lack of detailed spatial information on species distribution

further limits the potential to incorporate road locations, types, and densities in a state and species-wide assessment.

We also note that relative risk to negative road impacts is provided for both populations and species. Risk was elevated for species with small and isolated ranges and that are facing a myriad of other threats. Because of this, a few common widespread species scored high at the population-level but not at the species-level. This included gopher snakes (*Pituophis catenifer*) and western toads (*Anaxyrus boreas*) where road mortality has been identified as a threat to the persistence of local populations (e.g., COSEWIC 2012; Jochimsen et al. 2014).

To potentially aid in local assessments, we have provided distance estimates or "buffer zones" that contain estimates for 95% of population-level movements for all species (e.g., Semlitsch and Bodie 2003). We provide all references evaluated for distance estimates in Appendix 2. Meta-population movements can be very important to the stability of pond-breeding amphibians (e.g., Semlitsch 2008; Jackson et al. 2015) and are included in many of the buffer zone calculations. However, we note that buffer zones may not include meta-population-level movements if the rate of these dispersal movements was less than 5% in the studies we used for our analyses.

This should be considered an initial assessment of susceptibility to negative road impacts in a hierarchical framework (e.g., see Level 2; Hobday et al. 2011). Therefore, as previously stated it will be important to re-assess the risk of specific populations to roads within their habitat and to evaluate and compare alternatives at the local scale (e.g., Suter 2016). This may include more detailed information on specific road attributes (e.g., density, type, location), as well as species behavior (Jaeger et al. 2005; Rouse et al. 2011; Rytwinski and Fahrig 2013; Jacobson et al. 2016). Age structured and spatially explicit population viability models are valuable tools to predict long-term population responses to roads and to compare outcomes of multiple mitigation scenarios (e.g., Gibbs and Shriver 2005; Borda-de-Água et al. 2014; Polak et al. 2014; Crawford 2015). Need and placement of mitigation structures can be guided by local population or meta-population dynamics, landscape attributes, movement routes, and road mortality hot spots (e.g., Bissonette and Adair 2008; Langen et al. 2009, 2015b; D'Amico et al. 2016; Loraamm and Downs 2016).

The quantity and quality of life history information, particularly movement data, are highly variable among species (see confidence levels; Tables 9 and 10). Therefore it is important to re-assess risk as new information becomes available. Finally, this is a structured assessment of comparative risk across a range of target species; therefore specific values for high risk have not been established. The ranking or assessment methodology should be adaptive and updated with advancements of road ecology science (e.g., Linkov et al. 2006).

Conclusion

Although roads are a significant cause of mortality and habitat fragmentation for many wildlife populations, road-related risk rankings have been based largely on expert opinion due to a scarcity of literature on road effects for most species. Therefore, we developed an objective and scientifically-based comparative risk approach to assess the potential threat from negative road impacts using species life history and movement data. After applying it to over 160 herpetofaunal species (and subspecies) in the state of California, the results are consistent with road ecology literature in identifying known high risk species, and call attention to some species not previously identified. Overall, we found that snakes and chelonids had the largest proportion of species at high risk for negative road impacts due to longer movement distances (home range and/or migratory), lack of road avoidance, and relatively low fecundity in comparison to other herpetofaunal groups. Results also indicated that consideration of aquatic connectivity appears to be under-represented for semi-aquatic herpetofauna that use both terrestrial and stream, riverine, or wetland habitats.

In addition to informing transportation planning and mitigation considerations for California herpetofauna, we believe this approach may be useful for comparing the risk of road-related fragmentation and mortality for species elsewhere and for other taxonomic groups. The results can help to inform multi-criteria threat assessments for special status species or those in consideration for listing. Finally, this serves to highlight species that may deserve further study and consideration for aquatic and terrestrial road mitigation to reduce mortality and to maintain population-level connectivity.

This risk assessment approach compares the susceptibility of species to negative road impacts. Commonly, there are numerous populations within a species range that occupy areas with greatly differing road pressures. Therefore, the actual risk to specific species populations will depend upon local road densities, road-types, traffic, and road locations in relation to species habitat and movement corridors.

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How does climate change cause extinction?

Abigail E. Cahill†, Matthew E. Aiello-Lammens†, M. Caitlin Fisher-Reid, Xia Hua, Caitlin J. Karanewsky, Hae Yeong Ryu, Gena C. Sbeglia, Fabrizio Spagnolo, John B. Waldron, Omar Warsi and John J. Wiens

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Anthropogenic climate change is predicted to be a major cause of species extinctions in the next 100 years. But what will actually cause these extinctions? For example, will it be limited physiological tolerance to high temperatures, changing biotic interactions or other factors? Here, we systematically review the proximate causes of climate-change related extinctions and their empirical support. We find 136 case studies of climatic impacts that are potentially relevant to this topic. However, only seven identified proximate causes of demonstrated local extinctions due to anthropogenic climate change. Among these seven studies, the proximate causes vary widely. Surprisingly, none show a straightforward relationship between local extinction and limited tolerances to high temperature. Instead, many studies implicate species interactions as an important proximate cause, especially decreases in food availability. We find very similar patterns in studies showing decreases in abundance associated with climate change, and in those studies showing impacts of climatic oscillations. Collectively, these results highlight our disturbingly limited knowledge of this crucial issue but also support the idea that changing species interactions are an important cause of documented population declines and extinctions related to climate change. Finally, we briefly outline general research strategies for identifying these proximate causes in future studies.

1. Introduction

Anthropogenic climate change is recognized as a major threat to global biodiversity, one that may lead to the extinction of thousands of species over the next 100 years [1–7]. Climate change is an especially pernicious threat, as it may be difficult to protect species from its effects, even within reserves [8,9]. Furthermore, climate change may have important interactions with other anthropogenic impacts (e.g. habitat loss [2,6]). Given this, understanding the responses of species to modern climate change is one of the most pressing issues facing biologists today.

But what do we actually know about how climate change causes extinction? It might seem that limited physiological tolerances to high temperatures should be the major factor that causes climate change to threaten the persistence of populations and species, and many studies have justifiably focused on these tolerances [10–13]. However, there may be many other proximate causes of extinction, even when anthropogenic climate change is the ultimate cause. These proximate factors include negative impacts of heat-avoidance behaviour [14], the climate-related loss of host and pollinator species [15,16] and positive impacts of climate change on pathogens and competitors [17,18], among others. The relative importance of these factors is unclear and has not, to our knowledge, previously been reviewed, despite increasing interest in mechanisms underlying the impacts of climate change [19].

Identifying these proximate causes may be critical for many reasons. For example, different proximate factors may call for different conservation strategies to ameliorate their effects [20]. These different proximate factors may

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also influence the accuracy with which the impacts of climate change are predicted and may drive populations to extinction at different rates.

In this paper, we address three topics related to how anthropogenic climate change causes extinction. First, we briefly review and categorize the many proposed factors that potentially lead to extinction from climate change. Second, we argue that there is already abundant evidence for current local extinctions as a result of climate change, based on the widespread pattern of range contractions at the warm edges of species' ranges (low latitude and low elevation). Third, and most importantly, we perform to the best of our knowledge, the first large-scale review of empirical studies that have addressed the proximate causes of local extinctions related to climate change. This review reveals some unexpected results. We find that despite intensive research on the impacts of climate change, only a handful of studies have demonstrated a proximate cause of local extinctions. Further, among those studies that have identified a proximate cause, very few implicate limited physiological tolerance to high temperatures as the main, direct cause. Instead, a diverse set of factors are supported, with species interactions being particularly important. Finally, we outline some of the research approaches that can be used to examine the proximate factors causing extinction from climate change.

2. Proximate factors causing extinction from climate change

We briefly review and categorize the diverse proximate factors that may cause extinctions due to climate change. We organize these factors by distinguishing between abiotic and biotic factors (following the literature on species range limits [21]). However, all factors are ultimately related to abiotic climate change.

We make several caveats about this classification. First, we emphasize broad categories of factors, so some specific factors may not be included. Second, some factors are presently hypothetical and have not yet been demonstrated as causes of extinction. Third, we recognize that these factors are not mutually exclusive and may act synergistically to drive extinction. They may also interact with other, non-climatic factors (e.g. habitat modification [2,6]) and many different ecological and demographic factors may come into play as populations approach extinction [22]. Finally, we do not address factors that impede climate-induced dispersal.

(a) Abiotic factors

(i) Temperature (physiological tolerances)

Many effects of anthropogenic climate change follow from an increase in temperature. The most obvious proximate factor causing extinction is temperatures that exceed the physiological tolerance of the species [10,12]. This factor may be most important in sessile organisms and those with limited thermoregulatory ability, and in regions and time scales in which temperature increase is greatest.

The impacts of temperature may also be more indirect, but still related to physiological tolerances. For example, in spiny lizards (*Sceloporus*), local extinctions seem to occur because higher temperatures restrict surface activity during the spring breeding season to a daily time window that is overly short [23]. Similarly, increased air temperatures may both decrease activity time and increase energy maintenance costs, leading organisms to die from starvation rather than from overheating [14]. In aquatic organisms, increased water temperatures may lead to increased metabolic demand for oxygen while reducing the oxygen content of the water [24]. Variability in temperature may also be an important proximate cause of extinction [25], including both extreme events and large differences over the course of a year. In temperate and polar latitudes, a mismatch between photoperiod cues and temperature may be important, with fixed photoperiod responses leading to activity patterns that are inappropriate for the changed climate [26]. Here, both low and high temperatures could increase mortality rates and lead to population extinction.

(ii) Precipitation (physiological tolerances)

Anthropogenic changes are also modifying precipitation patterns [27], and these changes may drive extinction in a variety of ways. For example, decreasing precipitation may lead directly to water stress, death and local extinction for terrestrial species [28], and loss of habitat for freshwater species or life stages [29,30]. There may also be synergistic effects between heat and drought stress (e.g. in trees [31]). Changing precipitation may be more important to some species than changing temperature, sometimes leading to range shifts in the direction opposite to those predicted by rising temperatures [32].

(iii) Other abiotic factors

Other abiotic, non-climatic factors may drive extinctions that are ultimately caused by climate change. For example, climate change can increase fire frequency, and these fires may be proximate causes of extinction (e.g. in South African plants [33]). Similarly, increases in temperature lead to melting ice-caps and rising sea levels [27], which may eliminate coastal habitats and modify the salinity of freshwater habitats [34].

(b) Biotic factors

The biotic factors that are the proximate causes of extinction from climate change can be placed in three general categories.

(i) Negative impacts on beneficial species

Climate change may cause local extinction of a given species by causing declines in a species upon which it depends. These may include prey for predators [35], hosts for parasites and specialized herbivores [16], species that create necessary microhabitats [36] and species that are essential for reproduction (e.g. pollinators [15]).

(ii) Positive impacts on harmful species

Alternately, climate change may cause extinction through positive effects on species that have negative interactions with a focal species, including competitors [37,38], predators [39,40] and pathogens [41–43]. Warming temperatures can also benefit introduced species, exacerbating their negative effects on native flora and fauna [44].

(iii) Temporal mismatch between interacting species

Climate change may also create incongruence between the activity times of interacting species [45]. These phenological

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mismatches may occur when interacting species respond to different environmental cues (e.g. temperature versus photoperiod for winter emergence) that are not congruently influenced by climate change [46]. We consider this category to be distinct from the other two because the differences in activity times are not necessarily negative or positive impacts on the species that are interacting with the focal species.

3. Are there current extinctions due to climate change?

Our goal is to understand which proximate factors cause extinctions due to climate change. However, we first need to establish that such extinctions are presently occurring. Few global species extinctions are thought to have been caused by climate change. For example, only 20 of 864 species extinctions are considered by the International Union for Conservation of Nature (IUCN) [47] to potentially be the result of climate change, either wholly or in part (using the same search criteria as a recent review [9]), and the evidence linking them to climate change is typically very tenuous (see the electronic supplementary material, table S1). However, there is abundant evidence for local extinctions from contractions at the warm edges of species' ranges. A pattern of range shifts (generally polewards and upwards) has been documented in hundreds of species of plants and animals [48,49], and is one of the strongest signals of biotic change from global warming. These shifts result from two processes: cold-edge expansion and warm-edge contraction (see the electronic supplementary material, figure S1). Much has been written about cold-edge expansions [21,50], and these may be more common than warm-edge contractions [51]. Nevertheless, many warm-edge contractions have been documented [52–58], including large-scale review studies spanning hundreds of species [48,59]. These warm-edge populations are a logical place to look for the causes of climate-related extinctions, especially because they may already be at the limits of their climatic tolerances [60]. Importantly, this pattern of warm-edge contraction provides evidence that many local extinctions have already occurred as a result of climate change.

We generally assume that the proximate factors causing local extinction from climate change are associated with the death of individuals. However, others factors may be involved as well. These include emigration of individuals into adjacent localities, declines in recruitment, or a combination of these and other factors. The question of whether climate-related local extinctions occur through death, dispersal or other processes has received little attention (but see [61,62]), and represents another important but poorly explored area in climate-change research.

4. What causes extinction due to climate change? current evidence

Given that there are many different potential causes of extinction as a result of climate change, and given that many populations have already gone extinct (as evidenced by warm-edge range contractions), what proximate causes of climate-related extinction have actually been documented? We conducted a systematic review of the literature to address this question.

(a) Causes of extinction: methods

We conducted three searches in the ISI Web of Science database, using the following keywords: (i) (('locally extinct' OR 'local extinction' OR 'extinc*') AND (caus*) AND ('climate change' OR 'global warming')); (ii) (('locally extinct' OR 'local extinction') AND ('climate change' OR 'global warming')); and (iii) (('extinc*' OR 'extirpat*') AND ('climate change' OR 'global warming' OR 'changing climate' OR 'global change')). The first two were conducted on 7 December 2011 and the third on 4 February 2012. Each search identified a partially overlapping set of studies (687 unique studies overall). We then reduced this to 136 studies which suggested that climate change is associated with local extinctions or declines (see the electronic supplementary material, appendix S1).

Among these 136 studies, we then identified those that reported an association between local extinction and climatic variables and that also identified a specific proximate cause for these extinctions (see the electronic supplementary material, appendix S1). The evidence linking these proximate causes to anthropogenic climate change varied considerably, but included studies integrating experimental and correlative results [23,63], and those that also accounted for factors unrelated to climate change [64]. Although we did not perform a separate, comprehensive search for all studies of climate-related declines, we also include studies of population declines that were connected to potential local extinctions as a second category of studies. Studies of declines should also be informative, given that the factors causing population declines may ultimately lead to extinctions [65]. All studies reported declines in abundance but some also considered declines in other parameters (e.g. fecundity). We also included studies of impacts from natural oscillations (such as the El Niño-Southern Oscillation, ENSO) as a third category of results.

(b) Causes of extinction: results

(i) Proximate causes of local extinctions

Of 136 studies focusing on local extinctions associated with climate change (see the electronic supplementary material, appendix S1), only seven identified the proximate causes of these extinctions (table 1 and figure 1*a*). Surprisingly, none of the seven studies shows a straightforward relationship between local extinction and limited tolerances to high temperature. For example, for the two studies that relate extinctions most directly to changing temperatures, the proximate factor is related either to how temperature limits surface activity time during the breeding season [23] or to a complex relationship between extreme temperatures (both cold and hot), precipitation and physiology [25,63]. Most studies (four of seven) implicate species interactions as the proximate cause, especially decreases in food availability [35,64,66]. Many authors have predicted that altered species interactions may be an important cause of extinction resulting from climate change (e.g. [67,68]), and our results empirically support the importance of these interactions (relative to other factors) among documented cases of local extinction.

(ii) Proximate causes of population declines

Seven studies identified proximate causes of population declines (table 2). The frequency of different proximate causes is intriguingly similar to those for population extinctions (figure 1*a*,*b*). Specifically, species interactions are the

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Table 1. Studies documenting the proximate causes of local extinction due to anthropogenic climatic change.

species	location	hypothesized proximate cause of local extinction	reference
American pika (*Ochotona princeps*)	Great Basin region, USA	limited tolerance to temperature extremes (both high and low)	[25,63]
planarian (*Crenobia alpina*)	Wales, UK	loss of prey as result of increasing stream temperatures	[35]
desert bighorn sheep (*Ovis canadensis*)	California, USA	decrease in precipitation leading to altered plant community (food)	[64]
checkerspot butterfly (*Euphydryas editha bayensis*)	San Francisco Bay area, CA, USA	increase in variability of precipitation corresponding with reduction of temporal overlap between larvae and host plants	[66]
fish (*Gobiodon* sp. A)	New Britain, Papua New Guinea	destruction of obligate coral habitat due to coral bleaching caused by increasing water temperatures	[36]
48 lizard species (genus *Sceloporus*)	Mexico	increased maximum air temperature approaches physiological limit, seemingly causing decreased surface activity during the reproductive season	[23]
Adrar Mountain fish species	Mauritania	loss of water bodies due to drought	[30]

proximate cause of declines in the majority of studies, with declines in food availability being the most common cause [69,71,72], along with disease [70]. Drying of aquatic habitats is the cause in one study [29]. Two studies show physiological tolerances to abiotic factors as responsible for declines, with the declines being due to desiccation stress in desert trees [28], and due to oxygen limitation at high temperatures in a fish [24]. However, we find again that no studies show a straightforward relationship between population declines and temperatures exceeding the critical thermal limits of physiological tolerance.

(iii) Proximate causes of extinction due to 'natural' climatic oscillations

Among the 136 studies, four documented proximate causes of climate-change related extinctions that were associated with climatic oscillations (table 3). These oscillations may increase in frequency and severity due to anthropogenic impacts ([77], but see [78]). All four studies reinforce the importance of species interactions as the proximate cause of many extinctions attributable to climate change (figure 1*c*), including climate-related losses of food resources [73,75], loss of an algal symbiont ('coral bleaching'; [74]) and pathogen infection [76].

Two of the most widely discussed examples of climate-change related extinctions involve chytrid fungus in amphibians and coral bleaching (including many examples given above [36,70,74,75]). In both cases, local extinctions are strongly connected to natural climatic oscillations (e.g. [74]), but the links to anthropogenic climate change are still uncertain. For example, Pounds *et al.* [42] concluded that chytrid-related declines and extinctions in the frog genus *Atelopus* are related to anthropogenic warming, but Rohr & Raffel [70] subsequently suggested that chytrid spread in *Atelopus* was largely due to El Niño events. The link between anthropogenic climate change and local extinction of coral populations through bleaching also remains speculative [79]. For example, severe climate anomalies can cause bleaching and coral mortality [80], but bleaching itself does not always lead to mass mortality [81].

(c) Proximate causes of extinction: synthesis

Our review of the proximate causes of population extinctions and declines due to climate change reveals three main results, which are concordant across the three categories of studies (extinctions, declines and climatic oscillations). First, very few studies have documented proximate factors (18 of 136). Second, a diversity of proximate causes are empirically supported. Third, changing interspecific interactions are the most commonly demonstrated causes of extinctions and declines (figure 1). Specifically, changes in biotic interactions leading to reduced food availability are the single most common proximate factor (figure 1). In contrast, limited physiological tolerances to high temperatures are supported only infrequently and indirectly (figure 1). Interestingly, the impacts of species interactions may be particularly difficult to document, inviting underestimation. However, we caution that these generalizations are based on few studies. For example, all three datasets (tables 1–3) are dominated by vertebrates, with only one plant study represented. Thus, the frequencies of documented proximate causes may change as the pool of studies becomes more taxonomically representative.

Finally, we note that we did not specifically address global species extinctions associated with climate change in our review. However, IUCN lists 20 species as extinct or extinct in the wild that potentially declined because of climate change (see the electronic supplementary material, table S1). Of these 20 species, seven are frogs that were possibly infected by chytrid fungus, which may be facilitated by climate change (see above). Four are snails, which may have become extinct as a result of drought. Two are freshwater fishes that lost their habitats because of drought. Among the six birds, two were also potentially affected by drought. The other four birds are island species possibly impacted by storms (the severity of which may be related to climate change), but these all had clear non-climatic threats. A similar pattern occurs in one island rodent species. In almost all cases, the links between extinction and anthropogenic climate change are speculative (but see [82]), which is why these cases were not included previously in our review. Intriguingly, none of the 20 is clearly related to

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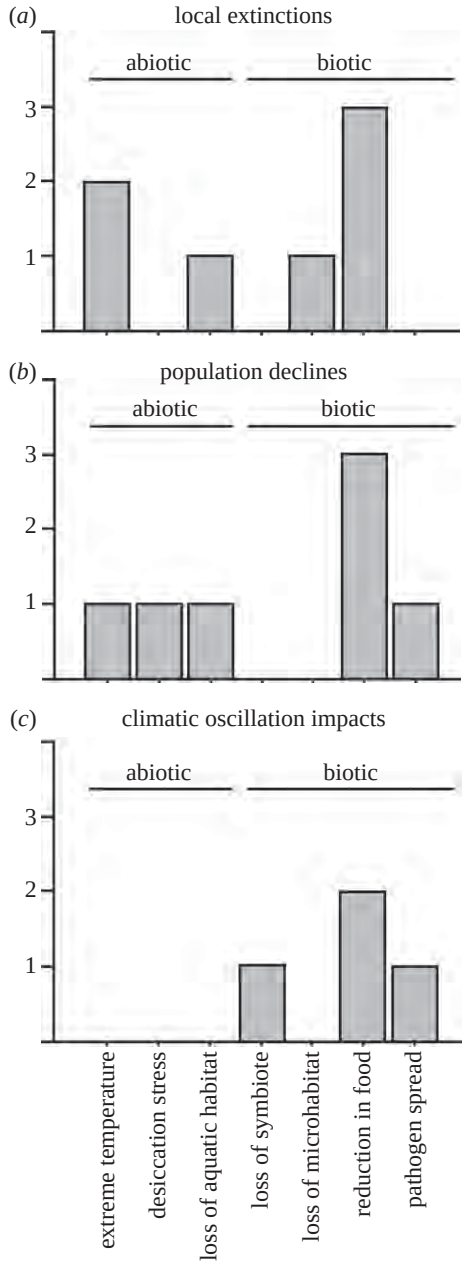

Figure 1. Summary of the frequency of different proximate causes of extinction due to climate change, among published studies. (*a*) 'local extinctions' refers to studies of local extinctions related to anthropogenic climate change (table 1), (*b*) 'population declines' refers to studies of declines in population abundance related to anthropogenic climate change (table 2), whereas (*c*) 'climatic oscillation impacts' refers to studies showing declines related to natural climatic oscillations (table 3) (but these oscillations may also be influenced by human factors, see relevant text). We note that there is some ambiguity in assigning some studies to a single, simple category.

limited tolerances to high temperatures (see the electronic supplementary material, table S1).

5. Approaches for finding the proximate causes of climate-related extinction

Our review demonstrates that disturbingly little is known about the proximate causes of extinctions due to recent climate change. How can this important gap be filled? Many approaches are possible, and we very briefly summarize two general frameworks that are beginning to be used. One focuses on individual species at multiple localities [23,25,63], the other on species assemblages at a particular locality [83–85]. These approaches are summarized graphically in the electronic supplementary material, figure S2.

Focusing on individual species (see the electronic supplementary material, figure S2), one must first document local extinctions or declines. To test whether populations have gone extinct, the present and past geographical ranges of the species can be compared. These analyses need not require surveying the entire species range, but could focus on a more limited series of transects (e.g. near the lowest latitudes and elevations, where ranges may already be limited by climatic factors [69,86]). The historical range can be determined from literature records and/or museum specimen localities [87]. These latter data are becoming increasingly available through online databases (e.g. GBIF; http://www.gbif.org/). Next, the species range (or select transects) should be resurveyed to document which populations are extant [23,56]. Evaluating whether populations persist is not trivial, and recent studies [56,88] have applied specialized approaches (e.g. occupancy modelling [89]). Furthermore, resurveys should account for false absences that may be misinterpreted as extinctions and for biases created by unequal sampling effort in space and time [87,90,91].

Documenting climate-related declines presents different challenges than documenting extinctions, given that most species lack data on population parameters over time. Some populations have been the focus of long-term monitoring, facilitating detailed studies of climate change impacts [86,92]. Large-scale databases on population dynamics through time are now becoming available. For example, the Global Population Dynamics Database [93] contains nearly 5000 time-series datasets. However, for many species, resurveying ranges to document local extinctions may be a necessary first step instead.

Given demonstrable local extinctions or declines, the next step is to determine whether these are related to large-scale trends in global climate change. Peery *et al.* [94] summarize six approaches that can be used to relate environmental factors to population declines [95]. These same approaches can be applied to connect global climate change and local extinctions. Relationships between changes in climate over time and population extinction versus persistence can be tested using GIS-based climatic data for relatively fine time scales (e.g. each month and year; PRISM; [96]). These analyses should preferably include data on other potential causes of local extinction not directly related to climate change, such as human habitat modification [64]. These analyses should help establish whether the observed local extinctions or declines are indeed due to climate change. If so, the next step is to understand their proximate causes.

Correlative analyses can be carried out to generate and test hypotheses about which proximate causes may be involved. Biophysical modelling [97] may be especially useful for these analyses, as it can incorporate many important factors, such as microclimate [98] and related variables (e.g. shade, wind speed, cloudiness, humidity) and relevant behavioural, ecological, demographic and physiological parameters [14,23]. Dissecting the specific aspects of climate that are most strongly associated with local extinctions may be important (e.g. is it warmer temperatures in the hottest part of the year, or the coldest?). Correlative studies can also test potential biotic factors, including the association between population extinctions or declines and the abundance of other species with negative impacts on the species in question (e.g. competitors, pathogens) or reductions in

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Table 2. Studies documenting the proximate causes of declines in abundance due to anthropogenic climatic change.

species	location	hypothesized proximate cause of decline	reference
aloe tree (*Aloe dichotoma*)	Namib desert	desiccation stress owing to decreasing precipitation	[28]
four species of amphibians	Yellowstone National Park, USA	increasing temperature and decreasing precipitation cause a decline in habitat availability (pond drying)	[29]
plover (*Pluvialis apricaria*)	United Kingdom	high summer temperatures reduce abundance of craneflies (prey)	[69]
eelpout (*Zoarces viviparus*)	Baltic Sea	oxygen limitation at high temperatures	[24]
frogs (genus *Atelopus*)	Central and South America	climate change facilitates spread of pathogen (chytrid fungus)	[70]
grey jay (*Perisoreus canadensis*)	Ontario, Canada	warm autumns cause rotting in hoarded food, compromising overwinter survival and breeding success in the following year	[71]
Cassin's auklet (*Ptychoramphus aleuticus*)	California, USA	changes in upwelling timing and strength lower both adult survival and breeding success by changing food availability	[72]

Table 3. Studies that report proximate causes of declines in abundance or fitness associated with El Niño-Southern Oscilliation (ENSO) events.

species	location	hypothesized proximate cause of decline	reference
fig wasps (Hymenoptera: Agonidae)	Borneo	ENSO event causes obligate host trees (*Ficus* sp.) to fail to produce inflorescences, resulting in local extinction of pollinating wasps	[73]
corals	Panama and Ecuador	high sea surface temperatures cause bleaching and mortality	[74]
butterflyfish	Indian Ocean	climate-related loss of coral food source	[75]
toad (*Bufo boreas*)	Western USA	warming reduces water depth in ponds, which increases ultraviolet-B exposure of embryos, which in turn increases risk of fungal infection	[76]

species necessary for persistence (e.g. prey, hosts). Two-species occupancy models [99] could be applied to test for the impacts of these and other types of interspecific interactions. Identifying the particular interactions that are responsible for climate-related extinctions may be challenging, given the diversity of interactions and species that may be involved. However, our results suggest that changing biotic interactions may be the most common proximate causes of climate-related extinction (figure 1).

Once potential factors are identified with correlative studies, these can be tested with mechanistic analyses. These could include experimental tests of physiological tolerances to relevant temperature and precipitation regimes [10,24,86,100], and laboratory and field tests of species interactions [39]. Transplant experiments that move individuals from extant populations into nearby localities where the species has recently gone extinct [100] may be particularly useful (for species in which this is practical). In many ways, experimental analyses can provide the strongest tests of the hypothesized causes of local extinctions. However, these should be informed by broader correlative studies. For example, simply testing the physiological tolerances of a species to extremely high temperatures may say little about the causes of climate-associated local extinction in that species if those extinctions are actually caused by warmer temperatures in winter or the spread of a competitor.

The second major approach (see the electronic supplementary material, figure S2) is to focus on species assemblages at single localities over time [83–85], rather than analysing multiple localities across the range of one or more species. Given data on species composition at different points in time, the local extinctions or declines of certain species can be tested for association with temporal changes in climate. These losses can then be related to specific biological traits (e.g. greater loss of species with temperature-cued flowering times versus those using photoperiod, or species for which the site is near their southern versus northern range limits [84]). These relationships can then point the way to more mechanistic and experimental studies.

6. Questions for future research

Understanding the proximate factors that cause climate-related extinctions should be an urgent priority for future research and should open the door to many additional applied and basic questions. Are there specific conservation and management strategies that can be matched to specific

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extinction causes? Are there phylogenetic trends or life-history correlates [20] of these factors that may allow researchers to predict which factors will be important in a species without having to conduct lengthy studies within that species? Do different factors influence the ability of niche models to accurately predict range shifts and extinctions due to climate change (e.g. physiological tolerances versus species interactions)? Can species adapt to some potential causes of extinction and not others?

7. Conclusions

Climate change is now recognized as a major threat to global biodiversity, and one that is already causing widespread local extinctions. However, the specific causes of these present and future extinctions are much less clear. Here, we have reviewed the presently available evidence for the proximate causes of extinction from climate change. Our review shows that only a handful of studies have focused specifically on these factors, and very few suggest a straightforward relationship between limited tolerance to high temperatures and local extinction. Instead, a diverse set of factors is implicated, including effects of precipitation, food abundance and mismatched timing with host species. Overall, we argue that understanding the proximate causes of extinction from climate change should be an urgent priority for future research. For example, it is hard to imagine truly effective strategies for species conservation that ignore these proximate causes. We also outline some general approaches that may be used to identify these causes. However, we make the important caveat that the relative importance of different proximate causes may change radically over the next 100 years as climate continues to change, and limited physiological tolerances to high temperatures may become the dominant cause of extinction. Nevertheless, our review suggests the disturbing possibility that there may be many extinctions due to other proximate causes long before physiological tolerances to high temperatures become predominant.

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Population persistence in landscapes fragmented by roads: Disentangling isolation, mortality, and the effect of dispersal

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ABSTRACT

Linear infrastructures, one of several forms of land-use, are a major driver of biodiversity loss. Roads impact populations at many levels, with direct road mortality and barrier effect contributing to decreased population abundance, higher isolation and subdivision, and therefore to increased extinction risk. In this paper, we compared the effect of road mortality and of the barrier effect on population isolation, persistence and size, and assessed the interaction of these effects with dispersal. We used a spatially explicit, process-based model of population dynamics in landscapes fragmented by varying levels of road density. We modelled a barrier effect independently from road mortality by varying the probability with which individuals avoid crossing roads. Both road mortality and the barrier effect caused population isolation. While road mortality alone had stronger negative effects than the barrier effect without extra mortality, the latter also resulted in decreased population size. Yet, road avoidance could, in some cases, rescue populations from extinction. Populations with a large dispersal distance were more negatively affected as road mortality increased. However, when there was no road mortality they maintained larger sizes than populations with a short dispersal distance. Our results highlight the much higher relative importance of road mortality than the barrier effect for population size and persistence, and the importance of assessing relevant species traits for effective long-term transportation planning and conservation management. Our model can be used in species-specific situations and with real landscape configurations in applications such as conservation planning.

1. Introduction

The current biodiversity crisis is mainly driven by land-use change (Pereira et al., 2012; Maxwell et al., 2016). Roads, one of many forms of land-use, cause major impacts on populations. As the road network is predicted to strongly increase in the coming years (van der Ree et al., 2015), it is crucial to assess its impact on populations, in order to apply suitable mitigation measures, and improve conservation and road planning.

Roads cause habitat loss and fragmentation, and decrease habitat quality. Roads also cause direct mortality through wildlife collisions with vehicles, and act as a barrier to movement (van der Ree et al., 2015). These direct and indirect impacts of roads can contribute to population isolation and subdivision, to decreases in population abundance, and therefore can increase population extinction risk (van der Ree et al., 2015; Ascensão et al., 2016), although there are also positive effects for some species (e.g., see Rytwinski and Fahrig, 2012, 2013).

Species traits can also influence population-level responses to land-use change (Pereira and Daily, 2006), and should be considered when assessing the effects of roads. Specifically, dispersal has been identified as an important factor but its influence on population persistence is still not fully understood. For example, while the role of dispersal is beneficial in metapopulation models (e.g., Hanski, 1998), because more patches can be colonized if dispersal is large, in source-sink models or reaction-diffusion models (e.g., Skellam, 1951; Pulliam, 1988) dispersal affects populations negatively, because it can lead to colonization of habitats where population growth rates are negative (sink habitats) (Pereira and Borda-de-Água, 2013). Moreover, dispersal can be associated with increased mortality risk (e.g., Nathan et al., 2012), with some studies suggesting there is an optimal intermediate dispersal rate

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for persistence in disturbed habitats (Casagrandi and Gatto, 1999).

The detrimental effect of dispersal in disturbed habitats is supported by several empirical studies (e.g., fragmented forests: Gibbs, 1998; Van Houtan et al., 2007). In the specific case of roads, a higher mobility has been related to negative effects of roads in mammal and bird species (Rytwinski and Fahrig, 2012). Furthermore, using a theoretical approach, Borda-de-Água et al. (2011) predicted that the larger the mean dispersal distance in a population, the larger would be the minimum area necessary for this population to persist in a landscape fragmented by roads.

In this paper we focus on dispersal movement as the process whereby individuals leave their initial location, move across a more or less suitable environment, and settle in a new location (Clobert et al., 2012; Matthysen, 2012). Our model does not currently include other types of movement (such as daily movements).

Direct road mortality introduces an additional source of mortality besides natural mortality. In addition, roads can also act as a barrier that does not introduce additional mortality, when the animals do not cross the roads. This barrier effect can be due to physical structures (such as fences) or to road avoidance behavior (e.g., Jaeger and Fahrig, 2004; Grilo et al., 2012), and for simplicity in this paper we refer to it simply as barrier effect. Although this can rescue individuals from road mortality to some extent, the negative consequences of habitat loss and fragmentation may be higher when such barrier effect is present, since road avoidance can lead to population isolation and to higher exposure to demographic and environmental stochasticity (Rytwinski and Fahrig, 2012; Ascensão et al., 2016). Moreover, the effects of road mortality and of road avoidance can be confounded and are still to be properly disentangled. For example, reduced population abundance near roads may be due to direct road mortality, or due to road avoidance behavior (e.g., Fahrig et al., 1995).

Although there is evidence that the effects of roads on population abundance are in general negative (Rytwinski and Fahrig, 2015), the impact of roads on population persistence has not been so commonly addressed (but see, for example Borda-de-Água et al., 2014 and Ceia-Hasse et al., 2017).

The key issue addressed in this paper was to disentangle the influence of an additional source of mortality (direct road mortality) versus the influence of a barrier effect to movement that does not introduce such additional mortality on population isolation, persistence and size, as well as the influence of dispersal, in fragmented landscapes. We addressed this using roads. We use a spatially explicit, process-based model of population dynamics. Our questions were: (1) What is the importance of road mortality versus isolation, for population persistence and size in landscapes fragmented by roads?; (2) How does dispersal influence the size and the persistence of populations under varying levels of road mortality and of a barrier effect?

2. Materials and methods

We used an individual-based toy model of population dynamics to perform a theoretical study on the effects of road mortality, barrier effect and dispersal on population isolation, size and persistence of a virtual species. Our study is not based on any empirical data and thus is more appropriately considered under the virtual ecology rationale (e.g., Grimm, 1999; Zurell et al., 2010).

2.1. Model description

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing agent-based models (Grimm et al., 2006, 2010). The model was implemented as an ANSI C++ program, which can be downloaded from https://github.com/anaceiahasse/landsim.

2.1.1. Purpose

The purpose of the model is to simulate population dynamics in fragmented landscapes. Specifically, in this study, the model simulated population dynamics in landscapes fragmented by roads, with special emphasis on the effects of road mortality, of a barrier effect without mortality, and on the influence of dispersal distance.

2.1.2. Entities, state variables, and scales

The entities of the model are the landscape and the individuals, i.e., the model keeps track of the features of the landscape and of the female population (the model only considers female individuals for simplicity).

The landscape is a two-dimensional grid of N x N square cells with reflecting boundaries. An alternative approach to deal with edge effects would have been to consider periodic boundary conditions (i.e., torus geometry) instead of reflecting boundaries. However, given a dispersal step size of only one cell and the large size of the grid, both approaches can lead to similar outcomes. Each cell of the landscape is assigned to one of n possible types with values varying between 0 and 1. In the present case, each cell belongs to one of two possible types, "high-quality" habitat (non-road) or "road", with values of "1″ and "0″, respectively. We generated several landscapes with different proportions of road cells, where roads were placed perpendicularly to one another (Fig. 1, Table 1). We used simple hypothetical regular road networks because our main objective was to disentangle the effects of sink mortality versus those of a barrier effect that does not introduce additional mortality. Sink mortality here corresponds to road mortality, and it is the probability that an individual dies when crossing a road (see Section 2.1.7.3 below). Our goal was to derive general principles that can be the basis to understanding and model more specific or complex cases.

Individuals are characterized by the following state variables: age, developmental stage (juvenile or adult), position in the landscape; and by the following attributes: fecundity, age at first breeding, natural survival probability, home range size, dispersal distance, road mortality probability, road avoidance probability (Table 1).

2.1.3. Process overview and scheduling

Each simulation time step consists of the following sequential events (Fig. 2, Table 1): reproduction; natural mortality; dispersal of juveniles; juvenile density-dependent mortality. Section 2.1.7 describes the submodels implementing these processes. Juveniles that establish a home range are inserted into the adult population at the end of each simulation time step, thereby updating population size and landscape cell availability for the following time step. At the beginning of each simulation time step, the age of each individual is updated (increased by 1), and the sequential steps listed above ensue.

2.1.4. Design concepts

2.1.4.1. Basic principles. Roads can contribute to population isolation, decreased size and increased extinction risk through direct mortality and barrier effects (e.g., van der Ree et al., 2015; Ascensão et al., 2016). Dispersal can also influence how roads impact populations (e.g., Borda-de-Água et al., 2011; Rytwinski and Fahrig, 2012). The model allows assessing the relative importance of these factors for population isolation, persistence and size, which is not yet fully understood.

2.1.4.2. Emergence. Population dynamics emerges from the model (i.e. from the set of rules defined, parameter values used and landscape configuration).

2.1.4.3. Adaptation. Juveniles choose the direction in which they disperse according to cell type (road versus high-quality habitat cell) and occupancy (they may avoid dispersing into road cells with a given probability and they do not disperse to occupied cells, respectively).

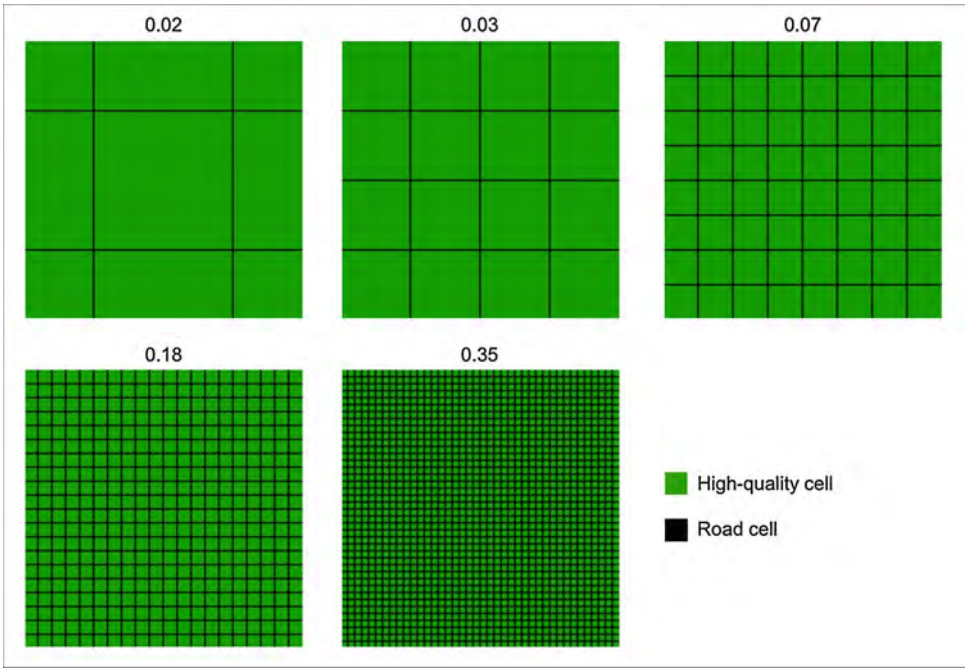

Fig. 1. Landscape configurations used in simulations. Each landscape is a grid of 200 × 200 cells composed of high-quality habitat cells, and road cells. Numbers on top of each panel indicate the proportion of road cells in each landscape.

Table 1
Model parameters and values used in the simulations.

Parameter	Value	
	1st set of simulations	2nd set of simulations
Landscape size (*N x N*)	200 × 200 cells	
Initial population size	10 individuals	
Number of replicates	100	
Number of time steps	1000	
Fecundity (b_i)	2	
Survival probability (s)	0.4	
Dispersal distance (d)	5 or 50 cells	
Road mortality, Road avoidance (m_{RM}, p_{RA})	(0.0, 0.0); (0.0, 1.0); (1.0, 0.0)	varied from 0 to 1 in steps of 0.1
Proportion of road cells in the landscape	0.02, 0.03, 0.07, 0.18, 0.35	0.07, 0.35

2.1.4.4. Sensing. During dispersal, juveniles evaluate cell type (road versus non-road cell) and occupancy.

2.1.4.5. Interaction. Juveniles do not disperse through cells that are already occupied.

2.1.4.6. Stochasticity. Stochasticity was incorporated in several processes (reproduction, natural mortality, dispersal of juveniles); see Section 2.1.7 for details.

2.1.4.7. Observation. For each model run, we recorded population size at the end of each simulation and averaged population size across replicates. We calculated the probability of extinction as the proportion of replicates in which populations went extinct before the end of the simulation.

2.1.5. Initialization

The model starts by settling an initial population of females at breeding age in the landscape. After the initial population is created, each simulation time step consists of the events described in Section 2.1.7 (Submodels). In all simulations, the initial population size was 10 individuals, set at random in the landscape. See Table 1 for the remaining parameter values used in the simulations and Fig. 3 for a representation of the settlement of the initial population in the landscape and of the colonization of the landscape.

2.1.6. Input data

The model does not import data of driving environmental variables.

2.1.7. Submodels

2.1.7.1. Reproduction. Females reproduce after one year and once they have established their home range. The number of female juveniles that a breeding female produces follows a Poisson distribution with mean equal to its fecundity b_i.

2.1.7.2. Natural mortality. Adults and juveniles die with probability (1 - s). When an individual dies it is removed from the population and its home range cell is made available for dispersing individuals.

2.1.7.3. Dispersal of juveniles. In our model adults do not move, and do not get killed by direct road mortality. Only juveniles disperse. Each juvenile disperses a fixed number of cells from its mother cell. A dispersal step is always to one of the four neighboring cells (von Neumann neighborhood), and is composed of the following events (Fig. 2b): (1) the individual evaluates whether its four neighboring cells are occupied or free, and does not disperse to occupied cells; (2) the individual evaluates whether the free neighboring cells correspond to roads or not, and can avoid dispersing through road cells with probability p_{RA}; (3) if the individual disperses through a road cell, sink dispersal mortality (road mortality) is applied with probability m_{RM}. The dispersal process is not stopped when the individual finds a first suitable empty cell; instead it continues until the individual either dies (due to road mortality), or disperses over his dispersal distance, d. An individual is allowed to move back to a cell it has previously visited. Therefore, two neighboring unoccupied cells are sufficient for an individual to survive over any number of dispersal steps. Moreover, each juvenile disperses from its mother cell, but given natural mortality that cell may be freed, and in that case it can be occupied by a juvenile. The default probability of dispersing to any neighboring cell is 1. However, if all four neighboring cells are occupied, and since

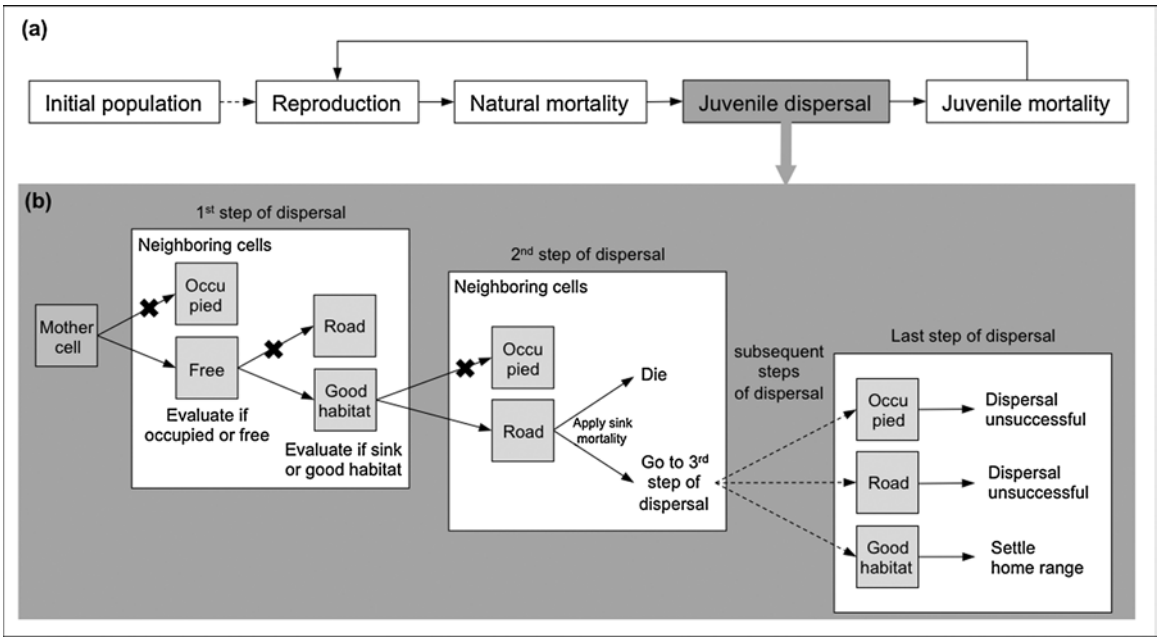

Fig. 2. Scheme of the model. (a) Schematic representation of the complete model simulation steps. (b) Schematic representation of juvenile dispersal. The x in (b) indicate that the individual does not disperse to occupied cells, and that it will disperse to a good habitat cell over a road cell.

individuals do not disperse to occupied cells, then the individual cannot move and dispersal is unsuccessful. If the cell in which the individual is at the end of dispersal is a road, dispersal is also unsuccessful. If dispersal is successful, the individual can settle a home range. In this study, we set the home range size to one cell and only one individual can establish its home range in each cell.

2.1.7.4. Juvenile density-dependent mortality. Following unsuccessful

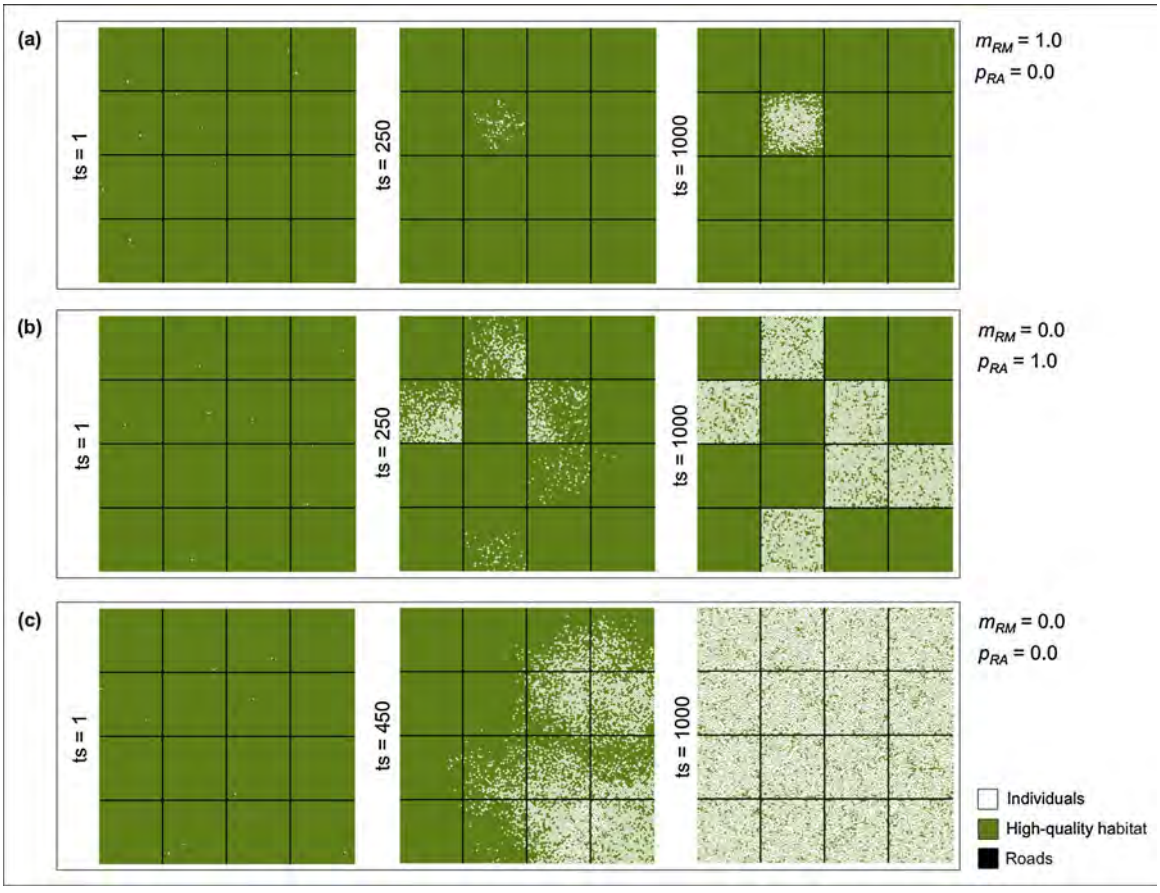

Fig. 3. Representation of the colonization of the landscape by a population under different combinations of values of road mortality probability (m_{RM}) and of road avoidance probability (p_{RA}), in different time steps (ts) of a model run. In the example shown, the dispersal distance is set to 50 cells (i.e. large dispersal) and the proportion of road cells in the landscape is 0.03.

dispersal, juveniles that did not establish their home range are removed from the population.

2.2. Simulations

We created five landscapes of 200 × 200 cells with perpendicular roads, each with a different proportion of road cells (Fig. 1, Table 1). We used two dispersal distances: short (5 cells), and large (50 cells), the latter of which we deemed reasonable considering the total size of the grid (40,000 cells). We modelled a barrier effect independently from sink mortality by varying the probability with which individuals do not cross roads while dispersing.

We performed two sets of simulations. In the first set of simulations, we assessed the effect of different extreme scenarios of road mortality and of road avoidance in landscapes with different proportions of road cells: (i) road mortality probability was one and there was no road avoidance; (ii) road avoidance probability was one and there was no road mortality; (iii) road mortality and road avoidance probabilities were both zero, for each dispersal distance and each road density. To assess the combined effects of road mortality and of road avoidance, in the second set of simulations we varied road mortality and road avoidance probabilities both at the same time independently from 0 to 1 in steps of 0.1 (i.e., using all combinations possible), for each dispersal distance (Table 1).

In all simulations, we used fixed values of the remaining parameters (Table 1), simulating the dynamics of hypothetical animal populations in hypothetical landscapes, because our main objective was to obtain general predictions on the differential effects of road mortality versus a barrier effect that did not introduce additional mortality (due to road avoidance behavior or physical structures such as fences), under different levels of dispersal.

We ran each simulation for 1000 time steps, to ensure that population size did not vary by more than 10% between consecutive simulation time steps, for at least the last 10 simulation time steps, and ran 100 replicates for each combination of values of parameters (Table 1).

Our computer program was extensively debugged, thus we are confident that the program is reproducing accurately the intended model. Being an individual-based model computer simulation, we performed our simulations under a set of assumptions that we deemed reasonable, and we tested them for a wide range of parameter values, obtaining the expected results.

Our model takes as input the model parameters and a two-dimensional matrix with the landscape. It produces a file containing the location of the home range of each adult in the landscape at each time step, and the population age structure at each time step. To apply the model to other species and landscape configurations, users can choose the values of the parameters specific to the species or population of interest, and a matrix with the desired landscape configuration.

3. Results

In our simulations, isolation occurred due to road mortality or to road avoidance (Fig. 3). With complete road mortality and no avoidance (Fig. 3a), or with complete avoidance and no road mortality (Fig. 3b), the landscape was only partially occupied. In contrast, when there was no mortality and no avoidance (Fig. 3c), the whole landscape was occupied.

When there was no road mortality and no road avoidance, the probability of extinction was higher and the population size was smaller at higher road densities, suggesting an effect due to habitat loss (Fig. 4). Nevertheless, with no road mortality and no road avoidance, the probability of extinction was zero or close to zero, even with high road density (Fig. 4a); and the population size was considerably larger than with either complete road avoidance, or complete road mortality (Fig. 4b). These results suggest that in such cases there was an effect of road avoidance or of road mortality, respectively.

The probability of extinction was higher and the population size was smaller when there was road mortality alone, than when there was road avoidance alone, except at the highest road density (Fig. 4). However, population size was much smaller at all road densities when there was road avoidance than in the case with no road avoidance and no road mortality (Fig. 4b).

When assessing the combined effects of road mortality and of road avoidance for different dispersal distances at the highest road density, the probability of extinction increased and the population size decreased with increasing road mortality (horizontal lines in Fig. 5). For a constant value of road mortality (vertical lines in Fig. 5), probability of extinction decreased and population size increased with increasing road avoidance. However, at this road density, the good habitat patches delimited by roads were small (16 cells), and populations went extinct when road avoidance was complete, even without road mortality.

The role of dispersal varied with road mortality. The probability of extinction increased and the population size decreased much faster with increasing road mortality for the large than for the short dispersal distance. However, when there was no road mortality, the probability of extinction was higher (Fig. 5a) and the population size was smaller (Fig. 5b) for the short dispersal distance.

Similar patterns were observed when assessing these effects at a lower road density (proportion of road cells in the landscape = 0.07; Fig. S1 in Appendix). However, they were less obvious than in the case of high road density, especially for the short dispersal distance: the probability of extinction was low, and the population sizes varied less. Nevertheless, population size strongly decreased with complete road avoidance, or with complete road mortality, for both dispersal distances, as in the case of high road density (Fig. 5).

Note that for the short dispersal distance and also for most of the large dispersal distance simulations in Fig. S1, while the probability of population extinction is close to zero, the population size is low, both when road mortality is one, and when road avoidance is one. This is because many individuals die on roads (when road mortality is one), or the population can only occupy part of the landscape (when road avoidance is one).

4. Discussion

Our results allow to make inferences about the differential effects of sink mortality versus those of a barrier effect without additional mortality, and the role of dispersal, on population persistence, isolation and size, which were the goals of this study. While habitat amount was kept constant when road mortality probability and road avoidance probability were varied with a same road density, it should nevertheless be taken into account that by generating landscapes with habitats and roads as grid cells, and by using a regular road network pattern, landscapes with higher road densities have lower total habitat amount and smaller habitat patches. In this sense, there were three effects present (i.e., road mortality, road avoidance, and habitat amount change).

4.1. Importance of road mortality versus a barrier effect without mortality for population persistence and size

Road mortality alone had a stronger negative effect on the probability of persistence and on population size than road avoidance alone. Road avoidance could also in some cases rescue populations under low to moderate road mortality from extinction, as suggested by other authors, since road avoidance decreases the probability that individuals cross roads, therefore reducing mortality caused by collision with vehicles (Jaeger and Fahrig, 2004; Rytwinski and Fahrig, 2013). Previous studies also suggest that the genetic effects of road mortality are stronger than those of the barrier effect without road mortality (e.g., Jackson and Fahrig, 2011; Ascensão et al., 2013).

In our simulations, population isolation occurred both when there was road mortality, or when there was a barrier effect without

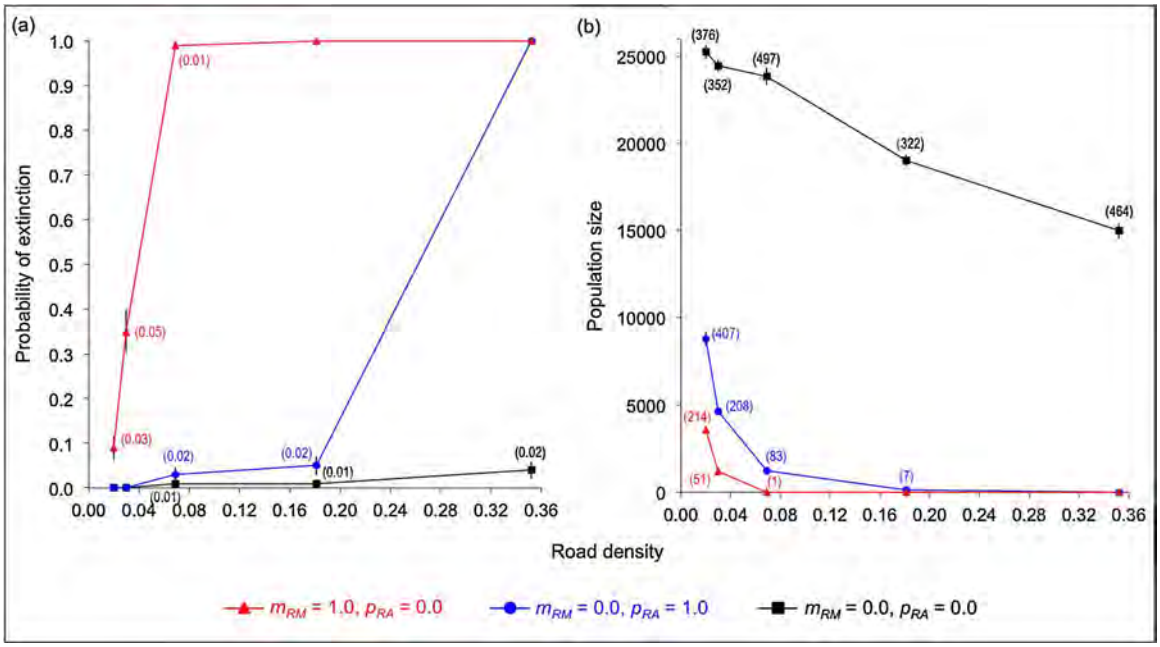

Fig. 4. Probability of population extinction (a) and population size (b) for the different proportions of road cells in the landscape, for different combinations of values of road mortality probability (m_{RM}) and of road avoidance probability (p_{RA}). Results shown are for the large dispersal distance (50 cells). Error bars correspond to the standard error of the mean, whose values are indicated in brackets (when different from zero).

additional mortality. Populations persisted even when road avoidance was very high, provided that the road mortality was low to moderate. Only complete road avoidance led populations to extinction, when road density was the highest. In those cases, individuals were isolated within the small patches of good habitat that were bounded by roads, and the resulting small populations exhibited an increased extinction risk due to demographic stochasticity (Lande, 1993).

Habitat fragmentation impairs species persistence and ecosystem functions. Moreover, the several effects of fragmentation are interlinked and can operate over long time scales (Haddad et al., 2015). In our analysis, population sizes were negatively affected when road avoidance was complete regardless of the road density, even if there was no road mortality. Population sizes were much smaller when compared to the cases with no road avoidance (and no road mortality). This may influence population persistence in the long-term, especially if other factors of disturbance come into play. For example, we did not vary habitat quality (all non-road cells had maximum habitat quality), because our aim was to obtain general predictions on the differential effects of road mortality versus those of a barrier effect without mortality. However, habitat quality can influence how roads affect populations (e.g., Grilo et al., 2014) and therefore the habitat quality of the non-road cells could be varied in more detailed studies, for example by including species-specific information on habitat preferences.

Moreover, although not included explicitly in our analysis, traffic volume is also important to consider when assessing the effects of roads on populations and in landscape connectivity studies, since traffic intensity may influence both road mortality and road avoidance, and thus population persistence (Jaeger et al., 2006; Jaeger, 2007; Charry and Jones, 2009; van Langevelde and Jaarsma, 2009; van Strien and Grêt-Regamey, 2016). Several studies suggest that road mortality may be higher at intermediate traffic volumes than high traffic volumes, because at higher traffic volumes road avoidance will be higher for many species (e.g., Seiler 2005; Grilo et al., 2015).

However, the focus of our analysis was on comparing the effects of road mortality vs. those of a barrier that does not introduce additional mortality, which can be due to road avoidance behavior but also due to physical structures such as fences (e.g., Jaeger and Fahrig, 2004; Grilo et al., 2012). Hence we modeled these directly as the probability of an individual dying on a road while crossing it, and the probability of an individual not crossing a road, regardless of the cause (e.g., road surface avoidance behavior, road avoidance due to traffic, fences), and therefore we did not consider traffic volume explicitly.

Additionally, while in our simulations individuals only evaluated their immediate neighboring cells in each step of dispersal, some species avoid roads from a distance (e.g., Jaeger et al., 2005), which may exacerbate the effects of habitat loss and fragmentation. Including microevolution in our individual-based model, which is fundamental to capture the response of organisms to changing conditions (Grimm and Berger, 2016), would also allow analysing eco-evolutionary responses to fragmentation (Haddad et al., 2015).

4.2. *Influence of dispersal distance on population persistence and size*

The role of dispersal distance varied depending on the values of road mortality. In fragmented landscapes, as was the case in all our simulations since roads were always present, populations with a larger dispersal distance showed a lower probability of extinction and maintained larger sizes, provided an additional source of mortality due to roads was not present. However, a large dispersal distance was detrimental for population size and persistence as road mortality increased.

We used fixed dispersal distances in our simulations. However, dispersal distance is usually stochastic (e.g., Nathan et al., 2012), and therefore it would not only be interesting but also add realism to the model by implementing dispersal kernels to determine dispersal distances (e.g., Austerlitz et al., 2004; Chipperfield et al., 2011), instead of using fixed dispersal distances.

Furthermore, in our simulations, dispersing individuals only evaluated their immediate four neighboring cells in each dispersal step, which can be considered as a biased random walk (e.g., Turchin 1998). While this has been a common choice to model movement with an orientation component (e.g., Börger et al., 2008), expanding the perceptive range of dispersing individuals would increase the realism and facilitate the transferability of the model to concrete situations.

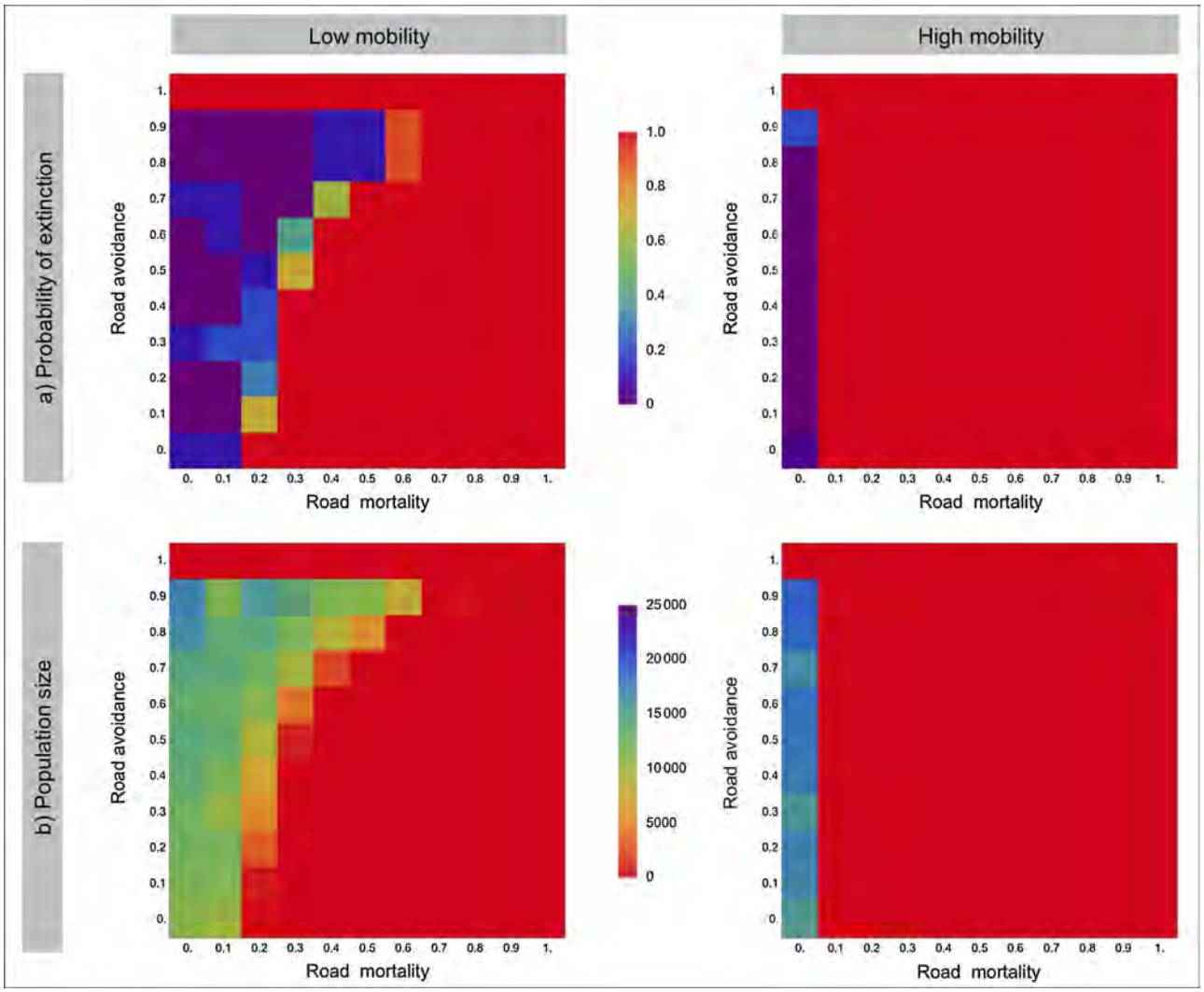

Fig. 5. Probability of population extinction (a) and population size (b) as a function of road mortality and road avoidance, for different dispersal distances (Low mobility = 5 cells; High mobility = 50 cells) in the landscape with the highest proportion of road cells in the landscape (0.35).

4.3. Limitations

The type of movement (juvenile dispersal) considered in our paper can have a large influence on individual fitness and population structure (Matthysen, 2012). However, our model does not currently include other types of movement (such as daily movements), and thus adults do not get killed due to road mortality. This is a simplification, because in real contexts animals will encounter roads during other types of movement as well. Therefore, it would be important to include such types of movement in the analysis.

Furthermore, in our model each juvenile disperses over a fixed number of cells, which implies that individuals may end their dispersal movement on a road (or right of way). This could correspond to situations where there are no other options for dispersal, e.g., all neighboring areas already occupied or corresponding to unsuitable habitat, but it should be considered as a simplification of real cases.

We used two dispersal distances in our simulations because we wanted to ensure that we were comparing the roles of contrasting dispersal distances, i.e., a short vs. a large dispersal distance. Including a wider range of dispersal distances could help further understand the role of dispersal in these fragmented landscapes, as some studies suggest there is an optimal intermediate dispersal rate for persistence in disturbed habitats (Casagrandi and Gatto, 1999).

We used a virtual species and simple hypothetical regular road networks because our main goal was to disentangle the effects of road mortality versus those of a barrier effect without such mortality. However, this implies that our results hold for the virtual species in the regular road network used.

4.4. Conclusions and future research directions

Our results highlight the much higher relative importance of road mortality than the barrier effect (without road mortality), and of assessing relevant species traits such as dispersal distance. We emphasize three results of our study: first, that even though population persistence was not impaired when road avoidance was complete (except when suitable habitat patches became too small to sustain viable populations), population size was considerably decreased, which is important to consider in long-term conservation management; secondly, that a large dispersal distance is not necessarily always detrimental for population size and persistence in fragmented landscapes if mortality in unsuitable habitats is low, which calls for further investigation; and thirdly, that population isolation occurred in extreme cases (i.e., complete road mortality or a complete barrier effect without road mortality). These may be especially important for species expected (Rytwinski and Fahrig, 2013) or observed (e.g., some snakes and turtles; Shepard et al., 2008) to avoid roads, and for species for which road avoidance increases with increasing traffic volume (e.g., carnivores and

ungulates; Dyer et al., 2002; Alexander et al., 2005; Leblond et al., 2013).

Finally, our model can stimulate other studies, either theoretical or empirical. Our results hold for the virtual species in the regular road network used, but our model can be applied to species-specific situations, by using the specific trait values of the species or population of interest. Information on model parameter values (initial population size, fecundity, age at first breeding, survival probability, home range size, dispersal distance, road mortality, or road avoidance) can be obtained from published databases, individual studies, or derived from related or ecologically similar species, and using allometric relationships (e.g., Jones et al., 2009; Borda-de-Água et al., 2014; Salguero-Gómez et al., 2016; Ceia-Hasse et al., 2017). For example, data on population density can be used to determine the initial population size. Data availability is usually higher for vertebrates and within these for mammals, followed by birds. This is also true for data on road mortality, and especially on road avoidance behavior, for which species-specific information is lacking for many species (Rytwinski and Fahrig, 2012).

Furthermore, although we used only simple hypothetical regular road networks in our simulations, the modelled landscape can represent real landscapes with real road configurations, and can hence also be used to evaluate the impact of different mitigation options for increasing population persistence, in environmental impact assessments, and for conservation planning.

Acknowledgments

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ecolmodel.2018.01.021.

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Rapid Range Shifts of Species Associated with High Levels of Climate Warming

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The distributions of many terrestrial organisms are currently shifting in latitude or elevation in response to changing climate. Using a meta-analysis, we estimated that the distributions of species have recently shifted to higher elevations at a median rate of 11.0 meters per decade, and to higher latitudes at a median rate of 16.9 kilometers per decade. These rates are approximately two and three times faster than previously reported. The distances moved by species are greatest in studies showing the highest levels of warming, with average latitudinal shifts being generally sufficient to track temperature changes. However, individual species vary greatly in their rates of change, suggesting that the range shift of each species depends on multiple internal species traits and external drivers of change. Rapid average shifts derive from a wide diversity of responses by individual species.

Threats to global biodiversity from climate change (*1-8*) make it important to identify the rates at which species have already responded to recent warming. There is strong evidence that species have changed the timing of their life cycles during the year and that this is linked to annual and longer-term variations in temperature (*9–12*). Many species have also shifted their geographic distributions toward higher latitudes and elevations (*13–17*), but this evidence has previously fallen short of demonstrating a direct link between temperature change and range shifts; that is, greater range shifts have not been demonstrated for regions with the highest levels of warming.

We undertook a meta-analysis of available studies of latitudinal (Europe, North America, and Chile) and elevational (Europe, North America, Malaysia, and Marion Island) range shifts for a range of taxonomic groups (*18*) (table S1). We considered $N = 23$ taxonomic group × geographic region combinations for latitude, incorporating 764 individual species responses, and $N = 31$ taxonomic group × region combinations for elevation, representing 1367 species responses. For the purpose of analysis, the mean shift across all species of a given taxonomic group, in a given region, was taken to represent a single value (for example, plants in Switzerland or birds in New York State; table S1) (*18*).

The latitudinal analysis revealed that species have moved away from the Equator at a median rate of 16.9 km decade^{-1} (mean = 17.6 km decade^{-1}, SE = 2.9, $N = 22$ species group × region combinations, one-sample t test versus zero shift, $t = 6.10$, $P < 0.0001$). Weighting each study by the √(number of species) in the group × region combination gave a mean rate of 16.6 km decade^{-1}. For elevation, there was a median shift to higher elevations of 11.0 m uphill decade^{-1} (mean = 12.2 m decade^{-1}, SE = 1.8, $N = 30$ species groups × regions, one-sample t test versus zero shift, $t = 7.04$, $P < 0.0001$). Weighting elevation studies by √(number of species) gave a mean rate of uphill movement of 11.1 m decade^{-1}.

A previous meta-analysis (*14*) of distribution changes analyzed individual species, rather than the averages of taxonomic groups × regions that we used, and also included data on latitudinal and elevational shifts in the same analysis (*18*). It concluded that ranges had shifted toward higher latitudes at 6.1 km decade^{-1} and to higher elevations at 6.1 m decade^{-1} (*14*), whereas the rates of range shift that we found were significantly greater [$N = 22$ species groups × regions, one-sample t test versus 6.1 km decade^{-1}, $t = 3.99$, $P = 0.0007$ for latitude; $N = 30$ groups × regions, one-sample t test versus 6.1 m decade^{-1}, $t = 3.49$, $P = 0.002$ for elevation (*18*)]. Our estimated mean rates are approximately three and two times higher than those in (*14*), for

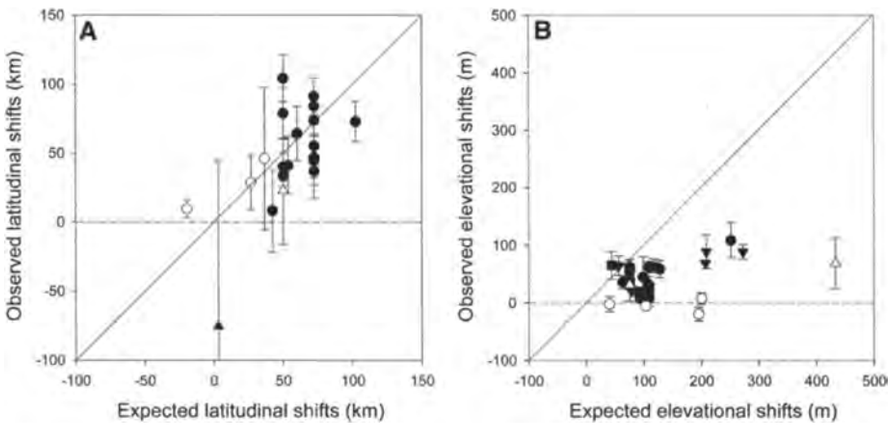

Fig. 1. Relationship between observed and expected range shifts in response to climate change, for **(A)** latitude and **(B)** elevation. Points represent the mean responses (±SE) of species in a particular taxonomic group, in a given region. Positive values indicate shifts toward the pole and to higher elevations. Diagonals represent 1:1 lines, where expected and observed responses are equal. Open circles, birds; open triangles, mammals; solid circles, arthropods; solid inverted triangles, plants; solid square, herptiles; solid diamond, fish; solid triangle, mollusks.

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latitude and elevation respectively, implying much greater responses of species to climate warming than previously reported (*18*). Most of the data we analyzed are from the temperate zone and from tropical mountains (table S1), where ecosystems are at least partly temperature-limited; different rates of change might be observed in moisture-limited ecosystems (*19*).

Published studies have shown nonrandom latitudinal and elevational changes (*1, 7, 13–17*) but have not previously demonstrated a statistical linkage between range shifts and levels of warming. We found that observed latitudinal and elevational shifts (the latter more weakly) have been significantly greater in studies with higher levels of warming (mean latitudinal shift versus average temperature increase; $N = 23$ species groups × regions, Pearson correlation coefficient (r) = 0.59, $P = 0.003$; mean elevational shift versus temperature increase; $N = 31$, $r = 0.37$, $P = 0.042$). Temperature gradients differ across the world, so a given level of warming leads to different expected range shifts of species in different regions (*20*), assuming that species track climate changes. To estimate the expected shifts, we calculated the distances in latitude (kilometers) and elevation (meters) that species in a given region would have been required to move to track temperature changes and thus to experience the same average temperature at the end of the recording period as encountered at the start (*18*) (table S1). We found that both observed latitudinal and elevation range shifts were correlated with predicted distances (Fig. 1A, $N = 20$ species groups × regions, $r = 0.65$, $P = 0.002$ for latitude; Fig. 1B, $N = 30$ groups × regions, $r = 0.39$, $P = 0.035$ for elevation), so our analyses directly link terrestrial range shifts to regional and study differences in the warming experienced.

Despite reports that many species lag behind climate change (*21–23*), nearly as many studies of observed latitudinal changes fall above as below the observed = expected line in Fig. 1A (9 points above, 11 below; $\chi^2 = 0.20$, 1 df, $P = 0.65$), suggesting that mean latitudinal shifts are not consistently lagging behind the climate. The lag in elevation response (Fig. 1B; 2 points above the 1:1 line, 28 below; $\chi^2 = 22.53$, 1 df, $P < 0.001$) is equally surprising because the required distances to track climate are much shorter than for latitudinal shifts (*20*). Real and apparent elevation lags may arise if suitable new conditions at higher elevations occur only in locations that cannot be reached easily (for example, on other mountain peaks), or they may reflect the topographic and microclimatic complexity of mountainous terrain [for example, cooler locations may be on poleward-facing slopes rather than higher (*24*)]; the need for finer-resolution analyses (*25*); and additional topographic, climatic, geological, and ecological constraints [for example, causing declines in cloud forest species (*26–28*)].

Taxonomic differences are not consistent predictors of recent response rates. For example, birds seem to have responded least in terms of elevational shifts but had a slightly greater than expected latitudinal shift (Fig. 1). Much greater variation is associated with differences among species within a taxonomic group than between taxonomic groups (Fig. 2 and table S2). For latitudinal studies, on average 22% (average of $N = 23$ species groups × regions) of the species actually shifted in the opposite direction to that expected. Similarly, 25% of species shifted downhill rather than to higher elevations (average of $N = 29$ species groups × regions). Thus, despite an overall significant shift toward higher latitudes and elevations, which is greatest where the climate has warmed the most, and despite around three-quarters of species shifting poleward and to higher elevations, we found that species have exhibited a high diversity of range shifts in recent decades.

At least three processes are likely to generate the high diversity of range shifts among species: time delays in species' responses, individualistic physiological constraints, and alternative and interacting drivers of change. Species may lag behind climate change if they are habitat specialists or immobile species that cannot colonize across fragmented landscapes (*17*, *21–23*), or if they possess other traits associated with low extinction or colonization rates (*29*). Species may also show individualistic physiological responses to different aspects of the climate, such as different sensitivities to maximum and minimum temperatures at critical times of their life cycles. These sensitivities will combine with variable wait times for different novel climatic extremes to take place (*30*). Species are also affected to different extents by nonclimatic factors and by multispecies interactions, which themselves depend on a diversity of environmental drivers (*21*, *28*). For example, a species might retreat toward the Equator at its poleward margin if it contracts with habitat loss faster than it expands through climate warming; whereas the poleward range margin of a species that thrives in novel agricultural landscapes may spread at a rate exceeding that expected, were warming the sole driver.

We found that rates of latitudinal and elevational shifts are substantially greater than reported

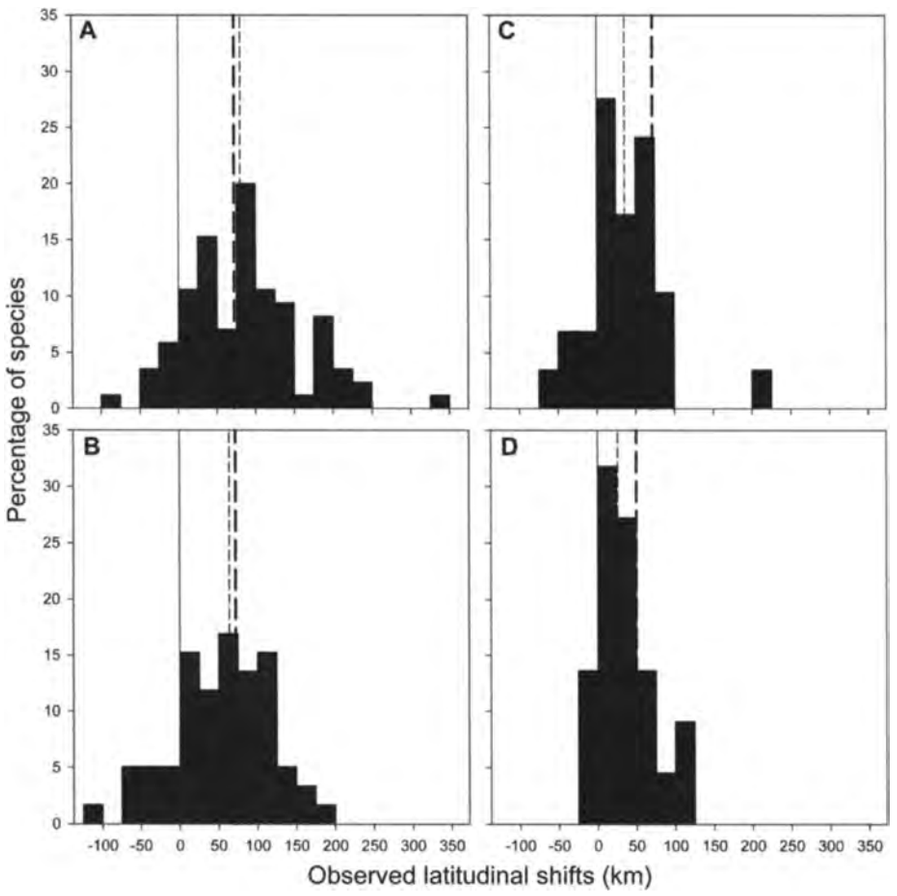

Fig. 2. Observed latitudinal shifts of the northern range boundaries of species within four exemplar taxonomic groups, studied over 25 years in Britain. **(A)** Spiders (85 species), **(B)** ground beetles (59 species), **(C)** butterflies (29 species), and **(D)** grasshoppers and allies (22 species). Positive latitudinal shifts indicate movement toward the north (pole); negative values indicate shifts toward the south (Equator). The solid line shows zero shift, the short-dashed line indicates the median observed shift, and the long-dashed line indicates the predicted range shift.

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in a previous meta-analysis, and increase with the level of warming. We conclude that average rates of latitudinal distribution change match those expected on the basis of average temperature change, but that variation is so great within taxonomic groups that more detailed physiological, ecological and environmental data are required to provide specific prognoses for individual species.

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Aneuploidy Drives Genomic Instability in Yeast

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Aneuploidy decreases cellular fitness, yet it is also associated with cancer, a disease of enhanced proliferative capacity. To investigate one mechanism by which aneuploidy could contribute to tumorigenesis, we examined the effects of aneuploidy on genomic stability. We analyzed 13 budding yeast strains that carry extra copies of single chromosomes and found that all aneuploid strains exhibited one or more forms of genomic instability. Most strains displayed increased chromosome loss and mitotic recombination, as well as defective DNA damage repair. Aneuploid fission yeast strains also exhibited defects in mitotic recombination. Aneuploidy-induced genomic instability could facilitate the development of genetic alterations that drive malignant growth in cancer.

Whole-chromosome aneuploidy—or a karyotype that is not a multiple of the haploid complement—is found in greater than 90% of human tumors and may contribute to cancer development (*1*, *2*). It has been suggested that aneuploidy increases genomic instability, which could accelerate the acquisition of growth-promoting genetic alterations (*1*, *3*). However, whereas aneuploidy is a result of genomic instability, there is at present limited evidence as to whether genomic instability can be a consequence of aneuploidy itself. To test this possibility directly, we assayed chromosome segregation fidelity in 13 haploid strains of *Saccharomyces cerevisiae* that carry additional copies of single yeast chromosomes (*4*). These aneuploid strains (henceforth disomes) display impaired proliferation and sensitivity to conditions that interfere with protein homeostasis (*4*, *5*). We measured the segregation fidelity of a yeast artificial chromosome (YAC) containing human DNA and found that the rate of chromosome missegregation was increased in 9 out of 13 disomic strains relative to a euploid control (Fig. 1A). The increase ranged from 1.7-fold to 3.3-fold, comparable to the fold increase observed in strains lacking the kinetochore components Chl4 or Mcm21. Consistent with chromosome segregation defects, 8 out of 13 disomic strains displayed impaired proliferation on plates containing the microtubule poison benomyl, including a majority of the strains that had increased rates of YAC loss (Fig. 1B).

Chromosome missegregation can result from defects in chromosome attachment to the mitotic spindle or from problems in DNA replication or repair. Defects in any of these processes delay mitosis by stabilizing the anaphase inhibitor Pds1 (securin) (*6*). Five out of five disomes (disomes V, VIII, XI, XV, and XVI) exhibited delayed degradation of Pds1 relative to wild type after release from a pheromone-induced G_1 arrest (Fig. 1C and fig. S1). Defective chromosome biorientation delays anaphase through the mitotic checkpoint component Mad2 (*6*). Deletion of *MAD2* had no effect on Pds1 persistence in four disomes, but eliminated this persistence in disome V cells (fig. S1). Disome V also delayed Pds1 degradation after release from a mitotic arrest induced by the microtubule poison nocodazole, which demonstrated that this strain exhibits a biorientation defect. Disome XVI, which displayed Mad2-independent stabilization of Pds1, recovered from nocodazole with wild-type kinetics (fig. S2). Thus, Pds1 persistence results predominantly from Mad2-independent defects in genome replication and/or repair (see below).

We next investigated whether aneuploidy could affect the rate of forward mutation. Disomes V, VIII, X, and XIV displayed an increased mutation rate at two independent loci, whereas disome IV displayed an increased mutation rate at *CAN1* but not at *URA3* (Fig. 2A). The fold increase ranged from 2.2-fold to 7.1-fold, less than the 9.5-fold and 12-fold increases observed in a recombination-deficient *rad51*Δ mutant and a mismatch repair–deficient *msh2*Δ mutant, respectively. Additionally, in an assay for microsatellite instability, we found that disomes VIII and XVI displayed increased instability in a poly(GT) tract (fig. S3), which demonstrated that aneuploidy can enhance both simple sequence instability and forward mutagenesis.

To define the mechanism underlying the increased mutation rate in aneuploid cells, we

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GLOSSARY OF ACRONYMS, INITIALISMS, AND ABBREVIATIONS

Each acronym, initialism, or abbreviation is spelled out for its first usage in each section.

AGENCY ACRONYMS, INITIALISMS, AND ABBREVIATIONS

CAL FIRE	California Department of Forestry & Fire Protection
Cal OES	California Office of Emergency Services
CHP	California Highway Patrol
County Ag. Comm.	Los Angeles County Agricultural Commissioner / Weights and Measures
County Animal Care	Los Angeles County Department of Animal Care and Control
County Emergency Management	Los Angeles County Office of Emergency Management
County Public Works	Los Angeles County Public Works
County Sheriff's Department	Los Angeles County Sheriff's Department
County Waterworks	Los Angeles County Waterworks District No. 29
DPH	Los Angeles County Department of Public Health
DPSS	Los Angeles County Department of Public Social Services
DRP	Los Angeles County Department of Regional Planning
EMC	Emergency Management Council
FEMA	Federal Emergency Management Agency
LA City Fire	City of Los Angeles Fire Department
LA County Fire	Los Angeles County Fire Department
Pepperdine	Pepperdine University
Red Cross	American Red Cross
SCE	Southern California Edison
SCVMA	Southern California Veterinary Medical Association
Ventura County Fire	Ventura County Fire Department

GENERAL ACRONYMS, INITIALISMS, AND ABBREVIATIONS

AAR	After Action Review
CEO	County Chief Executive Officer
Command and Control	P. Michael Freeman Command and Control Center
County EOC	Los Angeles County Emergency Operations Center
CSL	Community Services Liaison
DAC	Disaster Assistance Center
DOC	Department Operations Center
DRC	Disaster Recovery Center
EOB	County Sheriff's Department Emergency Operations Bureau
EOC	Emergency Operations Center
ICP	Incident Command Post
ICS	Incident Command System
IMT	Incident Management Team
JIC	Joint Information Center
MTZ	Mutual Threat Zone
NIMS	National Incident Management System

PCH	Pacific Coast Highway
PIO	Public Information Officer
PPDR	Private Property Debris Removal
RCC	Recovery Coordinating Center
RH	Relative Humidity
ROSS	Resource Order Status System
SEMS	Standardized Emergency Management System
SIB	County Sheriff's Department Sheriff's Information Bureau
UTF	Unable to Fill

CITYGATE TEAM TRANSMITTAL

It has been a privilege and honor for the Citygate Project Team to be of service to Los Angeles County. Throughout this effort, we have deeply considered lives lost, the personal impacts, the economic disruptions to residential and business communities, and the environment in the Santa Monica Mountains.

While this After Action Review includes critiques, we acknowledge many successful actions and respect the tremendous efforts of all responders in the face of the largest, fastest wildfire disaster in County history. Citygate's recommendations will improve agency response and community resilience in the next large area disaster.

Respectfully submitted,

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EXECUTIVE SUMMARY

The Woolsey Fire occurred in one of the most populous areas of the nation in an area well protected by emergency services. Thursday, November 8, 2018, began with a mass casualty shooting in Ventura County, a wildfire that enveloped and destroyed the town of Paradise in northern California, the fast-moving Ventura County Hill Fire, and, less than an hour after the Hill Fire, the Woolsey Fire started in Ventura County and spread into Los Angeles County.

In Los Angeles County, the responding agencies are large and capable. They are *extremely* experienced with large wildfires, as are many of the affected neighborhoods. While the size and speed of the Woolsey Fire in the first 33 hours challenged the coordinated agencies, the agencies and the public must recognize numerous significant accomplishments despite a *perfect storm* of factors that, when aligned, drove an event never experienced in the Los Angeles region:

- More than 250,000 people were successfully evacuated
- Casualties were limited to three, with no significant injuries to civilians or firefighters
- There were no significant aircraft or fire engine accidents
- Nine victim shelters and six animal shelters were opened
- Disaster Assistance Centers (DACs) were operational as soon as possible
- New private property debris removal practices were effectively implemented
- Significant care was provided for displaced animals of all types
- Significant health care was provided for the displaced populations in the shelters

Despite the numerous significant accomplishments in light of such a wildfire, the public understandably experienced frustration. Residents' prior experience and expectations regarding the agencies' capability to successfully confront a fast-moving wildfire were abruptly reset by the many obstacles present. No single fire had ever occurred in the mountains or the Malibu area that did not receive massive quantities of fire engines in time, but the Woolsey Fire was different.

While the Woolsey Fire disaster presented unprecedented challenges, it was still a single, focused incident; it was not Countywide. Imagine the challenges after a great earthquake or similar wide-ranging event. There are two primary, equally important lessons for the public, which are not new:

- Where wildfire threats are significant, buildings must be hardened against ember ignition and vegetation mitigations must be followed and maintained.
- The public must be prepared to receive information and follow the advice given.

There must also be an ongoing public policy discussion regarding significant development in Very High or High Fire Hazard Severity areas. A review of California's fire history indicates that five of California's *deadliest* (casualties) wildfires have occurred over the past two years, six of the

most *destructive* (structures) wildfires occurred over the past 10 years, and 15 of the *largest* (acreage) wildfires occurred over the past 19 years.

As terrible as the Woolsey Fire was, it was not the largest *megafire* in California. We cannot expect that all population growth in Very High or High Fire Hazard Severity areas can be protected simply by increasing resiliency[1] to wildfire and by adding more fire engines. Even if the current fire weather cycle stops, *it will return.* Governor Gavin Newsom's Strike Force Team, on April 12, 2019, observed that it is critical to "Make communities more resilient by considering updating codes that govern defensible space, encouraging cost-effective hardening of homes, strengthening evacuation, encouraging other emergency planning, *and improving land use practices to reduce the damage to life and property from wildfires*."[2]

These issues create real tension between public expectations and agency abilities which will require a concentrated effort to overcome. The Woolsey Fire clearly demonstrated that, while the agencies and public are prepared for a typical-to-serious emergency, there is room for improvement in catastrophic incident response and in reducing community vulnerability to a calamitous, fast-paced, dynamic event of any type.

WOOLSEY RESPONSE COMPLEXITIES

While the Los Angeles County Fire Department (LA County Fire), the Los Angeles City Fire Department (LA City Fire), and the Ventura County Fire Department (Ventura County Fire) regularly plan for and practice their response to a large fire in the region, they could not have planned for a complete exhaustion of California's limited firefighting resources brought on by a regional wildfire weather threat in conjunction with the Camp Fire, a mass casualty shooting in Ventura County, and the Ventura County Hill Fire, which began just before the Woolsey Fire started.

As is the case in all fires, the responding fire departments' top priority was to protect lives. During the initial stages of the Hill and Woolsey fires, all three departments were engaging in fire perimeter control, structure defense, and life safety actions. However, as the Woolsey Fire developed, the Camp Fire and Hill Fire consumed significant mutual aid resources and dry, northeast winds covered much of California, causing extreme fire behavior. As a result, by 2:30 PM on November 8, the southern California agencies that provided mutual aid resources to the Hill Fire now knew that no central or northern California agencies could send help south, and thus were very cautious about sending more of their resources to yet another local fire, which would leave their local areas vulnerable to the same conditions. Approximately 50 percent of requested resources were provided to the Woolsey Fire. Thus, as the Woolsey Fire grew Thursday evening, the fire services mutual aid system was already exhausted.

[1] Hardening buildings, fuels treatment, and vegetation management
[2] *Wildfires and Climate Change: California's Energy Future*, April 12, 2019

This necessitated the Woolsey Fire command team to strategically shift all resources to prioritize life safety as the fire rapidly grew, fanned by the Santa Ana winds gusting over 50 miles per hour. This strategy, along with a large, two-county sheriff's department evacuation force, successfully evacuated over a quarter of a million people and their animals from harm.

The initial emergency services response to the Woolsey Fire from two counties and the City of Los Angeles was proportionate to the initial fire; the experienced departments were ready and had planned for a severe fire weather day. Yet, the incident still presented unprecedented complexities:

- Multiple agencies (fire services, law enforcement, public works, and animal services) experienced an incident speed that, at times, outpaced their historically strong response efforts.
- Lives, structures, and critical infrastructure were threatened in the initial hours.
- Extensive evacuations across a multiple-jurisdictional area were required.
- Extensive infrastructure damage, at times, affected field operations, detoured evacuations, and delayed repopulation.
- The loss of the electrical system, due to wind and burned-down wooden power poles, created multiple challenges.
- Simultaneous neighboring and northern California fire incidents caused fire command's mutual aid requests to go significantly unfilled. Of those filled, the majority arrived after the fire reached Malibu.
  - Large Unable to Fill (UTF) mutual aid fire engine orders:
    - November 8: 175 engines UTF (58 percent)
    - November 9: 289 engines UTF (50 percent)
    - November 10 Noon: 874 engines UTF (53 percent)
- Relative humidity (RH), which plummeted to five percent, at times worsened the dry tinder fuel beds, many of which had not experienced fire for ten to forty years.
- Winds approaching hurricane force speeds and darkness Thursday evening combined to severely limit fixed-wing and rotor-wing aircraft firefighting drops, except for three LA County Fire Firehawk helicopters and LA City Fire helicopters.
- Although LA County Fire pulled as many resources as possible from its other fire stations to attack the Woolsey Fire, it was still required to maintain the resources necessary to respond to the nearly 1,100 daily 9-1-1 calls throughout the Department's 2,200-square-mile jurisdiction.
- All County personnel had to remain fully engaged without relief on the fire in the initial period.

Despite numerous significant accomplishments in life safety, the severe challenges in the fire response caused an understandable public frustration and desire to know what was preventable, and what was due to unprecedented natural factors.

THE WOOLSEY FIRE NUMBERS AT A GLANCE

- 96,949 acres, or 151.5 square miles, across two counties (appx. 1/3 the area of the City of Los Angeles)
  - 1,643 structures destroyed; 364 structures damaged in both counties
  - Los Angeles County (approximately 36 percent in the City of Malibu)
    - 184 homes and five commercial structures "damaged"
    - 1,075 homes and 46 commercial structures "destroyed"
    - Approximately 57,000 structures were not substantially affected
- The Woolsey Fire incident incurred approximately $52 million in fire suppression costs alone (not the full economic cost to the County or the communities); of this, the aviation cost was $7,717,795
- Insured losses are expected to total between $3 billion and $5 billion

THE FIRE'S DYNAMICS

It is hard to envision the speed of the Woolsey Fire from one map or photograph. LA County Fire, Ventura County Fire, and LA City Fire immediately sent resources to stop the Woolsey Fire from ever reaching Los Angeles County and to protect the residents of Los Angeles County and Ventura County, and the City of Los Angeles. This *standard, planned* multi-jurisdictional response was exponentially larger than that of a normal response from a single jurisdiction; however, the fire presented unprecedented complexities *immediately*. From ignition Thursday afternoon, the Woolsey Fire burned to the Pacific Ocean in Malibu by noon Friday. Most the fire growth occurred after the fire crossed Highway 101, taking about 6.5 hours to reach the ocean. This After Action Review (AAR) will discuss the fire's major dynamics that each presented new challenges:

- The location and topography, which presented severe challenges for initial attack
- The early November sunset, which grounded non-night-flying aircraft
- Early and mid-evening wind shifts when the fire was still outside heavily populated areas
- The fire's crossing of the 12-lane Highway 101 before dawn on Friday
- The defense early Friday of both sides of Highway 101 in the populated areas and in the mountain communities consumed the immediately available fire attack resources as the fire began the run to Malibu Friday after dawn

- Very limited initial resources in Malibu Friday morning due to fire ferocity, unfilled mutual aid requests, and fire- or wind-caused road damage blocking Santa Monica Mountain roads
- Road limitations on Malibu evacuation routes due to fire- or wind-caused impacts

EXPECTATIONS VERSUS REALITY

Even some of the largest, most experienced agencies in the United States were, at times, overwhelmed in the first hours by this incident's *speed and weight of impact*, exposing some limitations between the agencies and systems as they meshed into a single, wide-area regional response team in less than 24 hours. Prior experiences and expectations by community members regarding the agencies' capabilities to successfully confront a fast-moving wildfire were harshly reset by the many challenges presented by the Woolsey Fire:

- The expected fire behavior and rate of spread far exceeded the past experience of emergency responders, policy makers, and the public in the Santa Monica Mountains fire corridor areas.[3]
- The public expected a more robust firefighting army of resources in the Malibu coastal area, but many factors prevented that from happening.
- In large, dynamic wildfires, some life and structure loss are a tragic but expected possibility; however, what occurred in less than 24 hours was not anticipated by any prior plan or preparedness exercise. Three of the four historic Santa Monica fire corridors burning at once was beyond prior experience.
- The California Fire Master Mutual Aid System is a worldwide model; yet, contributing factors over two decades inhibited rapid resource movement to the Hill Fire and Woolsey Fire commensurate with each fire's rapid pace.
- The expectation of round-the-clock electrical power and internet connectivity became a myth, with no quick fallback for the public and emergency responders.
- Social media has led people to expect access to real-time information; yet, the infrastructure and processes could not meet the fire storm's pace demands.
- Throughout California, no single public communication system exists that successfully crosses social, economic, age, and generational abilities to receive emergency information.
- The public has not been educated and trained enough regarding evacuation routes and does not understand the complexities of returning. These unmet expectations, and others regarding the level of firefighting resources, are causing some people to consider ignoring the next evacuation orders.

[3] Canyon or drainage generally running to the ocean

The public has a perception that public agencies can always protect them. As an incident the size of the Woolsey Fire shows, this is not always possible. The public has a shared responsibility for preparedness which requires ongoing education programs by the agencies.

RECOGNITIONS

While the size and speed of the Woolsey Fire, at times, outpaced the early efforts of some of the largest and most experienced and capable agencies in the United States, they all should be recognized for their dedicated work. The following are some examples that deserve recognition:

- In the days leading up to the strong dry wind event, LA County Fire was preparing; placing additional resources on duty the day of the fire and ensuring its most experienced and qualified personnel were available and dispatched to the incident
- LA County Fire's early recognition that an unprecedented evacuation operation would be necessary
- A massive evacuation undertaking by the sheriff's departments of two counties
- Across the agencies, all available personnel reported for work and the initial *ground* crews and command chiefs went 36 to 48 hours without significant sleep
- Individual unit and personal initiative to overcome extraordinary conditions
- Aircrew/mechanic rotations to keep aircraft flying 24 hours per day
- Positive interagency relationships across all disciplines
- Annual joint training and planning efforts before the fire season
- Pre-positioning resources due to extreme fire weather the morning of November 8
- Public education programs such as Ready! Set! Go!
- Defensible space close to structures, where it existed, allowed defense of those properties as resource availability allowed
- By the first anniversary of the fire, the rebuilding effort has yielded nearly 100 reconstruction entitlements and ten building permits for affected structures and homes

THEMES FOR NEEDED IMPROVEMENTS

In many respects, an AAR must be a technical document. In the work to follow, the research yielded 155 findings and 86 actionable recommendations across four themes: The Response, Communication, Evacuation/Repopulation, and Transition to Recovery. At an aggregated level, the Los Angeles County Board of Supervisors and the public can focus discussion on three overarching themes:

Communication: All Los Angeles County agencies need to increase resource commitments to the crisis communication function. Public Information Officers (PIO) need more in-depth training for

their roles, to work together under a multi-agency, common incident communications strategy and have redundant tools with which to reach the public—*at the same quick pace that incidents grow.*

- During the initial phases of evacuations, the City of Malibu, the Los Angeles County Sheriff's Department (County Sheriff's Department), LA County Fire, and all other stakeholders worked on the evacuation of over 250,000 residences. While successful, the effort may not be reproducible as, in the early hours, there was not a clear, single, comprehensive voice speaking to evacuation, and not all notification tools were used or used often enough.
- There was an over-reliance on Twitter; care must also be taken to account for the digital divide in which not everyone is on Twitter or even the internet, creating the need for multiple methods of public emergency communication.
- Entry and repopulation policies were not well briefed to checkpoints or the public.

Collaboration: County leadership should strive for a more collaborative "One Team LA" mindset. This applies to not just the County agencies, but to the cities and special districts for wide-area multiple-county events. Every large area emergency must be framed as a unified command operation where key decision makers come together under an Incident Commander who uses policy direction to determine objectives, achieve unity of effort, and direct a single voice for communications. The public may not always know what agency directly serves them—but in these situations, every Southern Californian expects and deserves seamless collaboration.

- As this fire demonstrated, wildfires do not respect jurisdictional lines of agencies, cities, special districts, or counties. A Los Angeles sub-regional planning, response, and recovery dialogue must occur across county lines via a Multi-Agency Coordination System for large-scale wildfire, terrorism, and earthquake incidents.
- As the incident rapidly expanded, command post locations shifted to account for the Woolsey Fire's growing size and subsequent impact. This resulted in commanders not always being able to communicate face to face, which presents unified command communications challenges.
- The large Los Angeles County agencies are set-up with regional facilities and Department Operations Centers (DOCs) that routinely manage large emergencies without needing to depend on the Los Angeles County Emergency Operations Center (County EOC). As the Woolsey Fire grew, there was a stronger and less practiced need to work on the regional impact between the County EOC Woolsey Incident Command Post (ICP), the DOCs, and each independent city EOC.
- There is a need for greater inter-agency pre-incident evacuation and repopulation planning for the communities in Fire Hazard Severity Zones.
- No pre-prepared traffic evacuation plans/scenarios exist for the areas impacted by the Woolsey Fire.

- Evacuation plans also need corresponding repopulation plans at the earliest moment.

Situational Awareness: *Data-driven* knowledge from which to command *in real time*, at the *incident's tempo*, is crucial in the early hours of an emerging disaster. Most of the Woolsey Fire destruction occurred in the first 30 hours, not unlike what occurred in the communities of Paradise (2018 Camp Fire) and Santa Rosa (2017 Tubbs Fire). An emergency the speed and size of the Woolsey Fire does not wait for intelligence to be gathered slowly or normal incident command decision timeframes. Nighttime, smoke, technology failure, or any other obstacle also cannot be allowed to slow command decisions. As a result, the following are needed:

- Research and investment in emerging technologies to reduce the "fog of war"
- Increased practice, procedures, and technologies in melding the large County agency DOCs and Incident Management Teams (IMTs) into a virtual unified command, as if they were in one physical location, to reduce lag time in fast-tempo, complicated decisions
- Public education regarding alerting and the public's responsibility to understand incident severity and the need for Ready! Set! Go!
- Public education to increase awareness regarding public impact when a devastating fire incident shifts from direct control methods to Fire Front Following and Life Safety First tactics[4]
- Real-time display of fire perimeter, hazards, actions, shelters, and evacuation orders for public consumption

NEAR-TERM AGENCY ACTION RECOMMENDATIONS

Acquiring funding and implementing the technical recommendations across the themes beginning in **Section 5** are largely in the hands of agencies. Key highlights include:

1. Improve coordination of multiple-agency emergency public messages.
2. Increase the speed and use of all alerting tools in wide-area, fast-paced disasters.
3. Create more specific evacuation plans that can adapt to major road closures and a fast-paced disaster.
4. Help the public understand the risks and ramifications of not evacuating to protect their property when Fire Front Following and Life Safety First strategies are being utilized.

[4] Fire Front Following and Life Safety First are firefighting tactics described in Section 2.3.1

5. Address the impact of long-distance fire storm ember spotting through education and an emphasis on using layered buffer zones, including appropriate vegetation mitigations, improving soil moisture, and structure hardening techniques.

LONGER-TERM POLICY ACTION RECOMMENDATIONS

In addition, the Woolsey Fire incident shows the need for policy leadership from Los Angeles County and regional elected officials to enable significant changes for multiple agencies and public participation. Citygate suggests the following recommendations receive *policy leadership focus* from the County of Los Angeles Board of Supervisors:

Premise – Because wildfires and other emergencies do not respect jurisdictional lines, all public jurisdictions should adopt a cross-boundary philosophy that addresses how to prepare, fight, and recover from wildfires without creating silo actions and establish a sub-regional command model to bridge agency/political lines.

1. Utilize an oversight body to institutionalize the Woolsey Fire 2018 lessons learned to ensure that AAR recommendations become reality and will transcend staffing attrition in the future.
2. Advance an initiative with all applicable public agencies and private interest groups that are involved in the Santa Monica Mountains region to develop a unified, comprehensive, and strategic wildfire hazard reduction plan.
3. Encourage the major fire departments in the area to evaluate creating a sub-regional (three county) Multiple-Agency Coordination and Control Center within the State mutual aid system that will utilize technology to enhance situational awareness and create a shared, *real-time* intelligence, information, and command center on an around-the-clock basis. This concept should further existing agreements and enhance the ability of agencies to work collaboratively during the first one to two days of a catastrophic disaster, for the common welfare, at a pace faster than the Statewide mutual aid system can provide.
4. Reset the operation of the County EOC to the Los Angeles County Office of Emergency Management (County Emergency Management) to become the central coordination and support hub for all County agencies and the County Operational Area by activating and managing the County EOC.
5. Work with Federal officials to advocate Federal disaster reimbursement changes as needed. Federal approvals often cover many County costs, but other costs may not be reimbursable, including long-term animal housing costs for the Los Angeles County Department of Animal Care and Control (County Animal Care). As another example, some private property debris removal (PPDR) policies on items such as foundations do not work in California. In addition, the burn scars that result from wildfires are prone to mud and debris flows from winter rains. This subsequent loss

is not viewed as a continuation of the wildfire, but instead as a new stand-alone event which may not qualify for State and Federal disaster cost recovery.

If the desired end is more resilient communities to meet the current wildfire risks, the improvements suggested by the Citygate team, taken as a whole, should deliver an enhanced union of government services, community bonds, and personal involvement. Citygate's Project Team hopes the communities' common bonds to one another, and to their environmental treasures, will propel earnest conversations to deal with the wildfire lessons from the Woolsey Fire disaster.

NEAR-TERM NEXT STEPS

1. Absorb the issues identified in this AAR.
2. Direct staff to return in 90 days with an assignment and tracking plan for all the AAR recommendations by agency, the lead manager, and the completion timeline.
3. After the Los Angeles County Board of Supervisors reviews the assignment and tracking plan, ask the County Chief Executive Office and the finance teams of the agencies to estimate the cost of implementing the recommendations over feasible timelines.

CONCLUSION

This AAR details a firestorm of epic proportions; we do not use the cliché lightly. This document cannot tell all the stories of heroism, sacrifice, and professional, community, and individual leadership displayed by firefighters, law enforcement officers, public servants, volunteers, and community members who serve, work, and live in one of the most populated and arguably best prepared areas of the country. More than one senior public safety leader described the Woolsey Fire as "unimaginable in [their] career understanding to date, with a ferocity and speed over great distances that, at times in the early hours, overwhelmed the institutions."

The Woolsey Fire forever altered thousands of lives and generated enormous personal, business, and economic losses. Returning to normal is slow and, in some cases, never really occurs, but the individuals directly impacted by the Woolsey Fire can know as a result of this AAR, and other follow-up actions, that the agencies involved heard them, care deeply about their protective role, and will take seriously the recommendations in this review.

This review is also a recognition that planning for the unimaginable, in an area prone to wildfires and crossed by more than five major earthquake fault lines, is precisely what must be done.

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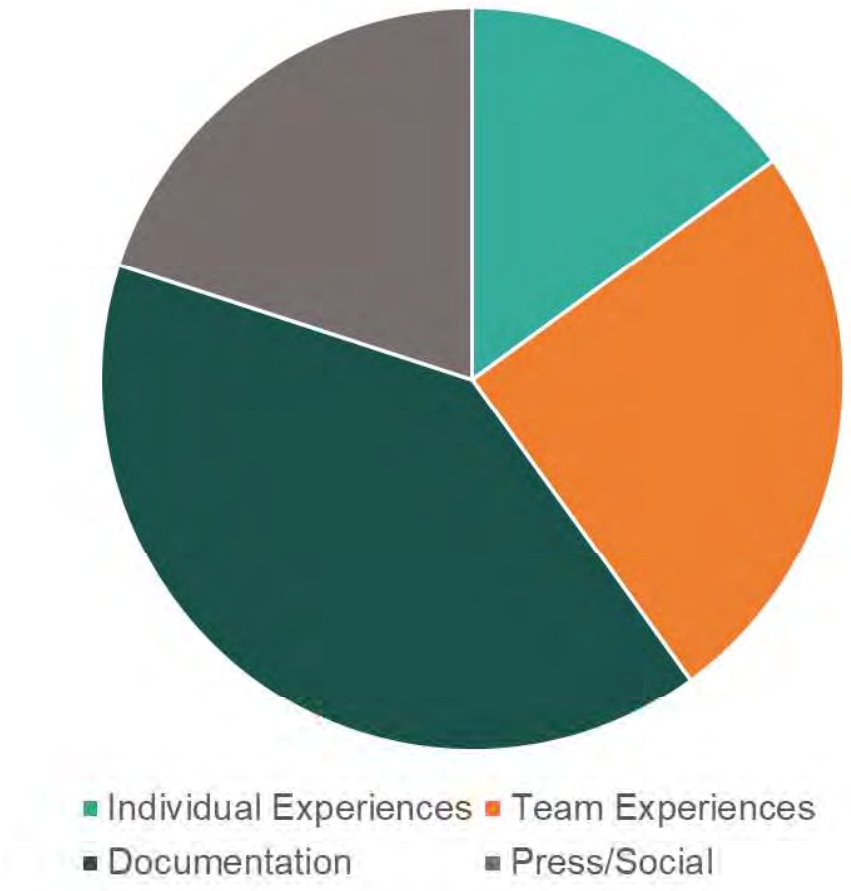
SECTION 1—AFTER ACTION REVIEW PROCESS

An After Action Review (AAR) of the Woolsey Fire tragedy allows for education based on fact-finding from what went well, and it provides recommendations for improvement. The elements of this AAR tell a 360-degree story of the event. While immersed in the event, no single person could know more than their own experience. Later, they learn more from others or the news, but even those interactions may not tell the entire story across such a huge disaster. The Citygate AAR team assembled and analyzed data, cross-checked against personal interviews, to detail the account for those who wish to study and learn from this incident. The incident affected thousands of people, and this report cannot tell every story in depth, nor can it cover every participant's experience; however, the Citygate team attempted to understand and learn from the individual experiences to represent the whole.

Figure 1—AAR Story Sources



1.1 Organization of This Report

1.1.1 Organization by Section

This AAR is organized into the following sections:

- Executive Summary
- Section 1—After Action Review Process
- Section 2—The Woolsey Fire Incident
- Section 3—Timeline of Significant Incident Events
- Section 4—Findings Across the Incident by Agency
- Section 5—Recommendations
- Section 6—Policy Leadership Recommendations
- Appendix A—History and Context Prior to the Woolsey Fire
- Appendix B—Background on Primary County Agencies
- Exhibit A—Santa Monica Mountains / Malibu Wildfire History
- Exhibit B—Fire Weather
- Exhibit C—Woolsey Fire Path Progression over the Geography
- Exhibit D—Woolsey Fire Area Fire History Map

1.1.2 How to Use This AAR

Citygate's AAR opens with a narrative description and timeline of the Woolsey Fire incident. However, for a comprehensive understanding of relevant background information, Citygate has provided information regarding involved agencies, fire history, weather patterns, and terrain records. As a result:

- If you are NOT familiar with wildfire history in the region of the Woolsey Fire, please read **Appendix A**.
- If you are NOT familiar with the involved agencies, their capabilities, and their roles in responding to the Woolsey Fire, please read **Appendix B**.
- For a list of wildfires in the Santa Monica Mountains / Malibu area, please read **Exhibit A**. For a map of fire history since 1970 in the Woolsey Fire area, see **Exhibit D**.
- For more information regarding the relevant fire weather at the time and region of the Woolsey Fire, please read **Exhibit B**.
- If you are NOT familiar with how the Woolsey Fire moved through the geography, please review **Exhibit C**.

1.2 Story of the After Action Review Process

1.2.1 Value and Purpose of the AAR

As the Federal Emergency Management Agency (FEMA) states in its 2015 document, "Operational Lessons Learned in Disaster Response," "There is a connection between evaluation and learning."[5] Such is the purpose and value of this AAR, including an improvement plan for the 2018 Woolsey Fire that devastated portions of Ventura and Los Angeles Counties.

Focusing on future improvement, an AAR serves many purposes, including:

- The creation of an official report on actions
- A fact-based response to questions and/or concerns expressed by the public, response agencies, and stakeholders
- An opportunity to capture previously unscripted acts of success
- An opportunity to assess perceived or real gaps in service
- An analysis of resources, agreements, and systems

Citygate followed FEMA's AAR principles for major disasters. FEMA identifies seven steps for conducting an AAR:[6]

1. Assign team leaders and members
2. Develop a work plan that includes, at a minimum:
    a. Scope of work
    b. Work schedule with deadlines and milestones
    c. Budget and resource needs
    d. Primary and secondary cooperating agencies/organizations/individuals
3. Initial data gathering
4. Conduct the after action workshop:
    a. Include key representatives of all the involved emergency response agencies
    b. Representatives must be able to address the emergency and incident operations of their respective organizations
    c. Concentrate on fact-finding and discovery of pertinent information related to the emergency response and recovery activities

[5] Federal Emergency Management Agency (FEMA), "Operational Lessons Learned in Disaster Response," June 2015, https://www.usfa.fema.gov/downloads/pdf/publications/operational_lessons_learned_in_disaster_response.pdf, 35.
[6] FEMA, 49.

d. Employ a facilitated process to ensure a fair and balanced inquiry

e. Allow for an atmosphere of openness with a forum to air concerns

f. Seek objective information on what went right and what did not

5. Compile and analyze the workshop data to begin preparation of the after action report:

   a. Compile the results of the survey, interviews, and workshop, and sort the information according to the areas covered in the after action report

   b. Review, analyze, and sort documentation according to the areas covered in the after action report

   c. The main purpose for analyzing the data is to verify and support comments and conclusions reached by participants and team members

6. Prepare after action report drafts and distribute for review and approval to the appropriate parties

7. Prepare the final AAR report and share it with interested parties

While conducting the AAR, Citygate subject matter experts:

- Reviewed over 4,700 documents
- Conducted small group and individual personnel interviews totaling over 111 personnel in over 98 hours of sessions
- Extensively toured the fire area and key neighborhoods by ground travel and helicopter
- Worked substantially with the following Los Angeles County agencies:
  - Los Angeles County Fire Department (LA County Fire)
  - Los Angeles County Sheriff's Department (County Sheriff's Department)
  - Los Angeles County Public Works (County Public Works)
  - Los Angeles County Office of Emergency Management (County Emergency Management)
  - Los Angeles County Department of Public Health (DPH)
  - Los Angeles County Department of Animal Care and Control (County Animal Care)
  - The Los Angeles County Department of Regional Planning (DRP)
  - Los Angeles County Agricultural Commissioner / Weights and Measures (County Ag. Comm.)

- Interviewed and obtained information from the following cooperating agencies:
  - Ventura County Fire Department (Ventura County Fire)
  - Ventura County Sheriff's Office
  - Ventura County Office of Emergency Services
  - California Highway Patrol (CHP)
  - City of Los Angeles Fire Department (LA City Fire)
  - California Department of Forestry & Fire Protection (CAL FIRE)
  - California Office of Emergency Services (Cal OES) Mutual Aid System
- Obtained community input via:
  - Listening at two Woolsey Task Force community input hearings
  - Conducting eight Woolsey Task Force Working Group meetings
  - Reviewing the records from agency-led community meetings during the event
  - Reviewing information from a web-based input survey hosted by LA County Fire
  - Following up on a limited basis with community individuals who testified and/or submitted information
  - Reviewing the media records, including various social media, regarding the Woolsey Fire


EXIT
FIRST
MED-FIRST

SECTION 2—THE WOOLSEY FIRE INCIDENT

2.1 PRE-FIRE AND IGNITION POINT FIRE WEATHER DATA

Recent data indicates that the climate has been changing or cycling, resulting in warmer-than-average temperatures, longer fire seasons, drought-stressed native fuels, and erratic/extreme fire behavior. Globally, 2018 was the fourth hottest year in recorded history, following the three previous years which earned the top three spots: 2017, third hottest; 2015, second hottest; and 2016 the hottest year.[7] In the past, Southern California fire seasons ran from May to November, with August and September as the peak fire activity months. Over the past decade, Southern California's heightened fire activity period has shifted to September through January. The term "fire season" is becoming outdated as wildfires are a real threat year-round. California is now referring to "fire years" and not seasons. California has recently experienced eight years of drought, with regionally intermittent relief. Drought and deteriorating forest health produce dry fuel moisture conditions at critical levels which are susceptible to fire. Experienced firefighters are witnessing fire behavior unlike anything they have witnessed in the past.

Monitoring fire weather is a year-round discipline for the California fire service. Regionally, on November 6, 2018, two days before ignition of the Woolsey Fire, meteorologist and fire technical staff saw evidence of increasing fire weather conditions. On November 7, per existing protocols, fire agencies upstaffed (adding units above the normal daily minimums) predetermined resources and the California Department of Forestry & Fire Protection (CAL FIRE) relocated resources across the State. On November 8, the relative humidity (RH) dropped from 100 percent at 7:00 AM to seven percent at 11:00 AM in the region that would be consumed by the Woolsey Fire. While the weather forecast called for moderate temperatures in the mid-70s, winds became sustained, hot, dry, and came from the east. At 2:30 PM, these Santa Ana winds were sustained at 23 miles per hour (mph) with gusts up to 37 mph. The conditions for a large-scale fire incident were perfect.

Summary fire weather data is provided in **Exhibit B**.

2.1.1 The Timing of the Woolsey Fire

Like the Thomas Fire of 2017, the Woolsey Fire occurred at a time of the year normally known more for rainfall than wildfires. This change in seasonal assumptions has many impacts, including the availability of resources throughout the State and the threat of post-fire rainfall debris flow immediately following the fire.

Historically, two distinct fire seasons exist in California depending on geography. The fire season in Northern California ends with precipitation toward the end of summer and beginning of fall,

[7] NOAA National Centers for Environmental information, Climate at a Glance: Global Time Series, published August 2019, retrieved on September 9, 2019 from https://www.ncdc.noaa.gov/cag.

and the Southern California fire season could extend past Thanksgiving. When the Northern California fire season ends early, Statewide firefighting resources are available to be redeployed to Southern California to stand ready for regional threats, such as extreme fire risks based on Santa Ana wind conditions.

Starting on November 8, the Woolsey Fire erupted late in the traditional fire season of Southern California, and there existed cooler daytime temperatures, but high winds and very low humidity. Compounding that issue, Northern California was still experiencing extreme fire weather conditions. When the Hill Fire and the Woolsey Fire ignited, there were no other new major fire events underway in the Southern California region. Once the major Hill Fire in Ventura County started in extreme fire conditions on the western Highway 101 corridor, the normally available mutual aid was quickly exhausted.

The second significant impact of the timing of the Woolsey Fire is related to flood and debris flow. When heavy rains follow a major fire, debris flows increase in likelihood as vegetation that previously held the soil in place has burned away. The extension of fire season deep into fall significantly shrinks the window for mitigation actions to lessen the impact of catastrophic flood and debris flows characteristic of fire-damaged chaparral lands receiving December rains. The full impact of this condensed catastrophe timeline was realized in Santa Barbara County (Montecito) when heavy rains fell soon after the destructive Thomas Fire in 2017, killing 21 people with two still missing. In the weeks following the Woolsey Fire, Los Angeles County faced the same threat faced by Santa Barbara County in 2017, which required that emergency management personnel continue to operate at heightened levels on two fronts due to heavy rainfall predictions even as firefighting resources were still working to fully extinguish the fire.

2.2 THE FIRE'S STORY AND DEMOGRAPHICS

2.2.1 Camp Fire

November 8, 2018 is a significant day in California wildfire history. Approximately 415 miles northwest of the point of origin for the Woolsey Fire is the community of Paradise, California. Approximately eight hours prior to the ignition of the Woolsey Fire, the deadliest and most destructive fire in California history, the Camp Fire, exploded in Butte County just east of Paradise. Before it was extinguished, the Camp Fire destroyed 153,336 acres of land, the town of Paradise, 18,793 structures, and took 85 lives. Significant to the Woolsey Fire is that over 1,000 fire personnel were assigned to the Camp Fire, pulling from the Statewide pool of firefighting resources; *however, on November 8, none were pulled directly from Los Angeles, Santa Barbara, Orange, or Ventura Counties.*

2.2.2 Hill Fire

The Hill Fire ignited less than one hour before the Woolsey Fire in the Hill Canyon area of Santa Rosa Valley, approximately 3.5 miles east of the City of Camarillo. The point of ignition for the

Hill Fire is approximately 14 miles west of the point of ignition for the Woolsey Fire. Both fires started in Ventura County.

The Ventura County Fire Department (Ventura County Fire) deployed a full brush fire ground and aerial unit response to the Hill Fire with on-duty staffing augmentation in place due to dangerous fire weather conditions (Red Flag Warning). A Ventura County Fire helicopter with a flight crew was first on scene and attacked the first spot fire. Immediately afterwards, it spotted another start across the road and that fire, driven by gusting, hot, dry winds, quickly ran through Hill Canyon toward the Newbury Park area of Thousand Oaks and Highway 101, including the Conejo Grade truck scales. Major infrastructure, including powerline corridors and Highway 101, occupied structures including commercial parks and schools, and suburban populations were in the path of the rapidly expanding Hill Fire.

Initial fire attack resources were outflanked by the fire. With a report of approximately 100 motorists trapped on Highway 101 in both directions, life safety became the primary mission. The strong winds out of the northeast pushed the fire and affected the business and residential areas of Newbury Park. Fire also rapidly grew to the south and west, expanding the fire front toward the City of Camarillo and flanking the Santa Rosa Valley area.

The fire quickly jumped Highway 101 within approximately 15 minutes from time of dispatch, running approximately *three miles in 15 minutes*. Figure 2 shows the fire approaching Highway 101. Crews were quickly overpowered, and direct operations were rendered ineffective by strong winds, steep topography, and flammable, drought-stricken fuels in the path of the fire.

Twenty Type 1 (structure fire) engine strike teams totaling 100 engines (each team comprises five engines plus a command chief) were initially ordered by Ventura County Fire for life threats and structure protection. Initial thoughts by Incident Commanders were that the fire would move quickly through the lighter fuel south of Highway 101 and advance toward California State University, Channel Islands. Based on initial conditions, the Hill Fire was believed to have the potential to reach the coast by nightfall. However, late in the evening, as the dynamic, moving Hill Fire burned into the burn scar of the 2013 Springs Fire, the erratic behavior calmed and the growth of the fire slowed significantly, allowing Incident Commanders to gain the upper hand.

Figure 2—Hill Fire Approaching Highway 101



With the serious potential for major impacts and loss of life, Ventura County Fire was already utilizing tremendous resources battling the Hill Fire when the Woolsey Fire erupted.

2.3 WOOLSEY FIRE: START TO STOP OF SPREAD

The Woolsey Fire's final size was enormous. As a point of reference, the 2003 Old Topanga-Malibu Fire burned 16,516 acres and 350 buildings. The following metrics show, in part, the scale of the Woolsey Fire:

- 96,949 acres, or 151.5 square miles, across two counties (appx. 1/3 the area of the City of Los Angeles)
- More than 250,000 people successfully evacuated
- Three deaths and no significant injuries to civilians and firefighters

- No significant aircraft or fire engine accidents
  - 1,643 structures destroyed; 364 structures damaged in both counties
  - Los Angeles County (approximately 36 percent in the City of Malibu)
    - 184 homes and five commercial structures "damaged"
    - 1,075 homes and 46 commercial structures "destroyed"
    - Approximately 57,000 structures were not substantially affected
- The Woolsey Fire incident incurred approximately $52 million in fire suppression costs alone (not the full economic cost to the County or the communities); of this, the aviation cost was $7,717,795
- Insured losses are expected to total between $3 billion and $5 billion
- Nine victim shelters and six animal sheltering sites opened

2.3.1 Key Firefighting Tactics in Extreme Conditions

Firefighting in the wildland area involves either *perimeter control* (directly attacking and controlling the outline of the fire) or *point protection* (protecting structures). During wind-driven wildfires, firefighters often employ point protection until wind conditions diminish. Point protection can be static at one location or, on dynamic moving fires, firefighters may use a tactic called *Fire Front Following*. When enough fire resources are available, *tactical patrols* will remain behind the fire front, watching for incipient fires igniting structures.

Additionally, when there are not enough resources for firefighting, the units available are directed into Life Safety First, in which all efforts are utilized to protect lives at immediate risk. The two terms regarding these tactics are here defined and used in this After Action Review (AAR):

1. Life Safety First: Units remain mobile to ensure civilians are evacuated out of harm's way and to answer 9-1-1 calls for help, rather than fully engaging in traditional structure defense operations.
2. Fire Front Following: When fire storm conditions are overwhelming, inhibiting firefighters' ability to breathe or even survive, the units find a safe refuge point and let the main fire front pass over/around them. When human activity is again possible, the fire units search for victims, effect perimeter control, extinguish spot fires around structures, control hot spots, and reduce ember production. This action is taken when there is insufficient time to safely set up ahead of the fire, or the intensity of the fire would likely cause injury to personnel located in front of the the fire.

On Friday, November 9, the Los Angeles County Fire Department (LA County Fire) dispatch center received approximately 1,800 *additional* calls for help (above the normal Countywide volume of about 1,100) from neighborhoods within the fire area. Even the engines assigned to

structure defense within Malibu early Friday could not keep up with the volume of 9-1-1 calls and, sometimes, by the time a unit had arrived, the caller was gone or wanted the fire engine to stay even though the situation did not yet warrant it. By informal estimates, in some threatened areas, almost half the 9-1-1 calls were not life threatening or no one was found upon arrival, significantly impacting the ability of very limited fire units to engage in life safety and structure defense operation.

However, there were multiple rescues, and some structures saved through heroic commitments. Dispatchers, firefighters, and field commanders were acting with the best information available, often putting themselves in harm's way.

2.3.2 Ignition and Firefighting Conditions

The cause of the Woolsey Fire is still under investigation, but it started on the old Santa Susana Field Laboratory property (Rocketdyne) in Chatsworth. On the afternoon of November 8, 2018, at approximately 2:24 PM, the Woolsey Fire was first reported at the Ventura County Emergency Communications Center as a request for a "smoke check," resulting in the initial deployment of the Rocketdyne Fire Department and one Ventura County Fire fire engine (#43). Initial ignition occurred in Woolsey Canyon of the Santa Susana Mountain range, which is now owned by The Boeing Company.

At 2:33 PM, before fire engines arrived on scene, the response was upgraded to a full wildland fire unit response, which also triggered LA County Fire and the City of Los Angeles Fire Department (LA City Fire) to respond per the established Santa Susana mutual threat zone (MTZ) agreement. The first two ground units and a helicopter arrived on scene between 2:45 PM and 2:51 PM. All reported a wind-driven fire growing from five to approximately 30 acres in six minutes. The initial wind direction was northeast (38–42 degrees), changing back and forth to east, which made the wind direction in alignment with the geographic canyon features conducive for a rapid fire run toward the Pacific Ocean. The full sequence of events is contained in **Section 3** of this AAR.

Exhibit C of this AAR contains aerial photos showing the topography and resultant challenges as the fire spread from the initial origin to the Pacific Ocean by noon the following day.

The extreme burning conditions on the afternoon of November 8 combined with inaccessible, challenging terrain stymied initial fire control efforts.

2.3.3 Immediate and Follow-On Fire Department Deployment

The Santa Susana MTZ agreement calls for a massive initial joint response from three fire departments: Ventura County Fire, LA County Fire, and LA City Fire. All the MTZ First Alarm resources were sent, except for three Ventura County Fire engine companies and one of its helicopters as their Hill Fire response was well underway. The Woolsey Fire also received four medium helicopters, four heavy helicopters, and two Super Scooper planes in the initial dispatch that coordinated with the ground attack. Unfortunately, due to the two other competing fires in the

State—primarily the Hill Fire before sunset—the Woolsey Fire only received two CAL FIRE fixed-wing retardant drops in addition to the air resources previously cited.

The following table shows the resource types, counts, and approximate time of arrival for the first hour of the fire:

Table 1—Filled / Unable to Fill (UTF) Resources at Early Critical Points

Department	Aircraft		Engines		UTF
Initial Attack (IA) on 11/8	Responded	UTF	IA	3:00 PM	3:00 PM
Ventura County Fire Department	0	1	2	3	3
Los Angeles County Fire Department	9	-	7	12	-
City of Los Angeles Fire Department	3	-	10	12	-
Subtotal	**12**	**1**	**19**	**27**	**3**

"Unable to Fill" (UTF) denotes when the local and eventually region and Statewide mutual aid system cannot fill the incident's resource requests. As seen in Table 2, the fire received 12 aircraft and 27 fire engines by 3:00 PM—only 40 minutes from first smoke check report; however, the combined forces in severe fire weather and rough terrain could not stop the fire.

In interviews with both ground fire commanders and senior fire helicopter pilots, three challenges existed from ignition to sunset on the first day:

- The front of the fire had multiple points and resisted efforts for flanking operations to *shoulder*[8] the forward advance of the fire at the point.
- The west flank was in flatter terrain against some service roads that somewhat assisted with slowing the fire, and the suppression efforts kept the fire from entering a major westward canyon that runs due west through Ventura County.
- The east flank toward the City of Los Angeles was very hilly, rocky, and was not conducive to direct attack by fire engines or hand crews. In one pilot's words, "The fire was spotting so badly in the rocks on the east, and with the multiple points at the front, given aircraft refill times, we could not keep enough water on it and the ground crews could not reach it and hold it while we refilled."

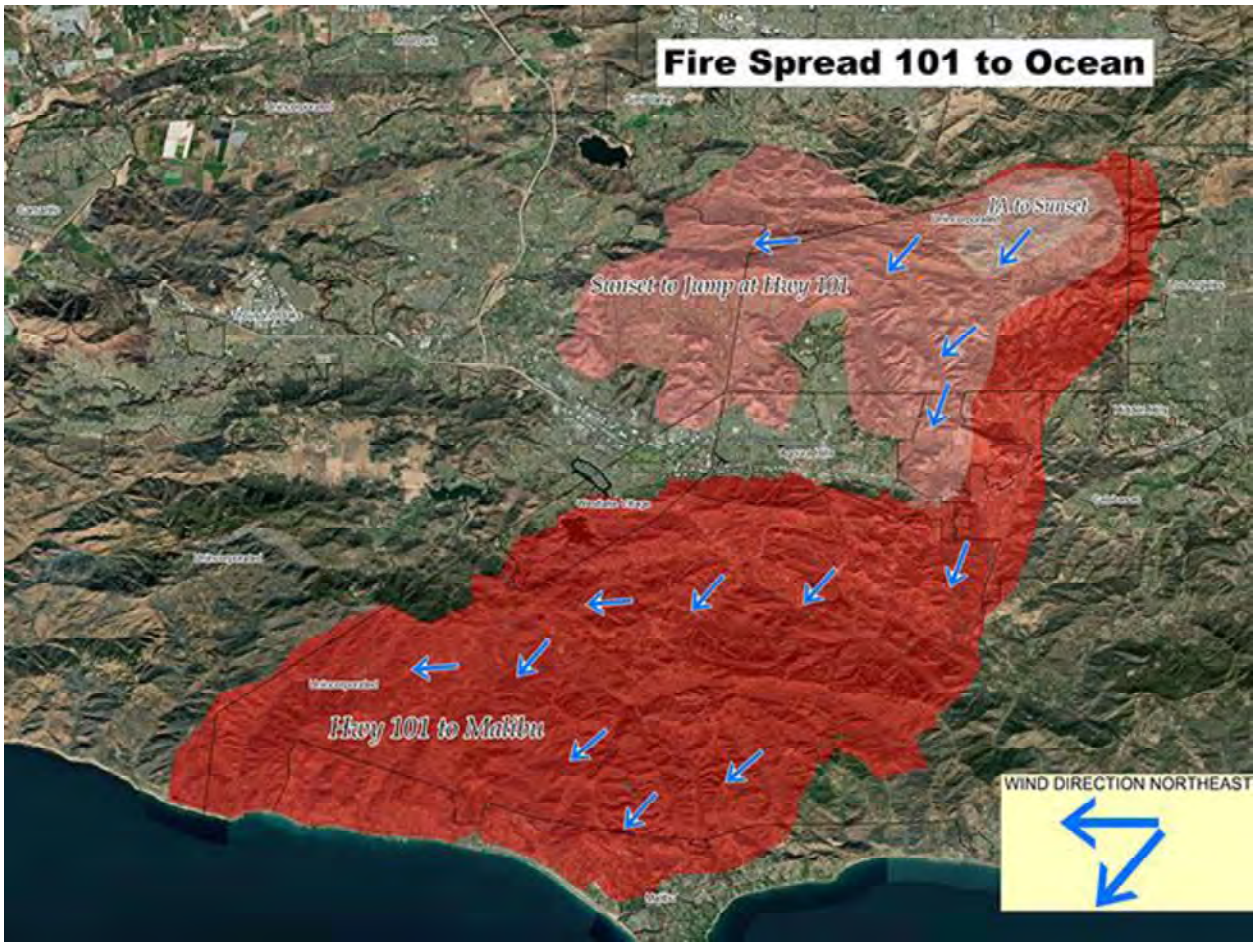
[8] Narrow the point of the fire by turning the flank inward, if possible.

2.3.4 The Fire's Three Main Movements to the Ocean

At sunset on November 8, the heavier, fixed- and rotary-wing aircraft that were not night-vision/drop capable had to stop flying. LA County Fire and LA City Fire helicopters that were night-vision/drop capable continued, Federal Aviation Administration crew standards and fire weather conditions permitting.

During the first 22 hours, the Woolsey Fire has three main movements, shown in the following map:

Figure 3—Three Main Fire Movements



- Movement 1: Thursday, November 8 – Fire origin to sunset (shaded nearly white)
- Movement 2: Thursday and Friday, November 8–9 – Sunset on November 8 to the Highway 101 jump at 5:15 AM on November 9 (shaded light red)
- Movement 3: Friday, November 9 – From the Highway 101 jump at 5:15 AM Friday morning, the fire's final run to the ocean, charring the core of the mountains and devastating Malibu in a little over six hours (shaded dark red)

The winds during the early evening of November 8, while largely out of the northeast, were wandering slightly to the north and more easterly. The fire spread over the evening and early morning hours, widening to the east *and the south.* In the early morning hours on November 9, the winds drove the now wider fire down onto the Highway 101 corridor cities.

As LA County Fire and Ventura County Fire engaged in aggressive structural protection with a substantial number of their engines on the north side of Highway 101, they planned for the fire to spot over the highway due to the strong winds and low RH. The most dangerous point was a set of low hills on both sides of the highway between Liberty Canyon Road on the east and the Palo Comado overcrossing on the west. Both sides of the highway were defended by ground units and night flying helicopters. The fire first spotted just south of the highway between the frontage road and the highway. Fire crews anticipated this fire behavior and extinguished the first spot fire. The dangerous spot over Highway 101 then occurred at approximately 5:13 AM, well up a hillside. This spot fire grew to an acre in less than one minute and several acres in less than five minutes. It was out of reach of the ground units and the water-dropping helicopter, due to refilling time, could not stop it.

Figure 4—Infrastructure Damage – Power Pole



While the fire continued to spot over Highway 101 west of this first major spot all the way to Westlake Village, this significant spot fire that jumped from hill to hill, high over the highway, was the start of the third phase: the run to Malibu.

The area behind the spot fire was also rough and, with even more spotting, the fire advanced into the subdivisions south of Highway 101 and into the mountain communities early in the morning. The fire departments deployed ground and air units into these areas. There were structures and lives saved in these areas.

Figure 5—Infrastructure Damage – Canyon Road



As is typical in severe fire storm conditions that endanger the firefighters when the fire burns over them, the plan was to follow the fire into the mountains and then into Malibu. However, with both a lack of mutual aid and severe wind and fire damage dropping wooden power poles and trees, the canyon roads became impassible. Due to the initial draw of resources for life safety and structure defense at Highway 101 and the inability to take dedicated engines off of the Highway 101 fire fight, the Ventura County Fire and LA County Fire unified command strategy for the Malibu coast early Friday morning was life safety.

Table 2 tells *two stories over time.* First, resources were frequently requested for the Woolsey Fire, and those requests went unfulfilled in the first 21.5 hours of the incident. The mutual aid request system records indicate that responding agencies kept requesting to no avail. Woolsey Fire incident

command chiefs personally called southland area fire chiefs urgently requesting catastrophic mutual assistance from Thursday night into Saturday morning, which is an unprecedented event. Table 2 shows the resources requested and not received up to the time the fire crossed Highway 101.

The second story is that of the firefighting resources in Malibu as the fire entered the coastal plain. Due to the Unable to Fill (UTF) requests and the fire storm's impact on roads through the mountains, units in Malibu consisted only of locally assigned units and a very small quantity of mutual aid. This is why the public observed that the normally heavy fire unit response was not occurring. As Friday progressed, more mutual aid arrived slowly in the Malibu area. Before noon on Friday, the Malibu coast only had between 7–26 engines, not the 100–200 mutual aid engines needed to immediately defend structures in highly developed areas. On Friday morning and early afternoon, the few engines present could not conduct structure defense, but instead were required to address an avalanche of 9-1-1 calls and conduct life safety missions. On Friday evening, there were still nowhere near the units requested. As a result, the public observation was, of course, valid; active structural firefighting in the coastal plain in the early hours of the fire was not possible. Unlike Malibu had ever experienced, nearly all available resources were committed from north of Highway 101 through the mountain communities before the fire began moving quickly to Malibu.

Table 2—Filled / Unable to Fill (UTF) Resources at Critical Points After the Initial Attack

	Tankers / Helicopters Deployed	Tankers / Helicopters UTF	UTF %	Engines Deployed	Engines UTF	UTF %
Midnight on 11/8	5/4	21/9	77%	124	175	58%
5:15 AM on 11/9 Hwy. 101 jump	5/4	21/9	43%	285	289	50%
Malibu area by 9:00 AM on 11/9				7		
Malibu area by 11:00 AM on 11/9				15		
Malibu area by noon on 11/9				26		
Incident total by noon 11/10	35/30	37/12	42%	768	874	53%

LA County Fire helicopters fought the fire through the mountains, helping to prevent the fire from entering Topanga Canyon after the Highway 101 crossing. As the fire approached the City of Malibu, helicopters successfully dropped water near the homes first threatened until the weight of the fire storm pushed them downslope, first to the Pacific Coast Highway (PCH) fire crossings, then finally to the ocean.

The LA County Fire Air Operations Section never gave up. Aircraft operated from the initial Highway 101 crossing until they were literally pushed to the ocean, where the helicopters had to follow the surf line under a very low smoke ceiling east to clear air. They saved several homes Friday morning by tanking from local swimming pools in inland Malibu. They continued Friday

afternoon and, as the fire storm winds abated a little, other air resources were brought in. Much of this was not noted on the ground due to the smoke conditions.

2.3.5 The Mutual Aid Response

Since the early 1970s, the California mutual aid system was designed for agencies to help each other. Before the deadly fires of the past few years, there were typically not multiple fires that would catastrophically empty the mutual aid system. However, due to the growth of fires, the changes to fire weather severity, and economic pressures on local government, the California mutual aid system has seen a decline in mutual aid being available during multiple fire events.

Table 3—Approximate of Total California Fire Engines (Type 1, 2, & 3) by Agency

Agency	Number of Engines
Local Governments	5,928
Cal OES	154
CAL FIRE	343
California Department of Corrections (Prison crews rarely leave site)	74
U.S. Forest Service	277
U.S. Bureau of Land Management	28
Bureau of Indian Affairs/Tribal	24
National Park Service	17
FWS	14
Department of Defense	41
Total	**6,900***

*The 6,900 total number of fire engines in the aid system represents seasonal resources and total inventory of resources. Not all fire engines are available for outside agency and immediate response.

The following table shows the historical count of mutual aid deployed to major fires and fire siege events.

Table 4—Past California Fire and Rescue Mutual Aid System Deployments

Fire or Fire Season	Number of Deployments
1991 East Bay Hills Fire	410 engines
1992 Fire Season	1,800 engines
1993 S. CA Wildfire Siege during October/November	1,525 engines
2003 Fire Siege	1,160 engines
2007 Fire Siege	1,150 engines
2008 Fire Season	4,895 engines
2009 Fire Season	2,125 engines
2010 Fire Season	475 engines
2011 Fire Season	495 engines
2017 Fires from 12/4/17 through 12/6/17 – Thomas (616), Creek (217), Rye (86)	919 engines
2018 Camp Fire (Paradise)	622 engines
2018 Woolsey Fire	619 engines

The following table shows the recent history of the California Mutual Aid system's inability to send large quantities of firefighting units, which has become a serious fire command issue.

Table 5—California OES Unable to Fill (UTF) Statewide Resource Summary

Year	2012	2013	2014	2015	2016	2017	2018
Engines / Water Tenders	134	214	403	958	3,029	6,134	2,724
Overhead/Command, etc.	1,073	1,404	2,315	4,758	4,034	4,867	3,375
Total	**1,207**	**1,618**	**2,718**	**5,716**	**7,063**	**11,001**	**6,099**

As seen in Tables 3, 5, and 6, the system cannot deploy sufficient resources to large incidents. This trend affected the Woolsey Fire response.

The Woolsey Fire unified command team *requested mutual aid early, often, and in high numbers*. Because the Hill Fire was more dangerous at first, it received the "normal, local" mutual aid that all Region 1 departments had pre-authorized to their dispatch centers to send the morning of November 8 as the departments prepared for a severe fire weather day. In fact, the Hill Fire received a five-engine strike team from LA County Fire as first responders. That team was already on the Hill Fire when the Woolsey Fire started. It was released back to the Woolsey Fire later on Thursday evening. From the start of the Woolsey Fire, there was frequent communication between the Incident Commanders of the Hill Fire and Woolsey Fire.

When the Woolsey Fire needed its initial unit request number and hundreds more, many agencies could not fulfill the request. Other jurisdictions may not have been willing to release additional firefighting resources due to their own exposure to fires during the Santa Ana wind conditions and the need to maintain staffing levels for regular life safety needs. As the Hill Fire became less threatening, Hill Fire command shifted units to the Woolsey Fire.

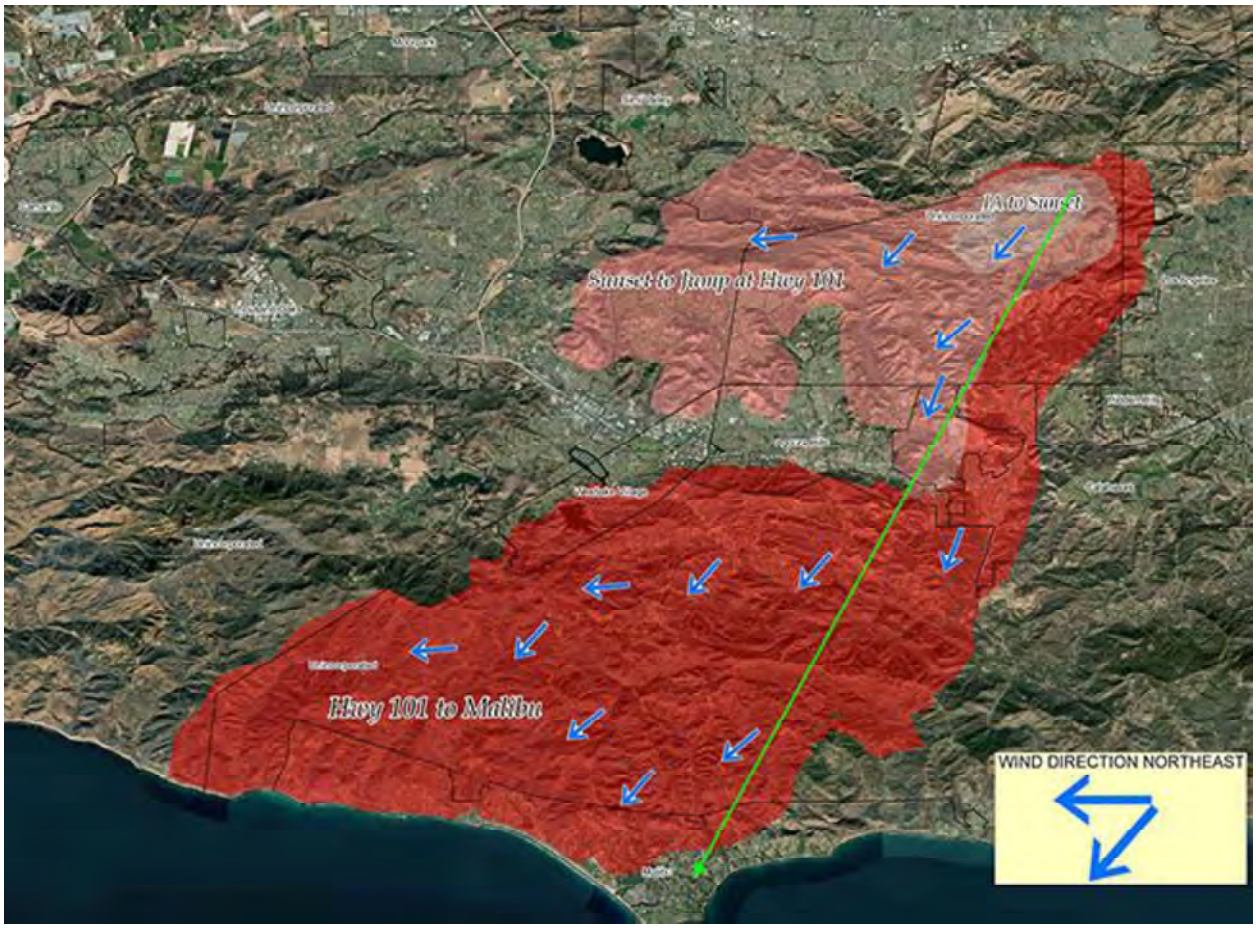
During the first two days of the Woolsey Fire, 53 percent of the fire engine mutual aid requests were unfilled. That totals a staggering 874 units, and the fire burned 96 percent of its final footprint in that time. LA County Fire deployed every unit it could from its own stock, including repairing units in the shop and lowering resources in multiple stations across the County. LA County Fire fielded 100 engines/units to the Woolsey Fire and still maintained coverage of its 2,200 square-mile area for routine 9-1-1 incidents. In addition, LA County Fire double shifted each of its assigned units to forego rest periods to ensure all 100 engines were on the road operating continuously within the impacted communities.

2.3.6 Firefighting Tactics in Woolsey

In the hours from ignition to the late evening on Thursday, November 8, fire command attacked the fire directly with the normal range of tools and procedures, all of which were well pre-planned in the Highway 101 corridor. The winds were variable which seemed to suggest the normal wildfire approach with a northeast wind would work. Three factors broke the plans:

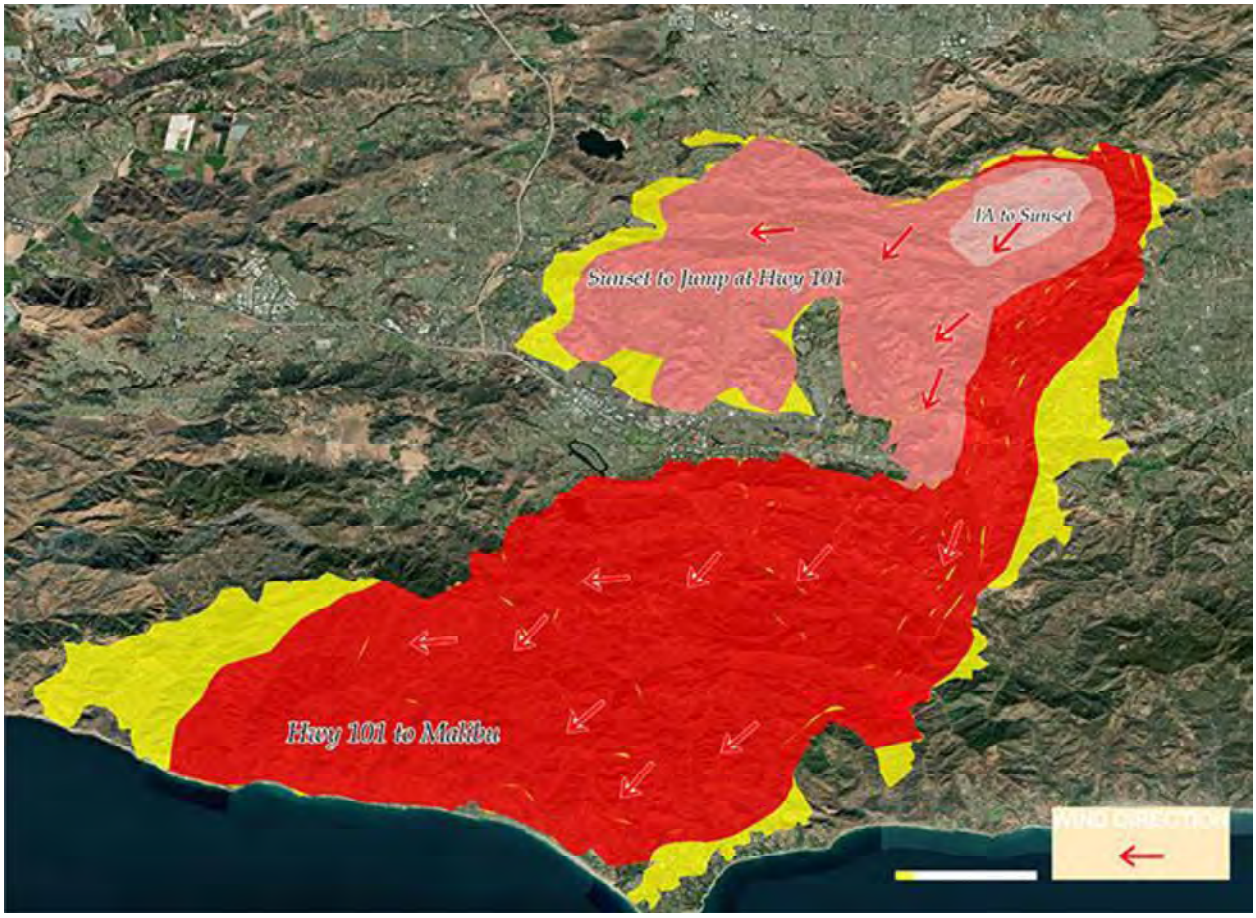
1. Very challenging terrain, especially after dark on Thursday / Friday morning
2. Winds shifting and increasing
3. An uninterrupted, open vegetation fuel bed line from the ignition area straight to Point Dume, as shown in Figure 6

Figure 6—Fuel Line from Ignition to Point Dume



The final Woolsey Fire footprint is shown in the following figure:

Figure 7—Final Woolsey Fire Footprint



After midnight on November 8, when direct control was no longer possible due to the fire entering multiple populated areas, fire command directed all units into Life Safety First and Fire Front Following to ensure evacuations were successful.

As the findings and recommendations in this AAR will show, both were compromised due to lack of resources and the strict application of the tactics even when local conditions warranted small deviations.

2.3.7 The Evacuation Response

During the day on November 8, LA County Fire chief officers were in a regular staff meeting at headquarters. They were monitoring the Camp Fire in northern California and their own fire weather conditions. The Hill Fire in Ventura County began and drew a response from LA County Fire, which was followed by the start of the Woolsey Fire. This prompted an all-command staff response from LA County Fire and the chief officers deployed to the Woolsey Fire Incident Command Post (ICP) in Ventura County. Another group of LA County Fire chief officers familiar

with the Woolsey Fire area in the Highway 101 corridor and Malibu went to LA County Fire Station #89 in Agoura Hills. Here they realized the potential for a devastating fire spread. They assumed the task to prepare their communities in case the Woolsey Fire crossed into Los Angeles County. The local Assistant Chief for the Santa Monica Mountains area made community connections at 3:30 PM on November 8, issuing voluntary evacuations all the way to Malibu.

The three LA County Fire chief officers then developed three evacuation zones based on past fire experience in the area:

- Zone 1 – Highway 101 east to Simi Valley
- Zone 2 – Highway 101 west to Mulholland
- Zone 3 – Mulholland to the PCH

By this point, the Los Angeles County Sheriff's Department (County Sheriff's Department) also had a liaison with the LA County Fire chief officers at Station #89. The evacuation zones were to be used under the general rule that, if the fire crossed a zone border, that would trigger an evacuation of the adjoining zone. This plan was incorporated into the incident action plan. The plan required a major response from the County Sheriff's Department. This plan was good on paper, but the fire spread quickly early Friday morning before dawn, accelerating the trigger points, requiring associated actions for community alerting.

Figure 8—Teamwork by County Personnel



The evacuation planning also triggers the need for mass care operations for humans and animals. As this care for the evacuated populace was being planned, law enforcement was already evacuating Zone 1 areas of Bell Canyon, Oak Park, Thousand Oaks, Agoura Hills, and Calabasas. The biggest challenge was notifying the public and community leaders and moving resources in the smoky conditions with many traffic hazards.

During the Woolsey Fire, law enforcement provided a significant force to notice evacuations, control road closures, conduct lifesaving 9-1-1 responses, and prevent civil disorder. The law enforcement commitment to the Woolsey Fire included:

- Approximately 6,400 law enforcement officers worked on the Woolsey event from start to finish and were assigned from:
  - County Sheriff's Department
  - Ventura County Sheriff's Office
  - CHP
  - City of Los Angeles Police Department
  - Mutual aid departments
- The law enforcement team had to maintain evacuation orders for 12 days

As the fire behavior and winds increased during the late evening of November 8, fire services and law enforcement commanders constantly monitored fire activity in relation to the evacuation decision points. At 1:20 AM, orders were given to evacuate Zone 2, focusing on the Malibou Lake area. At 5:15 AM, when the second spot fire jumped Highway 101, an LA County Fire Assistant Chief requested that mandatory evacuations begin all the way to the PCH. While Citygate cannot fully quantify the results, the evacuation planning and actions by all cooperating agencies fostered an environment in which over 250,000 people were successfully evacuated.

Occupant Support

Over the 2017–2018 fire seasons, there has been an increasing occurrence of residents not reacting to evacuation orders. People are forced back home due to road closures, caring for animals they were unable to evacuate, trying to prevent criminal looting, or just staying to protect their homes. Regardless of why people remain within evacuation areas, their emergency supplies (water, food, fuel, etc.) often deplete and they cannot resupply once evacuation road closures are enforced. CAL FIRE began a program during the 2017 Tubbs Fire in which it provided limited water and fuel to residents caught behind evacuation lines. Ventura County Fire enhanced this program during the 2017 Thomas Fire and LA County Fire took those lessons learned and enhanced the services, now referring to it as the "Occupant Support" program.

Figure 9—County Fire Occupant Support Team after a Successful Retrieval of a Cherished Ring



LA County Fire recognizes the harsh realities that some people are caught behind evacuation lines and may face critical supply needs. This program is not intended to encourage people to stay as LA County Fire still educates the public utilizing the Ready! Set! Go! program's tenets to leave early. Stay-behind survivor actions support humane needs behind the road closure lines and were followed by a parallel animal support program by Los Angeles County Department of Animal Care and Control (County Animal Care). Both programs worked well as small-area tests during this incident. There were not enough resources, due to the lack of mutual aid, to come even close to adequately providing occupant support. This effort should be expanded for future incidents in which the complexity and availability of assisting resources allows. Firefighting still must be substantially concluded as occupant support begins.

The Occupant Support program during the Woolsey incident utilized two task forces splitting the fire area in half. The task forces led by Battalion Chiefs consisted of personnel on fire engines, fire prevention light vehicles, and lifeguard response vehicles. Their mission was simple; logistically support those in the area who may have been running low on critical water, food, and supplies, and help those who may have had devastating losses as a result of the fire. They offered water, energy bars, generator fuel, and information on recovery, emotional support, contact to the outside world if needed, and, occasionally, when safe, assistance with the search for an important personal

item. Overall, the program offered compassion and showed the fire department caring beyond the last ember extinguished.

2.3.8 The Public Notification Response

The County Sheriff's Department Public Information Officer (PIO) program operates a decentralized media policy which dictates that individual stations are responsible for routine public information dissemination. This is accomplished through either a dedicated PIO position, or through the Lieutenant or Watch Commander if a station does not have a dedicated PIO. If a station needs assistance for an incident that grows large or is complex, they contact the 24-hour on-duty County Sheriff's Department Sheriff's Information Bureau (SIB) PIO.

When large incidents occur, the designated LA County Fire PIO on the Department's Type 3 Incident Management Team (IMT) usually takes the lead but, in the Woolsey Fire, the decision was made to keep each agency's lead PIO (six personnel) as a lead PIO team.

During the initial hours of the Woolsey Fire, PIO efforts occurred with Ventura County Fire, the LA County Fire PIO, and LA County Fire Community Services Liaison (CSL) staff who were eventually co-located. Initially, the LA County Fire Community Liaison was with the Fire Station #89 evacuation planning team.

The County Sheriff's Department PIOs assigned to the ICP were trying to communicate face to face with the fire services PIOs about evacuation information, even as they were initially driving out to the ICP.

The fire department PIOs used their dedicated Twitter accounts as their primary method of information dissemination, first via Ventura County Fire's official Twitter account, then via the LA County Fire PIO's Twitter account. The strategy was to use Twitter to reach local area media who would then communicate information to the affected public. The fire department PIOs were also fielding a high volume of media calls on their individual Department-assigned cell phones at what was described as a "relentless pace." At the Malibu Sheriff's Station, the Sheriff's Search and Rescue Unit's Twitter account was being utilized to disseminate fire and evacuation related information.

A Joint Information Center (JIC) was established at the Los Angeles County Emergency Operations Center (County EOC) at approximately noon on the second day of the fire (November 9). The JIC was staffed from 6:00 AM until 9:00 PM, with a JIC manager on site from 6:00 AM until 6:00 PM. The JIC was tasked with writing and disseminating news releases, once it obtained approval, and with keeping the 2-1-1 call center up to date.

On the morning of November 10, the initial attack PIO structure was significantly bolstered by the CAL FIRE Type 1 IMT's PIO section. Twice-daily fact sheets and daily news briefings were established and the routine use of American Sign Language interpreters and Spanish language PIOs were initiated under this structure.

When fire command ordered an evacuation, the PIOs used Twitter, email, texting, and voice calls to the partner cities in the fire area. They relied on the County Sheriff's Department Emergency Operations Bureau (EOB) team to use ALERT LA and other tools to notify residents in the unincorporated area. As time permitted, the PIOs answered or made calls to the local major media news outlets.

During the first two days, even when the PIOs were physically together, they had no unified strategy for notifications nor how to divide the workload. They all came from large organizations and were used to working in their "silo," which is not as effective in a large-scale incident.

2.3.9 The Care and Sheltering of Evacuees

Los Angeles County Code and the County Emergency Operations Plan designate the Emergency Management Council (EMC) as responsible for oversight of the preparedness activities of the various County departments, including preparation and approval of plans, training of County employees for emergency and disaster-related functions, and related emergency preparedness activities to ensure unity of purpose. The Los Angeles County Department of Public Social Services (DPSS) Director is a member of the EMC. The EMC subcommittee, which includes DPSS staff, assists the EMC, EMC Steering Committee, and the Los Angeles County Office of Emergency Management (County Emergency Management) in developing emergency plans.

DPSS is the care and shelter coordinator under the County Emergency Operations Plan and, as such, is responsible for developing any pre-disaster plans relating to caring for and sheltering disaster victims.

The American Red Cross (Red Cross) is the designated mass care service provider in Los Angeles County under the DPSS plan. The Red Cross has a designated seat next to the DPSS to staff the Mass Care and Shelter Branch within the County EOC Operations Section. The Red Cross is a non-profit entity, depends upon donations, receives no government funding, and is the designated shelter service provider during government-managed incidents throughout the United States.

During the Woolsey Fire, DPSS staffed the Mass Care and Shelter Branch within the County EOC to coordinate with the Red Cross and the Los Angeles County Department of Animal Care and Control (County Animal Care). DPSS identified and monitored sheltering needs. Shelter staffing is provided by the Red Cross without on-site assistance from DPSS.

The activated shelter sites did not exceed capacity; thus, additional sites were not developed. The DPSS team also checked on service populations with special needs and provided in-home services, as needed, for evacuees and during power outages in the evacuation area. DPSS provided CalFresh benefits (formerly known as Food Stamps) to service populations without power for more than four hours by obtaining the required documentation from Southern California Edison (SCE).

DPSS was challenged to staff its EOC position full time but provided phone support when not physically present. At times, the Red Cross was also challenged to physically fill all its staffing

assignments but, through phone calls and email, maintained adequate coordination with the County agencies.

At times, there was some confusion regarding where the shelters were located. In the early stages, information regarding where the shelters were located was not disseminated with evacuation notices. At least one shelter site in the City of Los Angeles, a school, was initially used without realizing the ramifications of that choice for a long-duration evacuation.

Figure 10—American Red Cross Shelter and Donations



Often, the donation of supplies to shelters by private centers and some elected official organizations was not well coordinated per existing County Plans. Given the sheer scale of the Woolsey Fire, a more robust control system is needed to manage the deluge of well-meaning donations and spontaneous volunteers. Solutions should be sought to foster enhanced coordination, especially in the early phase of catastrophic, multi-day incidents.

Los Angeles County Department of Public Health Role

Health care for those evacuated is a significant issue and is managed by the Los Angeles County Department of Public Health (DPH) within the County's emergency plans.

Figure 11—Health Shelter Personnel



For the duration of the Woolsey response, DPH participated in unified command with city, county, State, and Federal partners in the field and at the County EOC to coordinate interagency activities, request resources, and exchange response information and situational awareness. Its deployment included more than 100 staff in affected areas to support evacuation and sheltering operations, respond to the myriad of environmental health concerns, and address public health concerns related to repopulation missions. Specific activities included:

- Staffing the County's JIC to issue bilingual public health and safety messages and materials to the public and incident management personnel on fire safety, safe debris cleanup, food safety, boil water notices, hazardous material cleanup, mental health and well-being following a disaster, animal health, and other areas; utilized social media for up-to-the-minute situational updates.
- Providing staffing for four Red Cross shelters for fire evacuees with five round-the-clock public health nursing staff to assure protection against communicable diseases and provide influenza and tetanus vaccinations.
- Monitoring air quality data, issuing smoke and air quality advisories and alerts, consulting with school districts and County workplaces regarding indoor air quality

concerns for returning students and employees, and assessing water quality concerns to advise local water districts regarding boil water notices and orders.

- Developing protocols and coordinating with other County first-responder agencies and the State regarding solid waste removal and hazardous material and debris cleanup protocols; declaring a local public health emergency to ensure cleanup activities proceeded in a safe manner and prohibiting disposal of fire debris from residential properties without clearance from local fire or State agencies.
- Providing information on extremely vulnerable populations to local fire departments to assist with evacuating at-risk fire zones, including Medicare beneficiaries who are dependent on electric-powered medical equipment, dialysis, and other life-saving services.
- Supporting the Los Angeles County healthcare system in evacuating and transferring medically fragile patients from one skilled nursing facility and three congregate living facilities impacted by the fire.
- Conducting field community education outreach to establishments in areas impacted by the fire; talking with residents returning to their community and at entry checkpoints, and distributing health information and personal protective equipment.
- Inspecting nearly 500 restaurants in affected areas to ensure food safety following closures, fire damage, and power outages.
- Assessing and ensuring environmental health and safety at firefighter camp sites and shelters.
- Coordinating with Federal and State partners and performing independent air monitoring and other assessments in proximity to a decommissioned rocket testing, nuclear reactor testing, and liquid metal research facility to identify any potential health threats related to radiation; developing a press release to communicate findings.
- Supporting recovery planning and activities in the impacted areas by participating in community meetings and staffing the interagency Disaster Assistance Centers (DAC) to provide health messaging, distributing fact sheets, provide resource referrals, answering residents' questions, and providing tetanus and flu immunization services.

Overall, the DPH had the ability to support the County's emergency response command organization, to support evacuation and sheltering operations, and to respond to the myriad of environmental and public health concerns during both the response and recovery phases of the incident.

Recovery Phase

During the recovery phase of the incident, environmental health missions included management of debris clean-up, follow-up on odors, food salvage, drinking water concerns, and inquiries regarding septic tanks, contaminated debris management, structural ash, swimming pools, and mosquito breeding.

DPH participated actively in the Long-Term Disaster Recovery Group alongside several community and faith-based organizations and other government and non-government agencies to assess and serve the ongoing needs of the communities affected by the Woolsey Fire.

As the recovery phase continues with rebuilding, DPH provides residents with approved options for potable water and waste disposal when using a recreational vehicle or mobile home as temporary housing. To date, DPH has approved 36 temporary housing applications. In addition to monitoring temporary housing, DPH staff review plans for rebuilding septic systems. DPH anticipates 600 septic system plans to be submitted. To date, DPH has provided nearly 450 consultations to Woolsey Fire victims planning to submit rebuild plans.

Given the magnitude of the rebuilding needed after the Woolsey Fire, DPH has had staffing challenges to support the number of post-incident permit applications at a pace that clients and other County agencies need.

2.3.10 The Mass Care Response for Animals

County Animal Care is responsible for the daily operation of animal care centers as well as other duties in Los Angeles County and contract cities outside of the County, like the City of Thousand Oaks. While responding to the Woolsey Fire, County Animal Care fed and cared for over 2,000 animals in care centers every day, and still maintained its daily operational duties. County Animal Care has a great relationship with many volunteer groups and has expressed that it could not have succeeded without volunteer assistance.

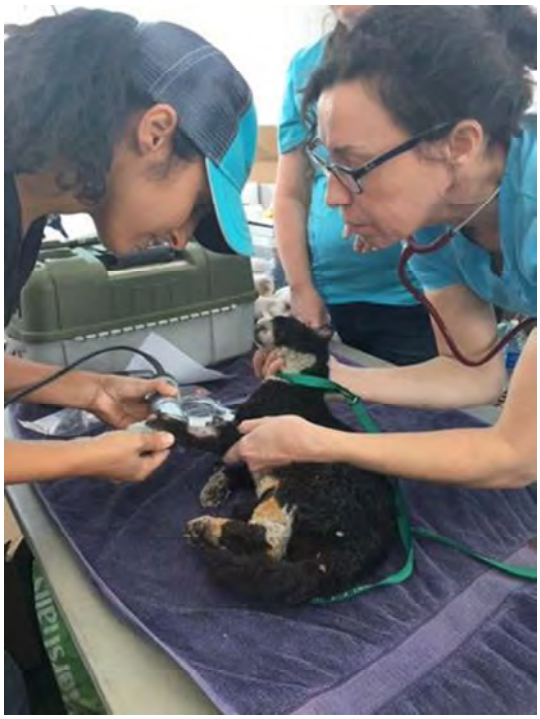
On November 8, at 3:30 PM, County Animal Care staff members concluded a tabletop exercise for the Department's Continuity of Operations Plan at its headquarters in Long Beach. This exercise was designed around the imagined evacuation of an animal care center. Just fifteen minutes later, at approximately 3:45 PM, the animal control manager in charge of the Agoura Animal Care Center observed a plume of smoke heading toward the Newbury Park community. The smoke was later identified as a result of the Hill Fire in the City of Thousand Oaks.

County Animal Care Officers reported to the Lost Hills Sheriff's Station and coordinated rescue responses with the County Sheriff's Department and LA County Fire. Other County Animal Care Officers were assisting owners with livestock rescues in the Cheseboro community of Agoura. Staff were assigned to field duties (assisting with evacuations of horses and other large animals) and to setting up emergency sheltering sites for animals.

County Animal Care worked closely with the County Sheriff's Department and County Emergency Management to coordinate animal mass care support in conjunction with human mass care sites. All attempts were made to keep animal owners connected with their animals so they would evacuate the fire area. Normally, the Red Cross does not allow pets at mass care sites, but creative workarounds were achieved to accomplish the task. Large animals were not limited to horses and there were unique challenges with some exotic species.

County Animal Care sought a sheltering site to support Thousand Oaks community animals that needed to be evacuated. The site provided parking for County Animal Care's emergency sheltering vehicle (AnimalSafe trailer) for household pets from the Thousand Oaks community. AnimalSafe trailers are trailers that County Animal Care uses to co-locate evacuees and their pets at sheltering sites. County Animal Care also had to protect and then evacuate the Agoura Hills Animal Care Center. They successfully completed this task and later found the care center suffered minor damage.

Figure 12—Animal Care Medical Team



Late Thursday evening, as Red Cross shelters opened at Taft High School and Pierce College, County Animal Care staff were activated to set up AnimalSafe trailers at these locations in response to the shelters opening. Into early Friday morning, County Animal Care supported an animal receiving site at Hansen Dam and then opened another at the Thousand Oaks Teen Center. Before dawn Friday, the County Animal Care Director of Volunteer Services issued a mass

notification to Department volunteers for assistance with County Animal Care's responsibilities for animal care and sheltering along with identifying mutual assistance partners for assistance.

Friday morning, County Animal Care received mutual aid support from spcaLA, the Pasadena Humane Society and SPCA, and Los Angeles City Animal Services. These agencies reported to the staging area at Whizin Market Square in Agoura.

A sizable challenge was to provide animal support to animals that could not be evacuated. These animals, especially horses, required food, water, and some improvement to enclosures. County Animal Care requested Los Angeles County Public Works (County Public Works) to deliver water inside the evacuation areas.

County Animal Care also teamed up with Veterinary Angels, a non-profit organization that assisted at the sheltering sites, working with County Animal Care's medical team to bring medical support to pets and owners affected by the fires. The MASH-type unit established with Veterinary Angels' support was so beneficial that the Los Angeles County Animal Care Foundation has committed to funding a mobile clinic for County Animal Care to use in future events. To support this resource, County Animal Care called the Southern California Veterinary Medical Association (SCVMA). Through its network of volunteers, the SCVMA was able to offer voluntary medical staff at its sheltering sites. An average of six SCVMA volunteers assisted County Animal Care each day.

Overall, County Animal Care provided care to 791 animals during the incident. Twelve of these, including several chickens and goats, reported receiving burns of varying degrees. One llama died from burn injuries. County Animal Care's Senior Veterinarian treated 12 animals for burns. In addition, County Animal Care's medical team monitored animals that were sheltered at Pierce and Hansen Dam.

The use of County Animal Care's Animal Care Center volunteers to supplement the Equine Response Team volunteers was also an innovation during this event. Although the Equine Response Team has been activated in many prior emergencies, County Animal Care volunteers have never before been used as additional support. County Animal Care's volunteers assisted at the sheltering sites to clean and care for evacuated animals. They also assisted with donations and greeting the public. Overall, County Animal Care Animal Care Center and Equine Response Team volunteers donated 7,821 hours of service during the fire.

After the fire, County Animal Care participated in the DACs at the Agoura Community Center and Malibu Court House. County Animal Care received 204 requests for assistance (for a total of 351 animals) from owners who were impacted by the fire. These requests were for medical care, temporary housing, and temporary food supply. Financial assistance to provide this medical care was provided by the Los Angeles County Animal Care Foundation. County Animal Care has been made aware of various community members and organizations that lost animals during the fire.

However, not all losses or injuries to animals were reported to County Animal Care during the event.

During the transition phase of the incident, County Animal Care staff formulated costs for expenses during the fire and found that many of the expenses were outside the Federal-Emergency-Management-Agency-eligible parameters. These exclusions were partially covered by volunteer donations, but there seems to be a gap in funding for animal cost recovery expenses.

County Animal Care's review after the incident identified many of the same challenges to its teams and systems as other County agencies during Woolsey Fire. The following key items are improvements that County Animal Care staff is working on or has already completed:

- Developed a process for ongoing training for new staff that do not have experience responding to emergencies. This was completed by July 31, 2019.
- Established a revised process to identify resource needs based on prior natural disasters so that a baseline for the resources needed is established.
- Working with the County Animal Care Information Technology team to expand abilities to track and communicate with County Animal Care officers in the field.
- Developing a process to manage a high volume of spontaneous volunteers.
- Establishing a more robust process to receive donations via phone, internet, email, and in person.
- Improving communications during an incident to all responders, staff, and volunteers.

2.3.11 Disaster Assistance Centers and Recovery

Recovery Coordinating Center (RCC) operations were activated by County Chief Executive Officer (CEO) with the goal of opening the LA County Fire DACs by Saturday, November 17. Staff from other County agencies were specifically assigned to the RCC because of their backgrounds.

The County team understood that at least two local DACs would be needed to serve fire victims: one in the Malibu area and another in the Highway 101 corridor.

This was the earliest in a disaster event the County had opened a DAC; prior philosophy/practice was to have a longer preparation period between the conclusion of the incident and the opening of the DAC. The Federal Emergency Management Agency (FEMA) Area Field Office opened in Westlake Village on December 18.

The DACs were staffed by 60 to 100 or more employees and volunteers representing over 50 local, State, and Federal agencies, cities, and non-governmental organizations.

The Agoura Hills DAC transitioned to a Disaster Recovery Center (DRC) on December 18, and then the DRC closed on January 11, 2019. The Malibu DAC closed on January 9, 2019.

Figure 13—Disaster Assistance Center



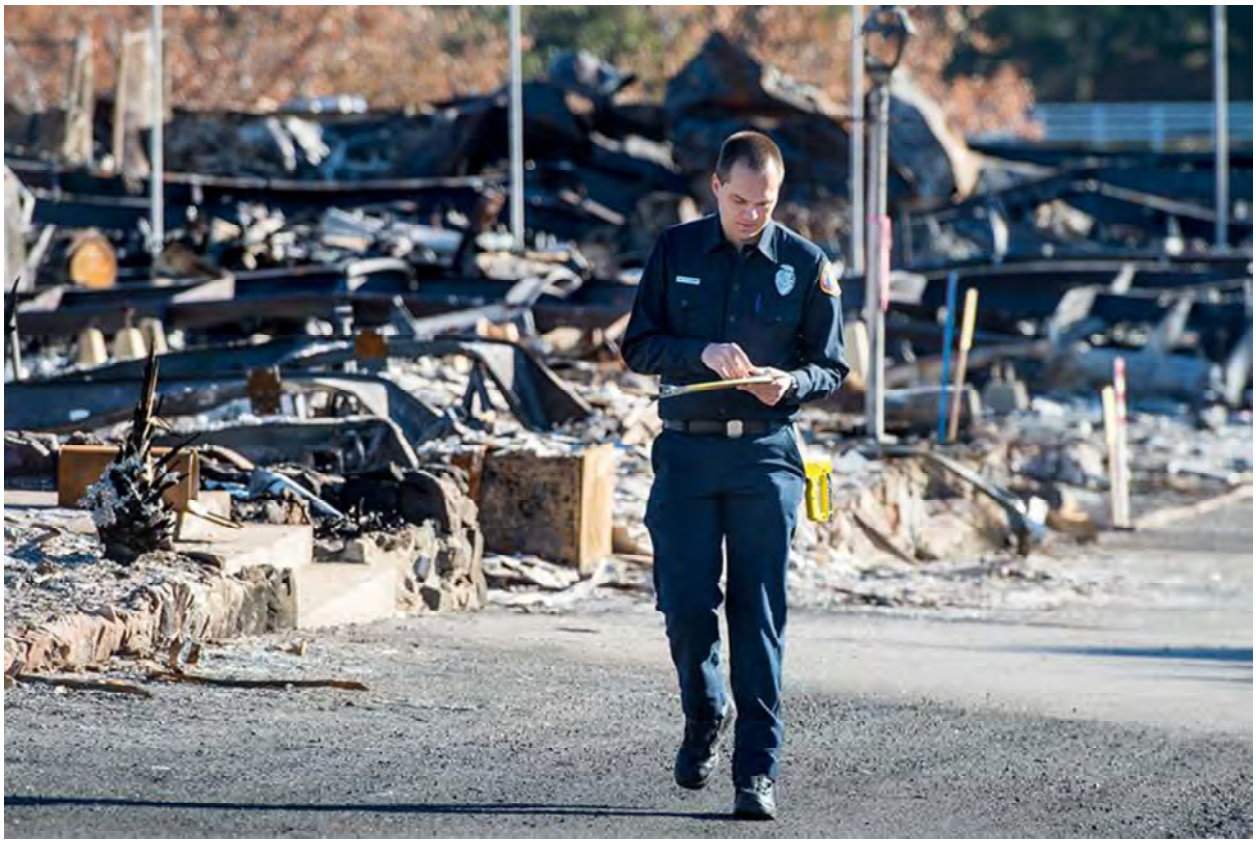
The DRC continues to this day. From the beginning, the County team led by the Los Angeles County Department of Regional Planning (DRP) has carried the burden of coordinating the rebuilding process; this effort will continue for approximately five years. In addition to the County planning, building, and fire regulations, the California Coastal Commission has requirements in the area regarding rebuilding. By October 1, the County approved 79 plans for rebuilding, issued 29 rebuilding permits, and is ahead of schedule in many respects.

2.3.12 Damage Assessment and Debris Removal

As the Woolsey Fire was being contained, LA County Fire and County Public Works dispatched several teams of engineers, inspectors, and Public-Works-Safety-Assessment-Program-certified members to survey the sites affected by the Woolsey Fire to confirm the extent of damage for residential, commercial, or County-owned buildings. In a matter of two weeks, over 400 residential and commercial sites were surveyed with a total of 658 structures classified as demolished, moderately damaged, or lightly damaged. Most sites were labeled with either a red tag or yellow tag. A rapid evaluation report accompanied by pictures was produced for every site surveyed. County Public Works also provided substantial assistance to the affected cities, especially the City of Malibu, to assess the damages to private property. Damage assessment continued on or about

November 10 (Day 3 of the Woolsey Fire) by County agencies and a CAL FIRE Damage Inspection Specialist Unit under the Unified Incident Command Planning Section.

Figure 14—County Damage Assessment



During the first week of the Woolsey Fire, County Emergency Management communicated with the California Office of Emergency Services (Cal OES) and FEMA to identify a timeline and critical components of debris removal needs. Considering this was the County's first utilization of a new State and Federal process for Private Property Debris Removal (PPDR), there was an associated learning curve. In partnership with Cal OES and CalRecycle, a unified command PPDR IMT was developed.

The RCC Operations Section subsequently established a Disaster Services Group to, among other responsibilities, coordinate debris removal pursuant to a DPH declaration of a local public health emergency. The Disaster Services Group subsequently tasked County Public Works with private property debris removal around November 19 (Day 11). County Public Works coordinated with other County departments, affected cities, and State and Federal agencies, including the California Environmental Protection Agency, Cal OES, and FEMA.

Figure 15—Hazmat Cleanup



Memorandums of Understanding were executed with affected cities to allow the County to execute a one-stop "Consolidated Debris Removal Program" for all affected property owners, which included right-to-enter and hazard abatement authorization. CalRecycle was awarded a contract for all debris removal under this program. Approximately 900 private parcels had hazardous debris removed. Property owners not opting into the PPDR program had to proceed at their own expense and gain the necessary environmental permits from the RCC.

2.3.13 County Water Supply in the Greater Malibu Area

Los Angeles County Waterworks District No. 29 (County Waterworks) was established in 1959 by the Board of Supervisors through a public election that authorized the formation of the District. The water systems in the Topanga and East Malibu Mesa areas were installed between 1962 to 1967. The water systems in the East Malibu Coastal region and areas west of Las Flores Canyon Road were installed between 1928 to 1970. After the construction of the major transmission line along the PCH that delivers water from the Metropolitan Water District of Southern California to Malibu, Topanga, and Marina del Rey, the District was petitioned to purchase several nearby mutual and privately-owned water companies. The District purchased Hillside Water Company in 1967 and Malibu Water Company in 1971.

The District currently serves approximately 22,300 people through 7,500 metered connections. The District purchases nearly 100 percent of its water supply from the Metropolitan Water District of Southern California through an intermediary wholesaler, the West Basin Municipal Water District. Water is delivered through a 35-mile-long transmission main that conveys purchased water from an interconnection with the Metropolitan Water District of Southern California in Culver City to the west boundary of the City of Malibu. Due to the single source of supply and the mountainous terrain of Topanga Canyon and Malibu, the water system has been laid out as a "tree system" with very few redundant pathways or pipeline loops. This "tree system" is vulnerable since a break in the system will stop water flowing to all service connections downstream of the break.

Public water systems serve two primary purposes: (1) domestic water service for drinking, cooking, bathing, irrigation, and sanitation; and (2) fire protection. To accomplish these purposes, public water systems are designed with storage and pipeline carrying capacities to provide water to simultaneously meet the highest domestic demand and the fire-flow requirements for a *single structure fire* per the version of Los Angeles County Fire Code adopted at the time that the water system *was built*. Water distribution systems are not, and cannot be, practically designed to fight wildfires due to multiple design considerations, including water quality decay if not enough water is used on a day-to-day basis. Many development areas in the mountain communities depend on wells for domestic and firefighting water. Widespread power failures also cripple these systems.

During the Woolsey Fire, County Waterworks was able to maintain storage and pressure—*as the system was designed.* However, due to a very high demand by firefighters, residents, and pipe breaks in burned structures, some neighborhoods had insufficient or no pressure at times.

As the fire front passed, County Waterworks employees turned off broken, leaking service at damaged structures. At no time during the firefighting or the recovery effort did County Waterworks turn off supply to neighborhoods or intact buildings; there was just not enough pressure at times to meet large demands as a result of the incident.

2.4 THE WOOLSEY FIRE INCIDENT RESPONSE SUMMARY

The following, in various forms, all contributed to the Woolsey Fire. Many are no different than past fires. Citygate observed:

1. Fire intensity was extreme, and there were unrealistic expectations of fire department behaviors based upon past experiences in which communities saw large quantities of fire units protect their community.
2. This fire behaved like no previous fire in the Santa Monica Mountains area. The Woolsey Fire burned through three of four historic corridors at once, with a wide fire front with a half-mile to one-mile-or-more ember cast. Previous fires burned as narrow ribbons; this fire fanned out widely and quickly through areas loaded heavily with dense vegetation.

3. The Malibu coastal plain area also has many long, dead-end canyon roads, which makes evacuation and firefighting access very challenging.
4. With the shortage of resources and the extreme fire behavior, the initial fire response in the Malibu PCH corridor could only meet life safety needs.
5. The speed and intensity of the fire overwhelmed the resources on scene.
6. This fire created highly stressful conditions for the public and emergency responders due to the extreme fire behavior and associated losses.
7. In the first 24-hour operating period and slightly beyond, command chiefs and fire services and law enforcement crews operated without adequate sleep and quality information regarding the Woolsey Fire situation.
8. Fire Front Following and Life Safety First fire unit tactics are not fully understood by the public nor policy makers.
9. Historical fires have occurred after the first couple of east wind days, whereas this fire occurred during the first wind day, when the winds are at a higher and unsettled intensity.

Figure 16—Recovery Center



10. The wind was blowing in an optimal direction to drive the fire wide and fast to the coast.
11. Ornamental landscaping is more readily ignited than many native species and thus contributes to structure ignition.
12. Vinyl fencing and weathered / aged wood exposures are more susceptible to ignition.
13. Social media influences create a demand for rapid-tempo updates.
14. Fire and/or wind caused early and wide-area losses of critical infrastructure, such as electric power, bridges, key roads, and cellular communication sites.
15. Ventura County Fire and LA County Fire resource levels have remained static while population growth has placed more people in harm's way while the severity and frequency of wildfires are growing.
16. Constituents and policy makers at Federal levels do not understand nor accept the new normal for California fire behavior and Santa Monica Mountain fire impacts.
17. There is the need to understand that frequent, extreme fire conditions have greatly affected the natural ecosystem of the native chaparral, including the introduction of invasive species and the adverse effects that accompany them.
18. Individuals and organizations are at odds regarding how to address the wildland fuel/fire problem.
19. There is a lack of public participation in the Ready! Set! Go! program to harden their structures against heat and embers, and to create defensible space and perform structure/property maintenance.
20. The lack of adherence to evacuation orders and the resulting 9-1-1 calls impacted the ability of very limited fire responders to defend structures in some locations.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SECTION 3—TIMELINE OF SIGNIFICANT INCIDENT EVENTS

The following timeline of significant events is numbered for easy reference and, if available, is timestamped. Not all significant events are stamped with a precise time as, sometimes, a batch record exists of several events in a singular AM or PM period. Those events fall between other time stamp events, so such instances have still been placed chronologically.

3.1 WEDNESDAY, NOVEMBER 7, 2018

Weather/Fire Conditions: Forecast and Preparation

Significant Event 1: National Weather Service predicts peak fire-event forecast overnight Thursday and into the predawn hours on Friday. Strongest winds predicted to occur Thursday night through Friday morning.

Significant Event 2: Los Angeles County Fire Department (LA County Fire) Assistant Chief calls the affected western County cities during the evening to advise them of augmented staffing implementation and pending fire weather predictions.

3.2 THURSDAY, NOVEMBER 8, 2018

Weather/Fire Conditions

Significant Event 3: 6:00 AM – Due to the predicted Red Flag Warning, Lost Hills Los Angeles Sheriff's Station was in direct communication with LA County Fire. Lost Hills Station units were directed to begin Red Flag Warning patrol checks.

Additionally, County Departments were on stand-by due to a Southern California Edison (SCE) public safety power shutoff possibility.

Significant Event 4: 6:33 AM – The Camp Fire ignites east of Paradise, California, and expands in size at an unprecedented rate. Statewide firefighting resources shift to address the growing threat of this fire that will evolve to become the deadliest wildfire in California history. Due to local weather/fire conditions, California Office of Emergency Services (Cal OES) Region 1, including Los Angeles County, does not send resources to the Camp Fire on November 8.

Significant Event 5: 8:00 AM – In the area of the impending Woolsey Fire, the relative humidity (RH) is 78 percent.

Significant Event 6: 8:00 AM – Los Angeles County Public Works (County Public Works) opens Department Operations Center (DOC) at Level 3 status due to the SCE public safety power shutoff warning.

Significant Event 7: 10:00 AM – With strong Santa Ana conditions in the region, the local RH drops to five percent or less in Simi Valley. Local agencies are on heightened alert including LA County Fire, Los Angeles County Office of Emergency Management (County Emergency Management), and County Public Works.

Significant Event 8: 2:00 PM – The Hill Fire in Thousand Oaks ignites. The Hill Fire was a wind-driven fire in the Hill Canyon area of Camarillo and quickly consumed the geographical area's augmented fire resources. Other area fire departments are reluctant to deplete their reserve capability due to the potential for fires in other jurisdictions.

Fire Conditions/Response: Fire Start

Significant Event 9: 2:24 PM – Ventura County Fire Department (Ventura County Fire) Emergency Communications Center receives first report of the Woolsey Fire as a smoke check on the Santa Susana Field Laboratory property. The initial response to the smoke check is the Rocketdyne Fire Department and one Ventura County Fire fire engine.

Significant Event 10: 2:33 PM – Before arriving on scene, a responding Ventura County Fire fire officer requests an upgrade to a full brush response, which triggers the Santa Susana mutual threat zone (MTZ) agreement activation. Due to commitments at the fast-moving Hill Fire, Ventura County Fire could only contribute two engines, one dozer, and two command officers for initial attack. Ventura County Fire Deputy Chief advises LA County Fire and City of Los Angeles Fire Department (LA City Fire) that Ventura County Fire cannot fully support MTZ agreement due to the Hill Fire.

Significant Event 11: 2:35 PM – LA County Fire and LA City Fire send full brush responses to the Woolsey Fire in addition to Ventura County Fire's response.

Fire Conditions/Response: Initial Observations

Significant Event 12: 2:51 PM – LA County Fire Copter-14 arrives on scene and reports a five-acre fire with rapid rate of spread and structures threatened. Winds are 25–30 MPH from the southeast.

Significant Event 13: 3:00 PM – Fire Incident Commander reports two 30-acre fire spots traveling in a southwest direction threatening structures in Oak Park and the State Responsibility Area wildlands.

Fire Conditions/Response: Initial Tactics & Actions

Significant Event 14: 3:16 PM – Air Tanker 76 diverted from Hill Fire to Woolsey Fire; four air tankers were requested.

Significant Event 15: 3:26 PM – Experiencing no cell service, the Woolsey Incident Command Post (ICP) is moved from Rocketdyne to Ventura County Fire Station #43.

Evacuations

Significant Event 16: 3:30 PM – Three county fire chief officers deploy to LA County Fire Fire Station #89 in Agoura Hills to build an evacuation contingency plan.

Significant Event 17: 3:30 PM – LA County Fire Assistant Chief calls all the western cities in the LA County Fire service area to inform them to start voluntary evacuations from Calabasas area to the Pacific Coast Highway (PCH). As a result, the Lost Hills Sheriff's Station activated its emergency operations center (EOC), its 12-and-12 staffing model, and called in all search and rescue members. The station begins to initiate voluntary evacuations in Agoura Hills, Calabasas, Hidden Hills, and Westlake Village.

Significant Event 18: All Afternoon – Local emergency communications / 9-1-1 centers are inundated with calls reporting fire-related conditions.

Fire Conditions/Response

Significant Event 19: 3:30 PM (approximate) – The County Emergency Management Director receives initial notification of Woolsey Fire from LA County Fire Deputy Chief with information that the fire could spread into Los Angeles County.

Significant Event 20: 3:32 PM – LA County Fire Incident Management Team 3 (IMT-3) is activated.

Significant Event 21: 3:40 PM – Lost Hills Sheriff's Station EOC communicated with the American Red Cross (Red Cross) and Los Angeles County Department

of Animal Care and Control (County Animal Care) regarding shelter preparedness.

Significant Event 22: 3:47 PM – Lost Hills Station dispatches personnel to strategic positions in the mountainside to provide intelligence on the location of the fire line and its progression.

Significant Event 23: 3:54 PM – Unified command is established with Ventura County Fire, LA County Fire, and LA City Fire at Ventura County Fire Fire Station #43 in Simi Valley.

Significant Event 24: 4:05 PM – The Woolsey Fire is determined to be in the Ventura County State Response Area jurisdiction; therefore, Ventura County retains responsibility as the mutual aid unified ordering point.

Significant Event 25: 4:20 PM – County Sheriff's Department Emergency Operations Bureau (EOB) received a mutual-aid request from Cal OES to send 24 law enforcement personnel to assist the Ventura County Sheriff's Office with evacuations.

Significant Event 26: 4:47 PM – Sunset occurs and only two fixed-wing aircraft drops are accomplished before the sunset curfew discontinues fixed-wing aircraft operations. LA County Fire and LA City Fire helicopters continue to operate to the end of dusk, and their night-capable helicopters continued through the night.

Significant Event 27: 5:20 PM – The 24 law enforcement personnel were redirected by Cal OES to the Woolsey Fire burning in Ventura County.

Evacuations

Significant Event 28: 5:18 PM – Incident command issues the first mandatory evacuation at Saddlebow and Maverick Lane in Bell Canyon, City of Los Angeles.

Fire Conditions/Response

Significant Event 29: 6:00 PM – California Department of Forestry & Fire Protection (CAL FIRE) IMT-5 is activated for Ventura County Fire's Hill Fire, and County Emergency Management is present at the Woolsey Fire ICP to monitor the Woolsey situation.

Significant Event 30: 6:15 PM – Lost Hills Station requested North Division resources to assist in the evacuations and traffic control.

Evacuations

Significant Event 31: 7:09 PM – PUBLIC INFORMATION OFFICER (PIO) TWEET: "LAC closely monitoring fire. At this time, the fire remains in VNC's jurisdiction. Due to potential threat to the community of Hidden Hills, mandatory evacuations are in place north of the Highway 101 from Valley Circle to Lindero Cyn."

Significant Event 32: 7:33 PM – County Animal Care plans the possible evacuation of the Agoura Animal Care Center due to the erratic behavior of the fire.

Fire Conditions/Response: Transition from Initial to Extended Attack

Significant Event 33: Between 7:00 PM and 9:00 PM – LA County Fire Incident Co-commander estimates it is increasingly likely they will not catch the fire now.

Significant Event 34: 8:00 PM (approximate) – Command personnel from LA County Fire and Ventura County Fire conduct a night flight in a helicopter to assess the situation's rapidly evolving fire dynamics.

Significant Event 35: 9:00 PM – Fire reported at 8,000 acres and structures affected in Oak Park community within Ventura County Fire.

Significant Event 36: 9:00 PM – Weather data Cheseboro: Temperature is 65 degrees, RH is six percent, wind is at 29 MPH from the northeast with peak gust of 48 MPH.

Significant Event 37: 9:41 PM – The resource request entered into the California Fire Mutual Aid Resource Order Status System (ROSS) system is for 37 strike teams (185 fire engines) resulting in many "Unable to Fill (UTF)" responses.

Significant Event 38: 10:20 PM – Lost Hills Sheriff's Station lost power and began operating on generator power.

Significant Event 39: 10:33 PM – The Incident Commander places a second master resource order in the Statewide ROSS system for Woolsey Fire resources.

Significant Event 40: National Weather Service synopsis: Strong Santa Ana winds will continue across Ventura and Los Angeles Counties, with the peak winds anticipated for Friday morning starting at sunrise and continuing through the noon hour. These winds are anticipated to diminish but not

disappear in the afternoon. RH is anticipated to remain in single digits while the strongest mountain gusts will be in the 50–60 MPH range on Friday morning. Isolated gusts up to *70 MPH are expected around the Hills of Malibu* and across the Ventura and Los Angeles County mountains.

3.3 FRIDAY, NOVEMBER 9, 2018

Fire Conditions/Response

Significant Event 41: 12:00 AM – Weather for Cheseboro: 64 degrees, RH is six percent, and winds are at 26 MPH from the northeast.

Significant Event 42: 12:18 AM – Incident command establishes enlarged fire containment "box" to limit the extension of the fire to Valley Circle on the east, Highway 118 on the north, Highway 23 on the west, and Highway 101 on the south. There is now major fire activity at Lindero to Thousand Oaks Boulevard from Bell Canyon to Highway 101 with new fire start on Highway 118. Potential for fire to impact backside and outflank first fire. Woolsey Fire rapidly progressing to the west and heading toward Lang Ranch and Highway 23 to the east side of Thousand Oaks. Numerous structures on fire in Oak Park and Los Angeles County corridor needing heavy fire engine response.

Evacuations

Significant Event 43: 12:22 AM – Per Ventura County Fire, evacuations are needed from Kanan Road to Westlake Boulevard and from Highway 101 northbound to Kanan Road.

Significant Event 44: 12:30 AM – The EOB activates the Department's duty DOC, IMT, and the Los Angeles County Emergency Operations Center (County EOC) team.

Significant Event 45: 1:14 AM – PIO TWEET: "Fire has entered LA County, Multiple structures have been impacted in the Oak Park area, Reyes Adobe north of T.O. Blvd."

Significant Event 46: 1:20 AM – Mandatory evacuations are issued by LA County Fire for Malibou Lake south of Highway 101.

Fire Conditions/Response: Strategy Shift

Significant Event 47: 1:25 AM – Fire organization is broken up into four branches with the ability to break into more branches.

Significant Event 48: 1:25 AM – Due to the scope of the fire and the limited resources, **life safety and victim rescue is priority; not enough resources for structure defense.** (This is the moment fire command shifted from direct attack to Life Safety First and Fire Front Following).

Evacuations

Significant Event 49: 1:35 AM – PIO TWEET: "Mandatory Evacuations are now in place south of the Highway 101 to Mulholland Highway, west of Las Virgenes Rd. to Westlake Blvd."

Significant Event 50: 1:46 AM – Alert LA Message: "This is the Los Angeles County Sheriff's Department, the Los Angeles County Fire Department has issued a mandatory evacuation order for the following areas due to a fast moving wild fire. From Westlake Blvd east to Las Virgenes Road and Mulholland Highway north to the Los Angeles County Line. For further information please contact the Los Angeles County information line at 2-1-1."

Significant Event 51: 2:00 AM – The EOB receives an additional law enforcement mutual aid request from Cal OES for 175 law enforcement officers to help with evacuations in Ventura County.

Significant Event 52: 2:01 AM – Alert from Malibu: "Alert mandatory evacuations south of Highway 101, from Mulholland Highway to Las Virgenes to Westlake, and north of Highway 101 from Valley Vista to Reyes Adobe."

Significant Event 53: 2:34 AM – Mandatory evacuation ordered for Westlake Village.

Declarations

Significant Event 54: 2:50 AM – Fire Management Assistance Grant for Woolsey approved.

Fire Conditions/Response

Significant Event 55: 2:51 AM – PIO TWEET: "Fire is approximately 8,000 acres with 0% containment."

Evacuations

Significant Event 56: 3:00 AM (approximate) – Mandatory evacuation orders south of Highway 101 north of Potrero Road between Westlake Boulevard and Wendy Drive. Evacuations in Hidden Hills area of LA County Fire and LA City Fire operational area have been downgraded to voluntary.

Significant Event 57: 3:18 AM – Fire extending down Las Virgenes, north of Highway 101.

Evacuations

Significant Event 58: 3:52 AM – News Flash Malibu: "Mandatory evacs for Woolsey fire in parts of Agoura Hills, Calabasas and Westlake Village."

Fire Conditions/Response

Significant Event 59: 3:57 AM – Email from LA County Fire Community Services Liaison (CSL): "Of note, fire is now at 8,000 acres with no containment, and the City of Hidden Hills and the LA City portion extending east of Hidden Hills to Valley Circle have moved from mandatory evacuations to voluntary. This incident is now in Unified Command with VNC, LAC, LFD, Ventura County Sheriff's Department (VCSO), Los Angeles County Sheriff's Department (LASD), Los Angeles Police Department (LAPD) and Cal Fire."

Significant Event 60: 4:00 AM – The County EOC is activated at level 3.

Significant Event 61: 4:45 AM – Fire is just north of Highway 101 and is threatening to jump south of freeway between Kanan and Palo Comado.

Significant Event 62: 5:00 AM – LA County Fire units report and extinguish a two-acre spot fire south of Highway 101 near Cheseboro and Agoura Roads.

Significant Event 63: **5:13 AM – Fire jumps over Highway 101 between Liberty Canyon Road and Palo Comado Road overpass.**

Communications

Significant Event 64: 5:17 AM – Email from Malibu staff to Mayor and city council of Malibu: "Fire has jumped 101 near Cheseboro. In the process of sending out an Everbridge notice."

Evacuations

Significant Event 65: 5:30 AM – When fire crosses Highway 101, LA County Fire chief officer announces mandatory evacuation for Malibu.

Fire Conditions/Response

Significant Event 66: 5:58 AM – Fire is well established over Highway 101 / Cheseboro canyon at 50 or more acres.

Significant Event 67: 6:00 AM – Weather data Cheseboro: Temperature is 63 degrees, RH is six percent, wind is 30 MPH out of the northeast with peak winds at 52 MPH.

Significant Event 68: 6:00 AM –The primary focus of fire suppression operations transitions from the Highway 101 area to the north, which now includes Malibou Lake and the southern front from Highway 101 to the PCH.

Evacuations

Significant Event 69: 6:13 AM – Mandatory evacuation issued for the region between Liberty Canyon and Decker Canyon all the way to the PCH.

Significant Event 70: 6:57 AM – Malibu Alert notice: "Alert MANDATORY EVACUATION – (6:50 AM) all of City of Malibu, all areas S. of Highway 101, Ventura County to Malibu Canyon."

Communications

Significant Event 71: 6:59 AM – LA County Fire PIO TWEET: "Fire has jumped Highway 101 near Chesebro and is headed to Ocean - Mandatory Evacuations, Highway 101 to the coast between Las Virgenes Cyn/Malibu Cyn Rd. to the LA County line. Imminent threat! Malibou lakes residents must leave area immediately."

Significant Event 72: 7:12 AM – City of Malibu Disaster Notification System: "The Woolsey Fire has jumped the 101 at Liberty Canyon and Chesebro Roads. Prepare to evacuate. Large animals can be taken to Hanson Dam Equestrian Center."

Fatality

Significant Event 73: 7:30 AM – Approximate time of first confirmed human fatality. Victim is found on the porch.

Fire Conditions/Response

Significant Event 74: 7:45 AM – Civilians trapped at Castro Peak, call for rescue. LA City Fire helicopter conducted rescue operations successfully.

Evacuations

Significant Event 75: 8:26 AM – Message from Alert LA: "This is the Los Angeles County Sheriff's Department the Los Angeles County Fire Department has issued a mandatory evacuation order for the following areas due to a fast moving wild fire. From Las Virgenes Road / Malibu Canyon Road to the Ventura County Line. For further information please contact the Los Angeles County information line at 2-1-1."

Significant Event 76: 8:45 AM – Agoura Animal Care Center evacuation is complete.

Significant Event 77: 9:35 AM – Branch 9 requests road closure of Erbes and Avenida de Los Arboles.

Significant Event 78: 9:36 AM – On S. Lakeshore Drive, Malibou, a victim is on the lake, under a bridge in a kayak, trapped, and needs help.

Fatality

Significant Event 79: 10:00 AM – Approximate time two fatalities occur. Both victims are in a van.

Fire Conditions/Response

Significant Event 80: 11:44 AM – At Marvista Ridge Way in Malibu, the fire is reported coming over the hill approaching homes, and there are apparently no fire engines at this location.

Significant Event 81: 11:51 AM – A civilian who previously refused aid is now stuck on Malibou Lake. He states he is now afraid for his life and wants firefighters to rescue him.

Communications

Significant Event 82: 12:00 PM (approximate) – Joint Information Center (JIC) established at the County EOC.

Fire Conditions/Response

Significant Event 83: Los Angeles County Waterworks District No. 29 (County Waterworks) staff relocates equipment to support firefighting needs in the Malibu and Topanga areas.

Fire Conditions/Response

Significant Event 84: 12:05 PM – Request made to expedite response by SCE and County Public Works to Las Virgenes west on Mulholland Kanan to clear a road for rescue operations.

Significant Event 85: **12:11 PM – Fire jumps PCH in Malibu according to California Highway Patrol (CHP)**.

Significant Event 86: 1:26 PM – All air tankers are temporarily grounded due to severe wind conditions.

Significant Event 87: 12:29 PM – Fire is burning out of control and heading through the City of Malibu.

Evacuations

Significant Event 88: **12:41 PM – CHP opens all PCH eastbound lanes in a contraflow configuration for evacuation effort.**

Fire Conditions/Response

Significant Event 89: 1:41 PM – ALERT LA Message *for Topanga Canyon*: "Zone 1-6 evacuate northbound to San Fernando. Zones 7-9 evacuate southbound to PCH."

Significant Event 90: 1:42 PM – The fire crests the ridge above Corral Canyon.

Significant Event 91: 1:50 PM – Air attack recommits all fixed wing aircraft to Woolsey Fire following grounding due to wind.

Significant Event 92: 1:55 PM – Flames reach Broad Beach Road and Trancas Road, Malibu. South of PCH, fire extends to the Pacific Ocean.

Evacuations

Significant Event 93: 1:56 PM – Additional mandatory evacuations ordered for Monte Nido community and north to Mulholland and Topanga Canyon.

Significant Event 94: 1:57 PM – Email from LA County Fire CSL: "We have additional mandatory evacuations, as follows: Monte Nido community and north to Mulholland All of Topanga Canyon. For messaging purposes, please include the following in all your messaging that includes the Topanga Canyon evacuations: Topanga Zones 1 through 6 are to evacuate northbound on Topanga Canyon to the San Fernando Valley. Zones 7, 8, and 9 are to evacuate southbound on Topanga Canyon to PCH, then go east. Fire is at 14,000+ acres, still no containment. There are some areas of Malibu where the fire has now reached PCH."

Fire Conditions/Response

Significant Event 95: **2:24 PM – Fire jumps PCH for the second time at Kanan Dume Road**

Significant Event 96: 3:59 PM – Fire is reported closing in on the area of Broad Beach Road and PCH, and there are reports of no fire engines in the area.

Significant Event 97: 5:00 PM – There is a request to expedite the response of SCE to the Corral structure group due to powerlines and a pole down on a LA County Fire command vehicle.

Significant Event 98: 5:02 PM – Growing, uncontained spot fires reported on Newell Road (Corral Canyon).

Communications

Significant Event 99: 7:35 PM – RETWEET from account @LACoFireAirOps: "Earlier video of @LACoFireAirOps Firehawk helicopter working to save lives and property in Malibu, CA. We are experiencing high winds, extremely dry fuels, and frequent spot fires."

Fire Conditions/Response

Significant Event 100: 8:00 PM – Weather data Cheseboro: Temperature is 66 degrees, RH is four percent, and wind speed at 13 MPH out of the north.

Evacuations

Significant Event 101: 9:01 PM – At Pepperdine University (Pepperdine), students are sheltering in place inside Payson Library per the University's established emergency plan. Some families expressed concern about student safety.

Fire Conditions/Response

Significant Event 102: 9:19 PM – Email from LA County Fire CSL: "Woolsey Fire is 35,000 acres and growing, with still no containment. Added mandatory evacuation area in City of Los Angeles - west of Valley Circle between Roscoe and Vanowen (West Hills area) and in Calabasas."

Significant Event 103: 9:39 PM – Fire reported at Highway 101 at Parkway Calabasas.

Evacuations

Significant Event 104: 10:47 PM – Lost Hills Sheriff's Station received a phone call regarding Pepperdine students not being allowed to evacuate because of the campus shelter in place order. Lost Hills forwarded the contact name and number at Pepperdine to the County Sheriff's Department IMT. The County Sheriff's Department IMT called and spoke with Pepperdine. During that conversation, there was no emergency on the campus and there were less than 1,000 students and staff in the shelter-in-place mode.

The campus and LA County Fire had a very good shelter-in-place plan and agreement for years. Further calls and confusion by outside parties led to a mutual aid law enforcement team arriving on campus with mistaken orders to start an evacuation, which was halted after a clarifying conversation between the campus and Woolsey incident leadership.

Significant Event 105: 11:00 PM – PCH is closed.

Fire Conditions/Response

Significant Event 106: County Public Works reports 10 sewer pump stations are without power and operating on backup generator power. Affected stations include Mulholland, David's Road, Long Valley, Summit Point, View Ridge, Pickney, Ulmus, Jim Bridger, Broad Beach, and Lechuza. No overflows have been detected.

3.4 SATURDAY, NOVEMBER 10, 2018

Fire Conditions/Response

Significant Event 107: Weather conditions for Santa Monica Mountains area: Temperature is 74 degrees, RH is nine percent, and wind is eight MPH out of the north.

Significant Event 108: Weather conditions for the Cheseboro area: Temperature is 70 degrees, RH is six percent, and wind is 12 MPH out of the north.

Significant Event 109: 12:06 AM – A request is made for SCE to respond two miles up Corral Canyon from PCH. Downed lines preventing movement of fire personnel.

Significant Event 110: 5:37 AM – Manager performs a walkthrough at the Agoura Animal Care Center and confirms that the Animal Care Center has sustained minor damage.

Significant Event 111: 7:00 AM – CAL FIRE IMT-5 officially enters unified command with Ventura County Fire, LA County Fire, CAL FIRE, National Park Service, LA City Fire, the County Sheriff's Department, and the Ventura County Sheriff's Office.

Significant Event 112: 11:03 AM – Life Safety Alert issued for two people unaccounted for in the area of Newell Road.

Significant Event 113: 1:23 PM – Third Woolsey Fire mutual aid order (ROSS system) for 30 strike teams (150 fire engines).

Significant Event 114: 3:00 PM – Highway 23 at Carlisle Canyon to PCH is closed.

Significant Event 115: SCE providing seven generators to support County Waterworks infrastructure.

Evacuations

Significant Event 116: County EOC requests a portable water tank and operator to support large animal evacuation centers.

3.5 SUNDAY, NOVEMBER 11, 2018

Repopulation: Initial Actions

Significant Event 117: 7:00 AM – Repopulation begins in the Cities of Simi Valley and Westlake.

Significant Event 118: LA County Fire implements occupant support function to assist residents.

Fire Conditions/Response

Significant Event 119: 8:00 AM – Weather data at Cheseboro: Temperature is 66 degrees, RH is seven percent, fuel moisture is six percent, and wind is 29 MPH out of the northeast.

Significant Event 120: 11:14 AM – Looter suppression activities for region south of Mulholland, west of Topanga, east of Kanan Road, and north of Pacific Ocean.

Significant Event 121: 11:40 AM – Looter suppression activities for region north of Mulholland, west of Kanan Road, east of Ventura County Line, and south of Ventura County Line.

Significant Event 122: County Public Works field crews initiate safe route assessments in coordination with first responders and, at the request of Agoura Hills, County Public Works field crews deploy safe route signage in fire-damaged area.

Significant Event 123: SCE supplies eight generators for County Waterworks infrastructure, and County Public Works supplies an additional four generators.

Significant Event 124: County Public Works crews have a temporary bridge solution for the damaged bridge on Mulholland Highway at Triunfo Creek.

Significant Event 125: 2:20 PM – Mutual aid order cancellation: Any open pending operational overhead resources are cancelled as no longer needed.

Significant Event 126: Five looting suppression missions are operational.

Evacuations

Significant Event 127: 11:00 PM – Mandatory evacuation ordered for Las Posas to the County line on PCH.

3.6 MONDAY, NOVEMBER 12, 2018

Repopulation

Significant Event 128: 8:00 AM – Repopulation meeting is held with all cooperators. Discussed repopulation of Hidden Hills and areas of Calabasas.

Significant Event 129: 9:30 AM – Unified Incident Command meeting: Discussion about miscommunications and need for unified message. Rocketdyne reportedly is not posing a health risk to the public.

Significant Event 130: County Waterworks issues a boil water advisory for western Malibu.

Significant Event 131: The City of Malibu requests road debris removal, fuel, and safety assessment services from County Public Works.

Fire Conditions/Response

Significant Event 132: 12:00 PM – 91,572 acres consumed by fire.

Declarations

Significant Event 133: 11:12 PM – Presidential Disaster Declaration announced by California Governor's Office.

Repopulation

Significant Event 134: County Public Works initiates City of Malibu's request for road debris and fuel services. The request for safety assessments is pending further coordination and dialogue scheduled for November 13, 2018.

Significant Event 135: County Public Works tree crews assessing conditions and clearing debris on Kanan Dume Road.

3.7 TUESDAY, NOVEMBER 13, 2018

Repopulation

Significant Event 136: 8:00 AM – Repopulation meeting is held with discussion regarding the opening of Rambla Pacifico, Big Rock community, and soft closure on northbound PCH at Sunset Boulevard.

Fire Conditions/Response

Significant Event 137: Woolsey Fire is calculated at 96,314 acres, and the Hill Fire is contained.

Declarations

Significant Event 138: Local Emergency Declared by Los Angeles County Board of Supervisors.

Repopulation

Significant Event 139: County Public Works DOC notes: "Public Works is in regular communication with the Cities of Malibu, Agoura Hills, and West Lake Village, as well as, the Los Angeles County Department of Public Health (DPH) and the Los Angeles County Department of Regional Planning (DRP) for recovery coordination."

Significant Event 140: SCE provides an additional 19 generators to support County Waterworks operations, if needed. Four generators are operating at this point.

Communications: Town Hall Meetings

Significant Event 141: 7:00 PM – Malibu Evacuee Update public meeting is held at Santa Monica High School with all partner agencies in attendance.

Communications: Recovery

Significant Event 142: Press Release #14: "Woolsey Fire Recovery Planning Efforts Underway in Los Angeles County" communicates development of disaster recovery and assistance centers, which will include—among many other services—services related to reconstruction.

Repopulation

Significant Event 143: County Public Works field crews begin road clearing operations on Mulholland Highway between Calabasas and Las Virgenes Roads.

3.8 WEDNESDAY, NOVEMBER 14, 2018

Recovery

Significant Event 144: 3:25 AM – Planning team assessing areas of and personnel needed for repopulation during daylight hours.

Significant Event 145: 5:01 AM – Law enforcement coordinate escort for 35 Pepperdine professors at 8:00 AM.

Recovery: VIP Visits/Impacts and Repopulation

Significant Event 146: 9:00 AM – Incident Command meeting is convened with topics including: Fatalities, Ventura County Sheriff's Deputy funeral services, Damage Inspection Specialist process and data, VIP visits.

Repopulation meeting discussed repopulation of the Pepperdine community and Calabasas area.

Recovery

Significant Event 147: 3:00 PM (approximate) – Recovery Coordinating Center (RCC) operations activated by County Chief Executive Officer (CEO) with the goal of opening the LA County Fire Disaster Assistance Centers (DACs) by Saturday, November 17.

Significant Event 148: County Public Works crews assess field conditions and document infrastructure damage.

Communications: Repopulation Meeting, Malibu

Significant Event 149: 2:00 PM – A repopulation meeting is convened in the City of Malibu.

Communications

Significant Event 150: County Waterworks lifts the boil water advisory for western Malibu, including Point Dume, Encinal Canyon, and area north of Malibu High School.

Significant Event 151: Press Release #24: "Public Safety is Paramount in Repopulation Efforts for Areas Affected by Woolsey Fire" communicates coordinated efforts by County, state, and federal agencies, including the responsibility of County Public Works to inspect the condition of all roadways damaged by the Woolsey Fire and related activities.

3.9 THURSDAY, NOVEMBER 15, 2018

Recovery operations continue across all County agencies.

3.10 FRIDAY, NOVEMBER 16, 2018

Recovery

Significant Event 152: 1:00 AM – The County Sheriff's Department staff meeting is held to discuss staging area relocation and repopulation of next areas to open.

Significant Event 153: In collaboration with numerous County departments, state agencies, federal agencies, and local non-profits involved in disaster response, County Emergency Management develops staffing and support plans for two DACs, which will open on November 17. Services provided will address resident and business needs.

3.11 SATURDAY, NOVEMBER 17, 2018

Recovery

Significant Event 154: 10:00 AM – Local Assistance Centers / DACs opened in Malibu and Agoura Hills.

Communications: Recovery

Significant Event 155: 10:00 AM – Town Hall public meeting held at Seminole Springs Mobile Home Park, Agoura Hills.

Significant Event 156: 11:00 AM – Repopulation meetings continue, including discussions about planning for a visit from the President of the United States, the repopulation of Malibu Canyon to the City limits, and opening Latigo Canyon Road to PCH.

3.12 SUNDAY, NOVEMBER 18, 2018

Recovery

Significant Event 157: In collaboration with numerous County departments, state agencies, federal agencies, and local non-profits involved in disaster response, County Emergency Management provides recovery information, programs, and services for residents and business, including environmental, transportation, and buildings-related functions.

Communications

Significant Event 158: Press Release #45 "Woolsey Fire Safety Message" communicates guidance to residents and businesses related to general hazards, electrical hazards, natural gas hazards, water conservation, falling debris, and storm preparation.

3.13 MONDAY, NOVEMBER 19, 2018

Recovery

Significant Event 159: 5:00 PM – Data collection for damage assessment concludes.

3.14 TUESDAY, NOVEMBER 20, 2018

Communications

Significant Event 160: Press Release #47 "Woolsey Fire All Residents in Burned Areas are Urged to Prepare for Flood Safety" communicates the threat of mud

and debris flows in the areas affected by the Woolsey and Hill fires. Guidance is provided regarding evacuation orders, sandbag locations, and how residents should respond if confronted with a flood emergency at home or on the road.

3.15 WEDNESDAY, NOVEMBER 21, 2018

Communications

Significant Event 161: 10:00 AM – Press Release #49 "Reopening Areas of Kanan Dume Road Affected by Woolsey Fire" announces the reopening of Kanan Dume Road from the PCH to Highway 101.

Communications: Rehabilitation and Rain Preparation

Significant Event 162: Press Release #51 "Debris, Mud, Other Hazards Expected in Woolsey Fire Areas" communicates guidance for residents including information regarding evacuation orders, sandbag locations, and how residents should respond if confronted with a flood emergency at home or on the road.

3.16 THURSDAY, NOVEMBER 22, 2018

Fire Conditions

Significant Event 163: Total structures destroyed by Woolsey Fire is 1,643, and another 364 damaged. Experts estimate over 57,000 structures were not substantially affected.

3.17 FRIDAY, NOVEMBER 23, 2018

Recovery

Significant Event 164: 9:00 AM (approximate) – Federal Emergency Management Agency (FEMA) Area Field Office opens in Westlake Village.

Significant Event 165: 9:00 AM – Agoura Hills DAC transitions to a Federal Disaster Recovery Center (DRC).

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SECTION 4—FINDINGS ACROSS THE INCIDENT AND BY AGENCY

Citygate's findings are as a result of the totality of analyses for this After Action Review (AAR) and include a broad range of observations, statements for historical record, and analytical conclusion. As a result of this and other factors, not every finding is coupled with a corresponding recommendation. In addition, while the findings are largely organized by corresponding theme and/or agency, some findings also apply to other agencies.

4.1 INCIDENT-WIDE RESPONSE FINDINGS

Finding 1: At present, the Los Angeles County Office of Emergency Management (County Emergency Management) has limited coordination duties during an emerging major incident, resulting in the operating departments splitting their focus from field operations to wide area public engagement and information.

Finding 2: Each affected city initiated its own Emergency Operations Center (EOC), which, combined with the Los Angeles County Emergency Operations Center (County EOC), required representatives from fire services, law enforcement, and other County agencies to be present or at least establish a communications link stretching finite County and city personnel during such a large incident.

Finding 3: Some residents intent on protecting their homes/animals did not evacuate, which resulted in use of additional resources in a resource-deficient environment and impacted the ability of fire units to engage in structure defense efforts.

Finding 4: Residents who refused to evacuate generated an enormous volume of 9-1-1 calls for help or wellness checks, with many of these turning out not to be life threatening.

Finding 5: Fatigue was recognized as a negative factor for first responders.

Finding 6: Downed power lines made lateral movement of emergency personnel and the public on roads nearly impossible.

Finding 7: The ability to quickly move assets during the fire was most problematic through Kanan Road, Decker Road, Encinal Canyon Road, and Mulholland Drive.

Finding 8: Several critical infrastructure sites were compromised by the fire, such as cellular voice/data affecting public notifications and emergency communications / technology (e.g., web-based maps).

Finding 9: Due to the volume of critical communication needs by first responders across multiple jurisdictions, both safety radio networks and cellular networks were unable to meet demands at times.

Finding 10: Infrequent training and lack of familiarity with the Incident Command System (ICS) by some partner agencies made interfacing with key agencies problematic at times.

Finding 11: During the first 24 hours of the incident, the Incident Command Post (ICP) was relocated three times (Rocketdyne, Ventura County Fire Department #43, Conejo Creek Park), compounding a challenging unified command transition.

Finding 12: County-level coordination between LA County Fire, Los Angeles County Sheriff's Department (County Sheriff's Department), County Emergency Management, and Los Angeles County Public Works (County Public Works) was not robust.

Finding 13: Potential strategic assets, like the California Highway Patrol (CHP) and County Public Works, were not immediately engaged.

Finding 14: Air quality and proper personal protective equipment were concerns during early field operations, including support operations for non-firefighting personnel.

Finding 15: There were access issues, early in the incident, in which key elected officials and agency staff could not reach, as a result of road closures, or enter the ICP command site, including the lead CHP Officer.

Finding 16: LA County Fire educates and trains the public regarding evacuation practices using the Ready! Set! Go! program, but the public lacks similar knowledge of *repopulation* challenges.

Finding 17: Public participation in structural hardening efforts on existing buildings is not uniform. There is a lack of public participation in maintenance of defensible space and structure/property.

Finding 18: Outside agency fire and law enforcement staff lacked sufficient briefings, including regarding specific community area practices which would increase their knowledge of local neighborhoods for best possible community interactions.

Finding 19: There was no single, all-encompassing method to communicate with all residents. Varying social media platforms and critical infrastructure damage created obstacles for public notification/information.

4.2 FIRE FIGHTING RESPONSE

4.2.1 Pre-Incident Local Readiness

Finding 20: LA County Fire has good tactical structure defense maps for the areas south of Highway 101.

Finding 21: LA County Fire had its Incident Management Team 3 (IMT-3) primed and ready prior to the event, with all team members available to respond.

Finding 22: All LA County Fire air resources and support personnel were ready prior to the event.

Finding 23: LA County Fire operates a hazard reduction program for defensible space. LA County Fire refers non-compliant parcels to Los Angeles County Agricultural Commissioner / Weights and Measures (County Ag. Comm.) for defensible space abatement. County Ag. Comm. only needed to forward 17 parcels in 2018 to the County Office of the Assessor for reimbursement.

Finding 24: California Office of Emergency Services (Cal OES) authorized "pre-positioning" funds to staff fire resources before the outbreak of the Hill and Woolsey Fires.

Finding 25: LA County Fire implemented an augmented staffing plan prior to Woolsey, which included an additional Battalion Chief dedicated for the Malibu / Las Virgenes area, two strike teams, staffed water tenders, and patrols, but no safety/communication aids for field command chief officers.

Finding 26: When the Hill Fire and the Woolsey Fire ignited, there were no other new major fire events underway in the Southern California region.

Finding 27: LA County Fire conducted training with its partners in June 2018 on the Santa Susana mutual threat zone (MTZ) and completed a comprehensive chief officers wildland training in the weeks before the Woolsey Fire.

Finding 28: The residents, LA County Fire, the Los Angeles County Board of Supervisors, and California Department of Forestry & Fire Protection (CAL FIRE) adopted the Santa Monica Community Wildfire Protection Plan, a Federally identified process to address wildfire hazards and reduce risk.

Finding 29: Southern California Edison (SCE) did not implement the new California Public Utilities Commission public safety power shutoff provisions prior to the Woolsey Fire.

Finding 30: Weather predictions were accurate prior to the fire, and fuel moisture readings indicated volatile fuels in the region—at or near critical levels from November 5 through November 12.

Finding 31: In the fire perimeter, there were limited fully wildfire-prepared neighborhoods or communities and, given the nature and intensity of this particular fire, even a 200-foot defensible space was often not enough.

4.2.2 Fire Response Command

Finding 32: Ventura County, Los Angeles County, and Los Angeles City Fire and law enforcement resources were heavily committed, beginning with the Borderline shooting in Thousand Oaks during early November 8, and then again with the Hill Fire.

Finding 33: After the Woolsey Fire, later in the afternoon and evening, there were numerous new fires in Ventura County Fire Department (Ventura County Fire) (Briggs, Peak, Lynn), City of Los Angeles Fire Department (LA City Fire) (Rocky Peak, Toyon), and LA County Fire (Copco) jurisdictions being addressed at the same time as the Woolsey and Hill Fires, each consuming vital, scarce resources with the potential for additional escalating incidents.

Finding 34: Some members of the public complained about fire agency resources being held at fire stations or along roads while there was active fire in the Malibu area. Upon further review, Citygate found these resources were used for Life Safety First 9-1-1 response and, in one case, a Malibu-stationed fire engine had a mechanical breakdown within its station in view from the public street.

Finding 35: LA County Fire Reserve Program Fire Engine 271 was first staffed by paid-call firefighters and then by full-time firefighters, which conflicted with local expectations. However, LA County Fire ordered all reserve fire engines Countywide to be staffed with career personnel.

Finding 36: LA County Fire had 59 reserve fire engines on November 8 to be used during extreme situations.

- Only 21 reserve fire engines were immediately available for service due to fleet viability.
- Five additional reserve fire engines were quickly put into service to help support the two pre-position strike teams for a total of 26 reserve fire engines in service.

Finding 37: Fleet mechanics were called in and worked around the clock to put reserve engines back into service, resulting in all but 11 reserve engines returning to service by November 13.

Finding 38: LA County Fire did not initially staff Command / Safety / Communications Aid / Drivers for command officers because Cal OES guidelines do not allocate for these positions as part of the pre-positioning program. Many command officers later in the incident commandeered firefighters for drivers as needed.

Finding 39: A single mutual aid (outside agencies) strike team of five engines was assigned to the upper bowl area Corral Canyon and worked to protect it Friday evening just before the fire hit. Before the fire burned the area over, two units staged in El Neito partway up the road and three units staged in the southern edge section of upper Corral to assist as the fire front passed to provide safe structure protection operations.

Finding 40: Limited resources led to a severe lack of tactical patrols, which control fires from initially burned vegetation and homes to those the fire front did not burn.

Finding 41: During the application of the Life Safety First priority, some unit leaders may not have fully understood the rules of engagement to decide when to dedicate their limited resources to address limited structure protection needs in between managing 9-1-1 life safety responses. LA County Fire has been teaching all company officers and command officers TIER—Take Initiative Engage and Report—which empowers every LA County Fire company on the road to conduct needed tasks without asking for permission.

4.2.3 Infrastructure Challenges

Finding 42: Road closures greatly impeded emergency response movements, including:

- Highway 101 closed in both directions in Newberry Park (Hill Fire).
- Pacific Coast Highway (PCH) at Las Posas, closed eastbound at First (Woolsey Fire).
- PCH in Malibu, closed for contraflow evacuation.
- Highway 101 in both directions, closed as Woolsey jumped the freeway.
- All laterals closed, such as Kanan, Decker, Mulholland, and Topanga roads.

Finding 43: Given the cellular data network failures, fire crews had to depend upon previously loaded mapping tools to locate victims in hazardous areas.

Finding 44: As the fire grew, communications on the Ventura County command channel became marginal in some geographic areas.

4.2.4 County Sheriff's Department Response Findings

Finding 45: Limited participation in emergency management training due to staffing shortages at local units caused a delay of development in unity of effort. Infrequent training and lack of familiarity with the ICS made interfacing with key agencies awkward.

Finding 46: CHP learned of planning meetings and briefings indirectly due to limited information sharing; once the County Sheriff's Department IMT-1 was established, CHP brought its concerns to the County Sheriff's Department command staff for quick resolution.

Finding 47: CHP was not made aware of the severe traffic congestion on PCH until late morning on November 9.

Finding 48: CHP only has jurisdiction of two miles of PCH in the incident response area.

Finding 49: Law enforcement staffing road closure posts, at times, lacked current information, policy, and the reasons for closures to better advise the public with whom they interacted.

Finding 50: Managing resources, relieving Deputies, and providing water, food, and fuel were a challenge during the first operational days.

4.2.5 County Emergency Operation Center Activation Findings

Finding 51: A Finance/Administration Section was not established as part of the County EOC organization as the incident base and Department Operations Centers (DOCs) were managing costs.

Finding 52: An EOC Policy Group meeting was convened on November 9 without a clearly communicated agenda or meeting objectives, causing the meeting to fail to identify near-term strategic policy goals for the EOC Director. Further, some participants lacked the appropriate authority to commit their Departments to a course of action in response to the disaster.

Finding 53: EOC was largely ineffective at maintaining a common operating picture and situational awareness among the critical locations/functions of the County EOC, various DOCs, and involved cities.

Finding 54: The County's Mass Care and Shelter plan is not robust enough to meet long-term, large-incident, mass-care needs for an incident the size of or larger than the Woolsey incident.

Finding 55: The County EOC is 26 years old. The current emergency management demands for space, connectivity, and workflow exceed its original design intent, and a replacement strategy should be considered for the future. Further, the EOC has no dedicated, annual budget for the replacement of equipment and capital repairs. The working quarters are cramped and are not designed for the number of people who occupy them. The interior structure is not conducive to general collaboration during normal business or emergencies.

4.2.6 County Public Works Response Findings

Finding 56: County Public Works pre-deployed resources in the Woolsey Fire region due to the extreme weather forecast for November 8.

Finding 57: County Public Works, with the assistance of County Emergency Management, the Los Angeles County Department of Public Health (DPH), the Los Angeles County Department of Regional Planning (DRP), and LA County Fire's Hazard Materials Division, successfully implemented the State's new Private Property Debris Removal (PPDR) program for the first time in the County. This new system provided a more robust debris removal opportunity for property owners to help the community prepare for the rebuild process with funding from the State.

Finding 58: This State-funded PPDR program potentially created an expectation with the public that the program will be available in the future, which would not be so without Federal and State disaster reimbursement.

Finding 59: County Public Works had agency representatives and technician specialists assigned to the ICP.

Finding 60: County Public Works did not have enough medically cleared, trained, and equipped personnel certified for respiratory protection for all field operations conducted in the burn area, resulting in delays to wait for the environment to improve.

Finding 61: Productivity time was occasionally lost due to potentially avoidable traffic logistics related to field staff driving to a central location prior to being deployed to their area of operations. Additionally, some field crews and DOC staff did not have their personal needs, including meals, supported in a fashion similar to their public safety peers.

Finding 62: When access permitted entry, County Public Works deployed six inspection teams to the Santa Monica Mountain area to inspect accessible bridges. Over 60 bridges were inspected.

Finding 63: The City of Malibu requested fuel support from County Public Works, and the request was honored via the existing General Services Agreement.

Finding 64: During response operations and when declared safe for entry, County Public Works teams were dispatched to inventory damaged signage, striping, and markings. To enhance safety of responders and others, County Public Works fabricated signs to provide informative road closure information.

Finding 65: Road infrastructure conditions were collected using geographic information system software and provided to all County Public Works crews involved in the response efforts.

- Using information collected during this assessment and in coordination with unified command, County Public Works staff coordinated with unified command to plan debris removal and road repairs by identifying priority routes.

Finding 66: Four internal levels of closure were established for all major roads depending on existing road conditions and mapped on the damage assessment application: Road Closed to Everyone, Road Open to Recovery Crews, Road Open to Residents, and Road Open.

- Three of these levels of closure were published on the County Public Works Road Closure website for public use: Road Closed to Everyone, Road Open to Residents, and Road Open.

Finding 67: During the fire, power was lost at fire stations and County Public Works facilities within the footprint of the fire. Power was restored by bringing in generators.

Finding 68: County Public Works worked closely with the CHP to ensure all required / requested changeable road signs were properly positioned and operating. The region had a sufficient number of these signs to meet the requests. Numerous additional changeable signs were also located elsewhere in the County that could have been quickly deployed to the area if needed.

Finding 69: County Public Works operates and maintains Los Angeles County Waterworks District No. 29 (County Waterworks) that supplies water mainly to the City of Malibu and the Topanga community.

Finding 70: When red flag conditions were announced, County Waterworks topped off all water storage tanks. All tanks were at their greatest possible capacity prior to the Woolsey Fire.

Finding 71: County Waterworks utilized an Emergency Repair Contractor to complete repairs to the water system caused by the fire so County Waterworks staff could fully focus on recovery and normal operation of the system.

4.2.7 Los Angeles County Department of Animal Care and Control Response Findings

Finding 72: Los Angeles County Department of Animal Care and Control (County Animal Care) can only account for those animals that are legally licensed in the service areas, such as dogs and cats; livestock are not licensed through the County Animal Care. This makes pre-planning difficult. A voluntary large and exotic animals registration program was previously attempted with marginal results.

Finding 73: County Animal Care began incident actions as the Hill Fire started because it is under contract with the City of Thousand Oaks, which initially put it ahead of the service request curve.

Finding 74: County Animal Care had a representative at the Lost Hills Sheriff's Department substation.

Finding 75: County Animal Care welfare checks were not directly coordinated with occupant support functions.

Finding 76: County Animal Care had trouble responding to the incident due to heavy traffic congestion in non-fire areas due to normal traffic issues and because they do not have Code-3 vehicles.

Finding 77: County Animal Care has been following County directives for clean-energy vehicles, but those vehicles do not meet the operational needs for large animal transports, especially concerning horsepower and fuel type.

4.3 Communications – Public Notifications

4.3.1 Communications Findings

Finding 78: There was an insufficient number of redundant communication methods to adequately communicate with all the effected residents.

Finding 79: During the early stages of the Woolsey Fire incident, there was confusion regarding who was the lead Information Officer.

Finding 80: There was a lack of an identified, single, informed voice addressing community concerns. There was no single body that oversaw conflicting and/or complicated actions/messages between the Hill Fire and Woolsey Fire that affected Los Angeles and Ventura Counties and the various cities.

Finding 81: There is a lack of an effective communications plan for when technology fails.

Finding 82: The Alert LA County tool, including its application for wireless emergency alerts and the radio/TV Emergency Alert System (EAS), was vastly underutilized.

Finding 83: A review of the utilization of the Alert LA County mass notification system indicates that its promotion to the public needs to be increased to improve its adoption by the public and key stakeholders. Many features of the system were underutilized and can be incorporated into a comprehensive, multi-layered mass notification protocol.

Finding 84: An over reliance on Twitter failed to account for people not utilizing Twitter and those normally, or due to the disaster's power failures, without internet service. An overuse of internet tools creates a digital divide where people without that type of access do not receive emergency messages from their government.

Finding 85: The existence of multiple uncoordinated communication efforts by the County EOC, the Woolsey ICP, and various other communicators was not consistent with County policy for a single, integrated voice as outlined in the Emergency Public Information Annex of the Emergency Operations Plan, and this practice conflicted with ICS.

Finding 86: There was a clear lack of understanding of the Joint Information Center (JIC)'s role and responsibilities across many elements of the emergency management organization for this incident (County Chief Executive Officer (CEO), EOC, ICP).

Finding 87: The number of road closures in the same geographic area between the Hill and Woolsey Fires created a media information overload for the public to fully understand which access/direction to use.

4.3.2 LA County Fire Communications Findings

Finding 88: Many residents have not really heard that firefighters might not defend their homes due to poor access, water supply, topography, and fuel conditions. This sets up

conditions in which the public expectations during the Woolsey Fire were not in alignment with safe fireground operations.

Finding 89: Regional fire department Public Information Officers (PIOs) and Community Services Liaisons (CSLs) maintain positive working relationships with their local city partners and the news media.

Finding 90: There was a lack of sufficient LA County Fire PIO resources into November 10. There is little to no LA County Fire PIO surge capacity or bench depth. None of the LA County Fire PIO staff were ICS Type 1 Information Officers at the time of the fire.

Finding 91: LA County Fire PIO lacks a strategic plan for release of critical public information.

Finding 92: Due to lack of a formal and institutionalized communication protocol, PIO and CSL workload was unnecessarily high.

Finding 93: The decision to assign the LA County Fire PIO as lead for the incident instead of the IMT-3 PIO deviates from ICS protocol and standard fire department past practice.

Finding 94: LA County Fire PIO section had no chief officer or Type 1 strategic leadership qualified person for the initial 48 to 72 hours.

Finding 95: LA County Fire PIO lacked an established plan for answering/prioritizing media requests.

4.3.3 County Sheriff's Department Communications Findings

Finding 96: Station supervisors need training and checklists regarding the correct procedures to promptly send out Alert LA messages.

Finding 97: Because they were perceived to be indirect tools that cover too wide of an area, the EAS and Wireless Emergency Alerts were not utilized to provide emergency public notifications as identified in the Emergency Public Information Annex of the Emergency Operations Plan.

Finding 98: Multiple official County Sheriff's Department Twitter accounts exist, and the public cannot be expected to be required to monitor multiple accounts to obtain timely, accurate, and critical information.

Finding 99: Only one County Sheriff's Department Sheriff's Information Bureau (SIB) staff member has advanced PIO training.

4.3.4 County Emergency Management Communications Findings

Finding 100: An incident communications organization was in place on November 9. A JIC was established in the EOC by noon and managed by the County Emergency Management Associate Director.

Finding 101: The JIC was not staffed 24 hours per day.

Finding 102: There was good communication between the JIC and the 2-1-1 call center.

Finding 103: The JIC needed more workspace in the EOC.

Finding 104: During the first 48 to 72 hours, multiple requests for County Emergency Management to send a PIO to the ICP went unfilled, creating challenges with the flow of timely public information to the JIC.

4.3.5 County Public Works Communications Findings

Finding 105: County Public Works staff communicated cellular phone system weak spots to local carriers, AT&T and Verizon. AT&T deployed mobile cellular antennae to boost coverage and signal strength.

- Where County radio systems had weak spots in the mountains, County Public Works obtained and used satellite phones.

4.4 EVACUATION

4.4.1 Countywide Evacuation Findings

Finding 106: A repopulation group comprising the cities and both counties' law enforcement, fire services, public works, and utility companies was formed and worked together. Repopulation was delayed by multiple agency concerns for the public's safety and was further hampered by insufficient information available to Deputies staffing road closures.

Finding 107: Early repopulation dialogue and decisions did not engage or inform all key stakeholders.

Finding 108: LA County Fire staff should be commended for creating the three-zone evacuation plan at LA County Fire Fire Station #89 during the initial hours of the fire. Voluntary evacuation orders were given to the Malibu area at 3:45 PM on November 8.

Finding 109: Decisions to order mandatory evacuations were conducted appropriately, but the communication of the orders was not optimal.

Finding 110: The road closure access issues at the Hill Fire further exacerbated the access issues within the Woolsey Fire in the western sections of both counties along the Highway 101 and Highway 1 corridors.

Finding 111: Repopulation guidelines are not communicated to the public in a similar way evacuation is taught.

Finding 112: LA County Fire used shelter-in-place to save lives at Camp 13, Camp Kilpatrick, and Pepperdine University (Pepperdine).

Finding 113: The Pepperdine shelter-in-place operation was a pre-planned procedure and did not distract from tactical fire operations. There were communications conflicts, which created different media reports.

Finding 114: The contraflow evacuation action, when finally engineered on PCH on Friday, November 9, was led/actuated by a single CHP Officer.

Finding 115: LA County Fire learned from the Ventura County Fire Thomas Fire (2017) and created the occupant support function to assist residents.

4.4.2 County Sheriff's Department Evacuation Findings

Finding 116: Deputies/Officers in the field did not have accurate information for evacuating citizens, for counseling those seeking re-entry, nor to provide to those who stayed behind and were seeking to leave and return.

Finding 117: Outside of Topanga Canyon, there were no maximum traffic load and directional options as part of planning or instructions for evacuations.

Finding 118: Coupled with fire-related network connectivity outages, a lack of physical maps was an issue for Deputies unfamiliar with the area.

Finding 119: During community listening sessions, some community members expressed concern regarding instances of rudeness and lack of professionalism by some non-local agency Deputies.

4.4.3 County Animal Care Evacuation Findings

Finding 120: County Animal Care staff developed positive workarounds to create animal sheltering sites and welfare checks.

Finding 121: A County Public Works water tender teamed up with County Animal Care to deliver water to large animals that were left behind by their owners.

Finding 122: County Animal Care and the American Red Cross (Red Cross) worked well together, and the Red Cross allowed pets in shelters (against standard Red Cross rules) to encourage victims' attendance.

Finding 123: County Animal Care staff and volunteers had to evacuate the Agoura Hills Animal Care facility.

Finding 124: In an effort to utilize the co-location model of sheltering, County Animal Care was awaiting information and notification of human sheltering sites from the Red Cross.

Finding 125: County Animal Care has limited staff to respond to animal evacuations because it must still care for over 2,000 animals and maintain regular operations, such as responding to calls for service at seven animal care centers 24 hours per day, seven days per week.

Finding 126: County Animal Care relies heavily on mutual assistance partners and volunteer groups during adverse times for reserve capacity.

Finding 127: Damaged/destroyed homes and animal enclosures prevented timely return of animals, thus causing longer County Animal Care shelter operations and increased costs, which may not be reimbursable.

4.5 TRANSITION TO RECOVERY

4.5.1 Countywide Transition to Recovery Findings

Finding 128: Some staff from other County agencies were specifically assigned to the Recovery Coordinating Center (RCC) because of their specialized qualifications.

Finding 129: There was early realization that at least two local Disaster Assistance Centers (DACs) would be needed to serve fire victims: one in the Malibu area and another in the Highway 101 corridor.

Finding 130: This was the earliest in a disaster event that the County had opened a DAC; prior philosophy/practice was to have a longer preparation period between the conclusion of the incident and the opening of the DAC.

Finding 131: DACs were staffed by 60 to 100 or more employees, and volunteers representing over 50 local, State, and Federal agencies, cities, and non-governmental organizations.

Finding 132: Inter-departmental cooperation was instrumental in the major lift to getting DACs operational so quickly.

Finding 133: The Federal Emergency Management Agency (FEMA) Area Field Office opened in Westlake Village on December 18.

Finding 134: The Agoura Hills DAC transitioned to a Disaster Recovery Center (DRC) on December 18, and then the DRC closed on January 11, 2019.

Finding 135: The Malibu DAC closed on January 9, 2019.

Finding 136: There is no common, County-level, information collection database management process for the initial damage assessment efforts of LA County Fire and County Public Works. Early, accurate damage assessment information/data is critical to local, State, and Federal disaster/emergency proclamations/declarations.

Private Property Debris Removal

Finding 137: During the first week of the Woolsey Fire, County Emergency Management communicated with Cal OES and FEMA to identify a timeline and critical components of debris removal needs. Considering this was the County's first utilization of PPDR with an associated learning curve, the process went very well. In partnership with Cal OES and CalRecycle, a unified command PPDR IMT was developed.

Finding 138: Los Angeles County engaged in dialogue with PPDR leaders and technical experts from Cal OES and CalRecycle to develop the Woolsey Fire PPDR plan and operations.

Finding 139: Coordination was needed amongst all County departments before the County entered into memorandums of understanding with third party stakeholders to ensure uniformity and full coordination.

Finding 140: Phase 1 of PPDR involved participation by Federal Environmental Protection Agency, California Environmental Protection Agency, and the Los Angeles County Certified Unified Program Agency to perform a visual inspection and removal of "immediate life hazard hazardous chemicals," such as asbestos, unsecured chimneys, and exposed active utilities.

- Phase 1 is the only phase that is not optional for property owners.
- Phase 2 of PPDR addressed erosion control.

Finding 141: Phase 2 of PPDR addressed debris removal and related excavation of contaminated soil.

- Property owners representing approximately 900 properties opted in to participate in the government-sponsored PPDR program.
- Property owners representing approximately 450 properties did not want to participate in the government-sponsored PPDR program and opted to participate in the local program developed by County Public Works.
- Local debris removal policy requires property owners to independently perform debris removal following County Public Works developed requirements.
- Themes regarding those opting out of the government-sponsored PPDR program included: 1) concern about foundation condition and the property owner's desire to preserve their foundation and 2) a general distrust of government.
- Property owners who opted out of the government-sponsored PPDR program were put on a timeline for completing their required clean up through the local debris removal program.
- The first home was not removed until February 2019 due to delays waiting for FEMA to approve the hire of contractors for debris removal.
- State agency partners found that County staff offered superior customer service; however, sometimes in the delivery of this high level of service, County staff was tentative to firmly communicate unpopular facts.
- Particularly in the beginning, public education, information, and outreach was inconsistent and decentralized. The outcomes ranged from extreme satisfaction to confusion and frustration.
- Staff at the DACs received conflicting information, particularly about how and when to permit temporary housing applications when debris still existed on site. There was significant confusion related to the DPH declaration of a public safety hazard, whether that conflicted with FEMA regulations, and how that would impact temporary housing permits. In some cases, early on, planning staff was telling people they could place temporary trailers on site but then were directed to stop doing that without clear direction as to why. There was a lack of inclusive coordination between the CEO, County Counsel, the DPH, County Public Works, and the debris removal program during the early period of recovery. The DRP had handouts for temporary housing permits prepared as soon as 11/17, but information on the 100-foot

setback from debris piles was not clearly communicated for weeks. This resulted in the DRP providing incorrect information to early visitors to the DACs.

- With greater collaboration with County Emergency Management, the accuracy and satisfaction of public information increased.
- Some property owners conveyed their experience of being told conflicting facts about the PPDR program. Some were told that they could easily opt to keep their structure's foundation, only to later learn this was not the case.
- The website www.lacountyrecovers.com provided vital information to residents.
- The hotline phone number was very beneficial for customer service needs.
- Concrete foundations are not typically covered by FEMA disaster reimbursement under PPDR, a fact which exposes a huge financial liability to communities implementing PPDR programs.

Finding 142: Disparate systems of tracking structures (e.g., by parcel number or by address) created problems for field crews and created confusion for some property owners who sought to check the status of their structures.

Finding 143: With great support from FEMA officials, the Board of Supervisors staff, and the County CEO staff, PPDR-assigned personnel participated in many productive, highly beneficial public meetings.

4.5.2 County Emergency Management Transition to Recovery Findings

Finding 144: County Emergency Management recognized early in the response phase that local disaster assistance would be needed. RCC was activated by the CEO on the afternoon of November 14.

Finding 145: RCC section head positions were selectively filled utilizing the CEO Office's network of known County personnel based on their skill sets, which was instrumental to getting assistance centers established quickly and effectively and to the success and effectiveness of the overall recovery effort.

Finding 146: During the incident, response and recovery were overlapping, so the Damage Inspection Specialist Unit at the incident produced preliminary Damage Inspection Reports and, as the incident stabilized, this report was continually revised and updated.

4.5.3 County Public Works Transition to Recovery Findings

Finding 147: Initially, LA County Fire, DPH, County Public Works, and, later, the CAL FIRE IMT deployed teams of engineers, inspectors, and personnel certified in the Safety Assessment Program to survey the Woolsey Fire to confirm the extent of damage and whether damage was to residential, commercial, or County-owned buildings.

- There are approximately 200 County Public Works personnel trained and certified to function in the Safety Assessment Program.
- Within two weeks, over 400 residential and commercial sites were surveyed, with 658 structures classified as demolished, moderately damaged, or lightly damaged.
- A rapid evaluation report accompanied by pictures was made for every site surveyed.
- County Public Works also provided substantial assistance to the affected cities, most especially to the City of Malibu, to assess the damages to private property.
- Damage assessment teams were challenged by a lack of visible addresses on many structures due to the destruction caused by the fire.
- Damage assessment teams found that different County agencies were relying on different addressing data / databases.
- Damage assessment teams found stand-alone, handheld, satellite-based Global Positioning System devices to be the most reliable device for damage reporting by structure and location.

Finding 148: As soon as conditions permitted, the County Building Evaluation Team was activated through the County EOC to perform damage assessment operations on County buildings.

Finding 149: County Public Works staff were deployed to provide geotechnical assessments and recommendations to address rock falls, debris flows, and slope stability concerns.

Finding 150: While the Woolsey Fire was active, County Public Works staff began an analysis of potential drainage and mud/debris flow concerns and mitigations in preparation of the upcoming storm season.

Finding 151: Once inspection data was available and site area inspection operations were safe, County Public Works personnel worked diligently to assess and address drainage issues.

Finding 152: County Public Works provided homeowners with "Protecting Your Home from Debris Flow" guides to answer questions, reduce preventable damage, and inform the public.

Finding 153: When conditions were safe, County Public Works immediately evaluated and addressed the repairs needed to the rail and timber structures and inlets.

Finding 154: Communication between the County Public Works DOC and field operations were excellent. For example, when flashflood warnings were issued in the Trancas Canyon area, the field personnel were immediately informed to make sure no one was in harm's way.

Finding 155: When conducting sediment removal, County Public Works had pre-identified Sediment Placement Sites in the region.

- With the assistance of the Los Angeles County Department of Beaches and Harbors, the Zuma Beach parking lot was temporarily provided to support this operation.
- The Calabasas Landfill had a limit of depositing 3,500 tons per day, which initially limited daily debris/sediment removal operations. County Public Works negotiated with the Los Angeles County Sanitation District to increase the maximum limit allowed under an emergency waiver.
- To increase the rapid turnaround of vehicles going to the landfill, the landfill created an express lane for County Public Works vehicles when the lines at the landfill became too long.



SECTION 5—RECOMMENDATIONS

Any After Action Review (AAR) of an incident the size and scope of the Woolsey Fire will include many recommendations within a framework of continuous process improvement across all the agencies to varying degrees. Citygate's recommendations are based on its findings and, more importantly, the totality of analyses in the AAR. As a result, not every recommendation is coupled to any single finding or group of findings.

In Los Angeles County, the responding agencies are large and capable. They are *extremely* experienced with large wildfires, as are many of the affected neighborhoods. However, even some of the largest, most experienced agencies in the United States were, at times, overwhelmed in the first hours by this incident's *speed and weight of impact*, exposing some limitations between the agencies and systems as they meshed into a single, wide-area regional response team in less than a 24-hour period. This was more evident until the fire's pace slowed and sufficient response resources assembled for control and a transition to recovery.

To assist the user of this AAR, the following recommendations are categorized by the major themes established in the County's Woolsey Task Force process:

- The Response
- Communications
- Evacuation
- Repopulation
- Transition to Recovery

The following table includes consecutively numbered recommendations, organized by theme, and include columns indicating which agency or agencies are the primary organization to implement change as recommended. These agencies are:

LAC Los Angeles County Fire Department

LASD Los Angeles County Sheriff's Department

CPW Los Angeles County Public Works

OEM Los Angeles County Office of Emergency Management

DACC Los Angeles County Department of Animal Care and Control

5.1 THE RESPONSE

	Recommendation	LAC	LASD	CPW	OEM	DACC
1.	Memorialize the successes of the Woolsey responses and recovery effort into policies, guidelines, and procedures to ensure ongoing success.	X	X	X	X	X
2.	Reset the operation of the Los Angeles County Emergency Operations Center (County EOC) to the Los Angeles County Office of Emergency Management (County Emergency Management) to become the central coordination and support hub for all County agencies and the County Operational Area by activating and managing the County EOC.		X		X	
3.	Closely practice and communicate the understanding that the unified ordering point may start with the originating jurisdiction but may be best located at the jurisdiction that has the largest incident exposure.	X				
4.	Draft an addendum to the Santa Susana mutual threat zone (MTZ) agreement that delegates action if the other party cannot fulfill its obligations.	X				
5.	Review radio frequency coverage to ensure effective talk/receive capability on incidents. Add additional command frequencies or upgrade the radio system with repeaters to cover from the Cheseboro to Malibu areas.	X	X	X	X	X
6.	Ensure all staff have communications training for satellite phones and Countywide Interoperable Radio System radios.	X	X	X	X	X
7.	Develop plans to assign Command Aids / Drivers to field command chief officers during augmented staffing fire weather days and long-term incident response to enhance operational effectiveness.	X				
8.	Continue to train officers and commanders on TIER (Take Initiative Engage and Report) for Fire Front Following and Life Safety First implementation to allow flexible engagement.	X				
9.	Grow a program to assist with survival and support of individuals within evacuation areas.	X	X	X	X	X
10.	Reinforce existing triage criteria for critical infrastructure and key resources (residential, commercial, governmental) and other properties when firefighting resources are scarce and priorities must be set.	X				
11.	Update command and tactical maps for major threat areas throughout Los Angeles County.	X	X	X	X	X
12.	Ensure incident response / tactical maps can be sustained without internet connection and digitally or physically transferred to outside resources.	X	X	X	X	X
13.	Recognize and mitigate, as practical, the detrimental effects of fatigue on safety, operations, and decision-making.	X	X	X	X	X

	Recommendation	LAC	LASD	CPW	OEM	DACC
14.	Incorporate the concepts of Fire Front Following and Life Safety First into Department wildfire programs to educate the public and policy leaders.	X				
15.	Install Global Positioning System tracking technology on all County vehicles for safety and tactical location awareness.	X	X	X	X	X
16.	Increase participation at all Los Angeles County Sheriff's Department (County Sheriff's Department) Emergency Operations Bureau (EOB) trainings.		X			
17.	Conduct thorough briefings for all personnel prior to deployment. County Sheriff's Department Deputies will be able to make more informed decisions and provide better explanation of limitations to the public.	X	X	X	X	X
18.	Incident Command System (ICS) training should be conducted not by agency but via mixed discipline classes to build relationships and knowledge of shared experiences, including elected officials and their staff.	X	X	X	X	X
19.	Ensure County public safety agencies meet on at least an annual basis to discuss authority/responsibility/tactics in general terms and specific to challenging locations.	X	X	X	X	X
20.	Hold at least one annual training, in strategically identified operational areas, to include area County Sheriff's Department Deputies/leadership (including representation from Incident Management Teams (IMTs)), Los Angeles County Fire Department (LA County Fire) personnel/leadership, Los Angeles County Department of Animal Care and Control (County Animal Care), Los Angeles County Public Works (County Public Works), County Emergency Management, California Highway Patrol (CHP), and other appropriate strategic partners.	X	X	X	X	X
21.	The County Departments must embrace SEMS. Provide regular, ongoing Standardized Emergency Management System (SEMS) / ICS training for all Los Angeles County and city personnel likely to fill an Emergency Operations Center (EOC) and field ICS positions.	X	X	X	X	X
22.	OEM should review and revise the emergency organization of the County to better define the roles and responsibilities of the Emergency Management Council (EMC) members and provide training and exercises to strengthen the Council's capabilities.				X	
23.	Develop a Wildland Fire Plan annex to the Emergency Response Plan that addresses key response issues for all known high-hazard areas.	X			X	
24.	Expand the political and public notification role of County Emergency Management to allow initial incident command staff to focus on respective operational priorities.				X	
25.	Exercise the EOC more frequently to facilitate better EOC/incident communication, cooperation, and coordination.	X	X	X	X	X

	Recommendation	LAC	LASD	CPW	OEM	DACC
26.	Add an Information/Intelligence Section to the EOC.				X	
27.	Provide regular tabletop exercises for designated EOC staff, County department heads, County Chief Executive Officer (CEO) leadership, and County Board of Supervisors chiefs of staff.				X	
28.	Provide geographic information system awareness training for EOC and RCC staff, including capabilities and sample products.	X	X	X	X	X
29.	Conduct a wildland fire deployment study to establish an appropriate ratio of emergency resources in relation to population and animal risk factors. This study should also help to support funding changes as needed.	X	X	X	X	X
30.	Allow case-by-case diesel vehicle exemptions from the County's clean-air policy to allow for agencies to fulfill mission critical tasks.	X	X	X	X	X
31.	Consider establishing local government Type 1 Incident Management Teams within Region 1.	X				
32.	Pre-identify Incident Command Posts (ICPs) that have the size and technology capability to support command and control actions and pre-position a cache of support items.	X	X			
33.	Support the ongoing FIRESCOPE work in the California Mutual Aid System regarding increasing the tempo for catastrophic, fast-moving incident resource triage and resource availability.	X				

5.2 COMMUNICATIONS

	Recommendation	LAC	LASD	CPW	OEM	DACC
34.	Shorten approval tempo of evacuation alerts, use of alerting tools, and the notification process. This requires a more robust multi-department process.	X	X	X	X	X
35.	Increase the quantity, diversity, and redundancy of early public notification/communications tools for evacuations, especially for limited access areas (e.g., canyons).	X	X	X	X	X
36.	Plan a communications system that functions when cellular service and/or radio communications do not work.	X	X	X	X	X
37.	Recognize digital divide issues and design additional types of alert systems to gain public attention.	X	X	X	X	X

	Recommendation	LAC	LASD	CPW	OEM	DACC
38.	Reset Countywide public notifications policies to provide a strategic, single message across all platforms of traditional, auxiliary, and social media, to include a Public Information Officer (PIO) organization chart, information flow protocols, social media message templates, and a regularly updated 24-hour area media contact list.	X	X	X	X	X
39.	When multiple County departments or agencies respond to a major incident, they must implement a joint information system strategy for the incident and adhere to the Operational Area Emergency Public Information Annex.	X	X	X	X	X
40.	Develop and practice a low-tech back-up plan for relaying critical public information during high-tech infrastructure failure (AM radio, ham radio, etc.).	X	X	X	X	X
41.	Develop and annually maintain agreements with local AM radio stations regarding their role in critical public information dissemination.				X	
42.	Mandate common data sharing and and ensure all communications, intelligence, and decision support tools can interface with each County agency.	X	X	X	X	X
43.	Develop sustainable PIO surge capacity / bench depth for all agencies, including elected office resources.	X	X	X	X	X
44.	Develop a qualified PIO staff roster; County departments should invest in high-level PIO training for all personnel assigned as PIOs and include American Sign Language and Spanish language PIOs, as well as any other identified language needs.	X	X	X	X	X
45.	The personnel commitment to the Joint Information Service function must be greatly expanded and the manager of the JIS should be of sufficient rank to communicate to the highest levels of local, county, State, and Federal government representatives.	X	X	X	X	X
46.	Provide adequate space for a fully staffed Joint Information Center (JIC) at the EOC, and/or designate alternate site(s) that will meet the need.		X		X	
47.	Provide regular, ongoing training on the Emergency Public Information Annex of the Emergency Operations Plan for all County and Operational Area cities personnel potentially involved in emergency incident information management.				X	
48.	As part of training, practice using more traditional techniques for communications, intelligence, and decision-making. Future training exercises should include emergency operations problem solving without the use of commonly available technology. Problem-solving, without the use of technology, and demonstrated skills, such as map reading, should be part of a checklist of requisite skills.	X	X	X	X	X

5.3 EVACUATION

	Recommendation	LAC	LASD	CPW	OEM	DACC
49.	Dramatically increase the tempo of pre-alerting and evacuations.	X	X	X	X	X
50.	Prepare a playbook of detailed evacuation plans with traffic engineering capacity, to include, at a minimum: ➢ Areas defined by geography ➢ Pre-defined routes and the signage needed ➢ Estimated time frames for alerting and then areas to evacuate ➢ Pre-determined trigger points ➢ Contraflow plans for the Pacific Coast Highway (PCH)	X	X	X	X	X
51.	Create pre-planned evacuation management procedures in conjunction with law enforcement and County Public Works.		X	X	X	
52.	Establish a Standard Operating Order Process for monitoring traffic flow of vital ingress and egress routes.		X	X		
53.	Create a matrix to ensure that when a field entity orders an evacuation it is confirmed by the responsible entity facilitating the evacuation.	X	X	X	X	X
54.	Develop and provide additional instructions/handouts for residents during an evacuation.	X	X	X	X	X
55.	Conduct thorough safety training and issue personal protective equipment for Deputies prior to fire evacuation deployment, which should include LA-County-Fire-led training on fire behavior, the hazards associated with premature reentry, and how to explain these issues to the public in the field.	X	X			
56.	Working in conjunction with appropriate County health agencies and public utilities (medical baseline customer list), identify and develop a plan for individuals who may require a more specific notification process and evacuation assistance.		X		X	
57.	Build stronger LA County Fire / County Animal Care ties for evacuation information and possible synergies with the Occupant Support Team.	X	X			X
58.	Explore alternate long-term emergency animal sheltering sites with a funding mechanism for displaced animals.					X
59.	Continue to support, enhance, and build public support for the Ready! Set! Go! program.	X	X	X	X	X

	Recommendation	LAC	LASD	CPW	OEM	DACC
60.	Update the Mass Care plans, procedures, and mutual aid agreements to ensure that they reflect the need for government liaison-trained American Red Cross (Red Cross) response personnel to be actively involved in the Los Angeles County Emergency Operations Center (County EOC) and the Los Angeles Department of Public Social Services (DPSS) Mass Care and Shelter Branch during all Level 2 and Level 1 activations.				X	
61.	Invite DPSS and Red Cross personnel to participate in large scale exercises that will include an activation of the Mass Care and Shelter Branch.		X		X	

5.4 REPOPULATION

	Recommendation	LAC	LASD	CPW	OEM	DACC
62.	Redesign, as needed, the repopulation process and establish a decision-making process, including establishing the final authority regarding repopulation determination.	X	X	X	X	X
63.	Implement a program that allows safe, timely, and appropriate access for evacuees to see, grieve, and perform a quick salvage check on their property.	X	X	X	X	
64.	Conduct a public repopulation education campaign commensurate with evacuation training to manage expectations.	X	X	X	X	X
65.	Create a PIO decision flow process to pre-notice all affected agencies and announce repopulation decisions with phased timeframes.		X		X	
66.	Conduct annual repopulation training for all involved agencies (public and private).	X	X	X	X	X
67.	Develop a program to better manage and distribute spontaneous volunteer and donation efforts. Include coordination with the Occupant Support Team.	X	X		X	X

5.5 Transition to Recovery and Future Mitigations

	Recommendation	LAC	LASD	CPW	OEM	DACC
68.	Activate the RCC as early as possible for any emergency with a likely need for disaster assistance.				X	
69.	Update the Damage Assessment annex to the County Emergency Response Plan to include a common data structure and capture tool across all County agencies.	X		X	X	
70.	Develop and maintain a list of suitable pre-designated sub-regional Disaster Assistance Center (DAC) facility sites across the County to reduce the time/effort required to identify and acquire such facilities in the early phases of a disaster event.				X	
71.	Convene a debris management project team with representatives from California Office of Emergency Services (Cal OES), CalRecycle, County Emergency Management, County Public Works, the Los Angeles County Department of Public Health (DPH), Environmental Health, participating cities, and other regional stakeholders to develop a local program and team capable of activating a private property debris removal (PPDR) response without requiring the assistance of Cal OES or CalRecycle.			X	X	
72.	Secure standing contracts with approved, licensed vendors for debris assessment and removal if the County chooses to activate a locally funded PPDR program in smaller incidents.			X	X	
73.	With the DPH, adopt standards, protocols, resources, and timeline expectations for mitigating public health risks associated with post-emergence hazardous debris removal.			X	X	
74.	In a manner reflective of the Public Health Agency requirements, ensure hazardous debris removal is addressed at all scales of emergency, from a single-family house fire to loss of an entire community.			X	X	
75.	Review Federal Emergency Management Agency (FEMA) reimbursement requirements to ensure the County contract award process is aligned (or accept that FEMA does not recognize some contract award considerations reflective of Los Angeles County's interests around minority- and veteran-owned businesses, etc.).				X	
76.	Establish an IMT for PPDR operations, train local personnel to staff it, and adopt trigger points for PPDR implementation.			X	X	
77.	Work with FEMA to ensure inclusion of foundation removal reimbursement when necessary. This is not included in FEMA's debris removal program, which may be based on tornado and hurricane emergencies that do not typically affect foundations.			X	X	

	Recommendation	LAC	LASD	CPW	OEM	DACC
78.	Los Angeles County should develop and implement a standard policy regarding the collection of damage information and the release of the Damage Inspection Report by the Damage Inspection Specialist Unit.	X		X	X	
79.	Identify critical infrastructure sites and ensure associated defensible space needs.	X		X	X	
80.	Increase awareness for voluntary home/property safety inspections through which residents can hear from local firefighters regarding how safe their structures are and/or what the resident can do to enhance survivability and accessibility for firefighters.	X				
81.	Build a unified strategic vegetation management plan for the Santa Monica Mountains among private property owners and land managers for the County, the Federal government, the State, and non-profits. As appropriate, to manage the landscape, use the best-fit tool based on a strategic plan.	X			X	
82.	Create a layered fire defense approach using structure hardening and fuel reduction / change of fuel types to buffer development in relation to managing a neighborhood's expected fire intensity potential. Implementation is the property owners' responsibility.	X				
83.	Explore methods to enhance the soil's ability, through carbon and moisture retention, to increase fuel moisture in defensible landscaping plants.	X				
84.	Increase requirements for development/construction codes and public education programs to gain more hardening of structures.	X		X		
85.	Commit dedicated funds annually for County EOC equipment and building repairs.				X	
86.	Study and plan for the replacement and modernization of the County EOC facility to meet current and emerging standards.				X	



SECTION 6—POLICY LEADERSHIP RECOMMENDATIONS

In addition to departmental recommendations, the Woolsey Fire incident shows the need for policy leadership from Los Angeles County and regional elected officials to enable significant changes for multiple agencies and public participation. Citygate suggests the following recommendations receive *policy leadership focus* from the County of Los Angeles Board of Supervisors:

Premise – Because wildfires and other emergencies do not respect jurisdictional lines, all public jurisdictions should adopt a cross-boundary philosophy that addresses how to prepare, fight, and recover from wildfires without creating silo actions and establish a sub-regional command model to bridge agency/political lines.

1. Utilize an oversight body to institutionalize the Woolsey 2018 lessons learned to ensure that After Action Review (AAR) recommendations become reality and will transcend staffing attrition in the future.
2. Advance an initiative with all applicable public agencies and private interest groups that are involved in the Santa Monica Mountains region to develop a unified, comprehensive, and strategic wildfire hazard reduction plan.
3. Encourage the major fire departments in the area to evaluate creating a sub-regional (three county) Multiple-Agency Coordination and Control Center within the State mutual aid system that will utilize technology to enhance situational awareness and create a shared, *real-time* intelligence, information, and command center on an around-the-clock basis. This concept should further existing agreements and enhance the ability of agencies to work collaboratively during the first one to two days of a catastrophic disaster, for the common welfare, at a pace faster than the Statewide mutual aid system can provide.
4. Reset the operation of the Los Angeles County Emergency Operations Center (County EOC) to the Los Angeles County Office of Emergency Management (County Emergency Management) to become the central coordination and support hub for all County agencies and the County Operational Area by activating and managing the County EOC.
5. Work with Federal officials to advocate Federal disaster reimbursement changes as needed. Federal approvals often cover many County costs, but other costs may not be reimbursable, including long-term animal housing costs for Los Angeles County Department of Animal Care and Control (County Animal Care). As another example, some private property debris removal (PPDR) policies on items such as foundations do not work in California. In addition, the burn scars that result from wildfires are prone to mud and debris flows from winter rains. This subsequent loss

is not viewed as a continuation of the wildfire, but instead as a new standalone event which may not qualify for State and Federal disaster cost recovery.

If the desired end is more resilient communities to meet the current wildfire risks, the improvements suggested by the Citygate team, taken as a whole, should deliver an enhanced union of government services, community bonds, and personal involvement. Citygate's Project Team hopes the communities' common bonds to one another, and to their environmental treasures, will propel earnest conversations to deal with the wildfire lessons from the Woolsey Fire disaster.

6.1 Near-Term Next Steps

1. Absorb the issues identified in this AAR.
2. Direct staff to return in 90 days with an assignment and tracking plan for all the AAR recommendations by agency, the lead manager, and the completion timeline.
3. After the Los Angeles County Board of Supervisors reviews the assignment and tracking plan, ask the County Chief Executive Office and the finance teams of the agencies to estimate the cost of implementing the recommendations over feasible timelines.

APPENDIX A

HISTORY AND CONTEXT PRIOR TO THE WOOLSEY FIRE

APPENDIX B

BACKGROUND ON PRIMARY COUNTY AGENCIES

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GLOSSARY OF ACRONYMS, INITIALISMS, AND ABBREVIATIONS

Each acronym, initialism, or abbreviation is spelled out for its first usage in each section.

AGENCY ACRONYMS, INITIALISMS, AND ABBREVIATIONS

CAL FIRE	California Department of Forestry & Fire Protection
Cal OES	California Office of Emergency Services
CHP	California Highway Patrol
County Ag. Comm.	Los Angeles County Agricultural Commissioner / Weights and Measures
County Animal Care	Los Angeles County Department of Animal Care and Control
County Emergency Management	Los Angeles County Office of Emergency Management
County Public Works	Los Angeles County Public Works
County Sheriff's Department	Los Angeles County Sheriff's Department
County Waterworks	Los Angeles County Waterworks District No. 29
DPH	Los Angeles County Department of Public Health
DPSS	Los Angeles County Department of Public Social Services
DRP	Los Angeles County Department of Regional Planning
EMC	Emergency Management Council
FEMA	Federal Emergency Management Agency
LA City Fire	City of Los Angeles Fire Department
LA County Fire	Los Angeles County Fire Department
Pepperdine	Pepperdine University
Red Cross	American Red Cross
SCE	Southern California Edison
SCVMA	Southern California Veterinary Medical Association
Ventura County Fire	Ventura County Fire Department

GENERAL ACRONYMS, INITIALISMS, AND ABBREVIATIONS

AAR	After Action Review
CEO	County Chief Executive Officer
Command and Control	P. Michael Freeman Command and Control Center
County EOC	Los Angeles County Emergency Operations Center
CSL	Community Services Liaison
DAC	Disaster Assistance Center
DOC	Department Operations Center
DRC	Disaster Recovery Center
EOB	County Sheriff's Department Emergency Operations Bureau
EOC	Emergency Operations Center
ICP	Incident Command Post
ICS	Incident Command System
IMT	Incident Management Team
JIC	Joint Information Center
MTZ	Mutual Threat Zone

NIMS	National Incident Management System
PCH	Pacific Coast Highway
PIO	Public Information Officer
PPDR	Private Property Debris Removal
RCC	Recovery Coordinating Center
RH	Relative Humidity
ROSS	Resource Order Status System
SEMS	Standardized Emergency Management System
SIB	County Sheriff's Department Sheriff's Information Bureau
UTF	Unable to Fill


LOS ANGELES
FIRE DEPT.

APPENDIX A—HISTORY AND CONTEXT PRIOR TO THE WOOLSEY FIRE

A.1 FIRE HISTORY IN THE AREA

A.1.1 Vegetation, Topography, and Weather

The 2018 Woolsey Fire occurred in an area of Los Angeles and Ventura Counties with an extensive fire history. Between the point of origin and the Pacific Ocean end point lie approximately 17.3 miles of steep, rugged canyons that can direct Santa Ana winds. The terrain has two distinct fuel environments: a drier inland valley with grass, chaparral, and sparse density of oak trees, and a southwestern coastal flank of the Santa Monica Mountains with higher humidity, covered with lush chaparral extending to the Pacific Ocean. At 3,111 feet high, Sandstone Peak in the Santa Monica Mountains separates these two environments. The inland valley is more populated than the rest of the Santa Monica Mountain area, especially along the Highway 101 corridor. The Highway 101 development pattern creates a wildland-urban interface condition where development abuts heavy wildland fuel. The steeper terrain of the southwest, ocean-facing slopes supports less development, which creates more of an intermix condition where development occurs on larger parcels impacted by wildland fuels on all sides. The southwest side also provides access challenges, and the rugged, steep canyons and ravines can drive fire behavior with or without strong winds.

Figure 1—Southern California Landscape Featuring Chaparral

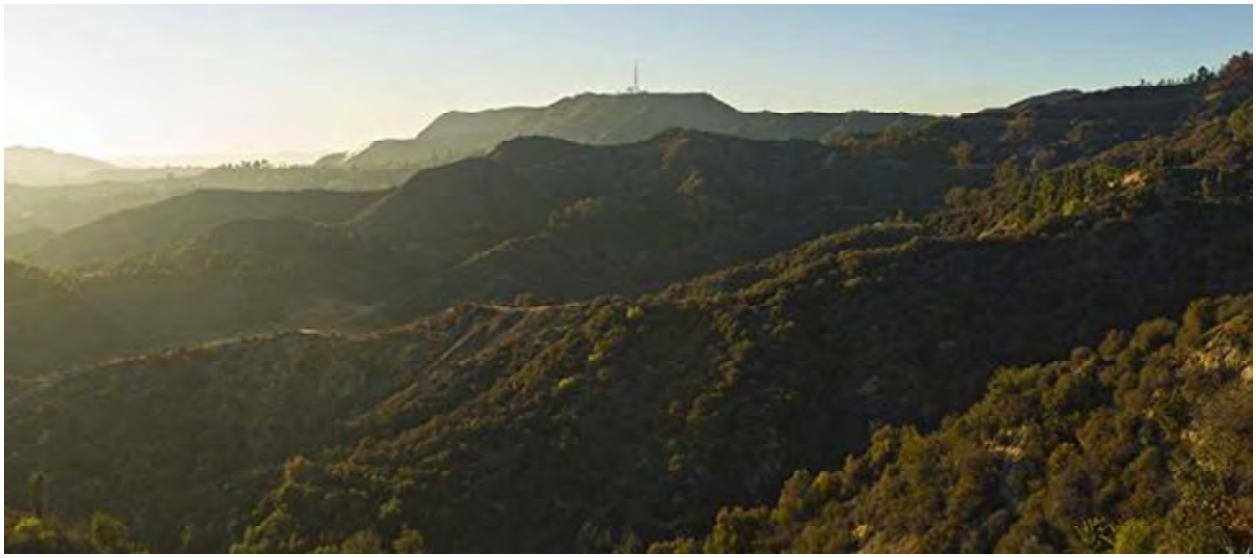


Chaparral is a generic term for the brush that dominates much of Southern California's natural environment. Plant species that typify the chaparral of this region include manzanita, ceanothus, chamise, scrub oak, grasses, and forbs. Plants of the chaparral environment are well known for

their reliance on natural fire behavior for seed germination. The Mediterranean climate of the Santa Monica Mountains supports a robust chaparral environment that is no stranger to wildland fires, even thriving on fire as part of its natural life cycle. Commonly referred to being "fire adapted," chaparral can be seen within weeks following a wildfire as seeds germinate and plants sprout. Wildland fire acts as part of the natural selection process to reduce fuel loads and initiate seed propagation. Alternatively, too frequent of a fire interval coupled with excessive high heat intensities can also interrupt the natural chaparral life cycle and allow invasive plant species to challenge this sensitive ecosystem.

The inland valleys have early grass fires that function as "ladder" fuels to carry fire into its adjoining chaparral beginning in late spring until late fall. Because of this fuel type and gentle sloping terrain, these non-wind-driven fires are somewhat easier to control, especially with a robust local first response system. On the ocean side of the mountains, the chaparral is on steep southwest-facing slopes that dry and pre-heat fuels from late summer to late fall. Dry chaparral coupled with its natural oils and resins creates a flammable mixture that can cause rapid topographical-driven fire spread.

Figure 2—Santa Monica Mountains



Weather patterns and the multiple challenging fire corridors of this region create a well-known active fire area. The fire history is attributed to the Santa Ana winds driving fires quickly through the chaparral-covered canyons of the Santa Monica Mountains. Historically, Santa Ana conditions ran from August through October; however, the window for Santa Ana winds now extends well into the traditional wet season of November through January.

Santa Ana wind conditions in Ventura and Los Angeles Counties are typically preceded one to two days by hot, dry sundowner winds in Santa Barbara County. Strong, dry, downslope winds of

35 to 50 miles per hour with sustained 50 to 80 mile-per-hour gusts typify Santa Ana conditions. The warm, dry conditions created by Santa Ana winds can linger for days or even weeks after the strong winds subside.

A.1.2 Development in the Region

The region of the Woolsey Fire is one of development extremes. Areas of dense retail along major transportation corridors dot this region of vast, rugged open space. The most prominent land feature of this region is the Santa Monica Mountains National Recreation Area, which is rich in historic, ecological, and recreational significance. The Woolsey Fire consumed over 80 percent of this Federal parkland.

The Woolsey Fire impacted the Highway 101 and Pacific Coast Highway (PCH) corridors. Commercial development along these corridors is largely composed of retail, professional services, and tourism-related businesses and accommodations.

Residential development in the Woolsey Fire area has spanned a wide variety of types and zoning density over decades. Private parcels develop under County building and fire code regulations at the time of their permit application. Larger parcels that involve subdivisions must entertain a California Environmental Quality Act process that addresses negative impacts of development and sets forth required mitigation actions before public policy approval is given. Along the Highway 101 corridor, master planned communities and multiple-family dwelling units typify the residential housing stock. In the canyons leading to the PCH, the house stock, construction characteristics, and neighborhood configurations vary greatly. Homes are often built with greater preservation of the natural topography at varying elevations and are accessible through long, narrow, and winding roads.

Throughout the Woolsey Fire region, because codes and regulations change over time, not all structures share the same level of fire code, building code, or land use compliance. Some areas and structures have *grandfathered* old patterns of subdivision (e.g., single entry/exit) or old, less-safe codes and regulations. This is why most structures, at present, are not hardened to resist ember intrusion during a wildfire, and some structures will be more expensive than others to retrofit.

A.1.3 Transportation Infrastructure

Two major transportation corridors traverse the footprint of the Woolsey Fire: Highway 101 and the PCH.

Highway 101 is the larger primary transportation corridor that connects Los Angeles to Ventura County and, further north, San Francisco. This section of Highway 101 is sometimes referred to as the Ventura Highway. In the area of the Woolsey Fire, Highway 101 comprises 12 lanes: four northbound, four southbound, plus emergency access lanes. The opposing lanes of Highway 101 are separated in most areas by a cement barrier. Also, there is sufficient space for emergency parking adjacent to the center and outside lanes of the highway in most areas of this region.

The PCH connects Santa Monica with Ventura County and runs closer to the coastline than Highway 101. In the area of the Woolsey Fire, the PCH is along the Pacific Ocean, and only in Point Dume does the PCH not afford quick access to the beaches along this route. Through much of this area, the PCH is a four-lane highway with intermittent northbound–southbound physical barriers, typically a raised curb and island.

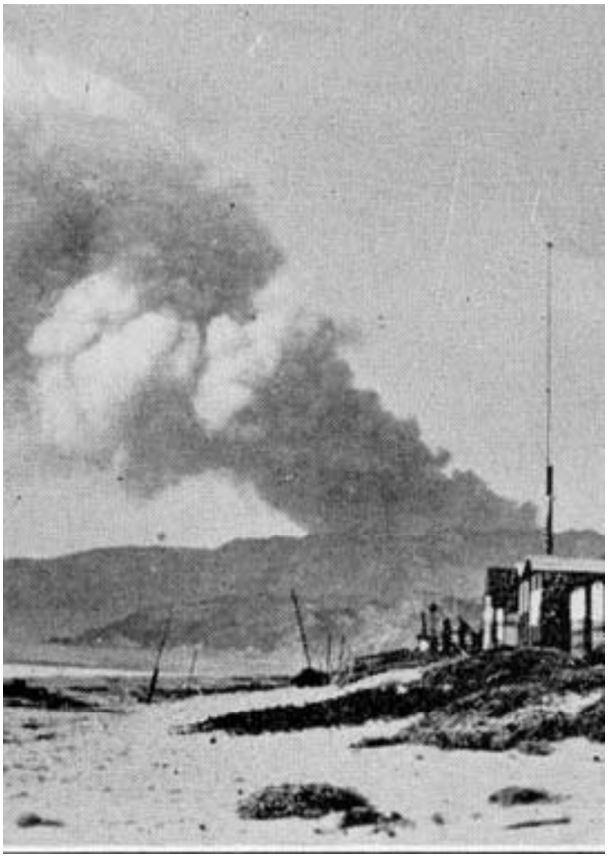
Winding canyon roads connect Highway 101 with the PCH. These include Las Virgenes Road, which becomes Malibu Canyon Road as it enters Malibu at Piuma Road; Kanan Road, which becomes Kanan Dume Road as it crosses Mulholland Highway; Westlake Boulevard, which becomes Mulholland Highway and then Decker Road; and Yerba Buena Road. These roads consist mostly of two-lane winding highways developed to rural highway standards with limited to no emergency parking pullouts.

A.1.4 Timeline and Outcomes of Historic Fires

The 2018 Woolsey Fire consumed a region with an extensive history of aggressive wildfires. While the footprint of the Woolsey Fire's destruction overlays previous fire scars, 2018 marked the first time in recorded history that the entire area burned in a single incident.

The Las Virgenes–Malibu geographic area has been the site for many large fires. These fires typically run from east to west, driven by strong Santa Ana winds. Historical fires started in the Santa Susana and Rocky Peak areas of Chatsworth and moved west toward Las Virgenes and Cheseboro Canyons. Before the widening of Highway 101 was completed in the 1960s, the then-four-lane highway offered little relief to fires jumping across the highway. When planning the expansion of Highway 101, it was hoped that the newly widened 12-lane freeway would create an effective firebreak to prevent fires from running to the ocean. Ensuing fires have shown that severe, wind-driven ember casts—which can deposit embers a mile or more ahead of an advancing fire—dashed these hopes.

Figure 3—Wildfire on December 31, 1917 in the Santa Monica Mountains



Historical fire records show a pattern of repetition in the Santa Monica Mountain region approximately every six to eight years. As population encroached in the fuel zone, increased fire suppression activities followed. Over years, urbanization, fire weather periods of longer duration, drought, and plant disease increased the potential for greater fire energy releases with an associated life and property loss result.

Figure 4—Wildfire in 1958 along Highway 101



Public sentiment and local government activity have been inconsistent—and sometimes at odds—regarding planned fuel reduction efforts. Opinions, priorities, and projects span a broad range from greater human control to habitat conservation to letting nature "run its course."

In response to significant fires, public officials often study fire losses to modify planning and building / fire code regulations to create a more fire-resistant community. One obvious problem of this evolving reactive approach is how to address the hazards of the existing community and the environmental protection afforded to this national recreation area. This includes the existing structures, landscape, transportation network, residential subdivision density, and water systems, which are typically *grandfathered* in despite significant changes in public policy and codes.

A review of California's fire history indicates that five of California's *deadliest* (casualties) wildfires have occurred over the past two years, six of the most *destructive* (structures) wildfires have occurred over the past 10 years, and 15 of the *largest* (acreage) wildfires have occurred over the past 19 years. Contributing fire threat and outcome factors include increased population growth in fire hazard areas, climatic cycles in and out of drought, disease and pest infestation, the cumulative effect of repetitive fires, an associated invasive species growth, and aging utility infrastructures.

Based on the table in **Exhibit A**, the area's fire history from 1897 shows a repetitive fire cycle in the Highway 101 corridor, the mountains, and the PCH, totaling 45 fires with 1,866 structures lost

and 584,404 acres burned *before* the Woolsey Fire. To see a map of the Woolsey Fire area fire history since 1970, see **Exhibit D**.

Table 1—Abbreviated Summary of the 121-Year Recorded History of Santa Susana / Malibu Area Fires*

Year	Fire Name	Location	Acres	Structures Lost	Deaths
1897	Great Drought	Malibu	Unknown or Unrecorded		
1903	Rindge	Malibu Canyon	10,000		
1913	Dry Canyon	Malibu Hills	10,000		
1917	Malibu Canyon	North of Malibu	2,000		
1921	Dume Canyon	Corral Canyon – Malibu	8,000		
1925	Latigo Canyon	Malibu	4,670		
1927	Cooper	Calabasas	3,118		
1929	Malibu Colony	Las Flores Canyon	274	13	
1930	Potrero	Decker Canyon	15,000		
1935	Malibu/Latigo/Sherwood	Kanan/Decker Canyon	28,599		
1935	Pt. Dume	Malibu	150		
1936	Cold Creed	Malibu	2,591		
1938	Topanga	Fernwood – PCH	16,500	350	
1942	Las Flores	Malibu	5,924		
1943	Las Flores	Malibu Canyon	5,800		
1943	Woodland Hills/Las Virgenes	Kanan/Decker Canyon	15,300		
1948	Topanga	Malibu	3,155		
1949	Susana	Simi – Chatsworth	19,080		
1955	Ventu	Thousand Oaks	12,638		
1956	Hume	Malibu	1,940		
1956	Sherwood/Newton	Kanan/Decker Canyon	35,537	120	1
1958	Warner	Malibu	4,040		
1958	Liberty	Malibu Canyon	17,860	107	
1958	Mulholland	Topanga Canyon	4,982		
1961	Topanga	Los Angeles City – Mulholland	8,750		
1967	Palmer	Chatsworth	14,248		

Year	Fire Name	Location	Acres	Structures Lost	Deaths
1967	Latigo	Malibu	2,868		
1970	Wright	Malibu Canyon	31,000	403	10
1970	Clampitt	Simi	107,103	80	4
1973	Potrero	Thousand Oaks	12,297		3
1973	Tripett	Topanga Canyon	2,770		
1976	Los Robles	Thousand Oaks	2,245	1	
1978	Kanan	Agoura – Malibu	25,385	230	2
1980	Las Virgenes	Calabasas	2,521		
1981	Oat Mountain	Chatsworth	17,786		
1981	Chatsworth Reservoir	Chatsworth – Los Angeles City	1,040		
1982	Dayton	Chatsworth – Malibu	42,540	74	
1985	Sherwood	Westlake Village	3,823		
1985	Piuma	Malibu Canyon – Corral Canyon	5,198		
1985	Decker	Malibu	6,526	6	
1985	Rocky Peak (Hummingbird)	Chatsworth	2,420		
1988	Keuhner	Chatsworth	3,818		
1989	Pacific	Malibu	3,180		
1993	Green Meadow	Thousand Oaks	38,152		
1993	Chatsworth	Box Canyon	2,036		
1993	Chatsworth	Chatsworth	37,571	43	
1993	Old Topanga	Topanga – Malibu	16,516	350	3
1996	Calabasas	Malibu Canyon to coast	12,377	10	
2005	Topanga	WB 118 Freeway to Calabasas	23,396	6	
2007	Corral	Corral Canyon – Malibu	4,901	49	
2007	Canyon	Malibu Canyon North of the PCH	3,782	14	
2008	Sesnon	Porter Ranch	14,703	63	1
2013	Springs	Newbury Park	24,000	15	
2016	Mulholland	Santa Monica Mountain	12		1
2018	Woolsey	Santa Susana / Malibu	96,945	1,643	3

* These are the notable 56 historical fires larger than 2,000 acres or with structure loss or deaths. A complete historical fire history chart of 157 fires is contained in **Exhibit A**.

A.2 Fire Loss Mitigation History

A.2.1 Government-Provided Fuel Mitigation Programs

The dry, sunny climate and variable terrain of Southern California combine to create an environment where wildfires are a part of the natural ecosystem and an almost year-round occurrence. This ecosystem fosters a diverse fire-adapted community of plants and animals. Although human-caused wildfires far outnumber naturally occurring wildfires within Los Angeles County, both have the potential to create situations in which structures in the Wildland Urban Interface can be at risk. All vegetation can eventually burn, even though irrigation has created a deceptively lush landscape of ornamental plants.

Following the loss of lives and structures during the 1993 wildfire season, the Los Angeles County Board of Supervisors created the Wildfire Safety Panel to offer recommendations aimed to reduce the threat to life and property in areas prone to wildfires. One such recommendation was to follow the findings of the Wildland Urban Interface Task Force, and another was to enforce the Bates Bill arising from the devastating Oakland Hills Fire in 1991. Jurisdictional fire departments had to establish guidelines and landscape criteria for all new construction in Fire Hazard Severity Zones. Fuel Modification Plans became a requirement within Los Angeles County in 1996. With these changes, all new construction projects, remodels of 50 percent or greater, parcel splits, and subdivision/developments within areas designated as Fire Hazard Severity Zones had to submit Fuel Modification Plans as a condition of approval. Los Angeles County Fire Department (LA County Fire) Forestry Division Fuel Modification Unit assumed responsibility for processing, reviewing, and approving these plans.

The California Department of Forestry & Fire Protection (CAL FIRE) maps and revises Fire Hazard Severity Zones for all land in California. These zone designations establish minimum standards for building construction and exterior landscape features to mitigate the increasing losses from the cycle of wildfire events. CAL FIRE categorizes the Fire Hazard Severity Zones as "Very High," "High," or "Moderate" for all State Responsibility Areas. In Local Responsibility Areas, the jurisdictional county or city determines the Severity Zones with approval from the State. Local ordinance or city councils then adopt these Fire Hazard Severity Zone designations.

The Los Angeles County Agricultural Commissioner / Weights and Measures (County Ag. Comm.) office is vested to protect the environment, the agriculture industry, consumers, and business operators through effective enforcement of Federal and State laws and County ordinances in the areas of health, safety, and consumer concerns of County residents. County Ag. Comm.'s highly diverse public services include ensuring a safe and wholesome supply of food and water, protecting consumers and businesses from fraud, preventing the misuse of pesticides, managing and excluding pests, minimizing fire hazards from weeds and brush, and providing useful consumer and agricultural information.

The County Ag. Comm. has four primary bureaus:

- Weights and Measures
- Weed Hazard and Integrated Pest Management
- Pest Exclusion and Produce Quality
- Environmental Protection

Within the Weed Hazard and Integrated Pest Management Bureau, the County Ag. Comm. addresses fire concerns by enforcing laws and ordinances requiring the removal of weeds, brush, and debris from vacant properties in unincorporated areas and contract cities to protect the health, safety, and property of residents. It also strives to improve environmental quality by eliminating hazardous and invasive weeds, fire hazards, and illegally dumped rubbish.

The Brush Clearance Program is a joint effort between the LA County Fire and the County Ag. Comm. Weed Hazard and Integrated Pest Management Bureau (Weed Abatement Division). This unified enforcement legally declares both improved and unimproved properties public nuisances and, where necessary, requires the clearance of hazardous vegetation. These measures create an up to 200-foot defensible space radius around structures for effective fire protection of property, life, and the environment. The Weed Abatement Division addresses vacant commercial properties throughout the County. Following devastating wildfires in 1993, LA County Fire began its Brush Clearance Unit. The LA County Fire Brush Clearance Unit enforces the adopted Uniform Fire Codes as they relate to brush clearance on improved parcels, coordinates inspections and compliance efforts with fire station personnel, and provides annual brush clearance training to fire station personnel.

Figure 5—Defensible Space



County Ag. Comm.'s efforts focus on unimproved parcels within the County while LA County Fire's efforts focus on improved parcels with structures. LA County Fire inspects all improved parcels, regardless if the parcel is owned, leased, rented or on Federal, State, special district, or private land. The local LA County Fire engine company, with a goal of establishing a minimum 100-foot defensible space in all High Fire Severity Zones and 200-foot defensible space in Very High Fire Severity Zones, performs these parcel inspections. Annually, LA County Fire engine companies inspect parcels and achieve an excellent property owner compliance rate with only 17 parcels referred to County Ag. Comm. in 2018 for clearance.

As climate conditions occur and fire frequency and intensities change, LA County Fire continues to evaluate parcels for inclusion into the program. Keeping enforcement and inspection workloads consistent with new development is difficult to manage.

A.2.2 Fuel Modification Plan Check Review

The defensible space buffer lessens the intensity from convective and radiant heat to structures and gives firefighters an area in which to protect structures. Defensible space has proven itself and should be extended further based upon local parcel placement due to wildland fuel type, slope, and natural wind effect considerations. During wind-driven events, a 200-foot defensible space buffer maintains a minimum protection distance from flying embers but does not ensure against structural ignition. Structures immediately adjacent to wildland fuels, and even within residential communities, are susceptible to flying embers, which often travel one mile or more.

The Fuel Modification Plan Check Review program applies to all parcels within Los Angeles County per the State's Public Resources Code 4290, which states:

> *The board shall adopt regulations implementing minimum fire safety standards related to defensible space that are applicable to state responsibility area lands under the authority of the department, and to lands classified and designated as very high fire hazard severity zones, as defined in subdivision (i) of Section 51177 of the Government Code. These regulations apply to the perimeters and access to all residential, commercial, and industrial building construction within state responsibility areas approved after January 1, 1991, and within lands classified and designated as very high fire hazard severity zones, as defined in subdivision (i) of Section 51177 of the Government Code after July 1, 2021.*

Fuel modification reduces the radiant and convective heat and provides valuable defensible space for firefighters to make an effective stand against an approaching fire front. Fuel modification zones are strategically placed as buffers to open space or areas of natural vegetation and would occur surrounding the perimeter of a subdivision, commercial development, or isolated development of a single-family dwelling. The objective is to create a defensible space, which is the minimum for effective fire protection in newly constructed and/or remodeled homes within High and Very High Fire Hazard Severity Zones.

A.2.3 Citizen-Focused Fuel Mitigation and Fire Prevention Programs (Ready! Set! Go!, etc.)

LA County Fire works with eight Fire Safe Councils and has several Community Wildfire Preparedness Plans that identify local hazards and list recommended mitigating actions. To date, resident focused fuel reduction actions comprise handwork, mechanical thinning, grazing, and prescribed fires. All follow the Ready! Set! Go! program implemented in 2009, following the horrific "Black Saturday" brushfires in Victoria, Australia, which killed 173 people within communities that largely embraced a stay-and-defend approach. The *Ready* portion focuses on getting citizens to harden their homes, creating defensible space, and maintaining structures against ember intrusion. The *Set* portion increases the public's situational and preparedness awareness as the chance of dangerous wildfires increases. Finally, *Go* encourages citizens to evacuate as soon as they know a dangerous situation exists or are directed by a law enforcement agency.

Forensic review of historical wind-driven wildfires shows that flying embers may travel long distances (one mile or more) and ignite receptive fuels/structures.[1] Within the home ignition zone, embers often land on protected areas, where they ignite, many times smoldering for hours until conditions are conducive for flame propagation and sequential ignition of the structure. Following the San Diego Witch Creek fire, the Insurance Institute for Business and Home Safety wind tunnel tests identified the following common ember hazards:

- Combustible roofs
- Leaf litter on roof valleys and rain gutters
- Organic mulch adjacent to combustible siding
- Wood fencing connected to a home
- Wood piles stacked next to homes
- Lightweight wood decking tied to a home
- Ornamental landscaping
- Combustible furnishings
- General exterior home maintenance

Home "hardening" is required throughout Los Angeles County if a certain percentage of a home is remodeled or during new construction due to revised building/fire codes. While these enhancements are worthy, the largest inventory of ember-susceptible structures is the existing inventory of structures already built. This is where the public can practice home hardening principles taught in Ready! Set! Go!, Firewise USA, or equivalent programs. Even having taken

[1] Insurance Institute for Business and Home Safety, San Diego County Witch Creek fire report, 2007.

these precautions, a homeowner still must maintain their home against ember intrusion throughout the year.

A.2.4 Unique Mitigation Efforts

69Bravo Helicopter Support / Water Site (Helistop)[2]

Helispot 69Bravo has become a unique asset to the firefighting ability of the LA County Fire and the mountain communities of Santa Monica, Topanga Canyon, and Malibu. It was privately developed, leased, and then purchased by LA County Fire. It provides refilling tanks for firefighting helicopters. Such sites significantly lower response refilling cycle times in the nearby mountains and canyons.

The site sits high atop the Santa Monica Mountain range, with two mountaintops covering 34 acres 2,400 feet above the Topanga and Malibu mountains. The Helistop provides emergency service resources 24 hours per day, seven days per week, 365 days per year, including:

- Two helipads with a landing/approach windsock and lighting
- A water well and eight fire hydrants along the property perimeter
- Two separate 6,000-gallon tanks for helicopter water extract
- 10,000-gallon water tank that maintains the water supply
- Line of sight to almost all of Los Angeles County, which allows for radio communications by emergency vehicles to central offices during a crisis

Figure 6—Helicopter Water Drop



[2] The following information comes directly from the 69Bravo website: http://www.69bravo.com/about.

Pepperdine University Shelter-in-Place Design and First-Aid Firefighting Abilities

Pepperdine University (Pepperdine) is on the edge of the Santa Monica Mountain range overlooking the Pacific Ocean. With a total enrollment of approximately 7,700 students, Pepperdine leaders tried to protect the campus and students from wildfires following the aggressive 1985 fire season. Wildfires are not the only risks Pepperdine takes seriously; the campus maintains a current and well-used 43-chapter Emergency Operations Plan that provides guidance for all known hazards.

Pepperdine designed and constructed three dual-purpose buildings that serve their primary function related to normal daily operations and the function of fire-safe shelters. Pepperdine utilizes a state-of-the-art communications system to communicate emergency information to students and parents, including information related to shelter operations. Pepperdine designed and maintains a fire resistive landscape to minimize fire propagation from the wildland interface to the campus core. This landscape design serves also as a fuel break for adjacent properties. The campus maintains a cache of potable water and emergency food rations to support prolonged shelter operations. Pepperdine maintains contracts with vendors to provide supplemental food supplies when necessary and logistically possible. Pepperdine can shelter-in-place all students. At the start of each new educational year, the president of Pepperdine communicates the university's emergency preparedness to all parents/guardians of students.

Healthy, familiar, professional relationships exist between Pepperdine leadership and regional LA County Fire personnel, and Pepperdine enjoys a long history of working closely with LA County Fire during pre-emergency and emergency operations. Fire personnel are commonly invited to review and provide guidance on campus fuel reduction efforts. When fires occur in the region, Pepperdine is typically the site of the Incident Command Post (ICP). This is due to many reasons, including the fire-protective nature of the campus, the campus features, and resources available to emergency responders, and the relationship the agencies enjoy. Some of the unique firefighting features and resources on campus include a helispot on the campus's front lawn for firefighting helicopter operations, space for ICP functions, and water reservoirs maintained for fire operations.

Pepperdine trains its security staff to function as a Fire Patrol group when fires occur. Security officers equipped and acting as Fire Patrol teams circle the campus in search of spot fires. When small fires are discovered, Fire Patrol teams can extinguish them before they grow out of control.

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APPENDIX B—BACKGROUND ON PRIMARY COUNTY AGENCIES

B.1 LOS ANGELES COUNTY FIRE DEPARTMENT



The mission of the Los Angeles County Fire Department (LA County Fire) is "to protect lives, the environment, and property by providing prompt, skillful, and cost-effective fire protection and life safety services." LA County Fire provides all-hazard emergency response services to approximately 4.1 million residents and businesses throughout 58 cities and the unincorporated areas of Los Angeles County. Responding to approximately 400,000 calls for service per year, the agency is one of the busiest in the nation. Under the leadership of Fire Chief Daryl L. Osby, the agency provides service to over 2,300 square miles of diverse geography and demographics and approximately 1.23 million housing units. With a 2017/2018 budget of $1.2 billion, LA County Fire employs approximately 4,700 employees.

B.1.1 LA County Fire Organization

Three major functional areas report to the Fire Chief: Emergency Operations, Business Operations, and the Leadership and Professional Standards Bureau. Led by a Chief Deputy, Emergency Operations is the arm of the Department responsible for leading and directing emergency response personnel. Regarding emergency response personnel, Emergency Operations is further divided into three geographic Bureaus: North Operations Bureau, Central Operations Bureau, and East Operations Bureau.

The Office of Emergency Management and the Emergency Medical Services Bureau are also under the direction of the Chief Deputy of Emergency Operations, as are Homeland Security and the Medical Director.

The three geographically divided operations bureaus of LA County Fire serve 58 cities and unincorporated communities with 22 battalions and nine divisions. An Assistant Chief commands each division, and three shift Battalion Chiefs command each battalion. A Community Services Liaison (CSL) and a Secretary support each of the nine Assistant Fire Chiefs. The CSL partners with the Assistant Fire Chief to develop and maintain strong working relationships with communities and the cities within the Division. The CSL represents the Department at community and civic events. The jurisdictional Assistant Fire Chief and CSL also facilitate emergency and non-emergency communications between the local board office, cities, and communities as needed.

The primary body of the Woolsey Fire occurred in LA County Fire Battalion 5, which includes 12 fire stations serving the incorporated cities of Agoura Hills, Calabasas, Hidden Hills, Malibu, and Westlake Village, as well as the surrounding unincorporated areas. Organizationally, Battalion 5 is one of 22 Battalions throughout LA County Fire and is part of Division 7. The Division 7 Assistant Fire Chief reports to the Central Region Deputy Fire Chief, who ultimately reports to the Chief Deputy of Emergency Operations under the Fire Chief.

B.1.2 LA County Fire Emergency Response Resources

At the time of the Woolsey Fire, LA County Fire maintained the following Countywide emergency response resources:

- 174 fire stations
- 179 engine companies
- 67 Paramedic squads
- 32 quints (ladder trucks that have water tanks)
- Specialized resources
  - Four Sikorsky S-70 Firehawk helicopters
  - Five Bell 412 helicopters
  - One seasonally staffed, contracted Erickson helitanker
  - Two seasonally staffed, contracted Bombardier CL-415 Super Scooper fixed-wing aircraft
  - 10 bulldozers
  - 10 fire camps with 26 crews
  - Five California Office of Emergency Services (Cal OES) Type 3 (wildland fire) engines
  - Four hazardous materials squads

- Five swift water rescue units
- Two urban search and rescue squads
- Two fire boats
- Lifeguard Division, Forestry Division, Prevention Division, Health Hazardous Materials Division (Certified Unified Program Agency)

LA County Fire is also the home of California Task Force 2 (also known as USA Task Force 2), an urban search and rescue team qualified to respond to local, national, and international disasters.

B.1.3 LA County Fire Communications

The P. Michael Freeman Command and Control Center (Command and Control) is the epicenter of communications for LA County Fire. This facility opened in 1990 as a state-of-the-art communications center. LA County Fire is one of the busiest fire departments in the nation, and in 2017 Command and Control dispatched over 394,000 emergency responses. Daily staffing includes 17 Dispatchers, three Dispatch Supervisors, one Fire Captain, and one Battalion Chief.

Command and Control also serves as the Cal OES Fire and Rescue Division Region 1 Mutual Aid Coordinator for the counties of Los Angeles, Orange, San Luis Obispo, Santa Barbara, and Ventura. Command and Control also serves as the Los Angeles Area B Operational Coordinator for Region 1.

Command and Control utilizes ultra-high (UHF) and very high (VHF) radio frequencies for dispatch and radio communications with field units. Interoperability for wildland responses is managed through predesignated communication plans that are VHF based.

LA County Fire enhances its communications capabilities with cell phone and satellite phone technology provided to selected chief officers. The Department also maintains an alpha-numeric paging system for regional disaster preparedness communications needs.

B.1.4 LA County Fire Wildland Firefighting Training

Wildland firefighting training is a key aspect of County organizational preparedness. LA County Fire firefighters are exposed to wildland firefighting in their recruit academy, and this training is reinforced and enhanced throughout their careers. All LA County Fire firefighters train for wildland firefighting operations with added emphasis on high hazard wildland firefighting areas. Training includes progressive hose lay operations, line control, helispot setup, and fire behavior. In addition, station personnel conduct defensible space inspections within their jurisdictional areas, providing enhanced insight and preplanning preparedness.

Besides overseeing the preparedness training of line personnel, all chief officers receive annual chief-officer- and wildland-specific training focused on key command and control issues.

The Department's Incident Management Team (IMT) program was developed after the 1993 Old Topanga Fire and has been a successful component of the Department's integrated response strategy to large-scale emergencies that take place within Los Angeles County. There are three Type 3 IMTs that carry command and general staff positions for day and night operations.

B.1.5 LA County Fire Situational Awareness Monitoring

LA County Fire maintains its situational awareness to weather, local emergencies, and regional emergencies on many fronts. Fire weather is monitored daily with the National Weather Service in Oxnard and through the Department's many weather stations and the Remote Automated Weather Stations throughout southern California. Based on the weather data and observed conditions, policies and procedures are in place for augmented and pre-positioned staffing.

To ensure Department-wide situational awareness during the fire season, a daily operations conference call is conducted with all on-duty chief officers and the on-call IMT. The conference call provides a fire weather overview, fire behavior synoptic forecast, and situational overview of wildland fire resources from air operations, camps, heavy equipment, and reserve unit availability.

The Command and Control center is responsible for monitoring local and regional incidents that may affect the Department, operational area, or Region 1. Communications with adjoining regions or the State's Southern Region Operations Center may take place if an incident is escalating and resources are ordered.

B.1.6 LA County Fire Regional Agreements

The Woolsey Fire broke out in the Santa Susana area of Ventura County. Due to this region's proximity to jurisdictions served by LA County Fire, the City of Los Angeles Fire Department (LA City Fire), and the Ventura County Fire Department (Ventura County Fire), the area is defined as a mutual threat zone (MTZ), and the three fire departments developed a regional agreement to address this area as a shared risk. Not only do these agencies commit to responding to fires in the region as a matter of mutual risk, the fire departments train together to ensure operational coordination and effectiveness. Prior to the Woolsey Fire, training specific to the Santa Susana MTZ took place in June 2018.

The MTZ agreement agencies further agree to ensure that only one Incident Command Post (ICP) is established and that Unified Command is positively created at the earliest moment possible. The Unified Command structure recommends whether an IMT is needed.

LA County Fire serves as the Area B Coordinator and Region 1 Coordinator for the California Master Mutual Aid System on behalf of Cal OES. The Mutual Aid Plan facilitates implementation of Chapter 7 of Division 1 of Title 2 of the Government Code entitled "California Emergency Services Act." Among the many duties of area and regional coordination include the following responsibilities:

- Evaluates requests for assistance from Area; determines the region resources from that region which can provide the timeliest assistance and initiates response thereof
- Determines if the timeliest assistance is from an adjacent region and, if so, requests assistance from that Region Fire and Rescue Coordinator (not to exceed five like resources) and must notify the State Fire and Rescue Coordinator of this action
- When resources are needed from more than one adjacent region, either for timely response or when the need is beyond region capability, the request must be made to the State
- Monitors and coordinates backup coverage within an area or region when there is a shortage of resources

B.2 LOS ANGELES COUNTY SHERIFF'S DEPARTMENT



The Los Angeles County Sheriff's Department (County Sheriff's Department) is the largest sheriff's department in the world. The County Sheriff's Department's mission is to enforce the law fairly and within constitutional authority; to be proactive in its approach to crime prevention; to enhance public trust through accountability; to maintain a constitutionally sound and rehabilitative approach to incarceration; to provide a safe and secure court system; to maintain peace and order; and to work in partnership with the communities it serves to ensure the highest possible quality of life. The County Sheriff's Department conducts this mission throughout Los Angeles County, including 44 cities that contract with the Sheriff's Department for law enforcement services.[3]

[3] Source: http://lasd.org/about_us_mission_creed_core.html

B.2.1 County Sheriff's Department Organization

The County Sheriff's Department employs approximately 18,000 employees, including 10,000 sworn and 8,000 non-sworn personnel. Under the leadership of Sheriff Alex Villanueva, sworn into office on December 3, 2018, the Sheriff's Department is organized into three primary operational areas: Custody Operations, Patrol Operations, and Countywide Operations. The Department has, approximately, a $3.2 billion budget.

B.2.2 County Sheriff's Department Emergency Response Resources

Within Patrol Operations, the County Sheriff's Department provides service from 23 patrol stations throughout the County. The Malibu / Lost Hills Sheriff's Station is at 27050 Agoura Road in the City of Agoura. This station serves the cities of Agoura Hills, Calabasas, Hidden Hills, Malibu, and Westlake Village, as well as the communities of Chatsworth Lake Manor, Malibou Lake, Topanga, and West Hills. The Malibu / Lost Hills Sheriff's Station is inside the footprint of the Woolsey Fire.

B.2.3 County Sheriff's Department Communications

Communications are decentralized in the County Sheriff's Department. Each Sheriff's station receives calls for service via separate business and 9-1-1 lines. Calls for service are then dispatched over the radio from a central dispatch center in Los Angeles at the Los Angeles County Sheriff's Communication Center. The communications system allows Deputies from different Sheriff's stations to communicate via radio. The system also can be patched, allowing interoperability whereby the County Sheriff's Department Deputies can communicate with other law enforcement personnel operating on different radio frequencies. The County Sheriff's Department issues cell phones to Department executives and specialized units. Specialized units are also supplied with satellite phones.

B.2.4 County Sheriff's Department Disaster Response Training

The County Sheriff's Department invested significantly in the organization's enhanced disaster response capabilities. The County Sheriff's Department maintains three Type 3 IMTs, three Los Angeles County Emergency Operations Center (County EOC) Teams, and three Department Operations Center (DOC) Teams. All team members must take National Incident Management System (NIMS) courses IS 100 "Introduction to the Incident Command System," IS 200 "ICS for Single Resources and Initial Action Incidents," ICS 300 "Intermediate ICS for Expanding Incidents," and ICS 400 "Advanced ICS for Command and General Staff."

B.2.5 County Sheriff's Department Situational Awareness Monitoring

The County Sheriff's Department Sheriff's Information Bureau (SIB) Operations Center is staffed around the clock. The SIB monitors operations within the Department and the Los Angeles County

Operational Area. SIB shares information with key stakeholder agencies that elect to receive SIB information and notifications.

B.2.6 County Sheriff's Department Regional Agreements

By law, the County Sheriff's Department is the mutual aid coordinator for law enforcement in Los Angeles County. To manage operations and resources more efficiently, the 88 cities of Los Angeles County are divided into eight geographical areas: A through H. To ensure continuity of operations, the County Sheriff's Department and mutual aid partners update mutual aid agreements annually.

B.2.7 County Sheriff's Department Emergency Operations Bureau

The County Sheriff's Department, under County Code 2.68, has the responsibility to activate and manage, in an emergency, the County EOC, including public notification tools such as Alert LA, the Emergency Broadcast System, and, lately, cell phone push notifications. The County Sheriff's Department Emergency Operations Bureau (EOB) also maintains Sheriff IMTs to respond to area emergencies and support an incident and/or regional sheriff's mutual aid requests. The IMT members are trained to a minimum ICS 400 series course level.

The EOB recognizes that it had become so technology dependent that losing some of its field unit communication technology during the Woolsey Fire created many obstacles.

B.3 Los Angeles County Office of Emergency Management



The Los Angeles County Office of Emergency Management (County Emergency Management) is responsible for comprehensively planning for, responding to, and recovering from large-scale

emergencies and disasters that impact Los Angeles County. County Emergency Management accomplishes this mission through partnerships and collaboration with first response agencies, other necessary County agencies, and non-profit, private sector, and government partners.

County Emergency Management provides disaster plan coordination and functional exercises with the 88 cities, 137 unincorporated communities, and 288 special districts in Los Angeles County. County Emergency Management also assists other County agencies in developing department emergency operation plans and County facility emergency plans. The Board of Supervisors and Emergency Management Council receive support and advice from County Emergency Management, with guidance provided to the Board of Supervisors in matters pertaining to their roles as elected officials during emergencies and disasters.

County Emergency Management maintains the approved Operational Area Emergency Response Plan, and the County EOC state of readiness is maintained by County Emergency Management in partnership with the EOB. County Emergency Management staff serve as the on-call first responders to the County EOC, with service available every minute of every day.

County Emergency Management maintains a cadre of County EOC team members trained in section and position responsibilities and in the use of the Operational Area Response and Recovery System. In addition, County Emergency Management provides ongoing training for County department Emergency Coordinators and building Emergency Coordinators.

County Emergency Management conducts public education campaigns for all hazards through the Emergency Survival Program, expos, and various media presentations in public venues. County Emergency Management maintains a multi-language emergency preparedness website at www.lacounty.gov/emergency.

The County EOC facility is perceived by the employees working there as antiquated and not built for effective collaboration. Relatively recent improvements in computer data bandwidth and communications connectivity have helped; however, not all in-house computer systems are integrated. The working quarters are cramped and not designed for the number of people that occupy them. The interior structure is not conducive to general collaboration during normal business or emergencies.

There is no regular, annual budget for scheduled replacement of equipment for the EOB or the County EOC. Equipment is largely acquired through one-time County funding. At times, grants are used but come with no emphasis on continuation of effort.

B.3.1 County Emergency Management Organization

County Emergency Management is housed in the County EOC Building in East Los Angeles, which also maintains the County EOC for coordination throughout the County Operational Area. Under the leadership of the Director and Deputy Director, County Emergency Management is staffed with 30 personnel organized into one administrative and three functional divisions:

- Administration includes the Director, Deputy Director, three administrative support positions, and a special projects position (six personnel)
- Preparedness Division includes public education, planning, and public information (nine personnel; three vacant)
- Response Division includes operations, training/exercises, operational integration, and homeless initiative (seven personnel; one vacant)
- Recovery Division includes public assistance and individual assistance (five personnel)

B.3.2 County Emergency Management Communications

County Emergency Management's primary communication hardware is triple redundant, consisting of landline, cellular, and satellite telephones, fiber optic internet, and backup satellite internet. For public alerting, County Emergency Management uses the County's numerous web pages, Twitter, and GovDelivery. County Emergency Management also administers the County's Alert LA mass notification system, with the County Sheriff's Department historically responsible for the content and timing of public alerts and warnings.

B.3.3 County Emergency Management Training

County Emergency Management provides emergency management training for County personnel. County Emergency Management is also responsible for coordinating and facilitating disaster/emergency management training and exercises for Los Angeles County Operational Area local jurisdictions under an annual training and exercise plan. County Emergency Management is further charged with developing Countywide emergency management capacity and developing a robust recovery training program.

B.3.4 County Emergency Management Situational Awareness Monitoring

County Emergency Management, as the Operational Area Coordinator, maintains a 24-hour, year-round point of contact as required by the California Standardized Emergency Management System (SEMS) guidelines and is responsible for reacting promptly to events in the County.

B.3.5 County Emergency Management Recovery Program Coordination

The County's 2017 Operational Area Recovery Plan identifies County Emergency Management's recovery role as follows:

> *The county's emergency management director oversees the day-to-day emergency management programs and activities. The emergency management director works with chief elected and appointed officials to establish unified objectives regarding the jurisdiction's emergency plans and activities. This role entails coordinating and integrating all elements of the community. This includes assessing the capacity and*

readiness to deliver the capabilities most likely required during and after an incident and identifying and correcting any shortfalls. The local emergency manager's duties often include:

- *Advising elected and appointed officials during a response or recovery*
- *Conducting response operations in accordance with NIMS*
- *Coordinating the functions of local agencies*
- *Coordinating the development of plans and working cooperatively with other local agencies, community organizations, private sector entities, and non-governmental organizations (NGO)*
- *Developing and maintaining mutual aid and assistance agreements*
- *Coordinating resource requests during an incident through the management of an emergency operations center*
- *Coordinating damage assessments during an incident*
- *Advising and informing local officials and the public about emergency management activities during an incident*
- *Developing and executing accessible public awareness and education programs*
- *Conducting exercises to test plans and systems and obtain lessons learned*
- *Coordinating integration of the rights of individuals with disabilities, individuals from racially and ethnically diverse backgrounds, and others with access and functional needs into emergency planning and response*

B.3.6 County Emergency Management Disaster Assistance Coordination

County Emergency Management is the lead agency for Local Assistance Center planning. Once the Recovery Coordinating Center (RCC) is established, establishing the Local Assistance Centers is the responsibility of the RCC Logistics and Operations sections; however, once established, County Emergency Management has the lead for managing them under the Local Assistance Center Plan functional annex. At the request of the Federal Emergency Management Agency (FEMA), the Local Assistance Centers for the Woolsey Fire were titled Disaster Assistance Centers (DACs).

The RCC Director is the County Chief Executive Officer (CEO), and the Deputy County Emergency Management Director is the RCC Deputy Director. Each RCC Section (Planning, Operations, Logistics, and Finance/Admin.) is led by a County department lead.

Disaster Recovery Centers

Disaster Recovery Centers (DRC) are Cal-OES led; however, a Local Assistance Center / DAC can also transition to a DRC, with Cal OES responsible for management. Sometimes, a DRC can be established without a Local Assistance Center / DAC being established.

Damage Assessment Process

Before an incident is fully concluded, the damage assessment process must set the stage for additional State and Federal assistance and operational priorities. This process starts with forming local Disaster Assistance Teams comprising mixed disciplines of Damage Inspection Specialists. Early on, this process may comprise a quick "windshield survey" to estimate initial damage data, to later be reinforced with more qualified staff. A final Damage Inspection Report is used to document damages.

Unincorporated Private Property Debris Removal

Mass debris management in the Operational Area is led by Los Angeles County Public Works (County Public Works) under the Unincorporated Area Mass Debris Management Plan.

B.3.7 Mass Care Shelters

The independent cities have primary responsibility for shelter needs within their communities, the County has the primary responsibility for the unincorporated communities, and the County provides for needs that exceed the cities' capabilities via request. Both the cities and the County have designated the American Red Cross (Red Cross) as the primary shelter provider.

The Red Cross is the designated mass care service provider in Los Angeles County under the Los Angeles County Department of Public Social Services (DPSS) plan. The Red Cross has a designated seat next to the DPSS to staff the Mass Care and Shelter Branch within the County EOC Operations Section. The Red Cross is a non-profit entity, depends upon donations, receives no government funding, and is the designated shelter service provider during government-managed incidents throughout the United States.

B.4 Los Angeles County Public Works



County Public Works is the largest municipal public works agency in the nation and serves over 10 million people in Los Angeles County over 4,000 square miles. Its mission is to deliver regional infrastructure and services to improve the quality of life for County residents. Under the leadership of the Director, six core service areas provide the diverse operations of Transportation, Water Resources, Environmental Services, Public Buildings, Development Services, and Emergency Management. The organization's annual budget is approximately $2.29 billion.

County Public Works' workforce comprises nearly 4,100 employees in over 500 job classifications, including professional, technical, clerical, and skilled crafts. Through these employees, County Public Works exercises its responsibility for the design, construction, operation, and maintenance of roads, traffic signals, bridges, airports, and sewers, as well as flood control, water supply, water quality, and water conservation facilities. As such, County Public Works had vast responsibility for roads, traffic operations, and waterworks in the Woolsey Fire area.

B.4.1 County Public Works Integrated Emergency Response Manual

Updated in 2018, the Department of Public Works Integrated Emergency Response Manual is the authoritative guide for the Department's internal disaster preparedness and emergency response policies and actions. Internally, this manual is also referred to as the Red Book. This 271-page manual is broken down into eight sections: I.) DOC / Emergency Response Activities; II.) DOC Reference Materials; III.) Communications; IV.) Public Information; V.) Vital Records; VI.) Disaster Claiming; VII.) Disaster Information Reporting Procedures; and VIII.) Policies.

The purpose of the Integrated Emergency Response Manual is "to incorporate and coordinate all the facilities and personnel of the Department into an organization capable of responding to any emergency using NIMS / SEMS, mutual aid and other appropriate response procedures" (p. viii). This manual "establishes the Department's emergency organization, assigns tasks, specifies policies and general procedures, and provides for coordination of planning efforts among the various divisions" (p. viii). Copies of the manual are distributed to each agency division and field office and to key personnel as determined by County Public Works.

As established by the Integrated Emergency Response Manual, each County Public Works division is charged with preparing and maintaining current plans to support their emergency response capabilities, and "all employees should know their role so they can carry out their duties effectively" (p. viii). The espoused culture of County Public Works is organizational planning and preparedness and team/individual knowledge and competence.

B.4.2 County Public Works Department Operations Center

At its Alhambra headquarters location, County Public Works maintains a 24-hour dispatch center and an on-call DOC. County Public Works regularly activates its DOC to support emergency incidents and planned events that have the potential for increased significance and community impact. During the research phase of this report, Citygate Associates witnessed the smooth and efficient opening of the DOC to support a large County Public Works project. The assigned DOC Director summarized the project to the DOC staff and provided a statement of the objectives of the DOC to support the event.

The opening of the DOC is scaled according to incident or event. Smaller events may cause a smaller DOC staff size whereas larger events or incidents can cause a full activation of the DOC. When fully activated, this dedicated workspace can accommodate approximately 50 DOC workers with functional workspaces and assigned seating.

When activated, the DOC is led by one of six County Public Works Deputy Directors. There is also a backup DOC at the Central Yard.

B.4.3 County Public Works Integration with the County Emergency Operations Center

The County EOC coordinates the overall emergency operations in the County for all 88 cities and unincorporated areas. County code identifies the County Sheriff's Department as the Director of Emergency Operations. County Public Works provides staff to the County EOC when deemed necessary by the County Sheriff's Department, CEO, and/or County Emergency Management. County Public Works staffs the Operations Section Construction & Engineering at the County EOC. The Department has designated three teams of four personnel (Senior Civil Engineer or higher) that rotate responsibility for this function monthly.

B.4.4 County Public Works Emergency Response Training

Like all County employees, County Public Works employees must complete Disaster Service Worker training. For employees with an expanded role during a disaster, County Public Works has a multi-tiered training program. DOC personnel must complete an in-house SEMS Emergency Operations Center (EOC) course and online courses NIMS IS 100 "Introduction to the Incident Command System," IS 200 "ICS for Single Resources and Initial Action Incidents," and IS 700 "Introduction to the National Incident Management System." DOC Directors and DOC Section Chiefs must also take IS 800 "National Response Framework," and these Department leaders attend the Situational Awareness / Common Operating Picture course.

When populating the disaster organization chart structure, County Public Works selects DOC Directors from the existing Deputy Director personnel, of which there are six. DOC Section Chiefs are selected from the pool of division heads, particularly those with a strong, broad understanding of Department operations.

Field personnel, including managers, must complete courses IS 100, IS 200, and IS 700. Additional coursework is offered, including the ICS 300 course and the O305 "All Hazard Incident Management Team" course. County Public Works employees selected to function as Agency Representatives must take all the required courses, plus additional in-house Agency Representative coursework. Agency Representatives are chosen by their ability to represent all aspects of County Public Works' mission.

County Public Works employees selected to function as Unified Commanders come from the ranks of County Public Works Principal Engineer and higher. These highly trained employees must complete all the requisite NIMS training and are selected based on their broad knowledge of County Public Works and ability to make decisions commensurate with their role.

B.4.5 County Public Works Communications Infrastructure

County Public Works field personnel utilize the Countywide Interoperable Radio System. The system operates on ultra-high frequencies and a secondary back-up radio system exists for system redundancy. County Public Works operates a 24-hour dispatch center that serves as a communications hub with field forces and with the public. The dispatch center is highly resourceful and integral to response.

B.4.6 County Public Works Facilities, Equipment, and Supply

The County Public Works fleet comprises approximately 3,360 pieces of equipment. The diversity of equipment is incredible, including on-road light-, medium-, and heavy-duty vehicles, which include electric/plug-in hybrid automobiles, pick-up trucks, vans, utility body trucks, large dump trucks, street sweepers, and vacuum jet trucks. There is also off-road and specialized equipment, such as backhoes, wheel loaders, and motor graders. County Public Works also maintains a robust inventory of portable equipment, such as pavement saws, stump grinders, and arrow boards.

County Public Works deployed a water truck to assist with watering animals during the Woolsey incident in cooperation with County Animal Care.

County Public Works maintains contracts for as-needed equipment and vehicle rentals. During normal operations and emergencies, County Public Works regularly executes these contracts to supplement its fleet of equipment.

County Public Works maintains a warehouse network that comprises a main warehouse and outlying satellite warehouses located strategically throughout the County. The warehouses stock a wide variety of materials ranging from road materials, traffic poles, pipes, stationary materials, street posts, signs, guardrails, safety items, seasonal items, emergency items, and thousands of other items. To support the Woolsey Fire, this warehouse system provided several critical items to the divisions deployed directly in the fire areas, including large quantities of traffic signs, barricades of numerous sizes, caution tape, emergency signs, traffic cones, glass beads, and traffic paint for road repairs. Other essential items provided were traffic signals, delineators, barricades, sheet metal, and personal protective equipment, such as safety vests, respirators, and safety glasses.

County Public Works operating divisions control the items the warehouse carries as standard stock. County Public Works also maintains numerous vendor procurement agreements capable of supplying provisions for emergency ordering of a wide variety of commodities. Given the size and duration of the Woolsey Fire, these vendor contracts quickly replenished necessary supplies.

B.4.7 County Public Works Situational Awareness Monitoring

County Public Works monitors and disseminates situational awareness information from the National Weather Service and County Emergency Management, as well as from numerous additional sources, including local news media, U.S. Geological Survey, city feeds, County department feeds, etc.

B.5 Los Angeles County Department of Animal Care and Control



Los Angeles County Department of Animal Care and Control (County Animal Care) is one of the largest and most progressive animal care and control agencies in the United States. County Animal Care's animal care centers serve unincorporated Los Angeles County and 43 contract cities, with a combined total population of over three million residents. The County Animal Care officers patrol over 3,400 square miles of cities, deserts, beaches, and mountains. County Animal Care has 442 employees and an annual budget of $52 million.

B.5.1 County Animal Care Organization

County Animal Care operates seven animal care centers in the cities of Agoura Hills, Baldwin Park, Carson/Gardena, Castaic, Downey, Lancaster, and Palmdale. These animal care centers provide safe, humane care for animals lost or no longer wanted by their owners. The animal care center staff and volunteers work tirelessly to reunite lost pets with their owners or to find new homes for homeless pets.

The Department employs sworn Animal Control Officers who serve as a key component of the community's public and animal safety program. County Animal Care's Animal Control Officers enforce State and local animal laws, respond to requests for service, and patrol neighborhoods seven days a week, 24 hours a day.

B.5.2 County Animal Care Emergency Response Resources

County Animal Care has one person assigned to emergency response. If an emergency occurs, support staff are provided by the seven animal care centers. The scope and size of the emergency dictates how many support staff will be dedicated for an event. During the Woolsey Fire response,

almost one-third of the County Animal Care workforce was deployed to respond to the emergency while simultaneously ensuring normal operations at seven animal care centers:

- Director
- Three Deputy Directors
- Six Animal Control Managers
- Three Lieutenants
- 13 Sergeants
- 29 Corporals
- 31 Animal Control Officers
- 23 Animal Care Attendants
- Three Veterinarians
- Three Registered Veterinary Technicians
- Three Intermediate Typist Clerks

Volunteers and mutual aid partners from six agencies were activated to support County Animal Care efforts.

County Animal Care has seven four-horse trailers, two command-post trailers with two Ford F-350 trucks to pull them, and four AnimalSafe (mobile shelter) trailers. All were deployed during the event.

B.5.3 County Animal Care Communications

The Department has the following methods of communicating during emergencies:

- Countywide Interoperable Radio System radios
- Cell phones
- Email
- Phone trees
- One ham radio (based at the Agoura animal care center)
- Tough books

B.5.4 County Animal Care Disaster Response Training

The Department requires all staff acting in the role of emergency responders to undertake Incident Command System (ICS) training from FEMA. County Animal Care emergency responders receive County Disaster Service Worker training, as well as on-the-job training for various departmental functions during an emergency. County Animal Care staff and key volunteers receive large animal

handling training to respond to livestock sheltering sites. Staff who pull trailers receive departmental training for this activity. All responding staff receive small animal handling training.

B.6 CALIFORNIA HIGHWAY PATROL



Statewide, the mission of the California Highway Patrol (CHP) is to "provide the highest level of safety, service, and security." Two primary CHP areas serve the area of the Woolsey Fire: The West Valley Area in Woodland Hills and the Moorpark Area located in Moorpark.

The primary functions of the CHP in the region affected by the Woolsey Fire include traffic enforcement on all freeway systems and traffic enforcement and traffic investigations on all roadways of unincorporated land. During disasters such as the Woolsey Fire, the CHP engages with their law enforcement partners, maintains a decision-making presence at the ICP, and provides traffic control operations, including road closures. While evacuation is not a primary function of the CHP, when necessary, CHP assists the local sheriff's Deputies with evacuation notification.

B.6.1 CHP Regional Organization

There are eight regional CHP divisions in the State of California. Each division comprises 12 to 20 CHP areas. The offices in these areas are the central point of CHP Officer assignment and deployment.

Officers assigned to the Moorpark area patrol approximately 650 linear miles of freeways, state routes, and unincorporated county roads, including US-101 from the Los Angeles County line to Camarillo Springs Road, State Route 23 from US-101, and State Route 118 from the Los Angeles County line to State Route 34. The Moorpark area also covers many unincorporated areas of

Ventura County, such as Oak Park, Newbury Park, Lynn Ranch, Somis, and Piru. The Moorpark area is led by a CHP Lieutenant.

Officers assigned to the Ventura area patrol the Pacific Coast Highway (Mugu Rock) to Camarillo and north to Santa Barbara.

Officers assigned to the West Valley area patrol an area of approximately 400 square miles. The bulk of the 400 square miles is within the San Fernando Valley, which is approximately 260 square miles. Within the boundaries of the West Valley response area, there are approximately 2.1 million residents, including residents of the City of Los Angeles, Hidden Hills, Calabasas, Agoura Hills, Westlake Village, Malibu, Lake Manor, Twin Lakes, and Topanga Canyon. The West Valley area is led by a CHP Captain.

B.6.2 CHP Regional Emergency Response Resources

The Moorpark area has an approved staff of 40 Officers, four Sergeants, and one Lieutenant. The Ventura area has an approved staff of 35 Officers and six Sergeants. The West Valley area has an approved staff of approximately 100 Officers, 10 Sergeants, two Lieutenants, and one Captain. During normal operations, the West Valley area has approximately 12 to 14 Officers on duty.

B.6.3 CHP Regional Communications

Statewide, the CHP divides communication systems by region. Two regional communications centers cover the footprint of the Woolsey Fire: the Los Angeles Communications Center and Ventura Communications Center. CHP Officers can easily communicate with CHP Officers based in other communications center regions. CHP mobile and handheld radios are programmable and allow for interoperability with local law enforcement agencies. A more common practice for interagency communications is to use the communications dispatchers as relays to other allied agencies.

B.6.4 CHP Regional Disaster Response Training

Every CHP Officer is trained in the ICS annually. Advanced ICS training is mandatory for all CHP personnel at the rank of Sergeant and above. CHP hosts regular training for Officers, including tabletop scenarios for emergencies like the Woolsey Fire. When possible, the CHP enjoys partnering with local law enforcement agencies for joint training. The CHP adopted a goal of ensuring that all field commanders discuss significant issues and training options on a quarterly basis to provide enhanced services to its partner agencies.

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EXHIBIT A

SANTA MONICA MOUNTAINS / MALIBU WILDFIRE HISTORY

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EXHIBIT A—SANTA MONICA MOUNTAINS / MALIBU WILDFIRE HISTORY

157 Historical "Malibu" Wildfires (Ventura and Los Angeles Counties)

Year	Fire Name	Location	Acres	Structures Lost	Deaths
1897	Great Drought	Malibu			
1903	Rindge	Malibu Canyon	10,000		
1904	Malibu	Malibu			
1909	Malibu 9/15/09	Malibu			
1909	Malibu 10/25/09	Malibu			
1910	Malibu	Las Flores – Temescal			
1911	Santa Monica	Malibu Mtns.			
1913	Topanga	Topanga – Escondido			
1913	Dry Canyon	Malibu Hills	10,000		
1917	Malibu Canyon	North of Malibu	2,000		
1921	Decker	Malibu	500		
1921	Dume Canyon	Corral Canyon – Malibu	8,000		
1923	Coopers Ranch	Topanga Canyon – Las Flores Canyon	50		
1924	Mulholland	Santa Monica Mtns.	300		
1925	Latigo Canyon	Malibu	4,670		
1925	Topanga P.O.	Trippet Ranch	150		
1926	Montgomery	Malibu	175		
1926	Old Topanga #2	Topanga	200		
1927	Malibu Junction	Calabasas	420		
1927	Cooper	Calabasas	3,118		
1928	Las Flores	Malibu	400		
1929	Malibu Colony	Las Flores Canyon	274	13	
1929	Encino Reservoir	Mulholland Highway	800		
1930	Tuna Summit	Topanga	157		
1930	Potrero	Decker Canyon	15,000		
1930	Picture City (Paramount Rh.)	Calabasas	400		
1935	Malibu / Latigo / Sherwood	Kanan/Decker Canyon	28,599		
1935	Pt. Dume	Malibu	150		
1936	Medea	Malibu	119		
1936	Cold Creed	Malibu	2,591		
1936	Escondido Canyon	Malibu	200		
1938	Bell Ranch	Calabasas	411		
1938	Topanga	Fernwood – PCH	16,500	350	
1940	Sequit	Malibu	182		
1940	Tuna Summit	Malibu	40		
1942	Malibu	Malibu Canyon			

Year	Fire Name	Location	Acres	Structures Lost	Deaths
1942	Las Flores	Malibu	5,924		
1943	Las Flores	Malibu Canyon	5,800		
1943	Woodland Hills/Las Virgenes	Kanan/Decker Canyon	15,300		
1944	McCoy	Calabasas – Las Virgenes	84		
1944	Summit Ridge	Topanga	47		
1946	Dume	Malibu	210		
1947	La Fouge (Triunfo Pass)	Malibu	640		
1948	Topanga	Malibu	3,155		
1949	Reindl	Malibu	215		
1949	Susana	Simi Chatsworth	19,080		
1951	Houston	Malibu	571		
1952	Topanga – Mulholland	Topanga Canyon	82		
1953	Udell	Malibu	560		
1953	Corral	Malibu	159		
1954	Triunfo	Malibu	169		
1955	Houston	Malibu	500		
1955	Ventu	Thousand Oaks	12,638		
1956	Hume	Malibu	1,940		
1956	Sherwood/Newton	Kanan/Decker Canyon	35,537	120	1
1958	Hertz	Topanga Canyon – Mulholland	191		
1958	Warner	Malibu	4,040		
1958	Liberty	Malibu Canyon	17,860	107	
1958	Mulholland	Topanga Canyon	4,982		
1959	Topanga	Two miles North of PCH	450		
1959	Stuart Ranch	Malibu Knolls	60		
1961	Murphy	Malibu	40		
1961	Topanga	Los Angeles City – Mulholland	8,750		
1963	Rocketdyne	Chatsworth	300		
1966	Susana Knolls	Black Canyon – Rocketdyne	1,100		
1966	Summit Drive	Calabasas Highlands	50		
1966	Rocketdyne	Chatsworth	301		
1967	Palmer	Chatsworth	14,248		
1967	Brown Canyon	Chatsworth	118		
1967	Round Meadow	Calabasas	100		
1967	Junction	Topanga Canyon	640		
1967	Latigo	Malibu	2,868		
1968	Stoney Point	Chatsworth	40		
1970	Stagecoach	Chatsworth	45		
1970	Stokes Canyon	Mulholland Drive – Malibu	50		
1970	Hoagland	Stokes Canyon – Malibu	50		
1970	Summit	Topanga Canyon	65		

Year	Fire Name	Location	Acres	Structures Lost	Deaths
1970	Golf Course	Calabasas	200		
1970	Wright	Malibu Canyon	31,000	403	10
1970	Clampitt	Simi	107,103	80	4
1973	Potrero	Thousand Oaks	12.297		3
1973	Tripett	Topanga Canyon	2,770		
1975	Thompson	Chatsworth	800		
1975	Stagecoach	Chatsworth	325		
1975	Potrero	Thousand Oaks			
1976	Landfill	Las Virgenes Canyon	60		
1976	Malibu	Malibu Canyon - South of Tunnel	35		
1976	Los Robles	Thousand Oaks	2,245	1	
1977	Canyon	Topanga Canyon	1,162		
1977	Carlisle	Westlake	1,368		
1978	Box Canyon	Chatsworth	100		
1978	Ramirez	Malibu	100		
1978	Mulholland	Seminole Hot Springs	50		
1978	Trancas	Malibu	200		
1978	Kanan	Agoura – Malibu	25,385	230	2
1979	Liberty Canyon	Agoura	157		
1979	Lost Hills	Agoura	170		
1979	Box Canyon	Chatsworth	945		
1979	Meyer	Chatsworth	40		
1980	Leota	Chatsworth	40		
1980	Hill	Thousand Oaks			
1980	Las Virgenes	Calabasas	2,521		
1981	Lindero	Westlake Village	111		
1981	Lindero Canyon	Westlake Village	47		
1981	Topanga (Skyline)	Topanga Canyon	60		
1981	Oat Mountain	Chatsworth	17,786		
1981	Chatsworth Reservoir	Chatsworth – L.A. City	1,040		
1982	Hall	Simi			
1982	Highlands	Calabasas Highlands	182		
1982	Dayton	Chatsworth – Malibu	42,540	74	
1984	Gun	Calabasas – Las Virgenes Road	125		
1984	Westlake	Las Virgenes Reservoir	228		
1984	Viewridge	Topanga Canyon	404		
1985	Sherwood	Westlake Village	3,823		
1985	Mulholland	Liberty Canyon – Las Virgenes Road	68		
1985	Piuma	Malibu Canyon – Corral Canyon	5,198		
1985	Decker	Malibu	6,526	6	
1985	Rocky Peak (Hummingbird)	Chatsworth	2,420		

Year	Fire Name	Location	Acres	Structures Lost	Deaths
1985	Box Canyon (Pioneer)	Chatsworth	1,238		
1986	Timberlake	Agoura	60		
1986	Browns	Chatsworth	117		
1986	Cornell	Agoura	40		
1986	Woolsey	Woolsey Canyon – Chatsworth	100		
1987	Lindero Canyon	Westlake Village	40		
1987	Agoura	Agoura	166		
1988	Cornell Rd	Agoura	75		
1988	Adobe	Agoura Hills	242		
1988	Agoura High	Agoura	60		
1988	Rolling Ridge Drive	Agoura	55		
1988	Keuhner	Chatsworth	3,818		
1989	Bowers Ranch	Chatsworth	100		
1989	Pacific	Malibu	3,180		
1992	Farralone	Chatsworth	46		
1992	Westlake	Kristen Lee Drive	50		
1993	Cheeseboro	Highway 101 – Agoura	50		
1993	Green Meadow	Thousand Oaks	38,152		
1993	Chatsworth	Box Canyon	2,036		
1993	Chatsworth	Chatsworth	37,571	43	
1993	Old Topanga	Topanga – Malibu	16,516	350	3
1994	Latigo	Latigo Canyon – Malibu	64		
1996	Calabasas	Malibu Canyon to coast	12,377	10	
1997	Rhapsody	Lindero Canyon – Augora	121		
2000	Calabasas	Las Virgenes Canyon – VNC	1,074		
2003	Pacific	Trancas Canyon – Malibu	797		
2005	Topanga	WB 118 Freeway to Calabasas	23,396	6	
2006	Latigo	Corral Canyon – Mesa Peak Mtwy.	37		
2007	Malibu Road	Pacific Coast Highway	20	5	
2007	Corral	Corral Canyon – Malibu	4,901	49	
2007	Canyon	Malibu Canyon North of PCH	3,782	14	
2008	Sesnon	Porter Ranch	14,703	63	1
2013	Old	NB 101 – Lost Hills Road, Calabasas	236		
2013	Springs	Newbury Park	24,000	15	
2016	Mulholland	Santa Monica Mountain	12		1
2016	Old	Mulholland Highway – Calabasas	516		
2017	Stokes	Calabasas	50		
2017	Topanga	Topanga	29		
2018	Woolsey	Santa Susana /Malibu	96,945	1,643	3

EXHIBIT B

FIRE WEATHER

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EXHIBIT B—FIRE WEATHER

The following figures illustrate weather data on November 8, 2019 in Cheeseboro and Malibu Hills.

Figure 1—Fire Weather Wind Gusts

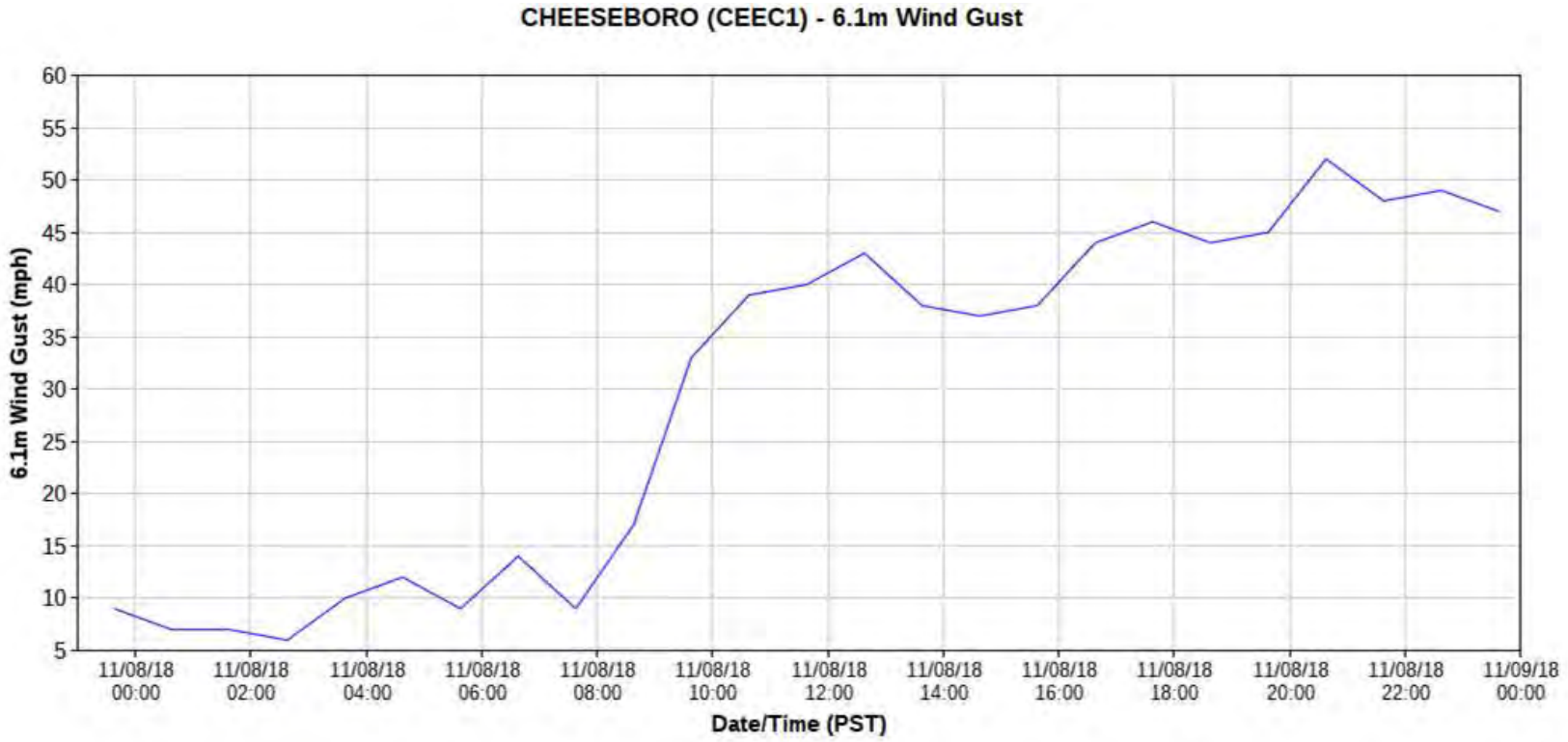

Figure 2—Fire Weather Humidity

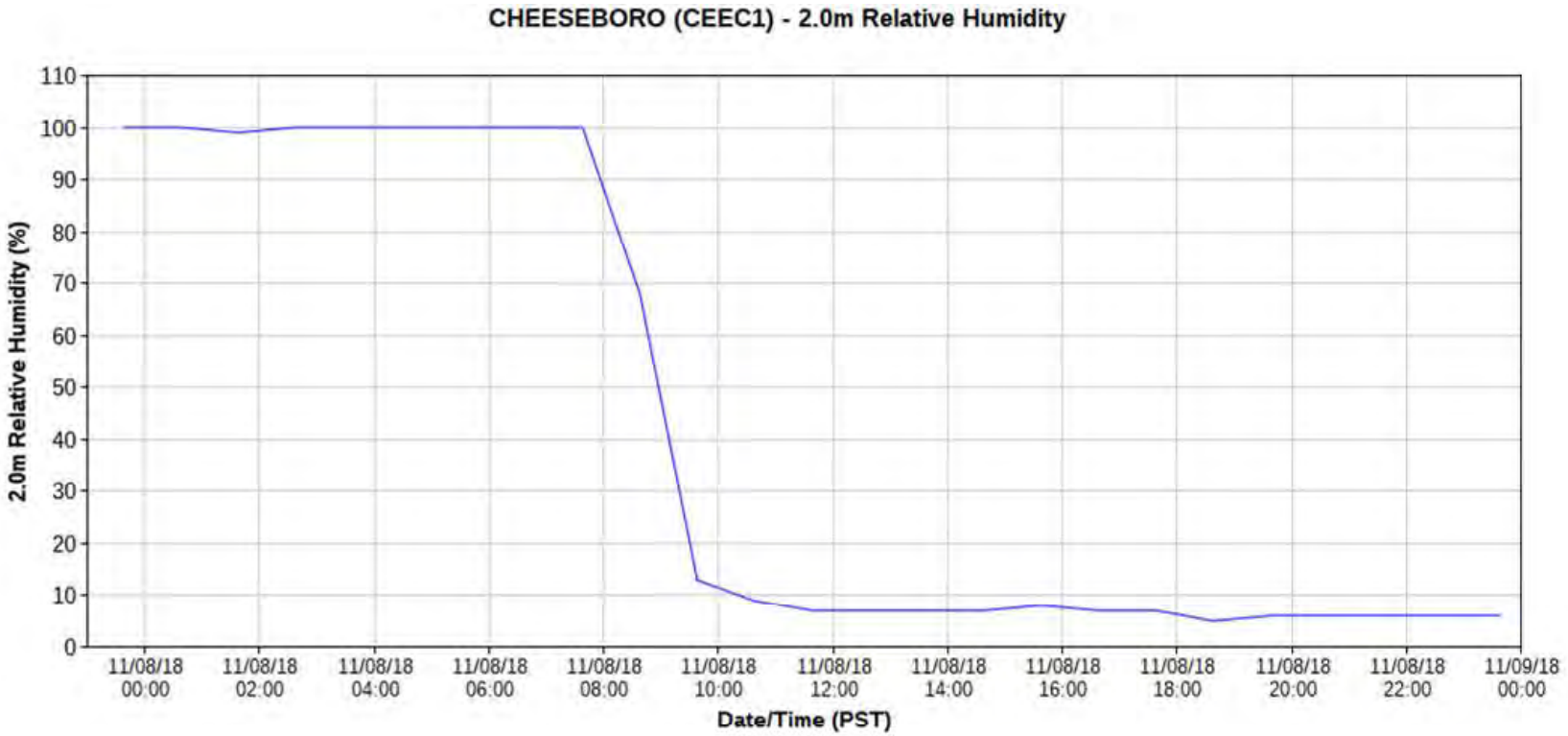

Figure 3—Malibu Hills Wind Gusts

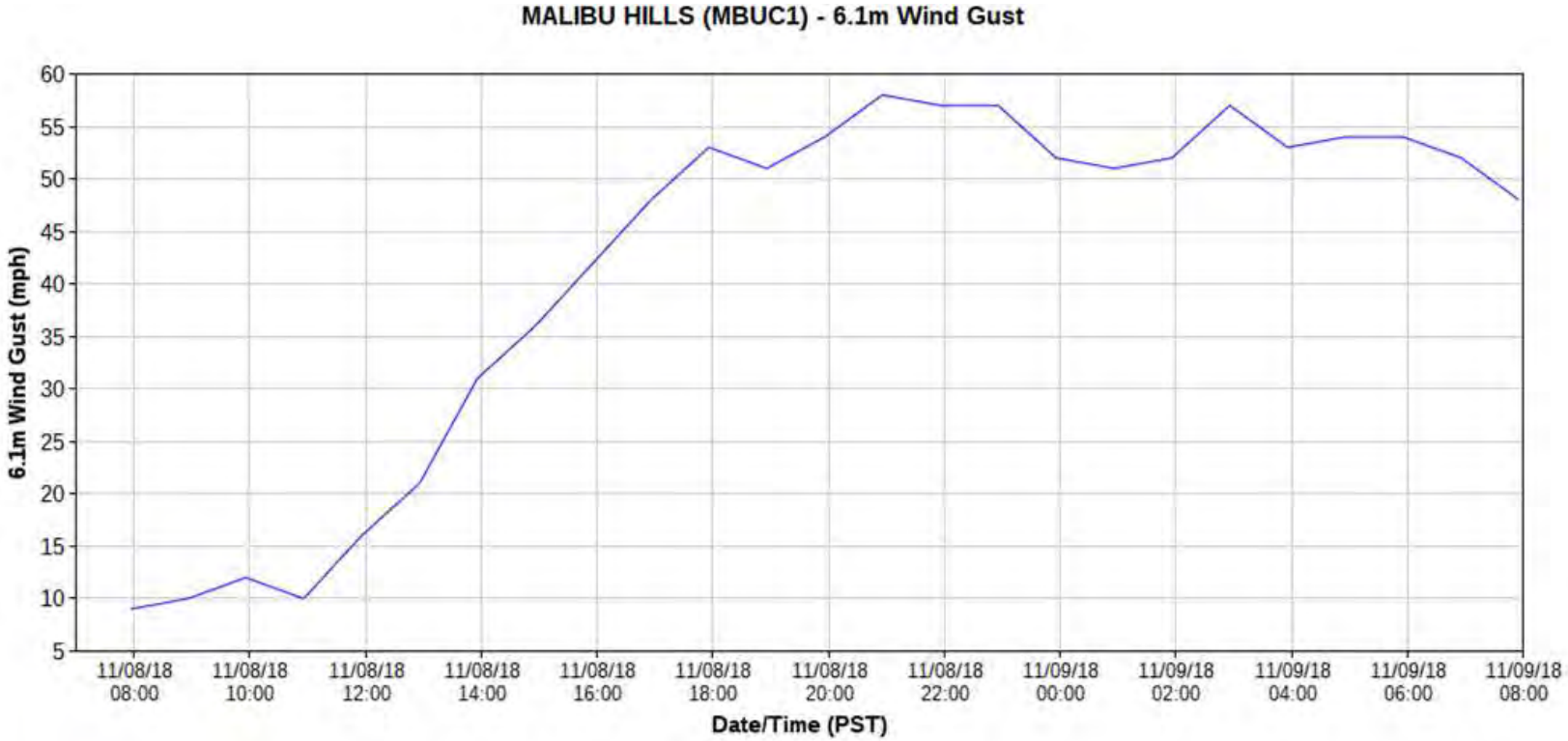

Figure 4—Malibu Hills Humidity

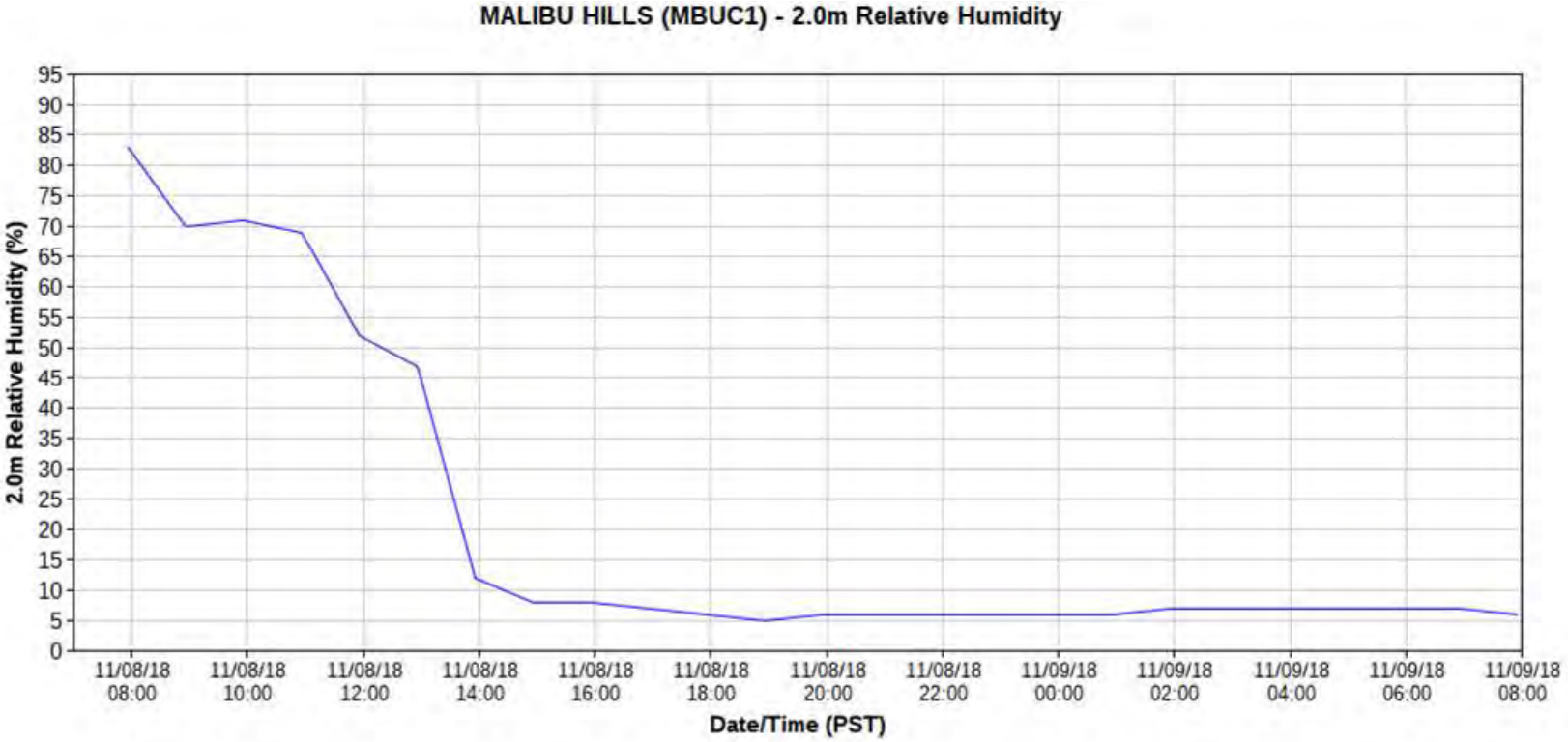

EXHIBIT C

WOOLSEY FIRE PATH PROGRESSION OVER THE GEOGRAPHY

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Fire Start Area to 2:24 – 4:00PM



Fire General Origin Area View to Southwest



Halfway Down Fire Origin



Fire at Sunset

Moorpark
Unincorporated
Simi Valley
Camarillo
IA to Sunset
Unincorporated
Los Angeles
Thousand Oaks
Hidden Hills
Agoura Hills
Westlake Village
Calabasas
Unincorporated
Unincorporated
WIND DIRECTION NORTHEAST
Malibu

Terrain Leaving Origin at Sunset



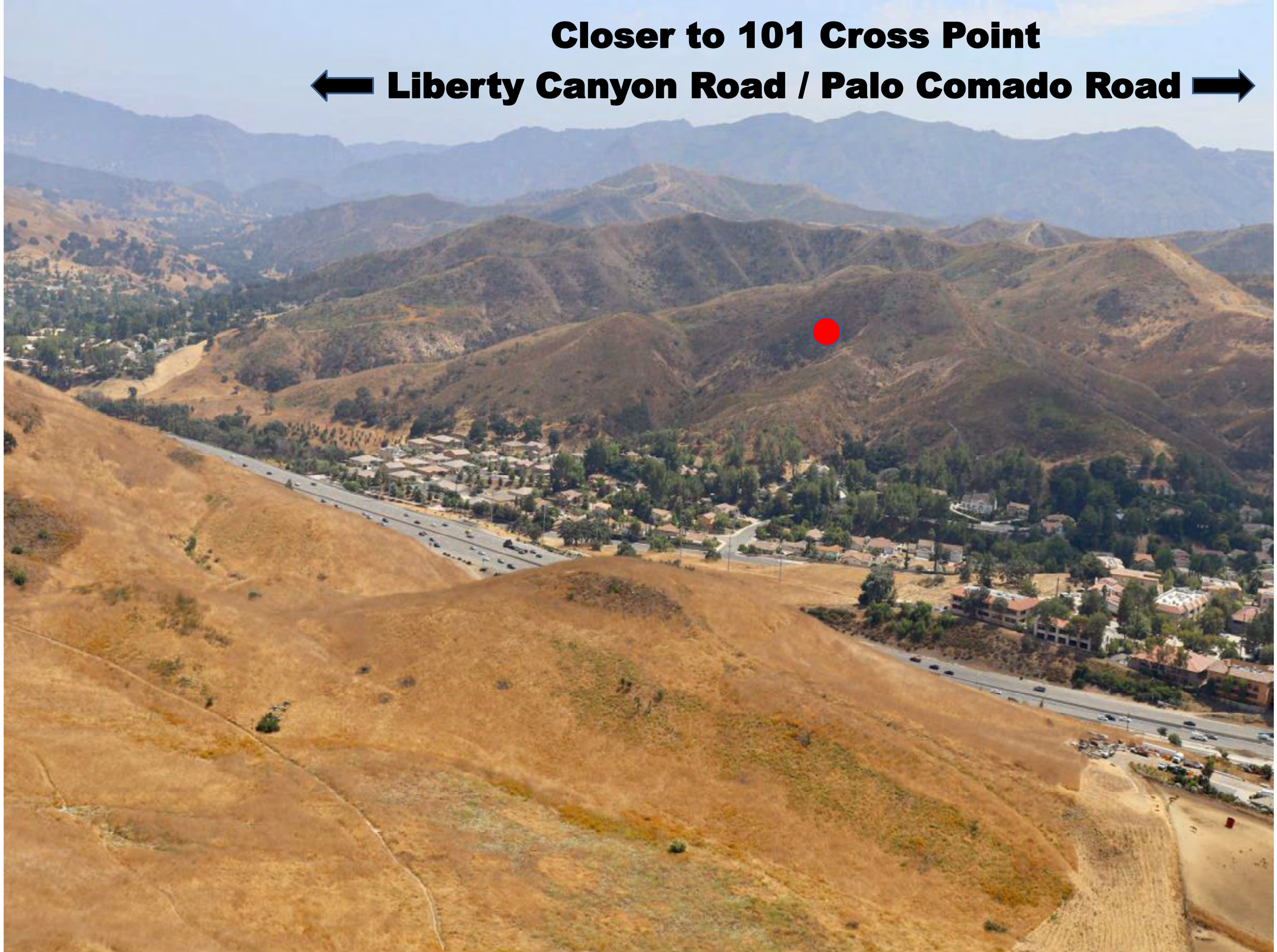
Fire Spread Sunset to 101 Jump

Moorpark
Unincorporated
Simi Valley
arillo
Unincorporated
IA to Sunset
Sunset to Jump at Hwy 101
Thousand Oaks
Los Angeles
Hidden Hills
Agoura Hills
Westlake Village
Calabasas
Unincorporated
Unincorporated
Malibu

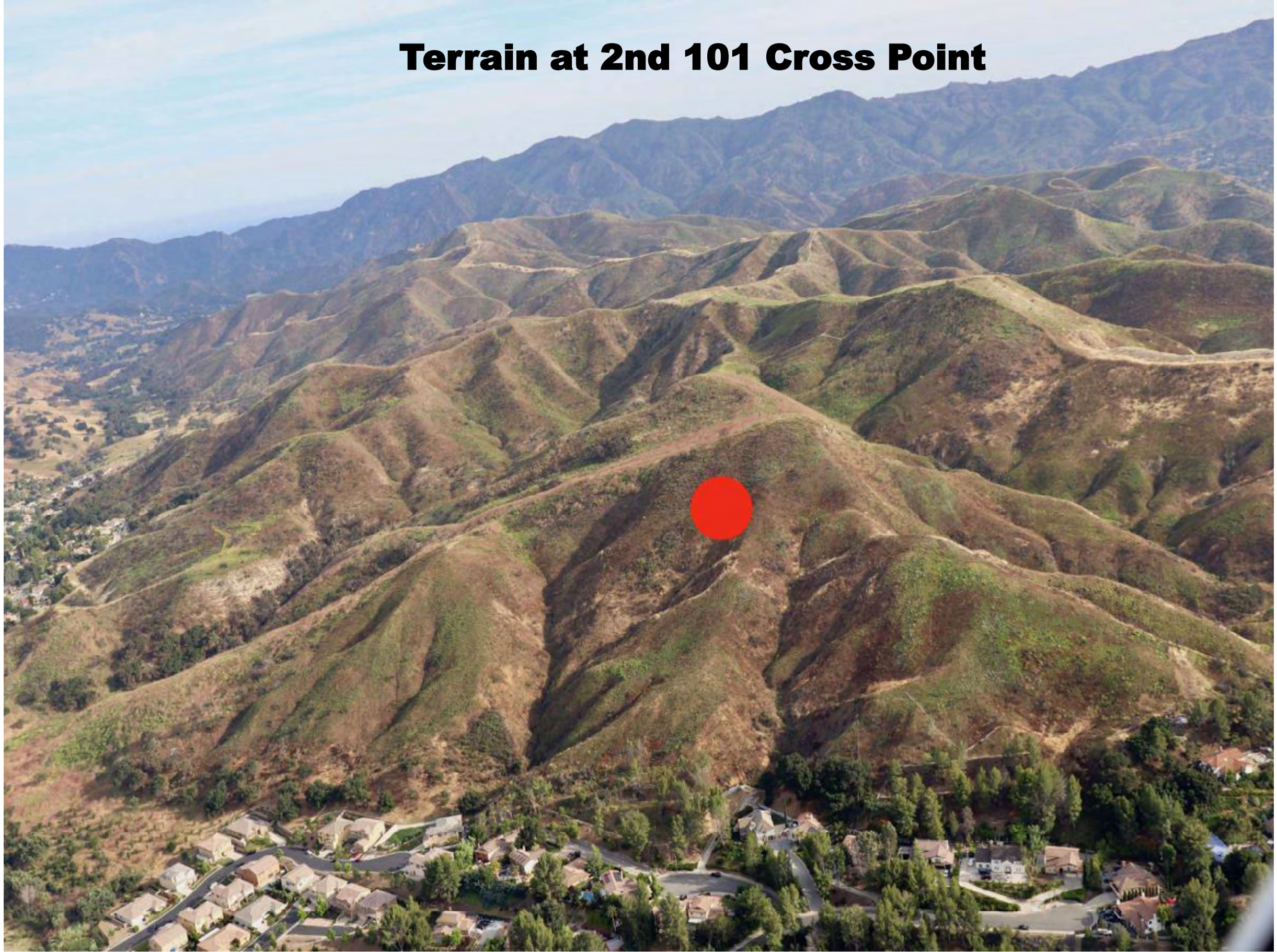
WIND DIRECTION NORTHEAST

Terrain Approaching 101 Cross Point




Closer to 101 Cross Point
Liberty Canyon Road / Palo Comado Road

Terrain at 2nd 101 Cross Point



101 Cross Point Looking NE to Origin



101 Main Cross Point Looking East



101 Cross Point Area Fire Behavior



101 Cross Point Upper Hillside Spread



Terrain Behind 101 Cross Point

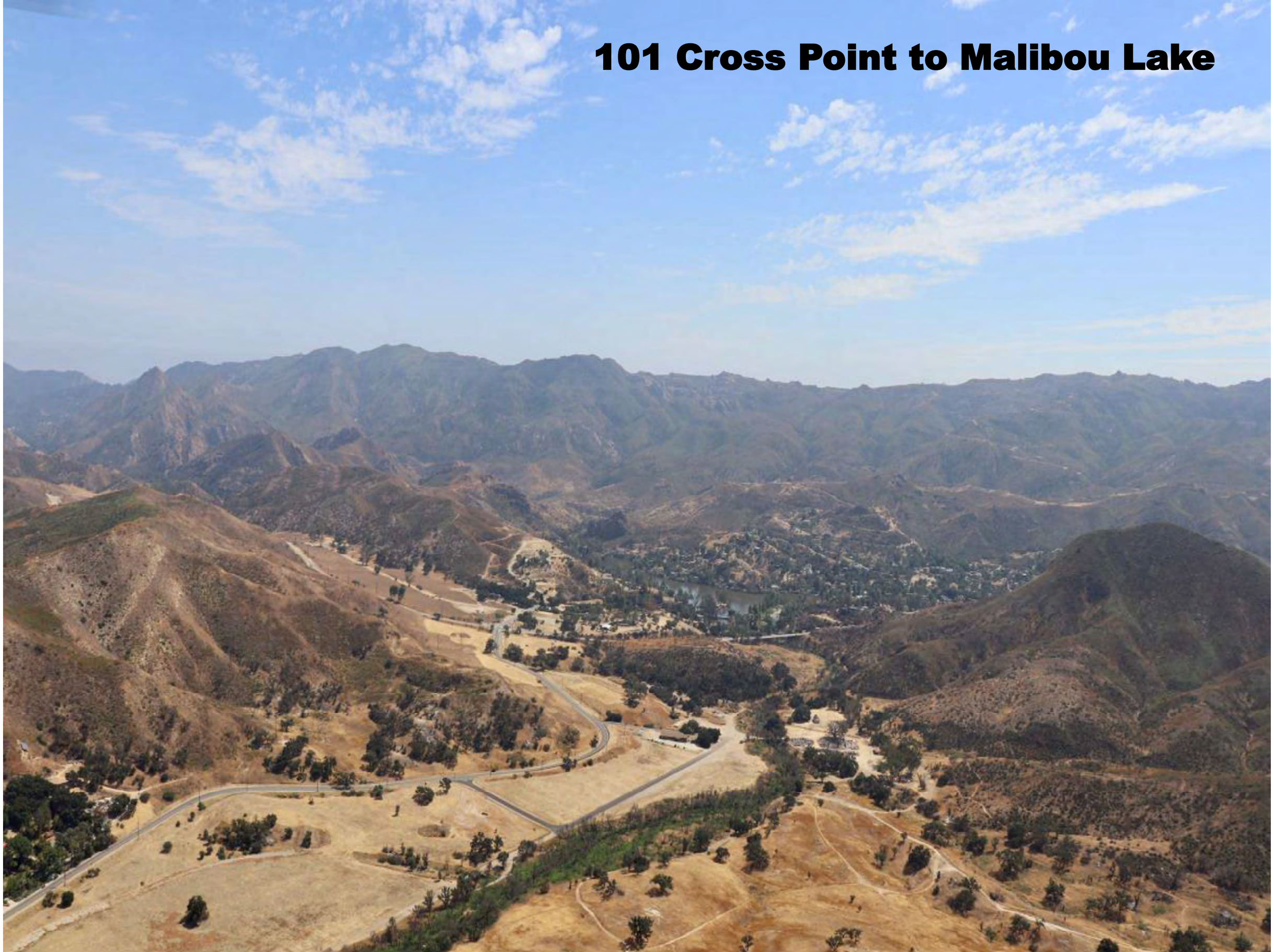


Fire Spread 101 to Ocean

Moorpark
Unincorporated
Simi Valley
Camarillo
Thousand Oaks
Unincorporated
IA to Sunset
Sunset to Jump at Hwy 101
Los Angeles
Hidden Hills
Agoura Hills
Westlake Village
Calabasas
Unincorporated
Unincorporated
Hwy 101 to Malibu
Malibu

WIND DIRECTION NORTHEAST

101 Cross Point to Malibou Lake



Malibou Lake

Fire Storm Entering Malibu City



Helicopter Work At Fire 1st Contact at Malibu



Terrain Approaching Malibu Inland Edge



First Contact Area to Ocean Distance



West of PCH Back to Mountains



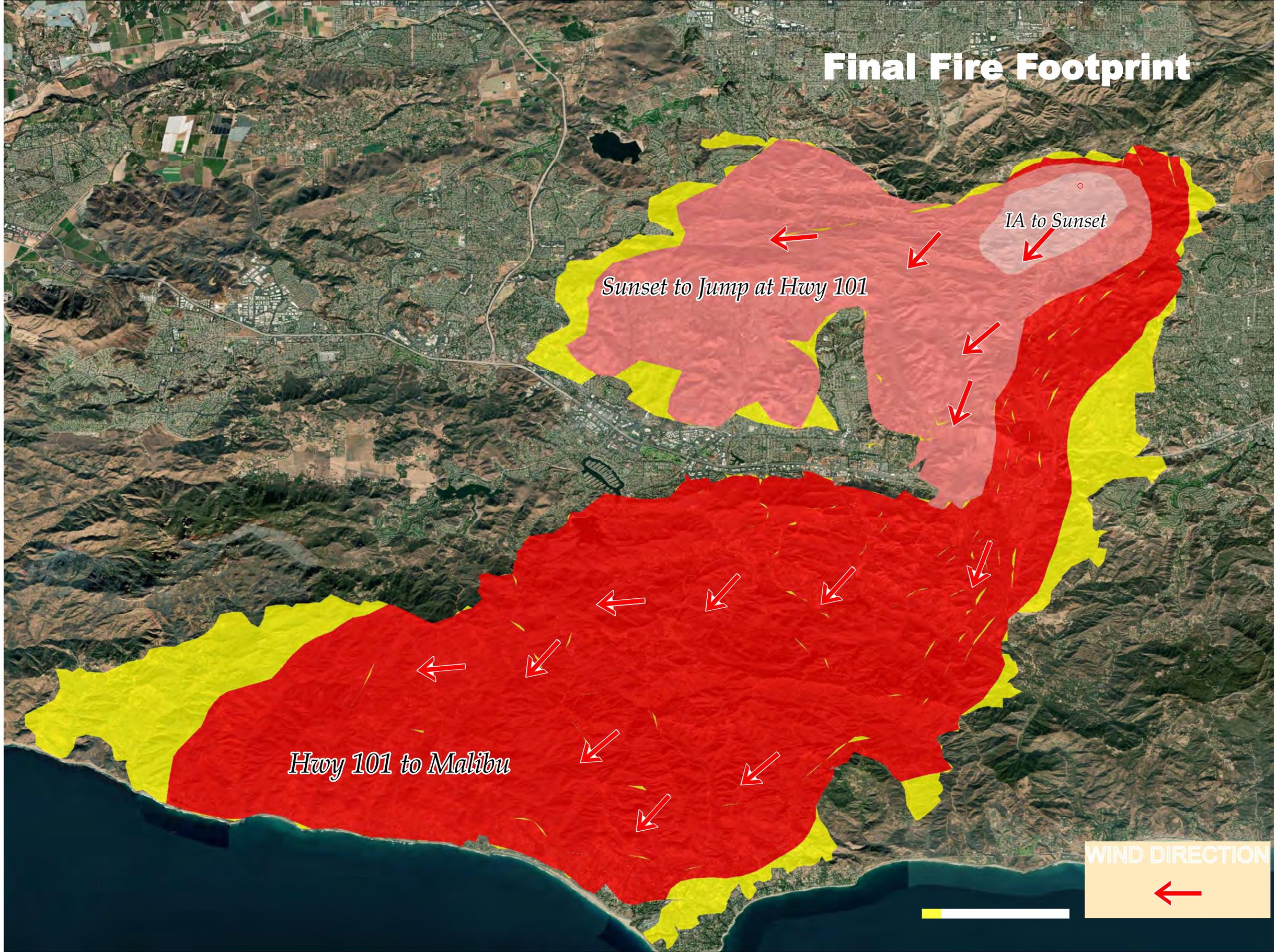
Daytime Fire Behavior



Daytime Fire Behavior



Final Fire Footprint



Structure Damage Locations

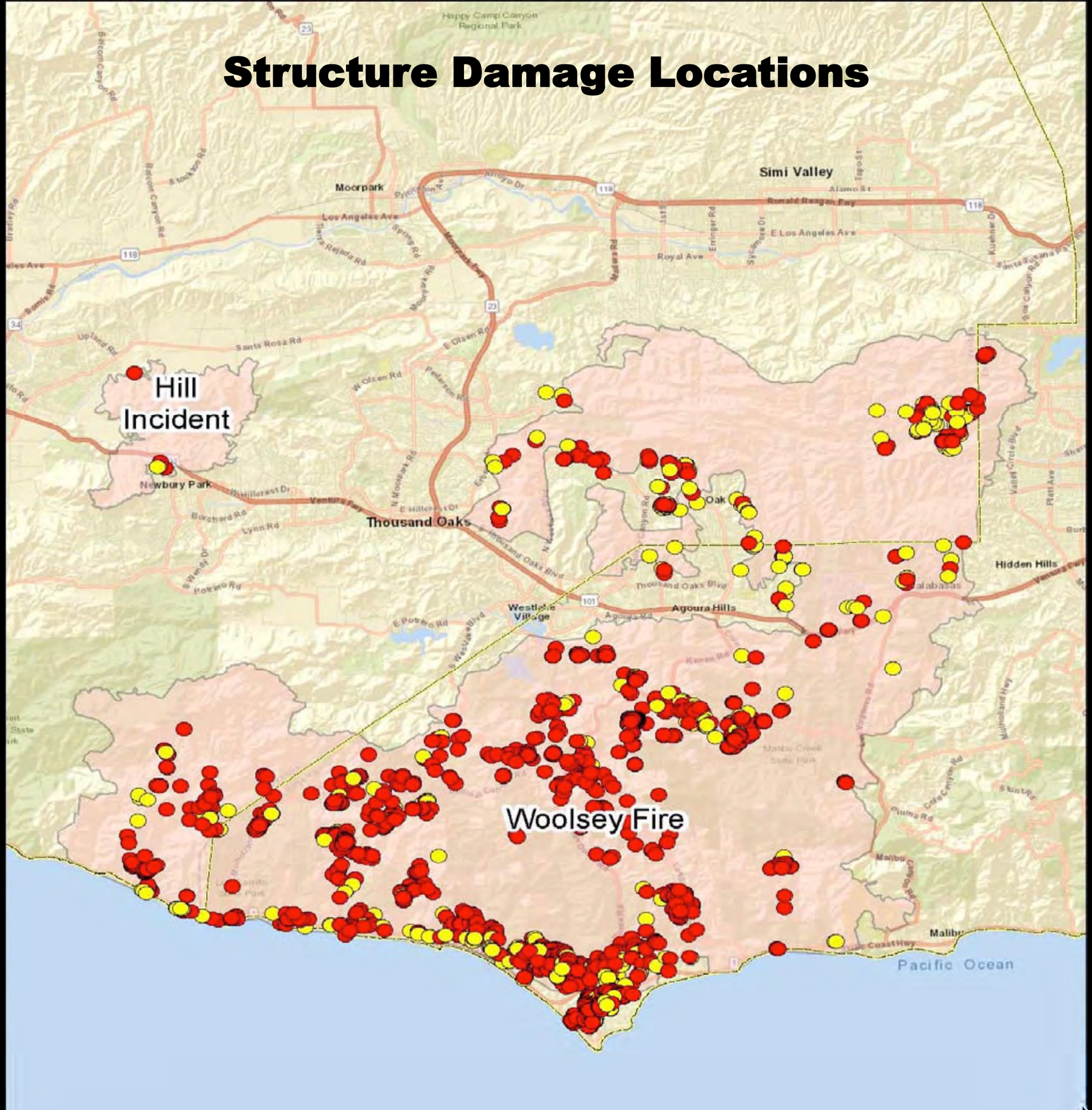


EXHIBIT D

WOOLSEY FIRE AREA FIRE HISTORY MAP

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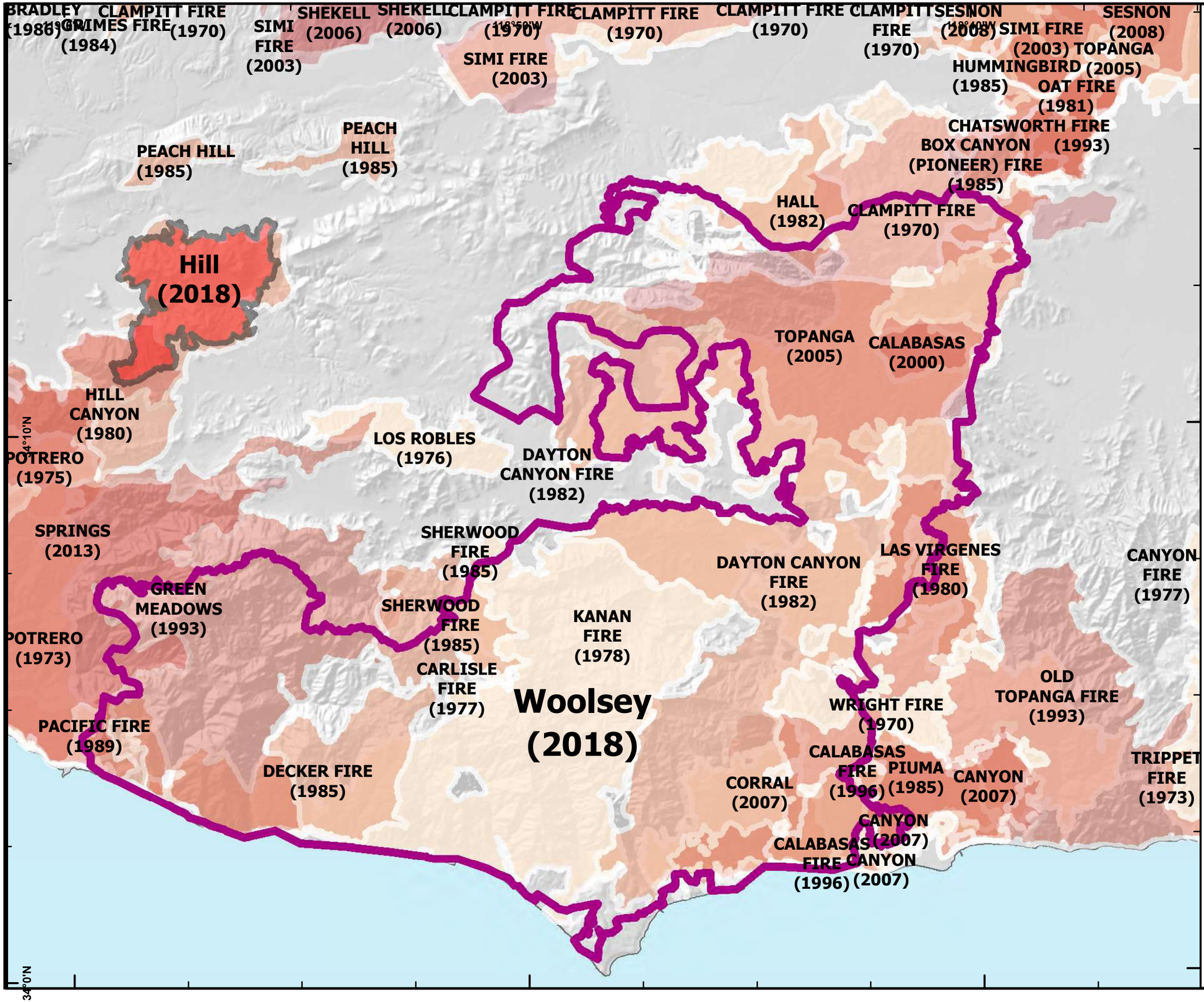

FIRE HISTORY MAP

Woolsey Incident
CA-VNC-91023
November 19, 2018

Fire History 1970 to Present

- 1970-1979
- 1980-1989
- 1900-1999
- 2000-Present
- Hill Fire 2018
- Woolsey Fire Perimeter

N
W E
S

1:125,000
NAD 83

0 2.5 5
Miles

Relative Sensitivities of Mammalian Carnivores to Habitat Fragmentation

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Abstract: *I examined the effects of habitat fragmentation on the distribution and abundance of mammalian carnivores in coastal southern California and tested the prediction that responses to fragmentation varied with the body size of carnivore species. I conducted track surveys for nine native and two exotic carnivore species in 29 urban habitat fragments and 10 control sites. Fragment area and isolation were the two strongest landscape descriptors of predator distribution and abundance. Six species were sensitive to fragmentation, generally disappearing as habitat patches became smaller and more isolated; three species were enhanced by fragmentation, with increased abundance in highly fragmented sites; and two species were tolerant of fragmentation, with little to no effect of landscape variables on their distribution and abundance. Within urban habitat fragments, the carnivore visitation rate increased at sites with more exotic cover and closer to the urban edge, a pattern driven largely by the increased abundance of fragmentation-enhanced carnivores at edge sites. Finally, body size, in conjunction with other ecological characteristics, partially accounted for the heterogeneity in responses to fragmentation among carnivore species. These differential sensitivities are useful criteria for choosing appropriate focal species for ecological research and conservation planning, a choice that depends on the scale of fragmentation in a region and the commensurate responses of carnivore populations at that scale.*

Sensibilidad Relativa a la Fragmentación del Hábitat de Mamíferos Carnívoros

Resumen: *Examiné los efectos de la fragmentación del hábitat sobre la distribución y abundancia de mamíferos carnívoros en la costa del sur de California y evalué la predicción de que las respuestas a la fragmentación variaban con el tamaño corporal de carnívoros. Se realizaron muestreos de huellas para nueve especies nativas y dos exóticas en 29 fragmentos de hábitat urbano y 10 sitios control. El área fragmentada y su aislamiento fueron los dos principales descriptores de la distribución y abundancia de depredadores. Seis especies fueron sensibles a la fragmentación, generalmente las especies desaparecían conforme los fragmentos eran más pequeños y aislados, tres especies fueron favorecidas por la fragmentación, con incremento en su abundancia en sitios altamente fragmentados, y dos especies fueron tolerantes a la fragmentación con poco o ningún efecto de las variables del paisaje sobre su distribución y abundancia. Dentro de los fragmentos de hábitat urbano, las tasas de presencia de carnívoros incrementaron en sitios con mayor cobertura exótica y cercanos al borde urbano, un patrón dirigido principalmente por el incremento en la abundancia de carnívoros favorecidos por la fragmentación en el borde de los sitios. Finalmente, el tamaño corporal, conjuntamente con otras características ecológicas, fueron parcialmente responsables de la heterogeneidad en respuestas a la fragmentación entre especies de carnívoros. Estas sensibilidades diferenciales son un criterio útil para seleccionar especies focales apropiadas para investigaciones ecológicas y la planeación de la conservación, una selección que depende de la escala de fragmentación en una región y de las respuestas apropiadas de las poblaciones de carnívoros a esa escala.*

Introduction

The destruction of habitat has been targeted as one of the most serious threats to biological diversity world-

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wide (Wilcove et al. 1998), and in areas with increasing urbanization, the loss and fragmentation of habitat is virtually inevitable. Mediterranean scrub habitats in coastal southern California are particularly threatened. Intensive development in the region over the past century has destroyed all but 10% of the native coastal sage scrub habitat (McCaull 1994). This habitat loss has created a "hotspot" of endangerment and extinction for the highly endemic biota in the region (Dobson et al. 1997). Mammalian carnivores are thought to be particularly vulnerable to local extinction in fragmented landscapes because of their relatively large ranges, low numbers, and direct persecution by humans (Noss et al. 1996; Woodroffe & Ginsberg 1998). The decline and extirpation of top predators from fragmented systems may generate trophic cascades that alter the structure of ecological communities (Crooks & Soulé 1999). Indeed, the persistence of these environmentally sensitive and ecologically pivotal species may be indicative of the integrity of entire ecosystems (Noss et al 1996). As such, mammalian carnivores can serve as useful tools for the study of ecological disturbances or for conservation planning and reserve design (Soulé & Terborgh 1999).

Mammalian predators are difficult to study, however, because of their low densities, nocturnal and secretive habits, and wariness of humans (Sargeant et al. 1998). As a result, the ecology of many carnivore species and their responses to ecological disturbances such as fragmentation are often poorly understood. Although considered members of the same ecological guild, carnivores may vary in their responses to fragmentation. In particular, differences in body size among carnivore species have been proposed as an important determinant of extinction probability (Brown 1986; Belovsky 1987). The relationship between body size and extinction risk in animals is complex, however, and has been the subject of considerable debate, with studies predicting and reporting positive, negative, or no relation of body size to extinction probability (reviewed by Johst & Brandl 1997). Few studies have evaluated if, how, or why carnivore species differ in their relative sensitivities to fragmentation effects.

My goal was to analyze the effects of the loss and fragmentation of habitat on mammalian carnivores in the urbanizing landscape of coastal southern California. Habitat fragmentation must be viewed as a multiscale problem, with fragmentation effects depending on the scale of fragmentation and the movement patterns of target species (Andren 1994). I therefore surveyed a suite of carnivore species that occur across a range of fragmentation levels and evaluated their responses to fragmentation at two spatial scales: (1) landscape-level heterogeneity among fragments and (2) local heterogeneity at sites within fragments. To allow for a more comprehensive assessment of relative sensitivities to fragmentation, I not only documented the presence or absence of each carnivore species, but also measured their relative abundance at each site. Finally, I tested the prediction that responses to fragmentation vary with body size in carnivore species, explored other ecological traits of these predators that may contribute to extinction risk, and used these differential sensitivities to evaluate the utility of mammalian carnivores as focal species with which to assess the degree of functional landscape connectivity.

Methods

Study Areas

I conducted carnivore surveys in 29 urban habitat fragments in coastal San Diego County from Fall 1995 through Summer 1997. Twenty-eight of these fragments were originally studied by Soulé et al. (1988). The fragments, completely surrounded by human-modified landscapes, are typically dendritic canyons dissecting coastal mesas, although a few also contain mesa-top habitat. The fragments support a mosaic of shrub habitat, including mixed chaparral, chamise chaparral, maritime succulent shrub, and coastal sage scrub, the dominant assemblage in most sites. Disturbed areas within fragments were typically dominated by ruderal weed species, ornamental plants invading from surrounding residences, fire-retardant ground cover such as South African iceplant (*Carpobrotus edulis*), and non-native trees (e.g., palms and species of *Eucalyptus* and *Acacia*) (Alberts et al. 1993).

From Fall 1995 through Summer 2000, I conducted carnivore surveys in less disturbed areas in coastal southern California to act as controls to the small, urban habitat remnants. These control areas varied in size and degree of isolation (Table 1), ranging from relatively small reserves isolated within urban developments (e.g., Point Loma Ecological Reserve) to large blocks of habitat relatively continuous with larger natural areas (e.g., Miramar Marine Corps Air Station).

Carnivore Surveys

I assessed the distribution and relative abundance of nine native and two non-native predator species through track surveys. Native species were the mountain lion (*Felis concolor*), bobcat (*Felis rufus*), coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), badger (*Taxidea taxus*), raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), western spotted skunk (*Spilogale gracilis*), and long-tailed weasel (*Mustela frenata*). Non-native target species were the domestic cat (*Felis catus*) and Virginia opossum (*Didelphis virginiana*), a marsupial introduced to California around 1910 (Jameson & Peeters 1988).

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Table 1. Landscape variables and distributions of 11 mammalian carnivore species for 10 control sites and 29 urban habitat fragments in coastal southern California (1, present; 0, absent).

	Area (ha)	*Age (yrs)*	*Distance Y (m)*	*Distance Z (m)*	*Long-tailed weasel*	*Spotted skunk*	*Badger*	*Mountain lion*	*Bobcat*	*Coyote*	*Gray fox*	*Striped skunk*	*Raccoon*	*Opossum*	*Domestic cat*
Control sites															
Miramar Marine Corps Air Station	5806	0	0	0	0	0	0	1	1	1	0	1	1	1	0
Chino Hills State Park	4452	0	200	200	1	0	1	1	1	1	1	1	1	1	0
Limestone Canyon/Whiting Ranch	4450	0	15	15	0	0	1	1	1	1	1	1	1	1	0
San Joaquin Hills	4219	22	5353	2930	0	1	0	0	1	1	1	1	1	1	0
Weir Canyon	1923	0	69	69	0	0	0	1	1	1	1	1	0	1	0
Santa Margarita Ecological Reserve	1763	0	30	30	0	0	0	1	1	1	1	0	1	0	0
Starr Ranch	1548	0	0	0	0	1	0	1	1	1	1	1	1	1	0
Tenaja	1191	0	0	0	1	0	1	1	1	1	1	1	1	1	0
Torrey Pines State Reserve	428	0	68	68	0	0	0	0	1	1	1	1	1	1	0
Point Loma Ecological Reserve	264	45	5700	5700	0	0	0	0	0	1	1	1	1	0	1
Urban fragments															
Florida	102	59	2100	233	0	0	0	0	0	1	1	0	0	0	0
Torrey Pines Extenstion	74	20	91	91	0	0	0	0	1	1	1	1	1	1	1
Balboa Terrace	56	43	121	117	0	0	0	0	0	1	1	1	1	1	1
Alta La Jolla	34	23	121	93	0	0	0	0	0	1	1	1	1	1	1
Kate Sessions	31	25	121	93	0	0	0	0	0	1	1	1	1	1	1
Zena	15	45	2865	467	0	0	0	0	0	1	1	1	0	1	1
Canon	12	67	1219	1167	0	0	0	0	0	0	1	1	1	1	1
Laurel	10	88	1554	350	0	0	0	0	0	1	1	1	1	1	1
32nd Street South	10	65	304	233	0	0	0	0	0	1	0	0	0	0	1
Pottery	10	23	45	70	0	0	0	0	0	1	1	1	1	1	0
Washington	9	83	365	187	0	0	0	0	0	1	1	1	1	1	1
Syracuse	9	27	40	70	0	0	0	0	0	1	1	1	0	1	1
Baja	8	40	670	70	0	0	0	0	0	1	1	1	1	1	1
Raffee	8	28	61	163	0	0	0	0	0	1	1	1	1	1	1
Solana	8	20	550	187	0	0	0	0	0	1	1	0	1	1	0
Acuna	7	31	110	47	0	0	0	0	0	1	1	1	0	1	1
Juan	7	32	228	70	0	0	0	0	0	1	1	1	1	1	1
Chollas	6	45	1005	467	0	0	0	0	0	1	1	1	1	1	1
Mil Cumbres	6	20	550	23	0	0	0	0	1	1	1	1	0	1	1
Chateau	6	29	110	47	0	0	0	0	0	1	1	0	0	1	1
Oak Crest	6	15	400	140	0	0	0	0	0	1	0	0	0	1	1
54th	4	29	609	187	0	0	0	0	0	1	1	1	1	1	1
60th	4	46	335	350	0	0	0	0	0	1	0	0	0	1	0
Spruce	4	95	1767	93	0	0	0	0	0	1	1	1	1	1	1
Titus	3	86	280	163	0	0	0	0	0	1	1	1	1	1	1
Montanosa	3	11	91	93	0	0	0	0	0	1	0	0	0	1	1
El Mac	2	41	883	163	0	0	0	0	0	1	1	1	1	0	1
Poinsettia	2	59	350	350	0	0	0	0	0	0	1	0	1	1	1
Talbot	2	64	1219	933	0	0	0	0	0	0	1	1	1	1	1
Urban fragment occupancy					0	0	0	0	2	26	25	21	19	26	25
Total occupancy					2	2	3	7	11	36	34	30	28	34	26

I established a series of track-detection stations at approximately 250-m intervals along dirt roads or trails (human and/or wildlife) along the main axis of each study area (Linhart & Knowlton 1975; Conner et al. 1983; Sargeant et al. 1998). Each track station consisted of a 1-m-diameter, 1-cm-deep, circle of freshly sifted gypsum baited with a liquid carnivore scent lure (Russ Carman's Pro-Choice and Canine Call, Sterling Fur & Tool, Sterling, Ohio) every other day. Track transects were checked and reset daily for 5 consecutive days. Tracks on each station were measured and identified to species; tracks with ambiguous identifications were omitted from analyses. Track surveys were conducted once each sampling quarter: fall (September–November), winter (December–February), spring (March–May), and summer (June–August). Each site was sampled for 1–2 years.

The track index of each carnivore species in each quarterly sampling session was expressed as the total number of visits recorded for a species, divided by the total sampling effort. I defined a visit as at least one track of a species on a track station (Conner et al. 1983). Mathematically, the track index (I) was calculated as

$$I = \ln[\{v_j/(s_j n_j)\} + 1],$$

where v_j is the number of stations visited by a species in transect j, s_j is the number of stations in transect j, and n_j is the number of nights that stations were operative in transect j. Thus, I for each species represents the visitation rate per track station per night in each study area. Although this index cannot be directly translated into numbers of individuals and hence does not measure absolute densities, it does provide an index of the relative abundance of a species at each sampling point (Conner et al. 1983; Sargeant et al. 1998). For each species, I averaged track indices across quarterly sampling sessions to derive a mean index at each study area for the duration of the study. Indices were log-transformed to meet normality assumptions in the statistical analyses. Overall, track surveys totaled 6540 station-nights ($s_j\, n_j$) among all study sites.

Landscape Variables

I used area, age, and isolation to assess the effects of landscape-level fragmentation on carnivore populations (Table 1). I measured the total area of each fragment based on digitized images of scaled aerial photographs taken in 1995. Total area of each control site was defined as the reserve boundaries within which the surveys were conducted. Because control sites were often adjacent to unfragmented habitat, area approximations represent minimum estimates.

Fragment age, defined as the number of years since isolation of the habitat fragment by urban development, was based on dated aerial photographs and building permit records (Soulé et al. 1988). Because fragment age is highly negatively correlated to the proportion of native shrub cover within fragments (Suarez et al. 1998; Crooks et al. 2001), I used age to measure a time effect per se in the fragments and to represent the cumulative loss of native habitat in the entire fragment since isolation. Age was scored as zero for control sites that were directly adjacent to larger natural areas (Miramar Marine Corps Air Station, Starr Ranch Audubon Sanctuary, Tenaja Corridor) or that were separated from such areas by only a roadway and not by urban development (Chino Hills State Parks, Limestone Canyon/Whiting Ranch, Santa Margarita Ecological Reserve, Torrey Pines State Reserve, Weir Canyon).

Two variables were calculated to characterize the degree of isolation of each site: distance Y, the distance to the closest habitat patch (measured from patch edge to patch edge) of equal or larger size (Soulé et al. 1988), and distance Z, the shortest distance to any other habitat fragment, reserve, or possible movement linkage to such sites (e.g., riparian channels, power line easements, golf courses). Isolation was scored as zero for control sites directly adjacent to a larger natural area and as the width of the roadway for control sites isolated from larger habitat blocks by a roadway.

All landscape variables were log-transformed to meet normality assumptions in the statistical analyses. When only the urban habitat fragments were considered, fragment age was positively related to distance Y ($r = 0.564$, $p = 0.001$) and distance Z ($r = 0.526$, $p = 0.003$), and distance Y was positively related to distance Z ($r = 0.362$, $p = 0.053$). When both habitat fragments and control areas were included, area was negatively related to age ($r = -0.813$, $p < 0.001$), distance Y ($r = -0.467$, $p = 0.003$), and distance Z ($r = -0.299$, $p = 0.065$); age was positively related to distance Y ($r = 0.741$, $p < 0.001$) and distance Z ($r = 0.597$, $p < 0.001$); and distance Y was positively related to distance Z ($r = 0.761$, $p < 0.001$).

SPECIES RICHNESS AND DISTRIBUTION

Island biogeography theory predicts that landscape variables such as size and isolation should help determine the number of species on islands (MacArthur & Wilson 1967). To test this prediction, I calculated two measures of carnivore species richness for each study area: (1) the number of carnivore species detected at the site during the course of the study and (2) the number of native carnivore species detected, excluding the non-native opossum and domestic cat. A species was present in a study area if it was detected on track stations within the site at least once during the course of the study. Presence was verified with a combination of remotely triggered cameras, scat surveys, and opportunistic visual sightings. Presence of a species does not necessarily imply that the site can support resident animals or populations. Like-

wise, failure to detect a species at a site does not indicate that the species has never visited the area, but rather that it was not recorded during sampling sessions.

I used backward-elimination multiple regression to identify which landscape variables (size, age, and isolation) were the best predictors of carnivore species richness in a study site. Independent variables with $p < 0.15$ were included in all regression models to minimize exclusion of important predictors from the model, and tolerance values were set at 0.10 throughout to control for multicollinearity (Tabachnick & Fidell 1996). Comparison-wide error rates were examined in all statistical analyses (Mead 1988; Stuart-Oaten 1995) ($p < 0.05$, statistically significant; $0.05 < p < 0.10$, marginally significant). I first conducted the multiple-regression analyses including only the 29 urban habitat fragments and then including all 39 study sites.

I used logistic-regression analyses to evaluate the effect of landscape variables on the distribution of individual carnivore species. First, I constructed bivariate logistic-regression models to evaluate the separate effects of area and isolation (distance Z) on the probability of occurrence for each species across all 39 study sites. Area and distance Z were chosen because preliminary analyses indicated that they were the two strongest predictors of carnivore distribution. For species with significant area and isolation effects, I plotted logistic-regression curves of the probability of occurrence of each species as a function of area, holding isolation constant by substituting its median value into a two-way (area $\times$ isolation) logistic model. Likewise, I constructed isolation curves after holding area constant by substituting its median value into the two-way logistic model. From these curves, I calculated the area and isolation at which the probability of occurrence of the species equaled 50% and used these estimates to represent the relative area and isolation requirements for each species (following Crooks et al. 2001). Finally, I used multiple-logistic-regression models to graphically evaluate the combined effect of area and isolation on probability of occurrence for each species.

Logistic-regression estimates of probability of occurrences and relative area and isolation requirements are not intended, however, to represent the actual fragment size or isolation necessary to ensure the long-term persistence of a population (Hinsley et al. 1996). Rather, probability of occurrence measures the probability of an individual visiting the study area at least once during the course of the study, and the area and isolation estimates generated are intended to function only as relative indices of sensitivity to fragmentation. Area and isolation estimates are likely to be more accurate for those species with the most detections.

RELATIVE ABUNDANCE

I used backward-elimination regression models to identify which landscape variables were the best predictors of the track indices of each species in each study area. The analyses were first conducted including only the 29 urban habitat fragments. Mountain lions, spotted skunks, badgers, and long-tailed weasels were omitted from these analyses because they were not detected in any urban habitat fragments. Bobcats, detected in only two fragments, were also omitted.

I repeated the multiple-regression analyses across all 39 fragments and control sites, including mountain lions and bobcats in the analyses. Spotted skunks, badgers, and long-tailed weasels were again omitted due to low detection rates. Because the track indices for mountain lions and bobcats were zero for many sites, the results of these regressions must be interpreted with caution. The final regression models were determined largely by the patterns of species' presence or absence across sites and not by variation in relative abundance among sites where they occurred. Nevertheless, I report regression models for mountain lions and bobcats to allow for further evaluation of the effects of landscape variables on these species and for further comparisons of their fragmentation sensitivities to those of other carnivore species.

Local Variables

Habitat heterogeneity within these urban habitat fragments is an important determinant of the persistence of native scrub-breeding birds (Soulé et al. 1988), rodents (Bolger et al. 1997), and invertebrates (Suarez et al. 1998; Bolger et al. 2000), all potential prey for carnivore species. I measured three variables to investigate the effect of habitat heterogeneity on carnivore populations: distance to the urban edge, percent cover of native shrubs, and percent cover of exotic vegetation. I estimated the distance of each track station to the nearest urban edge (the backyards of the houses bordering the fragment) and log-transformed these values to meet normality assumptions in the statistical analyses. I used a Braun-Blanquet categorical scale (Kent & Coker 1992) to estimate the percent cover of native shrubs and of total exotic cover within a 20-m radius around each track station. The cover scale was 0 (<1%), 1 (1–5%), 2 (6–25%), 3 (26–50%), 4 (51–75%), and 5 (76–100%). Distance to edge was positively related to shrub cover ($r = 0.281$, $p = 0.007$) and negatively related to exotic cover ($r = -0.341$, $p = 0.001$), and shrub cover was negatively related to exotic cover ($r = -0.694$, $p < 0.001$).

SPECIES RICHNESS AND RELATIVE ABUNDANCE

I calculated the total number of carnivore species and the number of native carnivore species detected at each track station in the 29 urban habitat fragments during the course of the study; two exotic species (opossum and domestic cat) and five native species (bobcat, coyote, gray fox, striped skunk, and raccoon) were detected

in the urban fragments and were hence included in the analyses. I then used backward-elimination multiple regression to identify which local variables were the best predictors of carnivore species richness at each station.

I calculated the mean track index for each species at each track station in the 29 urban habitat fragments to generate relative abundance indices. Again, mountain lions, spotted skunks, long-tailed weasels, badgers, and bobcats were omitted from these analyses due to low detection rates within fragments. I then used backward-elimination multiple regression to identify which local variables were the best predictors of the relative abundance of each species at a station. Some species were absent from some fragments, however, an absence driven in part by landscape variables such as area, age, and isolation. I therefore conducted the regressions for each species after excluding from the analyses all fragments where that species was never detected. By excluding these fragments I could account for the effects of landscape-level fragmentation on the presence or absence of a species and therefore more fully analyze the effects of local variables within fragments where that species occurred.

To further evaluate the effect of the urban edge on carnivores within fragments, for each species I graphed the mean track index at each station as a function of the distance of that station from the urban edge. Edge distances were classified into five categories: 0–24 m (n = 14 stations), 25–49 m (n = 35), 50–99 m (n = 16), 100–199 (n = 19), and >200 m (n = 7). Direct comparisons of track indices between species can be misleading, because the response of species to track stations may differ (Conner et al. 1983; Sargeant et al. 1998). To allow for more meaningful comparisons of track indices, I standardized the index for each species by dividing each value by the maximum track index recorded for that species. Therefore, these standardized track indices for each species ranged on a scale of 0 to 1.

Body Size and Fragmentation Sensitivity

I evaluated the relationship between body mass and sensitivity to fragmentation among carnivore species through linear-regression analysis. As an index of sensitivity to fragmentation, I calculated the average area of study sites occupied by each species, multiplying the area of each study site by the standardized track index (scale 0 to 1) of that species at that site. With area weighted by relative abundance per sampling point, the indices accounted not just for occupancy but also for differences in the relative abundance of a species among study sites. For example, for a given species, some study sites supported resident populations, whereas other study sites were only visited temporarily during the course of the study. Average area weighted by relative abundance accounted for such differences. In addition, I also compared body mass to typical home-range sizes and population densities reported in the literature for these species.

Results

Landscape Heterogeneity: Comparisons among Fragments

SPECIES RICHNESS AND DISTRIBUTION

The distribution of carnivore species varied across study sites (Table 1). Coyotes, opossums, gray foxes, domestic cats, striped skunks, and raccoons were detected in most urban fragments. Bobcats were detected in 9 of the 10 control sites but in only 2 urban habitat fragments, and mountain lions were detected in only 7 control sites and no urban fragments. I recorded few to no visits of mountain lions and bobcats in the habitat fragments, despite higher sampling intensity per unit area (station-nights/total area of site) in the 29 fragments (mean = 8.30 station-nights/ha, SE = 0.910) than in the 10 control sites (mean = 0.43 station-nights/ha, SE = 0.158) (t = 4.58, $p < 0.001$). Detections of spotted skunks, long-tailed weasels, and badgers were rare and occurred only in the larger habitat blocks.

Among the 29 urban habitat fragments, no landscape variables were retained as predictors of the total number of carnivore species in backward-elimination regression models (Table 2). When the opossum and domestic cat were excluded, however, the species richness of native carnivores exhibited a weak negative trend with fragment isolation (distance Z) and a weak positive trend with fragment age. When control sites were included in the analyses, both total carnivore species richness and native carnivore species richness increased with the area of the study site.

Logistic-regression models for each species indicated that the probability of occurrence across all sites was positively related to fragment area for coyotes (χ^2 = 5.57, p = 0.018), bobcats (χ^2 = 29.85, $p < 0.001$), mountain lions (χ^2 = 27.35, $p < 0.001$), spotted skunks (χ^2 = 5.85, p = 0.016), long-tailed weasels (χ^2 = 5.37, p = 0.021), and badgers (χ^2 = 9.73, p = 0.002). In contrast to these native carnivores, the probability of occurrence of domestic cats was higher in smaller fragments (χ^2 = 22.63, $p < 0.001$). Area was not a significant predictor of probability of occurrence for gray foxes (χ^2 = 0.24, p = 0.627), striped skunks (χ^2 = 1.81, p = 0.178), raccoons (χ^2 = 2.02, p = 0.155), or opossums (χ^2 = 0.357, p = 0.550).

Logistic-regression models indicated that probability of occurrence across all sites decreased with fragment isolation (distance Z) for coyotes (χ^2 = 6.92, p = 0.008), bobcats (χ^2 = 11.57, $p < 0.001$), and mountain lions (χ^2 = 11.88, $p < 0.001$). In contrast, probability of oc-

Table 2. Backward-elimination regression models of the effects of landscape variables on carnivore species richness and relative abundance among 29 urban habitat fragments and 10 control sites in coastal southern California.[a]

Variables	R^2	*Whole-model* p	*Coefficient*	p
Urban habitat fragments				
total species richness				
n.s.[b]				
native species richness	0.146	0.129		
distance *Z*			−0.408	0.067
age			+0.374	0.091
coyote	0.133	0.052		
area			+0.365	0.052
gray fox	0.114	0.074		
area			−0.336	0.074
domestic cat	0.393	0.002		
area			−0.550	0.001
distance *Z*			+0.246	0.122
opossum	0.164	0.029		
area			−0.405	0.029
striped skunk				
n.s.				
raccoon				
n.s.				
All sites				
total species richness	0.194	<0.001		
area			+0.440	<0.001
native species richness	0.372	<0.001		
area			+0.610	<0.001
coyote	0.15	0.015		
area			+0.388	0.015
bobcat	0.595	<0.001		
age			−0.921	<0.001
distance *Y*			+0.607	0.004
distance *Z*			−0.376	0.030
mountain lion	0.277	<0.001		
age			−0.526	<0.001
gray fox	0.197	0.005		
area			−0.444	0.005
raccoon	0.081	0.081		
area			−0.284	0.081
domestic cat	0.335	<0.001		
area			−0.579	0.001
opossum	0.241	0.002		
area			−0.491	0.002
striped skunk				
n.s.				

[a]*Independent variables are fragment area, age, and isolation (distance* Y *and distance* Z*). Independent variables with* $p < 0.15$ *were included in the final regression models.*
[b]*No independent variables were retained in the regression model (*$p > 0.15$*); n.s., not significant.*

currence was higher in more isolated fragments for domestic cats ($\chi^2 = 4.25$, $p = 0.039$). Isolation was not a significant predictor of probability of occurrence for gray foxes ($\chi^2 = 0.35$, $p = 0.553$), opossums ($\chi^2 = 1.88$, $p = 0.171$), spotted skunks ($\chi^2 = 0.18$, $p = 0.671$), striped skunks ($\chi^2 = 0.69$, $p = 0.407$), raccoons ($\chi^2 = 0.06$, $p = 0.811$), long-tailed weasels ($\chi^2 = 1.74$, $p = 0.187$), or badgers ($\chi^2 = 2.62$, $p = 0.106$).

After I controlled for isolation effects, the estimated area at which probability of occurrence was 50% was 1 ha for coyotes, 1.8 km^2 for bobcats, and 23 km^2 for mountain lions (Fig. 1a). The probability of occurrence for domestic cats dropped below 50% in fragments larger than 1.4 km^2; cats were never detected in the interior of control sites, and few if any feral cats occurred in these sites.

After I controlled for area effects, the estimated fragment isolation (distance *Z*) at which probability of occurrence was 50% was 883 m for coyotes and 6 m for bobcats (Fig. 1b). The probability of occurrence for mountain lions was <50% across the entire isolation range of fragments. In contrast, the probability of occurrence for domestic cats was >50% across the entire range of fragment isolation.

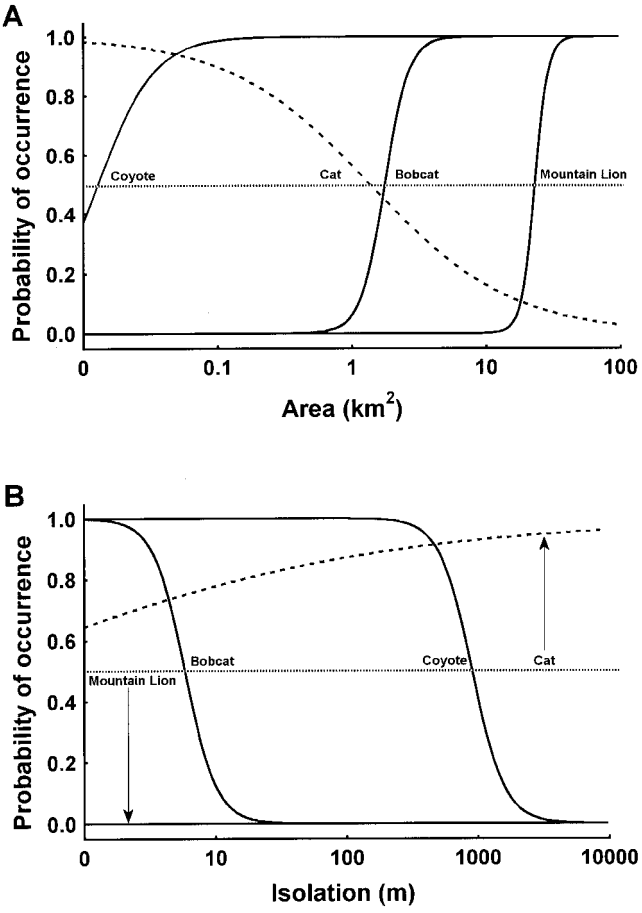

Figure 1. Logistic-regression models of the probability of occurrence of native (solid lines) and exotic (dashed line) carnivores as a function of (a) fragment area and (b) isolation. Area and isolation curves were constructed after the other independent variable was held constant by substituting its median values into a two-way (area × isolation) logistic-regression model. Only species with significant area and isolation effects are presented. Dotted line represents 50% probability of occurrence.

Multiple logistic-regression models of the combined effect of area and isolation on mountain lions, bobcats, and coyotes generated "extinction surfaces" that consisted of plateaus of occupancy at larger and less isolated sites that declined to basins of local extinctions at small and isolated fragments (Fig. 2). The effect of the area-isolation interaction, and hence the contour of the extinction surfaces, varied among species. The plateau for mountain lions was small and occurred only in the largest unfragmented sites, with large basins across all other study areas. The plateau for bobcats spanned a wider range of sites, but probability of occurrence dropped to zero in sites that were both small and isolated. Bobcats occurred in relatively small sites, but only those with little to no isolation. The plateau of coyotes was large, with a low probability of occurrence in only the smallest, most isolated urban fragments. Domestic cats exhibited a surface that was the inverse of these native predators. Their probability of occurrence was high in small and isolated fragments but lower in larger, less fragmented sites.

It should be emphasized, however, that the probability of residency or long-term viability of populations is undoubtedly lower than these probabilities of occurrence, particularly in smaller and isolated sites. For example, coyotes visited some fragments only temporarily during the course of the study. In some quarterly sampling sessions they were detected and in others they were not. Although the plateau of occupancy for coyotes encompassed most combinations of area and isolation, residency declined with fragment area. The average area of the 13 fragments in which coyotes came and went (mean = 0.75 [5.6 ha back-transformed], SD = 0.20) was smaller ($t = 3.01$, $p = 0.006$) than the average area of the 13 fragments in which coyotes were detected in every quarterly sampling session (mean = 1.19 [15.6 ha back-transformed], SD = 0.95).

RELATIVE ABUNDANCE

When only the 29 urban habitat fragments were included in the analyses, the relative abundance of coyotes at each sampling point was higher in larger fragments, whereas track indices of gray foxes, domestic cats, and opossums were higher in smaller fragments (Table 2). No variables were retained in the final model for raccoons and striped skunks ($p > 0.15$).

When control sites were also included in the regressions, coyote track indices at each sampling point again tended to be higher in larger sites. In contrast, the track indices of gray foxes, domestic cats, opossums, and raccoons were higher in smaller sites (Table 2). No landscape variables were retained in the models for the relative abundance of striped skunks.

When control sites were included in the regression models, fragment age was retained as the most significant predictor of the relative abundance of mountain lions and bobcats (Table 2); both species were less abundant in older sites. Mountain lions and bobcats were detected in relatively few sites, most of which were control areas not isolated by urban development (age = 0) and, for bobcats, a couple of recently isolated fragments (Table 1). This pattern generated the significant, negative slope between relative abundance and age for the two species.

The relative abundance of bobcats decreased with distance to the nearest movement linkage or natural area (distance Z) but, paradoxically, increased with distance to the nearest habitat patch of equal or larger size (distance Y). Bobcats were detected at sites that were relatively distant from larger natural areas (high values of

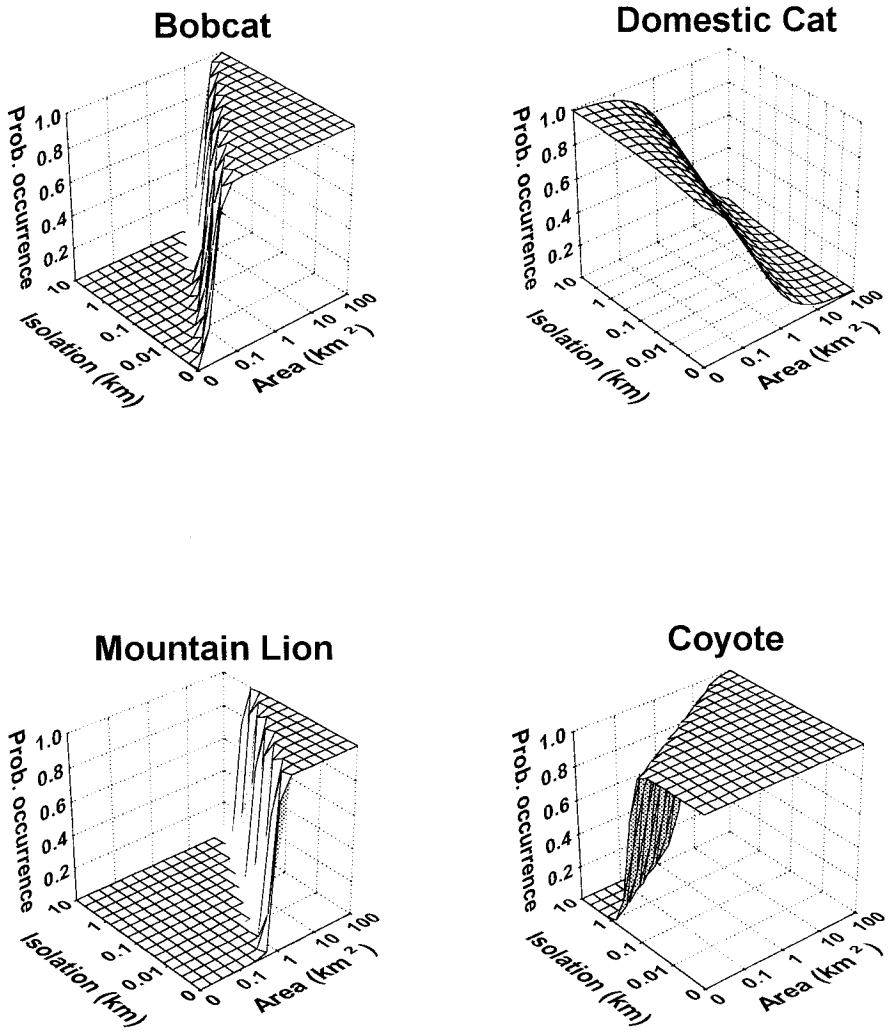

Figure 2. Multiple logistic-regression models of the probability of occurrence of mountain lions, bobcats, coyotes, and domestic cats as a function of fragment area and isolation. Only species with significant area and isolation effects are presented.

distance Y), but only if they were large or were near movement linkages to larger habitat blocks (low value of distance Z). For example, bobcats have persisted in the San Joaquin Hills, an isolated (distance $Y = 5353$ m) but large (4219 ha) habitat block. Bobcats were also detected in Mil Cumbres, a small (6 ha) urban fragment that was isolated from larger natural areas (distance $Y = 550$ m) but that was near a golf course (distance $Z = 23$ m), which likely served as a movement linkage to natural areas to the east.

Local Heterogeneity: Comparisons within Fragments

SPECIES RICHNESS AND RELATIVE ABUNDANCE

The number of carnivore species detected was greater at track stations closer to the urban edge (Table 3). This pattern was largely determined by non-native species. When exotic predators (domestic cats, opossums) were excluded from the analyses, the number of native species detected at each station did not vary significantly with any local variables.

The relative abundance of gray foxes and opossums was higher at track stations near the urban edge within fragments where each species occurred (Table 3). The abundance of domestic cat exhibited a weak negative trend with distance to urban edge. The relative abundance of striped skunks tended to be higher at greater distances from the urban edge. Domestic cats and raccoons tended to be more abundant at stations with more exotic cover. No local variables entered the model for the relative abundance of coyotes.

A graphical analysis revealed that the coyote rate of visitation to track stations was high both near the urban edge and into the interior of the urban habitat fragments (Fig. 3). The abundance of striped skunks also was relatively high in the interior of fragments. In contrast, the abundance of opossums, gray foxes, domestic cats, and raccoons was relatively high within 50 m from urban development, but then tended to decline into the interior of the habitat fragment.

Body Size and Fragmentation Sensitivity

When all species were included in the regression, the relationship between body mass (Table 4) and the average

Table 3. Backward-elimination regression models of the effects of local habitat variables on carnivore species richness and relative abundance at 92 track stations within 29 urban habitat fragments in southern California.[a]

Variables	R^2	*Whole-model* p	*Coefficient*	p
Total species richness	0.049	0.036		
edge			−0.222	0.036
Native species richness				
n.s.[b]				
Coyote (87 stations)				
n.s.				
Gray fox (85)	0.146	<0.001		
edge			−0.382	<0.001
Striped skunk (69)	0.042	0.095		
edge			0.205	0.095
Raccoon (62)	0.056	0.066		
exotic			0.237	0.066
Domestic cat (73)	0.143	0.005		
exotic			0.242	0.057
edge			−0.205	0.105
Opossum (79)	0.079	0.013		
edge			−0.281	0.013

[a]*Independent variables are distance to urban edge, native shrub cover, and total exotic cover. Independent variables with* $p < 0.15$ *were included in the final regression models. For each species, stations were included only in analyses for those fragments where the species was detected.*
[b]*No independent variables were retained in the regression model (*$p > 0.15$*); n.s., not significant.*

area of study sites occupied by each carnivore species, weighted by the standardized track index of each species at each site, was not significant ($r = -0.392$, $p = 0.233$) (Fig. 4a). Spotted skunks, long-tailed weasels, and badgers, however, appeared to be outliers to an otherwise positive relationship between body size and average area of sites occupied. When these three species were excluded from the regression, the positive relationship was significant ($r = 0.725$, $p = 0.042$). Body mass was also positively related to typical home-range sizes (Fig. 4b: $r = 0.720$, $p = 0.012$) and negatively related to typical population densities (Fig. 4c: $r = -0.705$, $p = 0.015$) recorded for these species (Table 4).

Discussion

Landscape Heterogeneity and Carnivore Populations

Fragment area and isolation were the two strongest landscape predictors of predator distribution and abundance. Badgers, long-tailed weasels, spotted skunks, mountain lions, bobcats, and coyotes appear to be the species most sensitive to fragmentation, with a lower probability of occurrence and relative abundance per unit area in smaller and more isolated habitat patches. In contrast, the probability of occurrence and relative abundance of domestic cats, gray foxes, and opossums tended to decrease with fragment area and increase with fragment isolation. Landscape descriptors had relatively little effect on the distribution and abundance of raccoons and striped skunks. Because some carnivores were fragmentation-sensitive, some fragmentation-enhanced, and some fragmentation-tolerant, landscape variables appear to affect species composition more than species richness.

The probability of occurrence of mountain lions, bobcats, and coyotes declined in sequence as habitat patches became smaller and more isolated (Fig. 1). Because mountain lions, bobcats, and coyotes generally occurred in fragments above some threshold of size and isolation, local extinctions of their populations in a fragmenting landscape appear deterministic and predictable (Brown 1986). Such thresholds also suggest that, depending on the species and the degree of fragmentation, a single large reserve would have a higher probability of supporting populations of these predators than archipelagos of similar but smaller isolates (Soulé & Simberloff 1986). For example, our models predict that the probability of occurrence of bobcats will be low in 10 1-km^2 isolates but higher in a 10-km^2 reserve, and that the probability of occurrence of mountain lions will be low in 10 10-km^2 isolates but higher in a 100-km^2 reserve (Fig. 1).

Unlike true islands, habitat patches are part of a landscape mosaic, and the presence of a given species in a patch may be a function not only of patch size and isolation, but also of how the species perceives the intervening matrix (Andren 1994; Rosenblatt et al. 1999). In previous studies in this system, fragment age and area were the most important landscape predictors of the distribution and abundance of native plants (Alberts et al. 1993), scrub-breeding birds (Soulé et al. 1988; Crooks et al. 2001), rodents (Bolger et al. 1997), and invertebrates

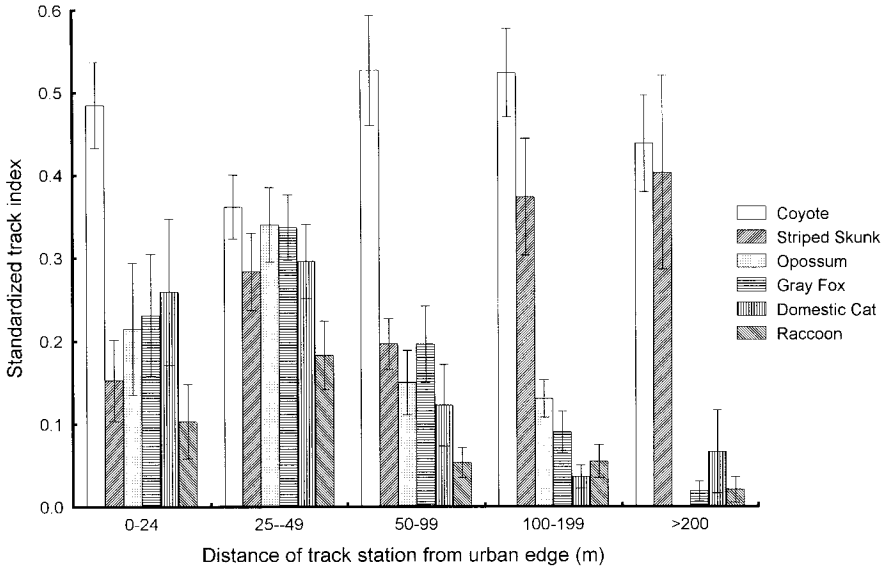

Figure 3. Track indices of carnivore species within urban habitat fragments as a function of the distance of the station from the urban edge. Track indices are standardized for each species.

(Suarez et al. 1998; Bolger et al. 2000). With limited exceptions, isolation effects were absent for these species, likely due to their strict habitat requirements and low dispersal capabilities (Soulé et al. 1992). For these taxa, little to no dispersal across developed areas resulted in complete isolation once fragmentation had occurred, with the fragments operating as true islands immersed within a relatively inhospitable matrix. My results also indicate that fragment isolation was not a strong predictor of the distribution and abundance of human-tolerant mesopredators, although the causal mechanisms differed. Unlike many native scrub-breeding birds, rodents, and invertebrates, mesopredator species such as raccoons, striped skunks, opossums, and domestic cats move through and reside within developed areas and thus perceive the urban matrix as somewhat permeable. High rates of movement through the matrix within which fragments are embedded should also minimize the effects of fragment isolation.

Local Heterogeneity and Carnivore Populations

Within the urban fragments, exotic cover and distance to the urban edge were the strongest local predictors of carnivore distribution and abundance. These two variables were correlated, with more exotic cover and less native shrub cover closer to the urban edge. Previous studies have found that scrub-breeding birds (Soulé et al. 1988), rodents (Bolger et al. 1997), and invertebrates (Suarez et al. 1998; Bolger et al. 2000) require native vegetation to persist in these fragments. Unlike many of these species, however, the mammalian carnivores detected in the habitat fragments are resource generalists that likely benefit from the supplemental food resources

Table 4. Ecological characteristics of mammalian carnivores detected in coastal southern California.[a]

Species	*Weight (kg)*	*Home range (km^2)*	*Density (km^2)*	*Reference*
Mountain lion	69.5 (36.0–103.0)	492 (112–829)	0.027 (0.005–0.048)	Beier & Barrett 1993; Nowak 1999
Coyote	13.5 (7.0–20.0)	5.69 (0.66–11.96)	0.3 (0.2–0.4)	Nowak 1999; Sauvajot et al. 2000
Bobcat	9.7 (4.1–15.3)	2.94 (0.24–5.63)	1.34 (1.15–1.53)	Lembeck 1986; Nowak 1999
Badger	8.0 (4–12)	2.0 (1.6–2.4)	2.70 (0.39–5.0)	Messick 1987; Nowak 1999
Raccoon	7.0 (2.0–12.0)	0.52 (0.39–0.65)	11.2 (2.3–20.0)	Nowak 1999
Gray fox	4.4 (1.8–7.0)	0.69 (0.22–1.87)	5.2 (0.4–10.0)	Nowak 1999; Riley 1999
Domestic cat[b]	3.9 (3.3–4.5)	0.40 (0.001–3.80)	150 (2–500)	Barratt 1997; Nowak 1999
Opossum	3.8 (2.0–5.5)	0.20 (0.05–2.54)	26 (2–116)	Nowak 1999
Striped skunk	1.6 (0.7–2.5)	0.21 (0.11–0.37)	3.3 (1.8–4.8)	Nowak 1999
Spotted skunk	0.6 (0.2–1.0)	0.49 (0.34–0.65)	24.4 (8.8–40)	Crooks & Van Vuren 1995; Kinlaw 1995; Nowak 1999
Long-tailed weasel	0.2 (0.09–0.34)	0.62 (0.04–1.20)	19.4 (0.38–38)	Nowak 1999

[a]*Estimates of body size, home range, and population density vary considerably (Nowak 1999). Values are typical averages and ranges (in parentheses). If no average estimate was provided, median values, calculated from the ranges, are presented. Body-mass estimates were taken from Nowak (1999). Where available, home ranges and population densities were taken from studies conducted in California.*
[b]*Estimates include studies from suburban, urban, rural, and island cat populations.*

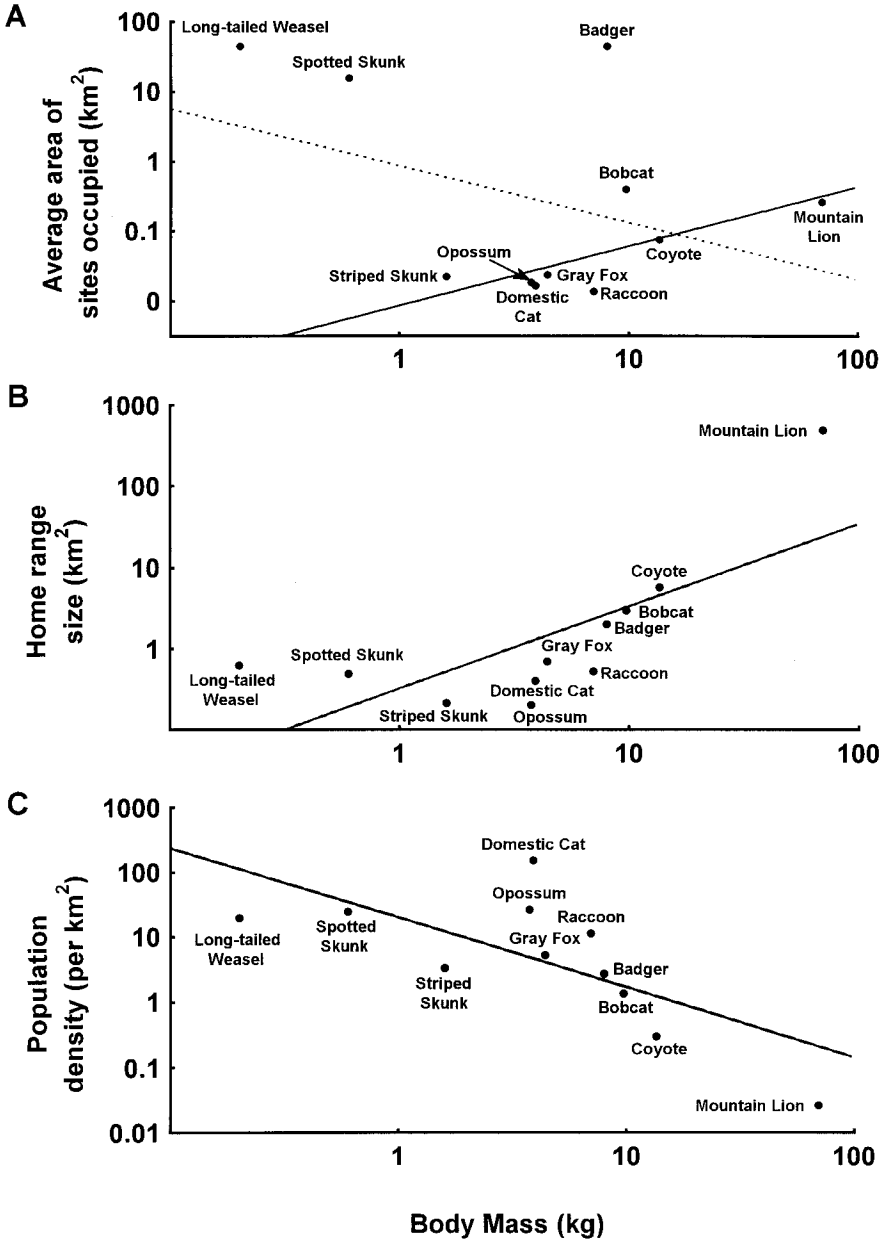

Figure 4. Relationship between log body mass and (a) log average area of sites occupied by mammalian carnivores, weighted by the relative abundance of each species at each site, (b) log home-range size (r = 0.720, p = 0.012; see Table 4 for values), and (c) log population density (r = −0.705, p = 0.015; see Table 4 for values). Dotted line in (a) is the least-squares regression fit including all species in the analysis (r = −0.392, p = 0.233), and the solid line in (a) is the regression excluding spotted skunks, long-tailed weasels, and badgers (r = 0.725, p = 0.042).

(e.g., garden fruits and vegetables, garbage, direct feeding by humans) associated with residential developments. As a result, the carnivore visitation rate actually increased at sites with more exotic cover and closer to the urban edge, a pattern determined largely by the increased abundance of fragmentation-enhanced mesopredators (gray foxes, opossums, and domestic cats) at edge sites within habitat fragments. Although some carnivores within the habitat fragments seem tolerant of disturbance, these fragments have already lost an entire suite of predator species, including mountain lions, bobcats, spotted skunks, long-tailed weasels, and badgers. Furthermore, the habitat fragments are relatively small (<100 ha), so the most "interior" sites within the fragments are still relatively near (<250 m) urban edges.

Unlike true islands, "edge effects" that emanate from the human-dominated matrix can increase the extinction probability of isolated populations (Murcia 1995; Woodroffe & Ginsberg 1998). Human-tolerant mesopredators in southern California represent such an edge effect. They occur within the developed matrix, are more abundant along the edges of habitat fragments, and are effective predators on birds, bird nests, and other vertebrates in this system and elsewhere (Crooks & Soulé 1999). Several factors likely account for increased numbers and activity of mesopredators in disturbed landscapes. Residential developments represent suitable habitat for some mesopredator species whose distributions are closely associated with human-dominated landscapes (Donovan et al. 1997). In addition to

habitat suitability, however, dominance interactions between carnivores affect mesopredator populations. When large, dominant predators disappear in fragmented systems, smaller, subordinant predators can subsequently undergo an ecological release, a pattern termed mesopredator release (Soulé et al. 1988; Crooks & Soulé 1999). In the San Diego habitat fragments, Crooks and Soulé (1999) found that lower visitation rates of coyotes in small, isolated remnants resulted in elevated numbers and activity of urban mesopredators, even after statistically controlling for potential confounding variables such as fragment area, age, and isolation. Mesopredator species therefore appear to be ecologically released by fragmentation not only because they can adapt well to urban environments, but also because such sites may provide refugia from dominant predators.

All Carnivores Are Not Created Equal

Although they are generally considered part of the same ecological guild, I found that carnivores were heterogeneous in their sensitivities to landscape and local fragmentation variables. As predicted, body-size differences partially accounted for this heterogeneity in response. Body mass was positively related to typical home-range sizes (Fig. 4b) and negatively related to typical population densities (Fig. 4c) recorded for these species, patterns consistent with those observed among mammals (Lindstedt et al. 1986). Due to their wide ranges and low densities, larger-bodied carnivores generally required larger areas (Fig. 4a), eventually disappearing in habitat fragments that were not connected by movement corridors. Obvious exceptions to the allometry of body size and fragmentation sensitivity, however, were spotted skunks, long-tailed weasels, and badgers, small- to medium-bodied species that exhibit relatively small home ranges and high population densities but that were detected only in the largest habitat blocks. Unlike the generalist urban mesopredators, these relatively specialized mustelids tend to be primarily carnivorous and somewhat restricted in their habitat preferences (Nowak 1999). Such specializations likely contribute to their patchy distribution in coastal southern California and increase their vulnerability to environmental disturbances. Clearly, in addition to body size, other ecological traits such as diet, resource specialization, social structure, and behavior contribute to species-specific responses to fragmentation effects.

Differential sensitivities to fragmentation can be useful criteria when focal species are chosen for ecological research and conservation planning. Mammalian carnivores can be excellent focal organisms with which to evaluate the degree of functional landscape-level connectivity, because they are area-dependent species that require movement corridors for persistence (Beier 1993; Noss et al. 1996; Soulé & Terborgh 1999). The choice of appropriate carnivore focal species, however, depends on the scale or intensity of fragmentation in an area and the corresponding responses of carnivore populations to fragmentation effects at that scale. As Figs. 1 and 2 make evident, the scale of landscape-level connectivity in southern California varies widely, ranging from small, isolated urban remnants to large, intact habitat blocks.

At one extreme of the connectivity scale are the highly fragmented landscapes of urban coastal southern California (e.g., patch size <1 km^2; Fig. 1a). Coyotes and urban mesopredators can be useful focal species with which to understand the effects of fragmentation at this scale. Fragmentation-enhanced predators such as opossums and domestic cats can function as direct, positive indicators of environmental disturbances associated with urban development, edge effects, and the invasion of exotic predators and competitors into natural systems. Coyotes have also persisted in developed areas in southern California. The remarkable behavioral plasticity of coyotes and their ability to succeed in disturbed areas limits their utility as an indicator of connectivity across much of coastal southern California. Nevertheless, coyote occupancy, residency, and relative abundance declined with fragment area and isolation, to the point of local extinctions of coyote populations in the smallest, most isolated urban remnants. Coyotes can therefore serve as useful indicators of functional connectivity in highly fragmented areas, particularly those sites that have already lost more vulnerable predators such as bobcats and mountain lions (Figs. 1 & 2). Furthermore, the ecologically pivotal role of coyotes (Crooks & Soulé 1999) warrants their inclusion in research and conservation plans, particularly in regions with active predator-control programs.

Mountain lions are situated at the opposite end of the connectivity scale (e.g., patch size >100 km^2; Fig. 1a) and appear extremely sensitive to the loss and fragmentation of habitat. The large body size and solitary behavior of mountain lions translate to large home ranges and low population densities (Table 4). Therefore, many of the isolated habitat remnants in urban southern California are likely too small and too isolated to permanently support any resident lion populations (Figs. 1 & 2) (see also Beier 1993). Consequently, mountain lions or other large, apex predators may not be the most effective indicator species with which to evaluate the degree of functional landscape-level connectivity in moderately to highly fragmented landscapes. The mountain lion's requirement for a large home range and its sensitivity to environmental perturbations, however, can make it a valuable focal species in larger, more intact habitat blocks (Beier 1993).

Finally, bobcats were intermediate in their sensitivity to fragmentation, a degree of sensitivity commensurate to the scale of fragmentation across much of coastal

southern California (e.g., 1 km^2 <patch size < 100 km^2; Fig. 1a). Bobcats were less sensitive to disturbance than mountain lions, which seldom occurred in fragmented areas, yet were more sensitive than coyotes and mesopredators, which were detected in even small urban habitat fragments. Bobcats are generally solitary and are strictly carnivorous (Nowak 1999), resulting in low densities and in resource specializations that likely increase their probability of local extinction. Landscape connectivity appears to be the key to the persistence of bobcat populations in developing landscapes. They can persist in fragmented habitats, but, as my results suggest, only in those landscapes with adequate movement linkages to larger natural areas. The status of bobcat populations is therefore a valuable indicator of the degree of functional, landscape-level connectivity across much of the fragmented landscapes of coastal southern California. In other systems, the choice of indicator species will require information on the level of fragmentation and connectivity in that region and how species respond to fragmentation effects at that scale.

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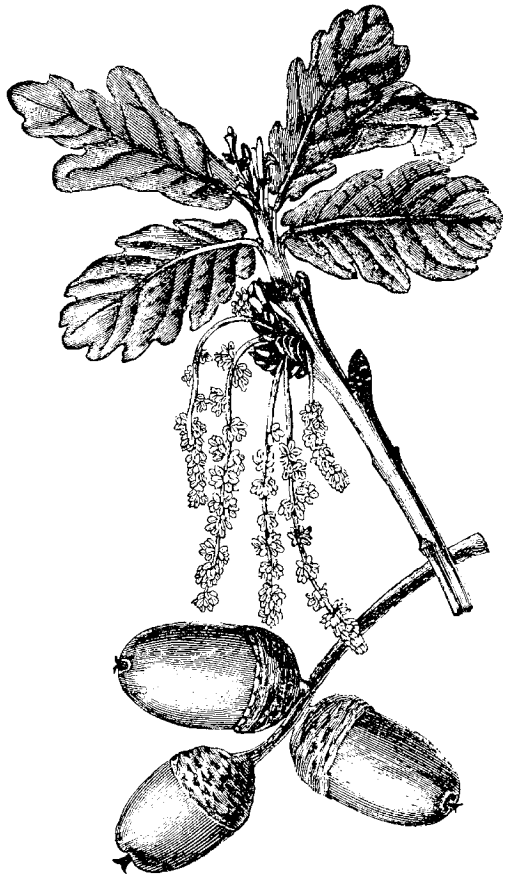

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Effects of habitat loss and fragmentation on amphibians: A review and prospectus

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ABSTRACT

Habitat loss and fragmentation are among the largest threats to amphibian populations. However, most studies have not provided clear insights into their population-level implications. There is a critical need to investigate the mechanisms that underlie patterns of distribution and abundance. In order to understand the population- and species-level implications of habitat loss and fragmentation, it is necessary to move from site-specific inferences to assessments of how the influences of multiple factors interact across extensive landscapes to influence population size and population connectivity. The goal of this paper is to summarize the state of knowledge, identify information gaps and suggest research approaches to provide reliable knowledge and effective conservation of amphibians in landscapes experiencing habitat loss and fragmentation. Reliable inferences require attention to species-specific ecological characteristics and their interactions with environmental conditions at a range of spatial scales. Habitat connectivity appears to play a key role in regional viability of amphibian populations. In amphibians, population connectivity is predominantly effected through juvenile dispersal. The preponderance of evidence suggests that the short-term impact of habitat loss and fragmentation increases with dispersal ability. However, species with limited dispersal abilities are likely to be equally imperiled by habitat loss and fragmentation over longer time periods. Rigorous understanding of the effects of habitat loss and fragmentation on amphibians will require species-specific, multi-scale, mechanistic investigations, and will be benefit from integrating large empirical field studies with molecular genetics and simulation modeling. Molecular genetic methods are particularly suited to quantifying the influences of habitat structure across large spatial extents on gene flow and population connectivity. Conservation strategies would benefit by moving from generalizations to species and process specific recommendations and by moving from site-specific actions to implementing conservation plans at multiple scales across broad landscapes.

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1. Introduction

1.1. *The extinction crisis and amphibians*

Earth is facing the largest mass extinction in 65 million years (Lawton and May, 1995; Vitousek et al., 1997; Wilson, 1999; Myers and Knoll, 2001; Balmford et al., 2003). Current global extinction rates for animals and plants are estimated to be up to 1000 times higher than the background rate in the fossil record (Wilson, 1999; Baillie et al., 2004). Vertebrate animal taxa are disappearing at disproportionately high rates, and amphibians are the group with the highest proportion of

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species threatened with extinction (Stuart et al., 2004; Beebee and Griffiths, 2005). The 2004 IUCN red list of threatened and endangered species identifies one in three of the world's amphibian species as threatened with extinction (Baillie et al., 2004).

1.2. *Vulnerability of amphibians*

The apparent vulnerability of amphibians (Pechmann et al., 1991; Houlahan et al., 2000; Kiesecker et al., 2001; Baillie et al., 2004) may be due to a complex of factors, including: (1) relatively low vagilities, which amplifies the effects of habitat fragmentation (Sinsch, 1990; Gibbs, 1998; deMaynadier and Hunter, 2000; Bowne and Bowers, 2004), (2) high vulnerability to death when moving across roads and through inhospitable terrain, which depresses population growth rates (Fahrig et al., 1995; Carr and Fahrig, 2001; Carr et al., 2002), (3) often narrow habitat tolerances, which exacerbates the effects of habitat loss, degradation, and edge effects (Findlay and Houlahan, 1997; Semlitsch, 2000; Houlahan and Findlay, 2003), and (4) high vulnerability to pathogens, invasive species, climate change, increased ultraviolate-B exposure and environmental pollution (Pounds et al., 1999; Broomhall et al., 2000; Kiesecker et al., 2001; Blaustein et al., 2000; Hecnar, 1995; Bridges and Semlitsch, 2000; Davidson et al., 2001; Stuart et al., 2004).

1.3. *Importance of habitat loss and fragmentation*

Habitat loss and fragmentation contribute directly to most of these threats (Carr and Fahrig, 2001; Bowne and Bowers, 2004; Houlahan and Findlay, 2003). Recent research has provided information on the relationships between certain amphibians and certain attributes of habitat loss and fragmentation, and has clearly implicated the effects of habitat fragmentation on juvenile dispersal as one of the key issues in the conservation of pond breeding amphibians (Sjögren, 1991; Sinsch, 1992; Sjögren-Gulve, 1994; Vos and Chardon, 1998). However, most studies of the influences of habitat loss, fragmentation, or related mortality risks have not provided clear insights into the population-level implications of these impacts (Carr et al., 2002). There is a clear need for studies that focus on the mechanisms that drive patterns of distribution and abundance (Marsh and Trenham, 2001; Bowne and Bowers, 2004).

1.4. *Moving from sites to landscapes; ponds to populations*

In order to understand the population-level implications of habitat loss and fragmentation, it is necessary to move from site-specific inferences to assessments of how multiple factors interact across large spatial extents to influence population size and population connectivity (Ruggiero et al., 1994; McGarigal and Cushman, 2002; Bowne and Bowers, 2004). Non-spatial studies conducted at local scales do not provide a basis for inferences at the landscape or regional level (McGarigal and Cushman, 2002). There is often a gross mismatch between the scale of ecological research and population-level responses (Kareiva and Anderson, 1988; Ruggiero et al., 1994). For example, correlations between organism abundance and the area of various landcover types within a certain distance of a breeding pond does not provide information necessary to infer how habitat patterns interact with the spatial distribution of breeding ponds to influence distribution and abundance. Landscape-level studies that represent the spatial patterns of the environment in a manner relevant to the organisms of question, and that address species-specific movement and abundance characteristics are essential to extend fine-scale species environment relationships to the population-level (McGarigal and Cushman, 2002).

1.5. *Purpose and goals*

The overall goal of this paper is to summarize the state of knowledge, identify information gaps and suggest approaches to provide reliable knowledge and effective conservation of amphibians in landscapes experiencing habitat loss and fragmentation. The paper is divided into four major components. The first is a review of current knowledge about relationships between habitat loss and fragmentation and pond-breeding amphibian populations at landscape and regional scales. Using this review as context, the second section identifies some important information gaps and research needs. Next, I propose several research approaches that may be effective at filling these information gaps. Then, I suggest several ideas to link research more effectively to conservation, and suggest interim conservation strategies.

2. The state of knowledge

2.1. *Habitat area in uplands*

Relatively few landscape-level studies of amphibian density and movement have been conducted (Houlahan et al., 2000; McGarigal and Cushman, 2002). Most existing studies have focused on relationships between forest cover and species occurrence. These have shown positive relationships between amphibian populations and area of forest in the surrounding landscape (Dupuis and Steventon, 1999; Knutson et al., 1999; Guerry and Hunter, 2002; Houlahan et al., 2000; Trenham and Shaffer, 2005), and negative relationships with urban development (Delis et al., 1996) and roads (Fahrig et al., 1995; Carr et al., 2002). Studies of landscape composition effects have found relationships between forest cover and amphibian presence at spatial scales ranging from 100 m to over 3000 m radii (Hecnar and M'Closkey, 1997; Knutson et al., 1999; Lehtinen et al., 1999; Guerry and Hunter, 2002; Houlahan et al., 2000; Trenham and Shaffer, 2005). Several studies also note a general pattern of increased species richness with increasing forest cover (Gibbs, 1998; Kolozsvary and Swihart, 1999; Houlahan et al., 2000).

Despite these generalizations, reliable inferences about habitat area effects require attention to species-specific ecological characteristics and their interactions with environmental conditions at a range of spatial scales. Species-specific characterization of habitat is essential if scientists are to evaluate the effects of habitat loss on populations. For example, the suggestion that forest cover in the landscape benefits amphibians may not apply to species that are fully aquatic or that depend on nonforested upland habitat. Also, some

populations of amphibians have been enhanced by human construction of ponds and wetlands in areas where breeding sites were previously limited, such as arid environments. In addition, the location and slope of critical thresholds in habitat amount are species specific, and related to reproductive potential, dispersal ability, home range size, habitat specificity, and other characteristics (Monkkonen and Reunanen, 1999; Fahrig, 2001). Thus, it is essential to explicitly link the habitat tolerances of a species to the extent and pattern of those habitats in the landscape if one is to produce reliable inferences about relationships between habitat area and species distributions.

2.2. *Habitat isolation*

Several studies have suggested that habitat area is often more important than habitat configuration (Fahrig, 1998, 2003; Cushman and McGarigal, 2004). The evidence for amphibians is equivocal on this question. Guerry and Hunter (2002) found positive associations between nine amphibian species, area of forested habitat and proximity of ponds to forest habitat. Seven of the nine species were associated with forest area. Three of the nine were associated with pond-forest adjacency. This indicates that habitat area and isolation are both important, and that the degree of importance is a species-specific property which likely reflects a combination of life-history and behavioral characteristics.

A growing body of work suggests that roads can have substantial negative effects on amphibian persistence (Vos and Chardon, 1998; Carr and Fahrig, 2001). Habitat fragmentation by roads and other barriers decreases dispersal (Gibbs, 1998; deMaynadier and Hunter, 2000), increases mortality (Fahrig et al., 1995; Carr and Fahrig, 2001) and reduces genetic diversity (Reh and Seitz, 1990). Habitat fragmentation leads to reduced patch size patches, increased patch isolation, and increased risk of demographic, stochastic and genetic events. This increases extinction risk by reducing demographic and genetic input from immigrants and reducing the chance of recolonization after extinction (Lande, 1988; Sjögren-Gulve, 1994).

2.3. *Connectivity: a key to persistence*

A number of researchers have proposed that habitat connectivity is a key to regional viability of amphibian populations (Hecnar and M'Closkey, 1996; Semlitsch et al., 1996; Semlitsch and Bodie, 1998; Skelly et al., 1999; Marsh and Trenham, 2001; Rothermel and Semlitsch, 2002). Amphibians generally have lower rates of movement per generation than invertebrates, mammals or reptiles (Bowne and Bowers, 2004). Low recruitment of dispersing individuals probably plays a major role in decline and extinction of amphibian populations in fragmented landscapes (Sjögren, 1991; Sinsch, 1992; Sjögren-Gulve, 1998; Vos and Chardon, 1998; Bulger et al., 2003). Breeding sites lacking connectivity to suitable terrestrial habitat may be population sinks due to high mortality of juveniles during emigration (Rothermel, 2004). A number of studies have indicated that populations may decline if immigration is prevented (Brown and Kodric-Brown, 1977; Harrison, 1991) and may not be recolonized following a local extinction (Semlitsch and Bodie, 1998). Connectivity seems to be of particular importance as even in unfragmented landscapes, amphibian populations experience relatively frequent local extinction and turnover (Edenhamn, 1996; Hecnar and M'Closkey, 1996; Alford and Richards, 1999; Trenham et al., 2003). Thus, dispersal is critical for recolonization of local populations and maintenance of regional populations (Hecnar and M'Closkey, 1996; Semlitsch et al., 1996; Skelly et al., 1999).

2.4. *Role of juvenile dispersal in population connectivity*

In amphibians, population connectivity is predominantly effected through juvenile dispersal (Madison, 1997; Preisser et al., 2001; Guerry and Hunter, 2002; Rothermel, 2004). Many studies have indicated that post-metamorphic dispersal contributes more to regional persistence than does adult dispersal (Sinsch, 1992, 1997; Sinsch and Seidel, 1995). For example, Preisser et al. (2001) found that adults of a variety of amphibian species move up to 125 m from breeding ponds, while juvenile *Ambystoma* sp. salamanders dispersed up to 670 m, and Wood frog (*Rana sylvatica*) over 1000 m. From this they concluded that juvenile dispersal is essential for landscape connectivity for these species. Other studies have reached similar conclusions based on the relatively small movement distances and philopatry of adults and relatively large dispersal distances of juveniles (Breden, 1987; Berven and Grudzien, 1990).

2.5. *Effects of fragmentation on population connectivity*

There are several important implications of habitat fragmentation on species persistence. First, a number of studies have shown that high levels of post-metamorphic survival are often required to maintain local populations. For example, one study found that survival to first reproduction had to exceed 18% in order to maintain local populations of the California tiger salamander (*Ambysotma californiense*) (Trenham et al., 2000). However, as they report survival to maturity of less than 5%, they conclude their study population is a sink that would be doomed to extinction in the absence of substantial immigration. In addition, a population model developed for marbled salamander (*Ambystoma opacum*) suggested that post-metamorphic survival had to exceed 70% to maintain local populations (Taylor and Scott, 1997). Second, a number of studies have shown substantial reductions in dispersal success and juvenile survival in fragmented landscapes. For example, Rothermel (2004) found an average of only 9% of juvenile spotted salamander (*Ambystoma maculatum*) released 50 m from a forest edge survived their initial migration to forest. Habitat loss and fragmentation can substantially reduce the abilities of juvenile amphibians to disperse across landscapes and the resulting reductions in post-metamorphic survival and population connectivity can threaten viability.

Recently, a number of studies have investigated the relationships between landscape structure and amphibian dispersal with experimental methods. Both spotted salamanders and wood frogs avoid crossing fields, pastures, clearcuts, lawns, and roads (Windmiller, 1996; Gibbs, 1998; deMaynadier and Hunter, 1999; Rothermel and Semlitsch, 2002; Regosin et al., 2003; Marsh et al., 2004). Wood frogs have also been

shown to orient toward forest (deMaynadier and Hunter, 1999). Rothermel and Semlitsch (2002) studied the orientation and movement of several amphibian species in open field and forest environments. They found that orientation of spotted salamander and wood frog is biased toward forest. Spotted salamanders moved three times as far into forest as into fields (Rothermel and Semlitsch, 2002). Lower recapture rates in fields reflected high mortality rates due to desiccation and predation. Also, avoidance of open-canopy habitats by juvenile American toads (*Bufo americanus*) indicates that predictions of dispersal behavior based on adult habitat use may be misleading (Rothermel and Semlitsch, 2002). Rothermel (2004) conducted an experimental study of movement of spotted salamanders and American toads in grass fields at distances of 5 or 50 m from a forest edge. Less than 15% of salamanders and toads released 50 m from the forest edge reached forest, suggesting that few juvenile amphibians would be able to migrate greater distances across pastures (Rothermel, 2004). The authors conclude that fields are substantially resistant, and thus forest fragmentation reduces dispersal rates for these species (Rothermel and Semlitsch, 2002; Marsh et al., 2004; Rothermel, 2004).

Recent research has also suggested that the short-term impacts of habitat fragmentation often increase both with population size and dispersal ability, but particularly strongly with increasing dispersal ability (Gibbs, 1998; Newcomb Homan et al., 2004). This pattern is opposite to what many researchers expect on theoretical grounds, namely that species with larger populations and larger dispersal abilities will be less impacted by fragmentation due to their relatively greater abilities to disperse between breeding sites in fragmented landscapes. For example, in a study of five amphibian species across a gradient of habitat loss, Gibbs (1998) found that organisms with low dispersal rates had better persistence in landscapes with low habitat area. This effect has also been seen in comparison of wood frog and spotted salamander habitat occupancy (Newcomb Homan et al., 2004). A possible explanation is that greater dispersal ability results in greater mortality risk in fragmented landscapes. Carr and Fahrig (2001) suggest that highly vagile organisms may be at a disadvantage in landscapes with roads because of increased likelihood of mortality. An example of this may be the response of red-spotted newt (*Notophthalmus viridescens*) in fragmented landscapes (Guerry and Hunter, 2002). Red-spotted newts appear to have high sensitivity to habitat loss and forest fragmentation. In one study, they were the first species to disappear from a fragmented landscape (Gibbs, 1998). The terrestrial stage of red-spotted newts may last seven years (Forester and Lykens, 1991) in which they may travel long distances from the natal pond (Gill, 1978). Declines in fragmented landscapes are probably often related to elevated losses of juveniles in the terrestrial period (Gibbs, 1998). The preponderance of evidence suggests that the short-term impact of habitat loss and fragmentation increases with dispersal ability. In a fragmented landscape individuals of species with large dispersal abilities will generally encounter roads and other anthropogenic barriers at higher rates than less vagile species. This will tend to increase mortality rates for these species. The combined effects of roads and landcover may result in high rates of death among dispersing juveniles, which can imperil local and regional populations by decreasing recruitment (Sinsch, 1992, 1997; Sinsch and Seidel, 1995).

It appears that species with large dispersal abilities and those with relatively small dispersal abilities are both threatened by habitat loss and fragmentation, but in different ways. Those with large dispersal abilities are vulnerable to elevated dispersing mortality, which appears sufficient to lead to local extinctions (Hecnar and M'Closkey, 1996; Semlitsch et al., 1996; Skelly et al., 1999). However, species with limited dispersal abilities are likely to be equally imperiled by habitat loss and fragmentation over longer time periods. Once these local populations are isolated by fragmentation they may be ultimately doomed to extinction. Amphibian populations experience relatively frequent extinction and turnover (Edenhamn, 1996; Hecnar and M'Closkey, 1996; Alford and Richards, 1999; Trenham et al., 2003), thus population connectivity is ultimately important even for populations of species that are not directly impacted by habitat loss or elevated mortality risks in dispersing.

3. Challenges to general knowledge

3.1. *Lack of species-level information*

Despite these generalizations, there are several obstacles that must be overcome before scientists will be able to reliably predict population-level responses of specific species to changes in habitat area or isolation. In most parts of world, there is very limited knowledge of the species–environment relationships of amphibians, their responses to habitat loss and fragmentation and the factors controlling population connectivity (Hazell, 2003). Knowledge is still quite rudimentary about the population-level implications of habitat area, edge, isolation, and road mortality relationships. The precision of knowledge about the habitat relationships, life-history, vagility and behavior of most amphibian species is insufficient. Few studies report population level effects of inter-patch movement and few document movement rates (Bowne and Bowers, 2004). In addition, those studies that do measure movements rarely produce results that can be generally applied, as dispersal data are highly sensitive to sampling scheme and landscape characterization (Carr and Fahrig, 2001). Amphibians exhibit a great range of habitat requirements and dispersal abilities (Stebbins and Cohen, 1995). Little is known about the factors influencing dispersal (Rothermel and Semlitsch, 2002; Rothermel, 2004). Information about the dispersal abilities and relative cost or risk of crossing various landcover types is insufficient for most species to reliably model responses to real landscape mosaics. Additional research is needed to determine appropriate threshold distances and cover-class resistance values for migrating amphibians (Rothermel, 2004). Furthermore, the high variability of population sizes through time confounds efforts to isolate mechanisms through correlative means (Alford and Richards, 1999). The combination of variable population sizes and imprecise knowledge of dispersal parameters and habitat tolerances presents a daunting challenge for researchers attempting to infer population-level impacts of habitat loss and fragmentation on amphibians.

Another obstacle to population-level predictions is that few landscape level studies of habitat fragmentation effects have been conducted. McGarigal and Cushman (2002) reviewed 134 papers on habitat fragmentation published between 1995 and 2000. They identified a paucity of experimental studies at the landscape-level. Most studies were patch-based, and poorly replicated or unreplicated, which greatly limits the inferences that can be reliably drawn. Importantly, they identified amphibians and reptiles as the animal taxa most poorly studied, accounting for only 4% of papers on the effects of habitat fragmentation.

4. Research needs

4.1. *Importance of species-specific, multi-scale, mechanistic investigations*

Survival of amphibian populations in fragmented landscapes depends on the interaction between the pattern of roads, landcover types, the distribution of breeding ponds, the population sizes in those ponds and the dispersal characteristics of the species (Fahrig, 1998; Carr and Fahrig, 2001). For example, Porej et al. (2004) emphasize the importance of considering scaling differences among species and the structure of the landscape mosaic when investigating thresholds and minimum patch sizes. Furthermore Marsh and Trenham (2001) suggest that pond isolation is often better explained by details of the structure of terrestrial habitats than the distribution of breeding habitats in that landscape, and urge researchers to focus on mechanisms underlying patterns of dispersal and abundance. Petranka et al. (2004) found that there is often a lack of demographic independence within clusters of local breeding ponds, and that the degree of spatial synchrony in local populations varied between species and in response to localized disturbances. Predicting such effects would require information about species specific responses to disturbance, population sizes, movement rates and abilities. Both Monkkonen and Reunanen (1999) and Fahrig (2001) predicted that the location and slope of critical thresholds in habitat amount should be species-specific, and based on a variety of traits including reproductive potential, emigration success, home range size, habitat specificity, dispersal ability and other behaviors.

Each species experiences and responds to ecological conditions in its environment uniquely. Thus, reliable understanding of interactions between species and their environments requires careful attention to both scale and the characterization of the environment. First, species-environment relationships may differ greatly among species across scales (Cushman and McGarigal, 2004). The environmental patterns that are important at one scale for a species may not be those that influence it at coarser or finer scales (Grand and Cushman, 2003). Thus, researchers must adopt multi-scale approaches that allow for assessment of the interaction of environmental patterns across scales (Wiens, 1989; Cushman and McGarigal, 2003). Second, the environment is experienced differently among species. Thus, researchers should select and characterize the environmental attributes on a species-specific basis. For amphibians, this often means assessing interrelationships between multiple environmental attributes, across a range of scales, for entire landscapes containing dozens or hundreds of local breeding populations. Only by analyzing species-relevant habitat patterns at scales relevant to the populations of those species will it be possible to obtain reliable inferences about the impacts of habitat loss and fragmentation on amphibian populations (McGarigal and Cushman, 2002).

5. Research approaches

5.1. *Empirical approaches*

There are at least four major ways that one could empirically test relationships between the presence or movement of a particular species and environmental structure at the landscape-level. First, one could conduct large-scale, correlative studies of distribution in relation to habitat composition and configuration at a range of scales (Hecnar and M'Closkey, 1996; Knutson et al., 1999; Kolozsvary and Swihart, 1999; Vallan, 2000; Guerry and Hunter, 2002; Weyrauch and Grubb, 2004). Such studies, if replicated sufficiently at the landscape level, can provide reliable information about relationships between landscape structure and the distribution of specific amphibians. The major challenges to such studies are obtaining sufficient replication at the landscape-level to achieve reasonable statistical power, sampling sufficiently large landscapes to allow adequate consideration of environmental patterns at a range of spatial scales, and representing environmental conditions and landscape structures in manners that are relevant to each species in question (McGarigal and Cushman, 2002). These types of studies are also limited in inference because they do not directly measure biological responses such as mortality, movement and productivity. Presence does not always equate to quality. Patterns of distribution do not necessarily reflect patterns of fitness with respect to environmental gradients and landscape patterns.

Two alternative approaches are mark-recapture and telemetry studies (deMaynadier and Hunter, 1999; Rothermel and Semlitsch, 2002; Rothermel, 2004). By quantifying movement rates, distances and routes of dispersing juveniles through complex environments researchers can describe species-specific responses to environmental conditions. Importantly, these methods are well suited for incorporation in manipulative field experiments in which the area and configuration of habitat are controlled to isolate the effects of habitat loss and fragmentation on organism movement and survival rates. These kinds of studies provide the most reliable inferences about relationships between survival rates, movement and ecological conditions (McGarigal and Cushman, 2002). The challenge in these studies is one of cost and sample sizes. Large-scale manipulative field experiments and mark-recapture metapopulation studies are exceptionally expensive to implement, take a number of years to produce reliable results, and generally do not provide large landscape-level sample sizes due to financial and logistical constraints. Likewise, telemetry studies are often limited by spatial scope, sample size and pseudoreplication (Litvaitis et al., 1994).

A fourth alternative involves using molecular genetic methods to empirically derive rates of gene flow among ponds and effective population sizes (Schwartz et al., 1998;

Manel et al., 2003; Curtis and Taylor, 2004; Funk et al., 2005). Molecular genetic methods offer a particularly attractive approach to quantifying gene flow across heterogeneous landscapes, as the logistical and financial costs of extensive mark-recapture study grids are obviated. The genetic characteristics of subpopulations at each sampled pond can provide both information on its effective population size and the degree to which it differs genetically from other ponds. Such methods allow one to quantify rates of gene flow between ponds, assuming time lags between landscape change and genetic response have been accounted for. This in turn allows researchers to test specific hypotheses about the role of specific landscape features and environmental conditions in affecting population connectivity (Manel et al., 2003).

5.2. *Simulation models*

Simulation models offer a flexible way to investigate the behavior of idealized ecological processes in idealized landscapes. It is important to understand that this idealization in simulation modeling is both a limitation and an asset. It is a limitation in that a simulation is never equivalent to the phenomena being simulated. Decisions are made on which processes to include, at which scales, their relative weights, the functional structure of each and how they interact. Similarly, decisions are made on how to represent the structure and composition of landscapes and how to represent the behavior and ecology of organisms. These decisions fundamentally determine the results, and error in them results inevitably in error in the predictions.

However, the fact that such decisions determine results can also be an advantage. By varying functional parameters, environmental characterization, and organism attributes, scientists can investigate hypotheses about the relative influence of different factors, their interactions, and ranges of organism characteristics, such as gradients of population size or dispersal ability. This provides a means for thorough evaluation of complexes of factors that would be impossible to investigate directly in the field.

5.3. *Integrating simulation models and empirical field studies*

Simulation results are not compelling unless verified by empirical data. Reliable model predictions depend on accurate algorithmic implementation of the process–pattern relationships that dominate the behavior of the phenomena being simulated. Models require extensive empirical understandings for their formulation, and require extensive empirical data for their verification. It can be said that models without data are not compelling, and data without models are not informative.

A powerful research paradigm is based on confronting models with rigorous empirical data to test the applicability and generality of relationships, and account for the influences of spatial patterns, temporal fluctuations and time lags (Kareiva and Anderson, 1988). It is an iterative process, with models proposing relationships, data refuting or supporting models, models being refined as a result and producing new predictions to be empirically tested. Field studies should be designed specifically to provide information needed to parameterize and test simulation models. In this effort, manipulative experiments may provide the best information, given their ability to isolate particular factors. However, the most promising area for integrating models with field data is in the area of landscape genetics (Manel et al., 2003). Simulation models can produce explicit predictions of the level of connectivity among populations across landscapes. Molecular genetics can quantify actual rates and patterns of gene flow. The intersection of these two provides a means to optimize the fit of simulation models to actual patterns of gene flow in complex landscapes. This optimization of the fit of spatial models to patterns of gene flow in real populations provides an unprecedented means to explore and understand the interactions between environmental patterns across a range of spatial scales and the connectivity of populations, which is among the most important questions in conservation biology.

6. Conservation strategies

6.1. *From general to specific*

A number of researchers have proposed generalized conclusions and conservation recommendations based on the observation that forest habitat area, habitat connectivity and road density are related to population persistence and population connectivity. These generalizations include that the effects of adjacent land use on amphibians can extend over large distances (Houlahan and Findlay, 2003), and that the proximity and area of upland/breeding habitat play a key role in determining occupancy (Laan and Verboom, 1990; Pope et al., 2000). It is clearly important to account for impact of uplands surrounding wetlands (Dodd and Cade, 1998; Semlitsch, 1998) as amphibian conservation often requires maintaining relatively large forest areas and relatively low road densities in the regional landscape (Houlahan et al., 2000). However, it is not clear how to translate these general understandings to specific management recommendations for individual species in any given landscape. There are large differences among amphibian species in terms of their habitat requirements and sensitivity to landscape change. Effective conservation requires specific predictions that can be applied to unique situations to produce conservation recommendations tailored to the system, species and situation.

6.2. *Core area conservation*

Several researchers have proposed conservation strategies based on protecting core areas based on limited adult migration and adult philopatry. For example, Bulger et al. (2003) suggested that specific protections for migrating California red-legged frogs *(Rana aurora draytoni)* were usually unwarranted and that protecting breeding sites is critical. Other researchers propose core zone widths based on adult migrations. For example, Semlitsch (1998) and Semlitsch and Bodie (2003) suggest core zones up to 218 meters for pond breeding amphibians and up to 290 meters for amphibians in general. Other researchers stress the importance of forest in core zones for persistence of spotted salamander, marbled

salamander, Jefferson's salamander (*Ambystoma jeffersonianum*), and wood frog, based on the fact that they are unlikely to persist and travel long distances in non-forest habitat (Whitford and Vinegar, 1966; Thompson et al., 1980; Douglas and Monroe, 1981; Kleeberger and Werner, 1983; deMaynadier and Hunter, 1998; Rothermel and Semlitsch, 2002). While these core zones have been advocated by some as a guide for setting biologically meaningful buffers for wetlands and riparian zones (Semlitsch and Bodie, 2003), they are insufficient as a basis for a conservation strategy for pond breeding amphibians. Any effective conservation strategy must consider more than critical core habitat for adults (Porej et al., 2004). Juvenile dispersal and habitat connectivity are at least as important (Carr and Fahrig, 2001).

6.3. *Landscape-level, population-based conservation strategies*

Just as it is necessary to move from site-specific to landscape-level analyses to understand the ecological relationships between amphibian populations and their environments, it is also necessary to base conservation planning on landscape-level and population-based approaches. Non-spatial conservation plans implemented at specific sites are unlikely to provide adequate conservation of populations that depend on dispersal across complex landscapes for persistence. Just as there is often a gross mismatch between the scale of ecological research and population-level responses, there is usually the same mismatch between the scale of conservation planning and the scale of population responses.

Effective conservation planning will require vast improvements in our understanding of the factors that influence vital rates, mortality and dispersal in complex landscapes. Given the urgency of the crisis facing amphibian populations (Baillie et al., 2004), it is imperative that conservation planners make the most effective use of the information currently available. This will entail extending information from empirical research on the relationships between population size, reproduction, dispersal, mortality and habitat factors across a range of scales to spatially explicit conservation proposals. These extensions can be made in a variety of ways, including through landscape genetic analysis and spatially explicit simulation models.

7. Summary

- Habitat loss and fragmentation are among the largest threats to amphibian populations.
- The extent, pattern and quality of terrestrial habitat in landscape mosaics are as important for many species as the quality of breeding sites.
- Many species of amphibians appear vulnerable to both the loss and fragmentation of nonbreeding upland habitat.
- Population connectivity appears to be a key to regional viability, and is primarily effected through juvenile dispersal.
- In fragmented landscapes, dispersal survival is often lower than required for population viability.
- The preponderance of evidence suggests that the short term impacts of habitat loss and fragmentation increase with dispersal ability.
- Species with limited dispersal abilities are equally imperiled by habitat loss and fragmentation over longer time periods.
- Combining molecular genetics and spatial modeling of organism movement provides a means to improve understanding of how habitat amounts and configurations influence dispersal, survival and population dynamics.
- Effective conservation of amphibian populations is limited by the lack of species-specific ecological knowledge, and lack of landscape-level studies of the effects of habitat loss and fragmentation on movement, survival rates, and population dynamics.
- Conservation strategies could benefit from taking multiscale, landscape-level approaches that integrate knowledge of species biology with broad-scale evaluations of the area and accessibility of both breeding and nonbreeding habitat.

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21

Biological corridors and connectivity

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hring utan ymbbearh, þæt heo þone fyrdhom ðurhfon ne mihte, locene leoðosyrcan laþan fingrum.

On his shoulder lay braided breast-mail, barring death, withstanding entrance of edge or blade.

Beowulf (Old English epic poem, c. 10th Century)

Introduction

The ability of individual animals to move across complex landscapes is critical for maintaining regional populations in the short term (Fahrig 2003; Cushman 2006), and for species to shift their geographic range in response to climate change (Heller & Zavaleta 2009). As organisms move through spatially complex landscapes, they respond to multiple biotic and abiotic factors to maximize access to resources and mates while minimizing fitness costs such as mortality risks. Habitat fragmentation decreases dispersal success (Gibbs 1998), increases mortality (Fahrig et al. 1995) and reduces genetic diversity (Reh & Seitz 1990; Wilson & Provan 2003). Local populations may decline if immigration is prevented (Brown & Kodric-Brown 1977; Harrison 1991) and may prevent recolonization following local extinction (Semlitsch & Bodie 1998).

The goal of this chapter is to describe the state of the art in quantitative corridor and connectivity modelling. We will review several critical issues in modelling, and provide expert guidance and examples to help practitioners implement effective programmes to preserve, enhance or create connectivity among wildlife populations. We first

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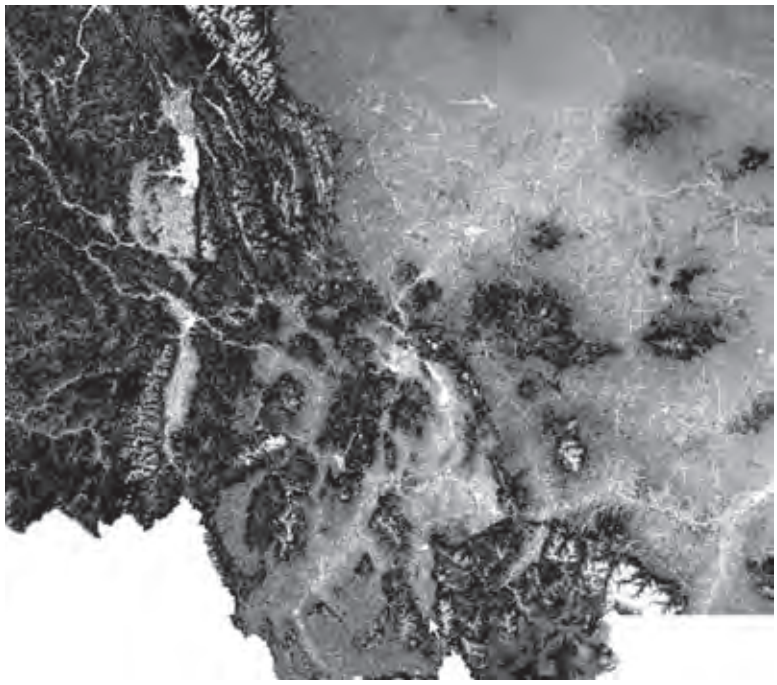


Figure 21.1 Example landscape resistance map for American black bear in an area of the US northern Rocky Mountains encompassing Montana and northern Idaho. Dark areas are low resistance for movement, while light areas are high resistance for movement. The resistance map was developed by Cushman et al. (2006) and validated with independent data by Cushman & Lewis (2010) and in multiple independent study areas by Short Bull et al. (2011).

review the fundamental task of estimating landscape resistance, comparing expert opinion and empirical methods. Next, we describe current methods of predicting connectivity from resistance surfaces. Then we discuss how to develop linkage designs that can maintain connectivity for multiple species, and under changing climate. We conclude with discussion of how effectively to validate connectivity model predictions.

Estimating landscape resistance

Most current methods of predicting population connectivity and mapping areas significant in facilitating animal movements begin with landscape resistance maps (Figure 21.1). Landscape resistance maps depict the cost of movement through any location in the landscape (pixel cell in a raster map) as a function of landscape features of that cell (e.g. high resistance might be assigned to a road or a body of water). In its most basic sense, landscape resistance reflects the local movement cost incurred by an animal. More formally, the resistance reflects the step-wise cost of moving through each cell for least-cost analyses (Singleton et al. 2002) or the relative probability of moving into the cell for circuit theory-based analyses (McRae et al. 2008).

Expert versus empirical estimation

Most published studies using landscape resistance maps have estimated resistance of landscape features to movement based on expert opinion alone (e.g. Compton et al. 2007). However, non-human species perceive landscapes in ways that may not correspond to human assumptions concerning connectivity and habitat quality (With et al. 1997). Using

unvalidated expert opinion to develop resistance maps has been a major weakness of most past landscape resistance modelling efforts (Seoane et al. 2005).

Methods for empirically estimating resistance

Habitat quality as surrogate for landscape resistance

Habitat quality can be predicted based on patterns of occupancy in relation to ecological conditions, such as through resource selection functions (e.g. Guerry & Hunter 2002; Weyrauch & Grubb 2004). The simplest way to estimate relationships empirically between population connectivity and environmental conditions is to assume that habitat quality directly equates to population connectivity. Predictions of habitat quality based on patterns of occurrence studies are limited because they do not directly measure biological responses such as mortality, movement and productivity (Cushman 2006). Patterns of species occurrence do not necessarily reflect patterns of fitness with respect to environmental gradients and landscape patterns (Van Horne 1983). More importantly, in the context of connectivity modelling, suitability for occupancy and suitability for dispersal may not be driven by the same factors at the same scales (e.g. Shirk et al. 2010; Wasserman et al. 2010). Habitat selection reflects the behaviour of individual organisms to maximize fitness within home ranges, while population connectivity is driven by dispersal, migration and mating events. These are functionally and biologically different processes. Few studies have formally evaluated the performance of habitat suitability models as surrogates for landscape resistance, but those that have generally have found them to perform poorly (e.g. Shirk et al. 2010; Wasserman et al. 2010). This highlights the importance of not assuming that habitat relationships optimally reflect the landscape features governing population connectivity.

Mark-recapture and experimental movement studies

By quantifying movement rates, distances travelled and routes of animals through complex environments, researchers can quantitatively describe species-specific responses to environmental conditions and landscape structure. For example, a study by Gamble et al. (2007) quantified dispersal in relation to topography and vegetation for several pond-breeding amphibians, demonstrating the value of mark-recapture approaches to evaluating population connectivity. In addition, these methods are well suited for incorporation in manipulative field experiments in which the area and configuration of habitat are controlled to isolate the effects of habitat loss and fragmentation on organism movement and survival rates. For example, Haddad & Baum (1999) used a large-scale experiment to find that three habitat-restricted butterfly species reached higher densities in patches connected by corridors than in similar, isolated patches.

These kinds of studies provide the most reliable inferences about relationships between survival rates, movement and ecological conditions (McGarigal & Cushman 2002). Unfortunately, large-scale manipulative field experiments and mark-recapture meta-population studies are expensive, take several years, and generally suffer from small sample sizes. Another potential limitation is that these studies focus on short-term, fine-scale movement path selection of individual animals, which may not scale up to population-level effects on migration and gene flow.

Telemetry

Advances in wildlife telemetry technology have enabled collection of very accurate and frequent location data for individual animals. Landscape resistance modelling based on telemetry is a powerful technique to address the factors that affect organism movement directly on scales of space and time greater than are possible with mark-recapture and experimental movement studies (e.g. Osborn & Parker 2003; Cushman et al. 2005,

2010a). GPS telemetry data enable direct assessment of the influences of landscape features on movement path selection. For example, Cushman et al. (2010a) modelled the influence of landscape features on elephant movement path selection using telemetry data, showing that elephants (*Loxodonta africana*) select movement paths near water, avoid human settlements and do not cross wildlife cordon fences. Similarly, Cushman & Lewis (2010) used satellite telemetry data to show that American black bears (*Ursus americanus*) choose movement paths that avoid roads and human residences and concentrate activity in forested areas at middle elevations. Directly associating movement paths with landscape features enables the development of species-specific landscape resistance models that are more reliable than those produced by expert opinion.

Landscape genetics

Gene flow among populations is necessary to support the long-term viability of populations, as it maintains local genetic variation and spreads potentially advantageous genes. Thus it is important to infer the functional connectivity among populations and across landscapes (van Dyck & Baguette 2005). The ultimate validation of any method of estimating functional connectivity lies in how well it explains gene flow (Cushman et al. 2006; Shirk et al. 2010; Wasserman et al. 2010; Short Bull et al. 2011). Genetic methods can directly measure dispersal and immigration (Waples 1998; Landguth et al. 2010). Logistical and financial costs associated with tracking individual animals are obviated and because genetic data integrate time and space, slow rates of dispersal through complex landscapes are measurable. Landscape genetic analyses enable direct association of movement cost across resistance surfaces with genetic differentiation, which enables empirical derivation and validation of connectivity maps. For example, Wasserman et al. (2010) used non-invasive monitoring to collect genetic data from several hundred individual American marten (*Martes americana*) across a 4000 square kilometer study area, and were able to use multivariate landscape genetic modelling to identify the landscape features that affect gene flow.

Combining multiple methods to produce robust estimates of resistance

Every method of estimation has its own limitations, so it is valuable to use multiple methods and independent data sets to estimate resistance. The strongest inferences are derived from multiple analyses of different kinds of data that produce a consistent result (Cushman & Lewis 2010). For example, landscape genetics and GPS telemetry are two complementary analyses that can be combined to produce robust estimates of landscape resistance. Using movement data to predict landscape resistance, and comparing that to landscape resistance predicted from landscape genetic analyses of the same species in the same study area, is a useful way to verify the robustness of landscape connectivity hypotheses (e.g. Cushman & Lewis 2010). In addition, such analyses would illuminate the multi-scale drivers of population connectivity, since mating and dispersal movement behaviours are the mechanisms through which gene flow operates in animal populations. At the present time, only a few research programmes have estimated resistance from a combination of approaches (Coulon et al. 2008; Cushman & Lewis 2010; Shanahan et al. 2011; see Box 21.1).

From landscape resistance to population connectivity

While resistance is point specific, connectivity is route specific (Cushman et al. 2008). Therefore, while resistance models can provide the foundation for applied analyses of population connectivity, they do not, in themselves, provide sufficient information to evaluate the existence, strength and location of barriers and movement corridors. Connectivity must be evaluated with respect to the paths, costs and success of moving across a landscape. The resistance model is the

Box 21.1 Combining landscape genetics and telemetry to estimate landscape resistance for American black bear

Cushman et al. (2006) used causal modelling with landscape genetics data to evaluate support for 110 alternative hypotheses describing the effects of landscape variables on population connectivity in an American black bear (*Ursus americanus*) population in northern Idaho, USA. Their analysis rejected hypotheses of isolation by distance and isolation by a geographical barrier, and affirmed a landscape resistance model which predicts that rates of gene flow are related to elevation, forest cover, roads and human development. Cushman & Lewis (2010) used conditional logistic regression to predict landscape resistance based on black bear GPS telemetry data in the same landscape. They used a path-level spatial randomization method to assess the effects of multiple landscape features on movement path selection (e.g. Cushman et al 2010a). The path-level randomization approach provides a robust means to compare the landscape features an animal encounters in its actual path with those that would be encountered in a large sample of available paths of identical length and topology. They found that consistent landscape factors influence genetic differentiation and movement path selection, with strong similarities between the predicted landscape resistance surfaces. Genetic differentiation among individual American black bears is driven by spring movement (mating and dispersal) in relation to residential development, roads, elevation and forest cover. The real value of this study is that it used two independent data sets and different kinds of analyses to validate the results, and it quantified the scale and strength of bear behavioural response to several landscape features. For example, it showed that gene flow is maximum at middle elevations due to impassable snow pack at high elevations in the dispersal season, and concentrated human populations in low-elevation valleys, and that bears strongly avoid roads and human resistances (e.g. near-total avoidance within a 200 m radius buffer around human structures).

foundation for these analyses, but it is explicit consideration of movement paths across the resistance surface that provides the key information for conservation and management.

Identifying corridors using least-cost modelling

In recent years least-cost (LC) modelling (part of graph theory, see below) has become the dominant modelling tool to evaluate functional landscape connectivity, especially in applied studies. This is mainly because:

- it produces an unambiguous corridor or path as an output, whereas most other approaches do not
- it is available in most commercial GIS packages as well as open source software
- LC models generate visually attractive and easy to communicate representations of connectivity (maps) and quantitative metrics of effective distance (cost values) in the same units (meters) as Euclidean distance (Adriaensen et al. 2003; Fagan & Calabrese 2006).

These attributes make LC modelling very well suited for quantitative landscape analyses and for evaluating effects of future scenarios on connectivity.

In LC models the only inputs are the map of sources and targets and the map of resistance values (R; Figure 21.2a). The cost layer is the first and central level of output of a LC analysis (see Figure 21.2a), and provides the functional cost distance values from the designated source to all locations in the geographical extent of the analysis. The least-cost path (Figure 21.2b) is the series of cells in the landscape which results in the minimum cumulative cost value (LC path value) to move from a source cell/cells to the target cell/cells under investigation. The LC path indicates the location of the cheapest route, but gives no information on how cost values are distributed over the landscape. For example, it does not indicate other zones in the landscape resulting in comparable costs (Figure 21.2c) or how wide the LC path zone is (Adriaensen et al. 2003; Pinto & Keitt 2009).

There are several methods available to produce biologically informative measures of landscape connectivity from such cost surfaces. One of these is the combination of several cost

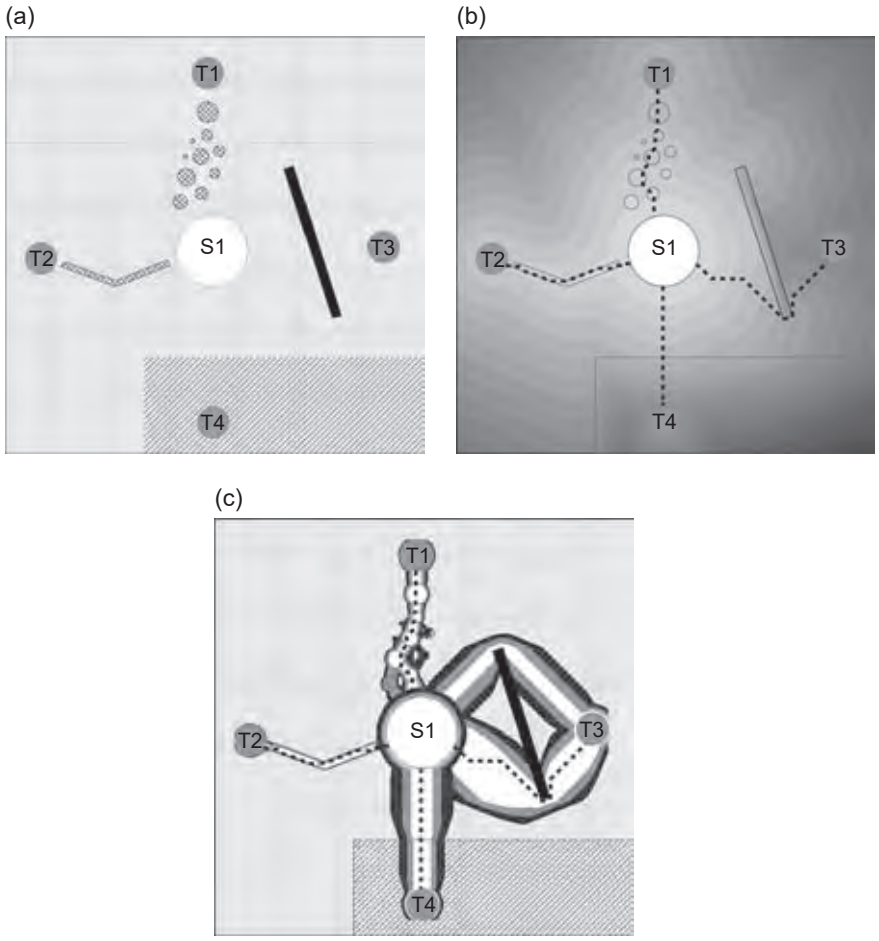


Figure 21.2 Input (a) to output (b-c) in LC modelling using a simple virtual landscape to show the basics of this modelling approach. (a) Landcover map showing a hypothetical landscape (source area S1: forest; target areas T1–4: woodlots; grassland (dotted); intensive cropland (hatched); hedgerow and bushes (cross-hatched); open water (solid black). (b) Cost layer from source area S1 and LC path to 4 target areas (dashed lines). (c) Corridor map showing 1–10% corridor buffers derived from bidirectional cost layers from source area S1. Result of 4 corridor analyses superimposed (targets=T1–4): white, increase in minimum cumulative cost less than 1% of LCP; light grey 1–5%; dark grey 5–10%.

layers into one 'corridor' layer (other names: bidirectional cost layer, conditional minimum transit cost [CMTC, Pinto & Keitt 2009]; see Figure 21.2c), in which the value of each cell is the overall cost to reach the target cell T from source cell S, but with the constraint to go through the cell under investigation. The LC path is a special case of this (with all cells having a value equal to the LC path value and thus the minimum present in the corridor layer). The LC path will always be the path of minimal corridor values but elsewhere in the landscape, there could be other zones with nearly equal cost values (see Figure 21.2c). Corridor maps give a more realistic view of the functionally cheapest routes in the landscape from the designated source to the destination (Adriaensen et al. 2003) (Box 21.2). For example, the width of corridors can be determined by taking percent slices of the landscape representing the lowest cumulative resistance (e.g. Singleton et al. 2002; Spencer et al. 2010) or by limiting

Box 21.2 Landscape connectivity in the Taita Hills

The Restoration and Increase of Connectivity among Fragmented Forest Patches in the Taita Hills, South-east Kenya project (CEPF project 1095347968; Adriaensen et al. 2007) included a detailed analysis of functional landscape connectivity in the area. In this project, evidence of the distribution and population status of bird species in the remaining small cloud forest patches on the hill tops (black patches) was successfully combined with output of LC models to support and prioritize habitat restoration actions in plantations with exotic trees (white patches). Forest restoration is now being implemented in a set of five pilot projects.

Least-cost models were used to model the location of exotic tree plantations in relation to modelled connectivity corridors for forest interior birds (dark grey zones), in order to evaluate their potential roles as stepping stones to promote recolonization after rehabilitation of the plantations. In the map shown, corridors between all pairs of remaining forest plots were superimposed (resistance set R1S5 for eco-type 'sensitive interior forest bird', including the critically endangered Taita thrush *Turdus helleri*).



corridors to a maximum cost-weighted cut-off distance above that of the LC path (WHCWG 2010). Regional connectivity assessments can require mapping corridors between hundreds to thousands of core area pairs (e.g. Spencer et al. 2010; WHCWG 2010). The development of GIS tools to automate corridor mapping, including decisions of which pairs

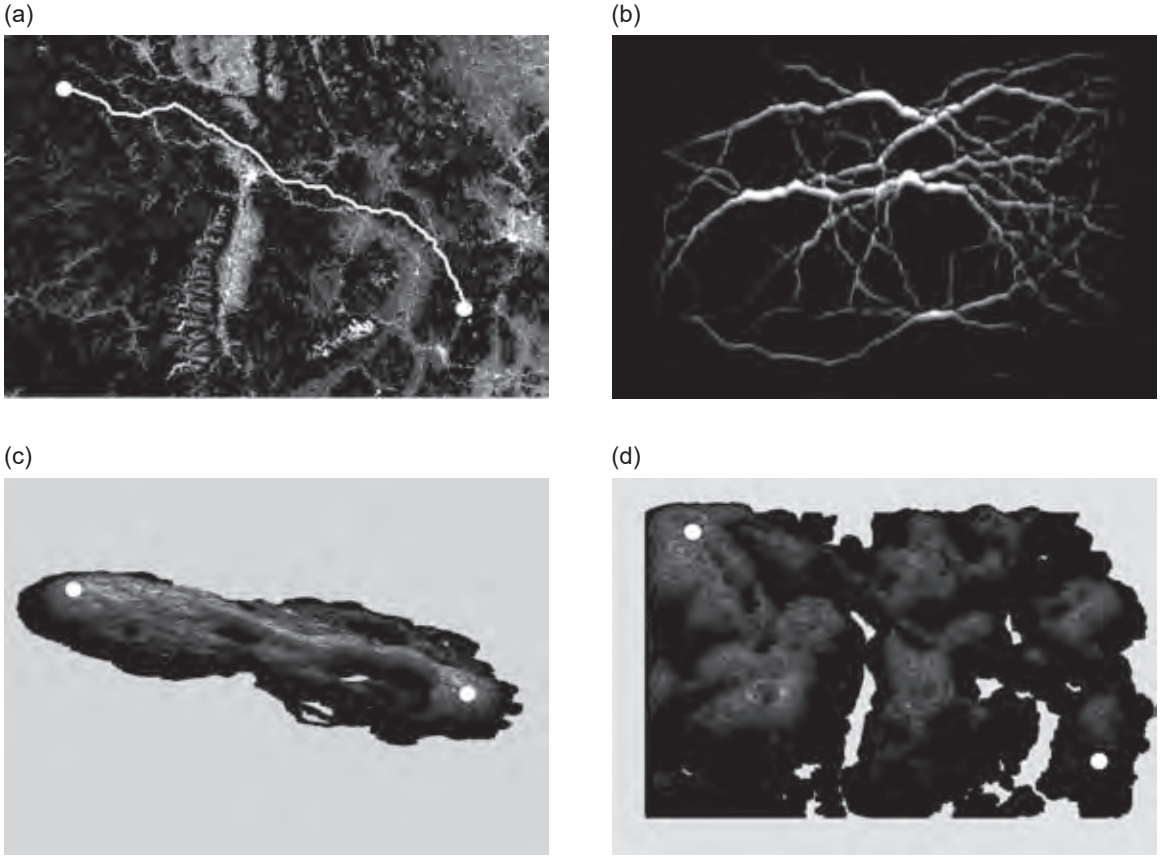


Figure 21.3 Comparison of four connectivity modelling methods applied to a single study area and resistance map. The study area is northern Idaho, USA. The resistance map is shown in panel (a) as a colour scale from blue (low resistance) to red (high resistance), and reflects landscape resistance to black bear gene flow (Cushman et al. 2006). Panel (a) shows a single least-cost path (white line) between two point locations (white dots). Panel (b) shows a factorial least-cost path analysis between several hundred source points. Panel (c) shows the least-cost corridor between the same two source points as in (a). Panel (d) shows the cumulative resistant kernel model of synoptic landscape connectivity.

of core areas to connect (e.g. McRae & Kavanagh 2011), makes this easy.

Factorial least-cost paths

One limitation of traditional LC path and LC corridor analyses is that they are limited to prediction of connectivity between single sources and single destinations (Figure 21.3a). While this may be ideal in the case where one is interested in the lowest cost routes between two focal conservation areas, there are many situations where a more synoptic analysis of connectivity is valuable. For example, it may be that there is a need to calculate corridor connectivity between thousands of sources and a single destination (e.g. Cushman et al. 2010a) or between hundreds of sources and hundreds of destinations distributed across a complex landscape (e.g. Cushman et al. 2008, Cushman et al. 2011; Figure 21.3b). For example, Cushman et al. (2008) used factorial least cost path analysis to predict the most important movement

routes for bears between Yellowstone National Park and the Canadian border in the United States Northern Rocky Mountains, showing that there are few major connections and locating several dozen potential barriers. This, in turn, focuses attention on where restoration and mitigation efforts would be most effective. A factorial implementation of least cost paths (e.g. UNICOR; Landguth et al. 2011) permits integration of a vast number of least cost paths to show synoptic connectivity across large and complex landscapes (Figure 21.3b). For example (Cushman et al. 2011) mapped regional corridor networks for several species of conservation concern across a vast area of the United States great plains using UNICOR (Landguth et al. 2011). The analysis identified which species have the most fragmented populations and mapped the most important corridor linkages among population core areas, focusing conservation efforts on the most important locations.

Other ways to analyse connectivity

Ecologists often use the term *graph theory* to refer to a family of analyses in which patches are reduced to nodes at patch centroids, with centroids connected by lines or 'edges' (e.g. Bunn et al. 2000; Urban & Keitt 2001; Minor & Urban 2007). Such graphs underlie many methods in connectivity analysis, including LC corridor modelling. Advances in computing and algorithms borrowed from other disciplines have allowed applications of graph algorithms to continuous landscapes instead of simple networks. Rayfield et al. (2011) review graph-based connectivity measures and provide a framework for classifying them as applications to connectivity conservation.

Circuit theory

Connectivity analyses based on electrical circuit theory use networks of electrical nodes connected by resistors as models for networks of populations, habitat patches or locations on a landscape connected by movement. Because connectivity increases with multiple pathways in electrical networks, distance metrics based on electrical connectivity are applicable to processes (e.g. gene flow; McRae 2006) that respond positively to increasing numbers of pathways. Additionally, previous work has shown that current, voltage and resistance in electrical circuits all have mathematical relationships with random walks (Doyle & Snell 1984; Chandra et al. 1997). Random walks can predict the expected routes that an animal with a preference for low-resistance habitat will take as it moves through a landscape. The precise relationships between circuit theory and random walks mean that circuits can be related to movement ecology and population genetics via random walk and coalescent theories, providing concrete interpretations of connectivity measures (McRae 2006; McRae et al. 2008).

Circuit and LC models represent two extremes in assumptions about movement and connectivity. Least-cost corridors calculate the routes expected to be taken by animals with perfect or near-perfect knowledge of the landscape, whereas current maps generated from circuit models predict movement routes taken by random walkers, with all possible paths contributing to connectivity. Neither will entirely correctly predict movement behaviour of real animals (Spear et al. 2010, and see below) but there are benefits to both models, as we show in the example in Figure 21.4. Least-cost analyses can show what routes/zones would permit the most efficient movement, which can be important for conservation planning; if a large portion of a landscape is likely to be developed, identifying those areas which, if conserved, provide the easiest movement routes will be important. Circuit theory has the advantage of identifying and quantifying 'pinch points' (see Figure 21.4), i.e. constrictions in corridors that, if lost, could sever connectivity entirely. Such areas can be prioritized for early conservation action because options are limited. Circuit algorithms also integrate across all movement pathways to

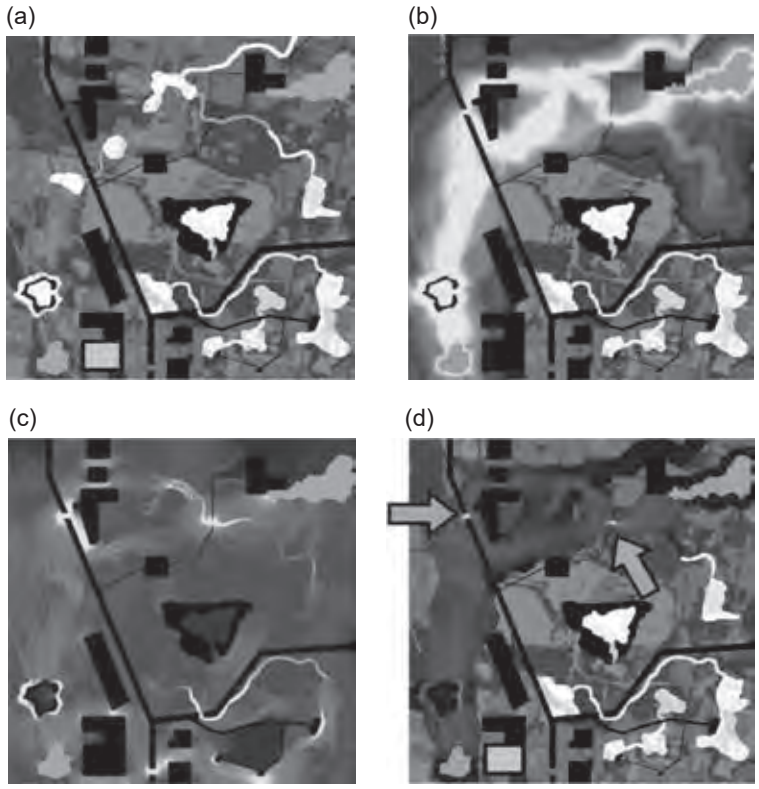


Figure 21.4 Example of how circuit theory can be used to identify and prioritize important areas for connectivity conservation. (a) Simple landscape, with two patches to be connected (green) separated by a matrix with varying resistance to dispersal (low resistance in white, higher resistance in darker shades, and complete barriers in black). (b) Least-cost corridor between the patches (lowest resistance routes in yellow, highest in blue). (c) Current flow between the same two habitat patches derived using Circuitscape (McRae & Shah 2009), with highest current densities shown in yellow (from McRae et al. 2008). Circuit analyses complement least-cost path results by identifying important alternative pathways and 'pinch points', where loss of a small area could disproportionately compromise connectivity. (d) A promising application is restricting circuit analyses to least-cost corridor slices to take advantage of the strengths of both approaches (from McRae & Kavanagh 2011). This hybrid approach shows both the most efficient movement pathways and critical 'pinch points' within them, which glow yellow. These could be prioritized over areas that contribute little to connectivity, such as the corridor at the top right of the map that has been coloured dark blue because it does not provide connectivity between the patches.

provide measures of redundancy, i.e. availability of alternative pathways for movement (see Figure 21.4). New applications allow identification of barriers that have a strong effect on connectivity, which can be useful for highlighting opportunities to restore connectivity, e.g. through re-establishment of natural vegetation or installation of highway crossing structures (McRae, unpublished data).

Centrality analyses

A promising graph-theoretic approach to connectivity modelling is centrality analysis, which ranks the importance of habitat patches or corridors in providing movement across an entire network, i.e. as 'gatekeepers' of flow across a landscape (Carroll et al. 2011). Centrality analyses can be based in LC path,

circuit theory or other connectivity analysis methods. The difference is that, instead of mapping corridors or current flow between single pairs of core areas, they add up results from connectivity analyses between all pairs of nodes (sites or cells) on a landscape. Centrality analyses can be applied to raster GIS data or networks to identify core areas, linkages or grid cells that are particularly important for overall connectivity. Because centrality metrics can incorporate connectivity between all pairs of nodes on a landscape, they can eliminate the need to identify specific pairs of habitat patches to connect. For example, betweenness centrality (Freeman et al. 1991) identifies the shortest paths connecting all pairs of nodes in a network, and sums the number of such shortest paths involving each intervening node. This procedure identifies areas lying on a large proportion of the shortest paths in a network, the loss of which can disproportionately disrupt connectivity across the network as a whole. The Connectivity Analysis Toolkit (Carroll 2010) specializes in centrality analysis, and supports metrics based on betweenness, current flow (Newman 2005), maximum flow (Freeman et al. 1991) and minimum-cost flow (Ahuja et al. 1993). It also allows time-series analyses of connectivity across landscapes where habitats shift through time (Phillips et al. 2008).

Resistant kernels

The resistant kernel approach to connectivity modelling is based on least-cost dispersal from some defined set of sources. The model calculates the expected density of dispersing individuals in each pixel around the source, given the dispersal ability of the species, the nature of the dispersal function and the resistance of the landscape (Compton et al. 2007; Cushman et al. 2010b). Once the expected density around each source cell is calculated, the kernels surrounding all sources are summed to give the total expected density at each pixel (see Figure 21.3d). The results of the model are surfaces of expected density of dispersing organisms at any location in the landscape. For example, Cushman et al. (2010b) used resistant kernel modelling to evaluate the interactive effects of roads and human land use change on population connectivity for a large number of pond-breeding species in Massachusetts (USA). The resistant kernel approach quantified expected density of dispersers in the upland environment as functions of breeding population size, dispersal ability and quantified the relative impacts of roads and land use on population connectivity (Figure 21.5).

The resistant kernel approach to modelling landscape connectivity has a number of advantages as a robust approach to assessing current population connectivity (Compton et al. 2007; Cushman et al. 2010b, 2011). First, unlike most approaches to mapping corridors , it is spatially synoptic and provides prediction and mapping of expected migration rates for every pixel in the whole study area, rather than only for a few selected 'linkage zones' (e.g. Compton et al. 2007). Second, scale dependency of dispersal ability can be directly included to assess how species of different vagilities will be affected by landscape change and fragmentation under a range of scenarios (e.g. Cushman et al. 2010b). Third, it is computationally efficient, enabling simulation and mapping at a fine spatial scale across large geographical extents (e.g. Cushman et al. 2010b, 2011).

Individual-based movement models

Individual-based (IB) models explicitly simulate the processes acting on the individual to predict movement. IB models predict movement paths of simulated dispersers based on parameters such as energetic cost of movement in different patch types, turning angles within patches and at patch transitions, movement speeds, duration of movement events, mortality risks in different patch types, and likelihoods of movements between patch types. Thus, IB models usually incorporate much more detail and thus greater realism than other

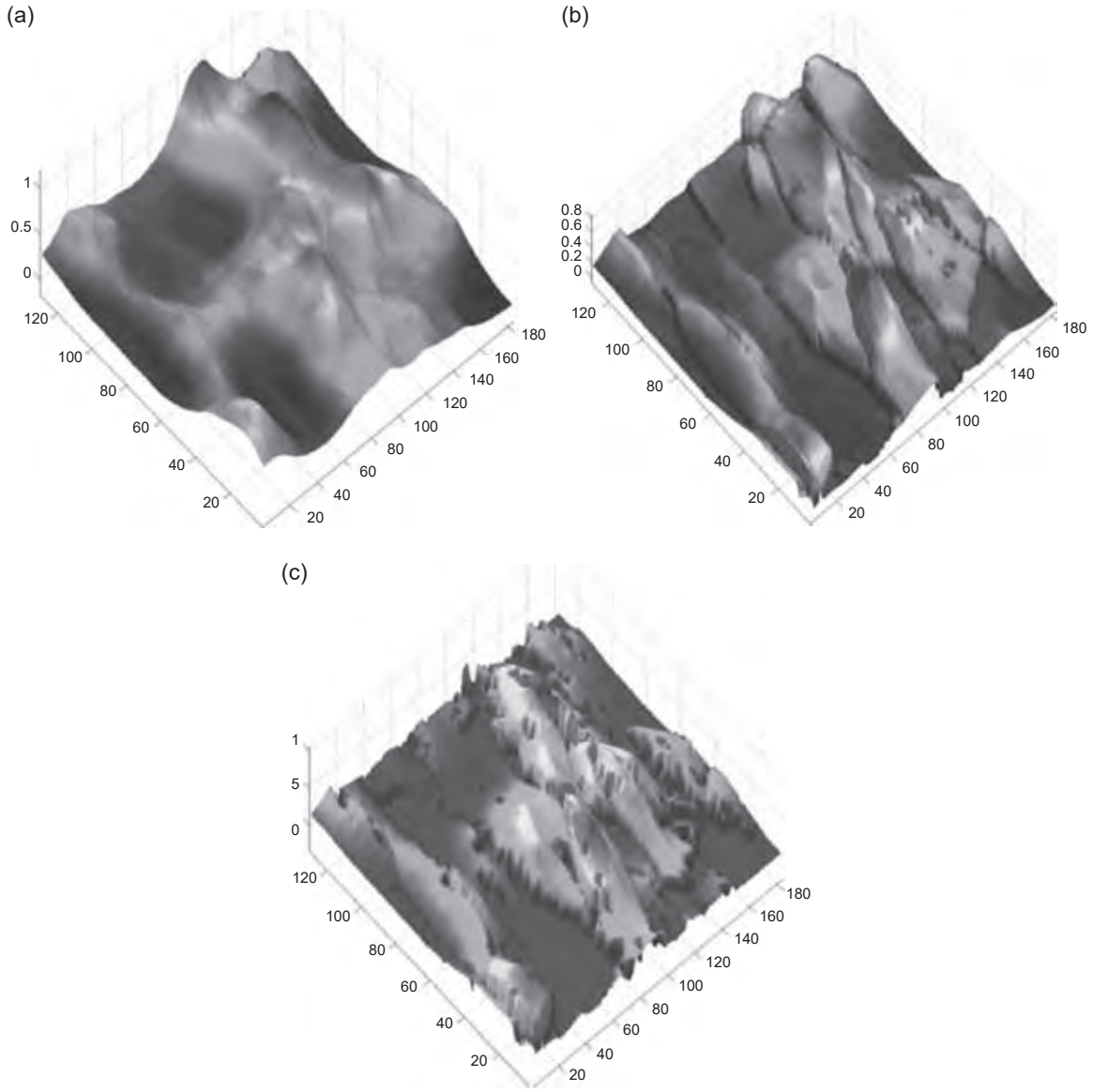


Figure 21.5 Example of resistant kernel results from Cushman et al. (2010b) showing predicted density of dispersing individuals in upland habitat under three hypotheses: (a) connectivity is unaffected by land use and roads and only a function of distance, (b) connectivity is reduced by roads but not by differences in land cover and land use, (c) connectivity is affected by roads and land use/land cover.

connectivity models, such as demographic and dispersal data, in addition to landscape characteristics.

There are three broad categories of models that simulate individual movement (raster based, vector based and network based), which differ according to whether the landscape is represented as fields, features or graphs. Conceived as fields, a landscape is a continuous surface defined by one or more variables (layers) that can be measured at any point within the field. Fields usually model continuous data such

as elevation, or temperature gradients, but can also represent categorical data such as habitat classification. If movement through the landscape is dependent on the variables of the field, then raster-based movement rules are most appropriate. Features are discrete entities that occupy positions in space, such as lines (rivers, roads, hedgerows) and polygons (lakes, woodland). The interiors of polygons are considered to be homogeneous. Movement between features is usually simulated using vector-based models. Finally, graphs represent the positional relationship between discrete elements in a landscape; a graph consists of a set of nodes that may represent continuous or categorical data, and a set of edges, which are dimensionless but describe how the nodes are connected to one another. Edges may be temporally referenced, indicating changes in graph connectivity over time. Network-based models are used to simulate IB movement in graphs. Examples of all three of these categories are discussed below.

Movement rules and models

Regardless of whether movement models are raster, vector or network based, they encode a series of rules that predict how the dispersal behaviour of individual animals is expected to interact with the spatial pattern of landscape structure (King & With 2002). Variations in patch quality, boundaries between patches, the nature of the mosaic, and overall landscape connectivity all affect the permeability of the landscape to dispersing individuals (Wiens 1997). The limited empirical information on the behavioural responses of animals to landscape structure (Turner et al. 1995; Lima & Zollner 1996) means that model parameters are usually based on observed habitat preference, dispersal rates in different patches, and how the energetic costs of crossing a landscape affect distance moved as well as direction taken. For example, the rules employed by Boone & Hunter (1996) simulated IB searching behaviour in grizzly bears by encoding permeability into the cells of habitat patches. Highly permeable habitat patches produced straight paths and long distance movements whereas patches of low permeability caused convoluted paths and short displacement.

Raster-based models

Raster- or grid-based representations of the landscape permit the greatest flexibility with which movement interacts with the landscape, and are appropriate where the dispersal matrix is heterogeneous (Wiegand et al. 1999). The landscape is represented as a series of tessellated shapes, usually square grid cells, and the model animal moves through each cell based on movement rules.

An advantage of this approach to modelling is the inclusion of a clear relationship between a cell and its neighbours, facilitating the description of local interactions by state transition rules. Each cell stores its own state variables that influence the decisions made by individuals through the landscape it represents. However, there are three principal disadvantages to raster-based models.

- The resolution of the grid is limited by memory capacity and simulation speed, and raster-based models have a tendency to be computationally demanding.
- The fixed spatial structure implies a fixed relationship between the spatial scale in the simulation and the scale of individual movements of the organism investigated.
- The geometry chosen to represent landscape in raster-based models (i.e. square grid, hexagonal grid, Dirichlet tessellation, etc.) can substantially affect the simulated behaviour of the individual dispersers even if the rules for movement and settlement are the same between different geometries (Holland et al. 2007).

Vector-based models

Vector-based models simulate organisms dispersing through continuous or homogeneous landscapes. If the motivations for these movements

are random or quasi-random search patterns, they can be simulated using correlated random walk algorithms (Kareiva & Shigesada 1983). Alternatively, if individual movements are targeted searches for resources with a particular spatial or temporal distribution, movement decisions will be informed by the underlying landscape structure. Finally, if motivation for movement is prompted by the desire to avoid or join conspecifics, it will result in density-dependent movement rules. Where motivations for movement are known and appropriate, IB models benefit from vector-based dispersal simulations, which are less computationally demanding than the raster-based alternative.

Network-based models

Network-based models differ from the other types in that they do not include a continuous representation of the landscape. Rather, connectivity between locations is represented by an edge between nodes. Network-based models usually specify an *a priori* representation of patch size, patch adjacency and other criteria (e.g. Lookingbill et al. 2010). Edges are formed when movement is possible between nodes. Dispersal corridors can be represented as nodes as well as edges in network visualizations of a landscape used as analytic connectivity models (McRae et al. 2008). They calculate walks through the network that minimize total weight, suggesting optimal pathways for dispersal. In IB models, network-based landscapes are utilized probabilistically (Lookingbill et al. 2010; Morzillo et al. 2011), and may result in biologically plausible but analytically suboptimal solutions. Graph-theoretic approaches to network analysis can be applied to the utilized networks of IB models to identify the nodes and edges that maintain cohesion of the network. For example, Gurnell et al. (2006) identified routes of entry for invasive grey squirrels into potential conservation areas for the endangered red squirrel in northern England through network analysis.

Corridors based on shifting climate envelopes

This approach produces 'temporal corridors' that track how a species' climatic envelope (suitable temperature and moisture regimes) might move across a landscape under climate change scenarios. Like some types of individual-based models, this approach avoids the concept of resistance that is central to most previous approaches. The heart of this approach is either a dispersal chain model (Williams et al. 2005) or a network flow model (Phillips et al. 2008), either of which identifies cells with suitable climate envelopes that are spatially contiguous for long enough to allow the species to establish new populations in cells as they become suitable. Although dispersal chain and network flow models are conceptually sound, they depend completely on the outputs of three other models, namely models of future emissions of greenhouse gasses, models of future climate resulting from how the atmosphere and oceans respond to these emissions, and climate envelope models for the focal species. Unfortunately, each of these latter three models is plagued with massive uncertainty (summarized in Beier & Brost 2010). In the future, ensemble modelling (building many alternative corridors based on various combinations of emission scenarios, circulation models and climate envelope models) might identify corridors robust across the range of assumptions in the ensemble.

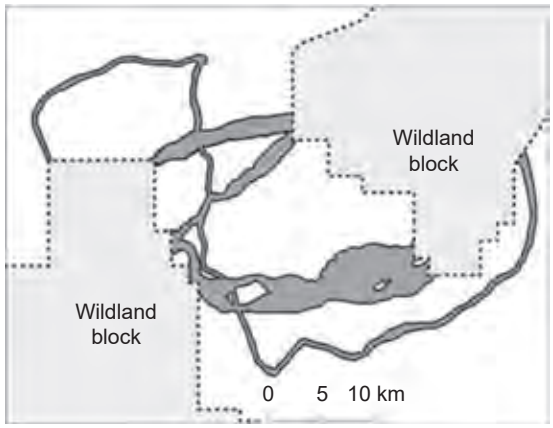
Beyond single species

From optimal corridors for single species to linkage designs for multiple species

Up to this point, we have described methods of mapping an optimal corridor, or areas important for connectivity, for a single species. Beier et al. (2008) proposed the term *linkages* to denote lands intended to support movement of

Box 21.3 Example of optimizing multispecies linkage

A hypothetical linkage design including optimal corridors for eight focal species, expanded to include patches of modelled breeding habitat for an additional five focal species for which corridor models were not appropriate, and a narrow riparian strand for fishes. Each strand needs to be >1 km wide in order to create large interior spaces free of edge effects, support meta-populations of species needing multiple generations to achieve gene flow through the corridor, and support ecological processes more complex than animal movement.



multiple focal species and ecosystem processes. To design linkages, conservation planners can select a suite of representative focal species suitable to serve as a collective umbrella for the entire biota. For instance, each of 27 linkage plans in California and Arizona (Beier et al. 2006, 2007) was designed to meet the needs of 10–30 focal mammals, reptiles, fishes, amphibians, plants and invertebrates. Focal species included species requiring dispersal for meta-population persistence, species with short or habitat-restricted dispersal movements, species tied to an important ecological process (e.g. predation, pollination, fire regime), and species reluctant to traverse barriers in the planning area. Although large carnivores are appropriate focal species and flagships (Servheen et al. 2001; Singleton et al. 2002), most of them are highly mobile habitat generalists and thus inadequate umbrellas for other species (Beier et al. 2009; Minor & Lookingbill 2010).

A simple unweighted union of single-species corridors is an obvious way to produce a linkage design to promote the goal of 'no species left behind' (Beier et al. 2006, 2007; Adriaensen et al. 2007; Cushman et al. 2011) (Box 21.3). But corridor models are not appropriate for some focal species, such as many flying animals, that do not move across the landscape in pixel-to-pixel fashion. To support movement of these species, Beier et al. (2008) recommend draping maps of known or modelled breeding habitat over the union of corridors, and enlarging the union to include patches that would decrease the inter-patch distances that dispersers would need to cross. The linkage design should be further expanded to include major riverine connections, which provide natural corridors for aquatic and some upland organisms, and promote other ecological processes and flows such as movement of sediment, water and nutrients.

Coarse-filter linkage designs for climate change

Climate change poses a challenge to all types of conservation planning, including linkage

design. As climate changes, existing land covers in some planning areas will not merely shift but will disappear as plant associations reassemble (Hunter et al. 1988; Lovejoy & Hannah 2005). Linkage designs should be robust to such changes, and should allow species to shift their ranges into and out of the planning area. To address this, one could attempt to model corridors for the shifting climate envelopes of all species (above). A simpler alternative is to design linkages with a coarse-filter approach based on the abiotic drivers of land cover and species distributions (Hunter et al. 1988; Anderson & Ferree 2010). This idea is grounded in the foundational ecological concept (Jenny 1941; Amundson & Jenny 1997) that biodiversity at any point in time is determined by the interaction of the recent species pool with climate, soils and topography.

Beier & Brost (2010) and Brost & Beier (2012) developed multivariate procedures to identify *land facets*, defined as recurring landscape units with uniform topographic and soil attributes, from readily available digital maps of elevation and soils. They used multivariate dissimilarity as a measure of pixel resistance for each land facet type. Finally, they used least-cost modelling to design land facet corridors, and joined these corridors into a linkage design. Other coarse-filter approaches are feasible. For instance, Rouget et al. (2006) suggest that species will shift their ranges by sequentially colonizing areas that lie along the most gentle and monotonic temperature gradients. Assuming these gradients in temperature are conserved in a changing climate, it may be possible to identify corridors along today's most gentle and monotonic temperature gradients, without the need for uncertain models of future climate.

Linkage designs should be produced by a combination of coarse-filter and focal species approaches. In each of three landscapes, Beier & Brost (in preparation) developed two linkages designs – one based on land facets and the other on focal species. The land facet linkage designs included optimal corridors for 25 of 28 focal species, whereas the focal species designs encompassed optimal corridors for 21 of 32 land facets. Neither approach on its own was likely to meet all conservation goals.

Validation of predicted corridors

Corridors resulting from models have sometimes been criticized because they lack supporting movement data (Simberloff et al. 1992; Rosenberg et al. 1997) and because they may contain errors in model parameters or incorrect assumptions (Spear et al. 2010). Therefore, additional vetting of modelled corridors in the field is strongly recommended.

Many field studies have evaluated the efficacy of existing corridors, such as corridors that follow linear features like fencerows or rivers (Hill 1995; Castellón & Sieving 2006), or that were constructed as part of experimental landscapes (Berggren et al. 2002; Haddad et al. 2003). There have also been tests of species' response to conservation action in established corridors (Duke at al. 2001; Shepherd & Whittington 2006). But field testing of modelled corridors, like the ones described in this chapter, have been scarce.

Modelled corridors may cover large spatial extents and span multiple land ownerships and management types, or even national borders, making the collection of field data logistically complex and resource intensive. If corridors are modelled for dispersal movement, capturing infrequent dispersal events is akin to finding a needle in a haystack, so collecting sufficient data to reliably test predicted corridors can be difficult. Finally, modelled corridors can only be truly validated if movement through the corridor is documented along with the outcome for which the corridor was intended, whether that be by successful migration to summer or winter ranges, successful recolonization of habitat patches, safe passage across a road, demographic rescue, or successful breeding and gene flow.

Even if all aspects of linkage cannot be validated, a partial field study will add confidence and transparency to a corridor project. For

example, Clevenger et al. (2002) developed two habitat models for black bears, one based on expert opinion and the other based on data from the literature. They identified road crossing zones from these models, and using data on crossings by real bears, they tested if the predicted linkages were used more than would be expected by chance. They found that the linkage models based on data from the literature outperformed the expert opinion models. The authors indicated that the expert opinion models may not have performed as well due to an overestimation of the importance of riparian habitat.

As an additional example of empirical field validation of corridors, Quinby (2006) used existing data from the annual breeding bird survey to test the utility of a proposed corridor. More bird species were found inside the corridor than outside it, confirming its validity. Chardon et al. (2003) used presence/absence data on the speckled wood butterfly from two different landscapes to compare the explanatory power of Euclidean distance and effective-distance connectivity models. They found that cost-distance was better able to predict connectivity than Euclidean distance. Zeller et al. (2011) used interviews with local residents to collect detection/non-detection data on jaguars and seven prey species in a grid-based design. The data were analysed by a site-occupancy model to determine probability of habitat use inside and outside the modelled corridor. It was found that probabilities of habitat use were mostly higher outside the modelled corridor, a conclusion which prompted a redesign of the final corridor.

The fact that there have been few studies to validate corridor models calls for more attention to this topic. Corridor validation techniques not only need to be improved upon, they need to be accessible to researchers and land managers working at different scales and on various species. Bridging the gap between corridor identification and corridor implementation will increasingly depend upon these validation studies, since land managers do not want to be left to implement a corridor of questionable efficacy, or be blamed for creating a sub-par corridor while more appropriate lands are unprotected from development and fragmentation (Hess & Fischer 2001; Morrison & Boyce 2008).

Conclusions

Population connectivity is critical for maintaining viable regional populations in the short term and to enable species to shift their geographic range in response to future climate change and other pressures such as land use change. In this chapter, we described the state of the art in quantitative corridor and connectivity modelling approaches. The first step in most quantitative connectivity analyses is to estimate and map landscape resistance. Traditional expert opinion is less useful for developing landscape resistance maps now that new and effective approaches using empirical data provide a much more reliable and robust means to map landscape resistance. There are a number of ways to predict or describe connectivity from resistance surfaces. Least-cost paths, least-cost corridors, circuit theory, centrality analyses, and resistant kernels are all powerful approaches suitable for different objectives. The efficient application of corridor analyses to future applied conservation problems must develop corridor designs to maintain connectivity for multiple species, and under changing climate. Finally, empirical validation of predicted corridors and linkages is essential to demonstrate their functionality and guide improvement of future corridor designs.

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PLANT ECOLOGY

Ongoing accumulation of plant diversity through habitat connectivity in an 18-year experiment

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Deleterious effects of habitat fragmentation and benefits of connecting fragments could be significantly underestimated because changes in colonization and extinction rates that drive changes in biodiversity can take decades to accrue. In a large and well-replicated habitat fragmentation experiment, we find that annual colonization rates for 239 plant species in connected fragments are 5% higher and annual extinction rates 2% lower than in unconnected fragments. This has resulted in a steady, nonasymptotic increase in diversity, with nearly 14% more species in connected fragments after almost two decades. Our results show that the full biodiversity value of connectivity is much greater than previously estimated, cannot be effectively evaluated at short time scales, and can be maximized by connecting habitat sooner rather than later.

Habitat loss and fragmentation are leading threats to biodiversity in ecosystems across the globe (*1*–*4*). In a world replete with small, isolated fragments, where 70% of the world's forest area is within just 1 km of an edge, biodiversity loss is mounting (*1*). Increasing habitat connectivity is a key conservation strategy to minimize biodiversity losses by facilitating dispersal and rescuing declining populations from extinction (*5*). However, it is not known if restoring connectivity among habitat fragments will increase biodiversity by promoting the colonization of new species.

A well-established body of ecological theory predicts the importance of connectivity for biodiversity. Metapopulation theory (*6*, *7*) illustrates how increasing connectivity is predicted to lead to greater regional population persistence by promoting colonization of new habitats, increasing recolonization of habitats where extinction has occurred (recolonization rescue), and buffering existing populations against extinction via increased immigration (demographic rescue). Metacommunity theory (*8*, *9*) and island biogeography theory (*10*) integrate these population-level effects of connectivity to yield predictions regarding biodiversity. These developments provide strong theoretical reasons to expect that modifying connectivity can increase biodiversity by increasing colonization and decreasing extinction, but they also caution that nonintuitive effects (e.g., synchronization of population dynamics or modification of interactions) are possible (*8*, *11*).

Despite the presumed importance of connectivity for community diversity in both basic and applied ecology (*12*, *13*), empirical evidence for predictions from theory has been mixed (*14*–*16*). A primary challenge in evaluating these predictions in empirical systems is that ecological processes vary greatly in space and time: The dynamic nature of colonization and extinction processes necessitates well-replicated, large-scale, and long-term studies to draw meaningful inference about the ultimate role of connectivity in affecting diversity. For example, changes in biodiversity due to either lost or restored connectivity do not occur instantaneously. In fragmented habitats, species can continue to persist for years before eventually going extinct (*17*), resulting in an "extinction debt" paid over decades or even centuries (*18*, *19*). Similarly, "colonization credits" can accrue when habitat connectivity is restored among species-impoverished habitats, catalyzing the potential for biodiversity gains (*20*–*23*). Species may not colonize immediately because of low dispersal rates, which are difficult to measure, making the extent of colonization credits unknown (*20*, *23*). This lack of information is important because colonization credits could forestall or even reverse extinction debt.

We tested the long-term effects of habitat connectivity on plant colonization and extinction dynamics and their resulting impacts on species richness over nearly two decades in a habitat fragmentation experiment at the Savannah River Site in South Carolina, USA. This experiment manipulates connectivity through the creation of habitat corridors—thin strips of habitat that connect otherwise isolated habitat fragments (*24*). Ten experimental landscapes each contain four 1.375-ha fragments of equal area that are either unconnected or connected to a central 1-ha fragment by a 150 m–by–25 m corridor (Fig. 1). Fragments and corridors are being restored to longleaf pine savanna, a threatened ecosystem within a global biodiversity hotspot (*25*), and are surrounded by dense pine plantations that limit herbaceous plant growth. For 18 years, we censused occupancy of all plant species as communities assembled after each restored fragment's creation. Connected and unconnected fragments were randomly assigned and did not differ in species richness at the start of the experiment [fig. S1; see also supplementary materials and methods (*26*)].

Habitat connectivity has increased rates of colonization and decreased rates of extinction. As communities assembled, connectivity increased the average annual species colonization rate by 5% and decreased the average annual extinction rate by 2% beyond expected successional dynamics (Fig. 2A and fig. S2). These apparently small differences in annual rates are persistent and have compounded over time, generating large increases in species richness in fragments connected by corridors, magnifying colonization credits (Fig. 2B and fig. S3). These impacts occur across 239 plant species with diverse life histories, including species of conservation and restoration concern from the longleaf pine ecosystem (fig. S6) and species that vary in their dispersal ability (fig. S7).

Higher colonization rates and lower extinction rates have shortened the average time for a species to colonize a fragment (Fig. 3) and have driven a large increase in plant species richness (Fig. 2B and figs. S3 and S5). Corridor-connected fragments now support, on average, 24 additional plant species compared with unconnected fragments (200 versus 176 in connected versus unconnected fragments, respectively; fig. S3), an increase of 14%. Notably, connectivity's effects on species richness continue to accumulate; our best-fit models of species richness differences over time show no asymptote. Moreover, connectivity's impacts on colonization and extinction rates remain consistent across the 18 years of this study (Fig. 2 and figs. S4 and S5) (*26*).

Our results underscore that typical experiments of 1 to 5 years in duration (*1*, *27*) likely underestimate the impact of long-term connectivity restoration on community diversity. Connectivity's impacts are not fully realized until the ongoing, lagged assembly processes and responses equilibrate. Theory from spatial ecology and community assembly predicts that connectivity's effect on diversity will eventually reach an asymptote because of local ecological processes constraining species richness (e.g., competition) and because local communities draw from a finite number of species in the region (*10*, *28*). Long-term empirical investigations of how landscape configuration alters colonization

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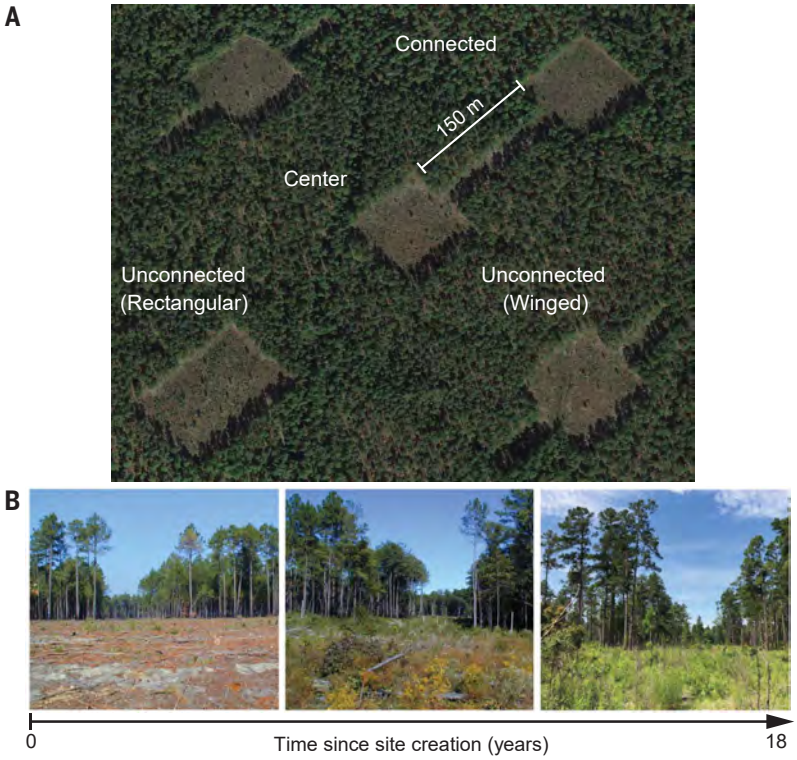

Fig. 1. A long-term habitat connectivity experiment. (**A**) One of 10 experimental landscapes (N = 10), each containing a center fragment that is connected or unconnected (winged and rectangular) to peripheral fragments of open longleaf pine savanna surrounded by dense pine plantations [additional details in (*26*)]. [Credit: Google Earth 2019] (**B**) Plant communities within fragments have assembled over nearly two decades and are being restored to native longleaf pine savanna using frequent, low-intensity fires that mimic the historic fire regime. See (*26*) for further information on the study design. [Credits (left to right): M. A. Burt, N. M. Haddad, and E. I. Damschen]

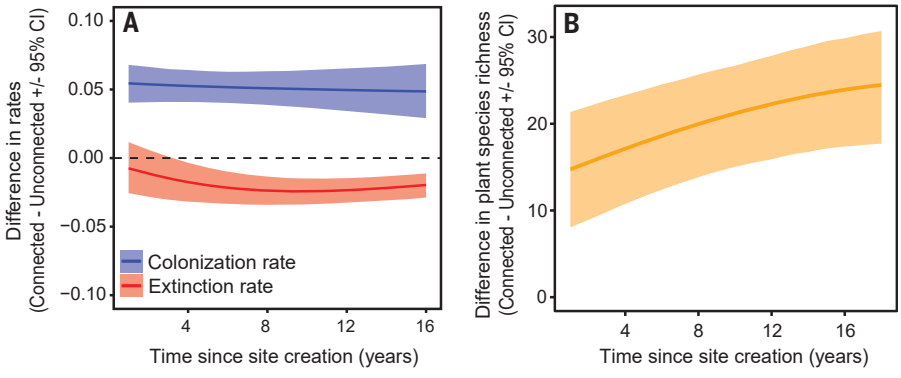

Fig. 2. Connectivity reduces extinction and increases colonization rates over two decades, resulting in accruals of species in connected fragments. (**A**) Average colonization rates are 5% greater and extinction rates are 2% lower for species in connected fragments than rates for those in unconnected fragments. These rates are constant over time. The net accrual of colonization credits increases biodiversity in connected fragments. (**B**) Plant species richness in connected fragments has increased at a greater rate than in unconnected fragments. Shown is the difference in estimated species richness over time, illustrating greater increases in richness in connected versus unconnected fragments. This rate increase has been consistent for nearly two decades and has resulted in connected fragments having 24 more plant species than unconnected fragments (fig. S3). A linear model (on the logit scale) is the best fit for the difference in species richness between connected and unconnected fragments over time (*26*). Shaded regions represent 95% confidence intervals.

and extinction rates are critical for determining and predicting human-induced changes to the environment; communities will almost never exhibit instantaneous responses or equilibrial dynamics (*29*).

We show that connectivity directly alters colonization and extinction dynamics among fragments, providing mechanisms for observed landscape-level biodiversity patterns (*30*). Our

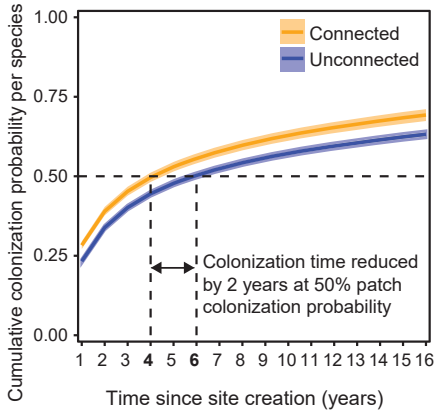

Fig. 3. Connectivity reduces colonization timing, resulting in colonization credits. The average cumulative probability of each individual species colonizing connected fragments is 1 to 6 years earlier than in unconnected fragments, resulting in reduced colonization lags and increased colonization credits. For example, the point at which a single species has a 50% likelihood of colonizing a habitat fragment (dotted lines) occurs a full 2 years earlier in connected versus unconnected fragments. Shaded regions represent 95% confidence intervals.

results contrast with hypotheses that attribute biodiversity change to habitat area alone and those that do not attempt to isolate underlying mechanisms (*14*). In our study system, connectivity leads to wholesale temporal shifts in community assembly, driven by lags in colonization that generate colonization credits, regardless of whether an equilibrium is achieved. Connecting fragments with corridors results in a 1- to 6-year reduction in the time it takes an individual species to colonize new habitat fragments, relative to the time needed for colonization of unconnected fragments (Fig. 3). For example, the 50% likelihood of a single species colonizing a fragment (dotted lines in Fig. 3) occurs a full 2 years earlier in connected fragments than for that same species in unconnected fragments (Fig. 3). These temporal shifts in the speed of colonization (Fig. 3 and fig. S8) have unexplored and potentially important ramifications for time-dependent ecological processes (e.g., priority effects). Although less explored, our results also suggest that corridor-mediated changes in the movement of individuals and alleles may affect evolutionary processes by altering effective population size and gene flow (*31*). Our results raise the need for theory to better integrate temporal duration in conservation and management.

Conservation strategies to mitigate biodiversity losses due to habitat fragmentation and loss are urgently needed, and habitat corridors feature prominently in global conservation plans (*4*). Our study shows that efforts to increase connectivity will pay off over the long term. Conservation plans that ignore connectivity, such as plans that focus solely on habitat area, will

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leave unrealized the substantial, complementary, and persistent gains in biodiversity attributable specifically to landscape connectivity (*30*, *32*).

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplementary Results
Figs. S1 to S8
Table S1
References (*34*–*61*)
Supplementary Code

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Science

Ongoing accumulation of plant diversity through habitat connectivity in an 18-year experiment

Ellen I. Damschen, Lars A. Brudvig, Melissa A. Burt, Robert J. Fletcher Jr., Nick M. Haddad, Douglas J. Levey, John L. Orrock, Julian Resasco and Joshua J. Tewksbury

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Habitat connectivity enhances diversity

Fragmentation of ecosystems leads to loss of biodiversity in the remaining habitat patches, but retaining connecting corridors can reduce these losses. Using long-term data from a large, replicated experiment, Damschen *et al.* show quantitatively how these losses are reduced. In their pine savanna system, corridors reduced the likelihood of plant extinction in patches by about 2% per year and increased the likelihood of patch colonization by about 5% per year. These benefits continued to accrue over the course of the 18-year experiment. By the end of monitoring, connected patches had 14% more species than unconnected patches. Restoring habitat connectivity may thus be a powerful technique for conserving biodiversity, and investment in connections can be expected to magnify conservation benefit.

Science, this issue p. 1478

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Supplementary Materials for

Ongoing accumulation of plant diversity through habitat connectivity in an 18-year experiment

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This PDF file includes:

Materials and Methods
Supplementary Results
Figs. S1 to S8
Table S1
Caption for Supplementary Code
References

Other Supplementary Material for this manuscript includes the following:
(available at science.sciencemag.org/content/365/6460/1478/suppl/DC1)

Supplementary Code (.pdf)

Materials and Methods

Landscape experiment

In 2000, we initiated a landscape experiment to test whether habitat corridors promote connectivity and impact community diversity. The experiment is at the Savannah River Site, a National Environmental Research Park in Aiken and Barnwell Counties, South Carolina, USA. Established by the U.S. Department of Energy, the site is managed by the US Forest Service under agreement with the Department of Energy.

The experiment consists of 10 replicate landscapes (experimental blocks), each comprised of five open-habitat fragments created by clearing mature pine plantation forest and restoring fragments to native longleaf pine savanna. There is a strong contrast between the open fragments and the surrounding closed-canopy pine plantation matrix. Eight landscapes were created prior to the 2000 growing season (i.e., before April) and two additional landscapes were created prior to the 2007 growing season. Two of the original eight landscapes were discontinued following the 2007 growing season due to management constraints and one was destroyed by a wind event following the 2015 growing season. The remaining five landscapes initiated in 2000 and the two landscapes initiated in 2007 continue through the end of this study. When examining patterns over time, landscapes are evaluated based on the number of years since that landscape was created. All available replicate landscapes (blocks) are used for each time point in this study. This staggered initiation of replicate landscapes also provides a benefit by separating connectivity effects due to time since replicate initiation from annual effects attributable to specific years.

Each landscape contains a center fragment (100 × 100 m, 1 ha) surrounded by four peripheral fragments that are each 150 m from the center fragment (Fig. 1). The center fragment is connected to one peripheral fragment by a 150 × 25 m corridor and the other three peripheral fragments are isolated from the center fragment by dense, mature loblolly (*Pinus taeda*) or longleaf pine (*Pinus palustris*) plantation forest. Unconnected fragments are equal in area to the connected peripheral fragment plus its corridor (1.375 ha) and are either rectangular (100 × 137.5 m) or winged. Winged fragments have two 75 × 25 m projections, each with the dimensions of half of a corridor, extending from each side of a 100 × 100 m fragment (Fig. 1). The identity of peripheral fragments (connected, rectangle, winged) was randomly assigned within each landscape, with one duplicate winged or rectangle fragment in each landscape. This study design allows us to separate influences of corridors mediated through connectivity from those mediated through differences in edge-to-area ratio. Specifically, impacts of connectivity are assessed by comparing response variables in winged and connected fragments (comparable edge-to-area ratio, different connectivity). Impacts of edge-to-area ratio are assessed by comparing the same variables in winged and rectangle fragments (comparable connectivity, different edge-to-area ratio). Because analyses used in this study showed no differences among unconnected fragment types (Table S1), response variables were averaged for those fragment types. The center fragment is not included in analyses comparing fragment types, therefore comparisons are always made for fragments of equal area. This approach is directly comparable to an earlier analysis of species richness in these fragments (*27*).

Through periodic prescribed fire and removal of establishing hardwood trees, we have restored fragments to their historical ecosystem type: open-canopy longleaf pine savanna. We used standard management practices in this ecosystem (*34*) and applied them consistently across experimental treatments (i.e., we managed all fragment types in the same way). Prescribed fires

are implemented and controlled by our partners at the USDA Forest Service-Savannah River consistent with the historic fire regime and with fire management in longleaf pine savanna conservation today (*35*). Low-intensity surface fires are ignited every two to three years during the dormant season (November - April) and are allowed to burn across large burn areas that include all experimental fragments for a given experimental landscape (block). Longleaf pine savanna species are fire-adapted and many species readily re-sprout after fire. Thus, ecological communities in our experimental landscapes recover quickly following fire, yet fire results in both mortality of resident species and recruitment opportunities for new species (*36*). Consistent with restoration practices in this ecosystem (*34*), we have also reduced woody encroachment in our fragments by cutting hardwood tree species with brush saws every three-to-four years and applying targeted herbicide to cut stumps and/or the base of individual stems. These management practices allow the fragments to undergo succession toward mature longleaf pine savanna, characterized by low density overstory longleaf pine trees and an understory dominated by highly diverse perennial herbs and grasses (*36*), while maintaining the contrast between our experimental fragments and surrounding matrix over the duration of the study.

Data collection

To quantify plant species richness and rates of extinction and colonization within our fragments, we annually survey each fragment for all plant species occurrences. We conduct surveys between May 15 and July 15, when most species in our system are visually identifiable. Here, we include data from 2001 through 2018 (except 2004 when active management prevented sampling). The goal of each survey is to census all species in each fragment by systematically walking the area of each fragment in a set pattern around permanent 3m-tall poles placed in a 12.5m grid. This grid consists of 88 small (12.5 × 12.5 m) sampling units in each fragment. For each census, we record all species in the first sampling unit and then record only new species in subsequent sampling units. This method allows us to consistently cover the entire area of each fragment and compile a list of all vascular plant species observed in each fragment as well as the order in which they were detected across the 88 sampling units. Over the entire 18-year time series, we have kept the number of observers to a minimum – three (Damschen, Brudvig, and Burt). These observers standardize sampling effort and taxonomic identification rules prior to each annual survey. Resulting estimates of species richness for each fragment are from equal areas (1.375 ha). Taxonomy follows (*38*) and (*39*). In rare cases where identification is not possible at the species level (2% of taxa), we combine species to the genus level.

We assigned each plant species one of three primary dispersal modes: wind, animal, or gravity. We chose these modes because they capture distinctive classes of seed movement. We determined dispersal modes by first searching the Kew Garden Seed Information Database (*40*). If species were not in that database, we searched the primary literature with ISI Web of Science for papers that described dispersal for the species and/or genus. In some cases, we also searched reliable plant natural history websites to cross-reference obtained information. All designations were independently reviewed by two plant ecologists within our plant ecology research team (E. Damschen, L. Brudvig, M. Burt, C. Warneke, Q. Sorenson). Any conflicting or missing designations were discussed and decided by this entire team and decided on based on morphological and field observations (11% of species). Wind dispersal included both wind and tumbling dispersal mechanisms. Animal dispersal included endozoochory and epizoochory by birds and mammals and myrmecochory by ants. Gravity dispersal included ballistic dispersal mechanisms and species lacking apparent morphology to assist dispersal.

We also determined whether each species was associated with longleaf pine savannas (i.e., "longleaf pine species"). We were interested in assessing the responses of these species because they are of particular conservation and restoration concern and could respond more strongly to the contrasting habitat differences between the fragments and matrix in our experimental landscapes. We classified species as longleaf pine indicator species if they met one or both of the following criteria: 1) designation as longleaf pine upland species in published species lists for the Savannah River Site (*41, 42*), or 2) designation as "indicator species" in previous analyses of longleaf pine savanna plant communities at the Savannah River Site (*43*).

Because soil moisture is an important determinant of plant diversity in longleaf pine savannas (*44, 45*), we quantified soil water holding capacity. We used the same methods as Damschen et al. (*27*) by collecting 96-136, 10-cm deep × 2.5-cm diameter soil cores, evenly distributed across each fragment. We then determined soil water holding capacity as (wet mass - dry mass)/dry mass for each sample (*46*) and used the average of all samples from a fragment in our analyses.

All data are available from the Environmental Data Initiative and Data One (*33*).

Analyses

We modeled changes in plant communities using multi-species occupancy models and their extensions to capture both changes in species richness and colonization-extinction dynamics (*47, 48*). Occupancy modeling provides two major benefits. First, it can account for species-specific imperfect detection (observation errors). Second, it estimates species directly rather than modeling summary statistics of communities (e.g., species richness), such that species identity is honored and tracked in the modeling process. The latter benefit also allows for understanding how species-specific characteristics (e.g., dispersal mode) may impact communities while also providing a means to derive community-level parameters (e.g., species richness). This general approach uses a hierarchical framework. To ensure that results were robust to the modeling framework we used, we used a negative binomial regression to contrast results to those from modeling species richness without accounting for imperfect detection.

As part of our occupancy modeling, we estimated imperfect detection using detection histories for each species in each fragment for each year. We used spatial replicates based on the long-term sampling design to create those detection histories. For each fragment, we pooled 88 samples that covered the entire fragment into $J = 8$ replicates. This sampling strategy is best viewed as a 'removal' design (*49*), where once a species is detected, it is no longer tracked in fragment *i*. For example, a detection history for species *k* at fragment *i* in year *t* could be [0 0 0 0 1 NA NA NA], where NA refers to no data, given the 'removal' design. For most analyses, we focus on comparing communities in connected (corridor) versus unconnected (rectangular and winged) fragments and did not include the center fragment in modeling (but see below for interpreting if colonization of corridor fragments arose from center fragments).

We first modeled the entire plant community ($K = 309$ species) to estimate potential effects of corridors over time on species richness. To model species richness over time, we used an 'implicit dynamics' formulation of the multi-species occupancy model (*50*). In this context, we modeled the probability of occurrence ψ for species *k* in time *t* at fragment *i* as:

$$z_{k,i,t} \sim \text{Bernoulli}\left(\psi_{k,i,t}\right) \quad (1)$$

where *z* is the latent occupancy state (0,1). We modeled ψ as:

$$logit\left(\psi_{k,i,t}\right) = \alpha_{trt,k} + \beta_{trt,k} time_t \quad (2)$$

such that each species *k* had a different, treatment-specific intercept and slope over time (i.e., an interaction of treatment*species*time). Note that in this model, we initially considered site as a random effect to account for within-site repeated measures over time, which provided similar results. We removed this effect in the final model to simplify model structure given the large number of latent parameters (e.g,. species-specific effects).

Our observation model was described as:

$$y_{k,i,t,j} \sim \text{Bernoulli}\left(z_{k,i,t} p_k\right) \quad (3)$$

Where $y_{k,i,t,j}$ is the detection of species *k* in fragment *i* at year *t* for replicate observation *j* and p_k is the probability of detection of species *k,* conditional on presence. We allowed detection to vary by species.

This model formulation assumes a linear effect of time since corridor creation (on the logit scale) on species-specific occurrence; however, this effect can appear non-linear on the probability (and species richness) scale, as in logistic regression. We also considered two types of non-linear functions (considering the log of time or adding a quadratic term of time), neither of which were supported by the data based on the Deviance Information Criterion, DIC (lower values indicate better fit; linear time: 93634; log time: 93840; quadratic time: 94352). We also initially considered the potential effects of soil moisture in this model, but found no support for its effect based on DIC (soils ignored: 93634; soils included: 99562). Thus, we did not include soil moisture in final models. We contrasted these results to modeling raw species richness with non-linear effects over time using a negative binomial regression, finding similar support for a linear effect of time and qualitatively similar patterns of changes in species richness as found in the multi-species occupancy model (Figs. S4, S5).

For a subset of the community (i.e., those species with > 10 detections over time; $K = 239$ species of the possible 309 species), we explicitly modeled colonization-extinction dynamics. While the entire community could be modeled to interpret colonization-extinction dynamics, little information is available for rare species to interpret treatment effects and how they change over time. Thus, such an approach would make the implicit assumption that rare species, which contribute a comparatively small amount of data on extinction and colonization, respond similarly to treatments as more common species, such that rare species dynamics do not have a large impact on conclusions (*48*). Because of this effect, we use the 239 species subset of more common species to make conclusions on colonization-extinction dynamics. We note, however, that modeling colonization-extinction dynamics of all species showed similar patterns.

We followed methods of Dorazio et al. (*48*), who extended the multi-species occupancy framework for capturing colonization-extinction dynamics. The dynamics of species occurrence can be described and estimated with time-series data by assuming a first-order Markov process, where $z_{k,i}$ at time *t* is contingent on $z_{k,i}$ at time *t* - 1, as well as local colonization, γ, and local extinction, ε, processes. If we define $\phi = 1 - \varepsilon$, then:

$$z_{k,i,t} = \text{Bernoulli}\left(z_{k,i,t-1}\phi_{k,i,t-1} + \left(1 - z_{k,i,t-1}\right)\gamma_{k,i,t-1}\right). \quad (4)$$

This framework requires estimating occupancy at time 1, and then colonization-extinction dynamics in subsequent time steps. We also considered an alternative parameterization that accounts for potential rescue effects ("pseudo-rescue effects" sensu Hanski 1999) replacing $\phi_{k,i,t-1}$ in equation 4 as (*51*):

$$\phi^*_{k,i,t-1} = \left(1 - \left(1 - \phi_{k,i,t-1}\right)\right)\left(1 - \gamma_{k,i,t-1}\right). \quad (5)$$

To further interpret support of rescue effects, we contrasted similar models as described in equations 4-5 but fit to single species (i.e., 'dynamic occupancy models'; *52*). We also note that

rescue effects are also often interpreted as occurring when connectivity (e.g., corridors) decrease local extinction rates, although it can be unclear if such patterns are driven by rescue effect mechanisms (*53*).

We allowed for ψ to vary by species (we also initially considered that ψ could vary by treatment; however, there was no support for this added complexity so we do not consider it further, See Fig. S1). We also allowed for γ and ε to vary by treatment over time for each species as:

$$logit(\gamma_{k,i,t}) = \alpha_{trt,k} + \beta_{trt,k} time_t \quad (6)$$

$$logit(\phi_{k,i,t}) = \alpha_{trt,k} + \beta_{trt,k} time_t \quad (7)$$

From this model, we then summarized the average ε and γ across species and associated 95% credible intervals for each treatment over time based on the species-specific posterior distributions of model parameters. We averaged unconnected treatments (winged, rectangular) because the rates of change for these treatments were similar (Table S1).

To determine if the results are consistent for species of conservation and restoration concern and to determine whether movement ability of species influences our results, we also summarize colonization-extinction dynamics on two types of species traits: 1) longleaf indicator status; and 2) dispersal mode (see Data Collection for descriptions of these characteristics).

To better interpret if colonization was driven by corridors, we re-ran the colonization-extinction model (using equation 4) and included the center fragment (Fig. 1) into the model. Based on this model, we determined if connected fragments tended to be colonized sooner than unconnected fragments for species that occurred (i.e., $z_{k,i,t}$ =1) in center fragments prior to other fragments within each landscape.

We assumed vague priors for all parameters ($N \sim (0, 100)$), and used uniform hyperpriors for standard deviation parameters ($U \sim (0, 10)$). We ran all models in jags using the jagsUI package to call jags from R. We ran four chains for 37,500 Markov chain Monte Carlo (MCMC) iterations and thinned chains by 50 after a burn-in of 15000 and an adaptation phase of 15000, ultimately saving 3000 samples from the posteriors. We assessed model convergence using the Gelman-Rubin statistic R-hat, assuming that an R-hat > 1.05 indicated convergence problems (*50, 54*).

Supplementary Text

Supplementary Results

Plant species in may have arrived in fragments through three different pathways. First, seeds could have arrived in the area where we created our experimental fragments before our experiment was created and remained in the soil seed bank. In our study system, the soil seed bank is dominated by annual herbs and graminoids, a small subset of the total species in our study system, and whose composition did not differ by fragment type at the start of our study (*27*). Second, plants were present in the pine plantation understory before our experiment was created, and some regrew after forest harvest. Our assignment of treatments to fragments was randomized and we have previously confirmed that species richness and composition did not differ by fragment type at the start of our study (*27*) (Figure S1). Third, species may arrive from the regional species pool into one of the fragments within an experimental landscape. The increased colonization rates and decreased extinction rates in connected fragments suggests that

species are more likely to move to a connected fragment than unconnected fragments. Based on temporal changes in $z_{k,i,t}$ from the colonization-extinction model that include all five fragments in each experimental landscape, we found species that first arrived in the center fragment of an experimental landscape (block) were more likely to next colonize a connected fragment than an unconnected fragment (Fig. S8). Our analysis of the order of colonization events showed that connected fragments were colonized sooner than unconnected fragments in 60% of the species (out of 120 species for which this situation occurred), but the distribution was highly skewed (Fig. S8), providing evidence of corridors facilitating colonization of species from center fragments. This evidence is bolstered by studies of individual species' movement in our experiment that overwhelmingly show increased rates of movement between connected fragments when compared to unconnected fragments (*55*).

It is also possible that rescue effects – instances where immigration prevents extinction (*5*) – are responsible for the lower extinction rates in connected fragments. When we evaluated the potential for rescue effects for the entire community, the model parameterization that included rescue effects (Eq. 5) did not fit the data as well as when no rescue effects were assumed (based on DIC: assuming rescue effect, DIC = 194,151.7, assuming no rescue effect, DIC = 192,533.7). Thus, there was no strong support for rescue effects at the community level. When evaluating whether models that included rescue effects were important for individual species, there was support for rescue effects for 54% of the 239 species based on DIC (i.e., lower DIC for the rescue effects parameterization than assuming no rescue effects). This support did not explain variation in species responses to corridors (i.e., variation in DIC did not correlate with corridor effect sizes based on treatment parameters in Eq. 6-7; $r < |0.07|$). Thus, we focused on the non-rescue effect model parameterization above for all general results in the main text. However, it is important to note that while rescue effects do not generally explain the community-level patterns we report, they can and do occur for some species.

Finally, once species arrive within fragments, connectivity may alter species interactions in ways that minimize species extinctions or promote colonization. For example, we have documented higher pollination rates in connected than unconnected fragments (*56, 57*), which may increase seed set and population size, thereby lowering the likelihood of extinction. Additionally, changes in seed predation caused by connectivity may create competition-free microsites that facilitate colonization (*58*). Corridors also increase the temperature at which prescribed fires burn, opening microsites for plant colonization and reducing dominance by woody species, which can increase persistence of subordinate herbs (*59*). Populations may also benefit from corridors by increasing gene flow and reducing impacts of inbreeding depression (*60*). Gene flow takes place through seed dispersal and pollination, both of which are facilitated by corridors in our study system (*56, 57, 61*).

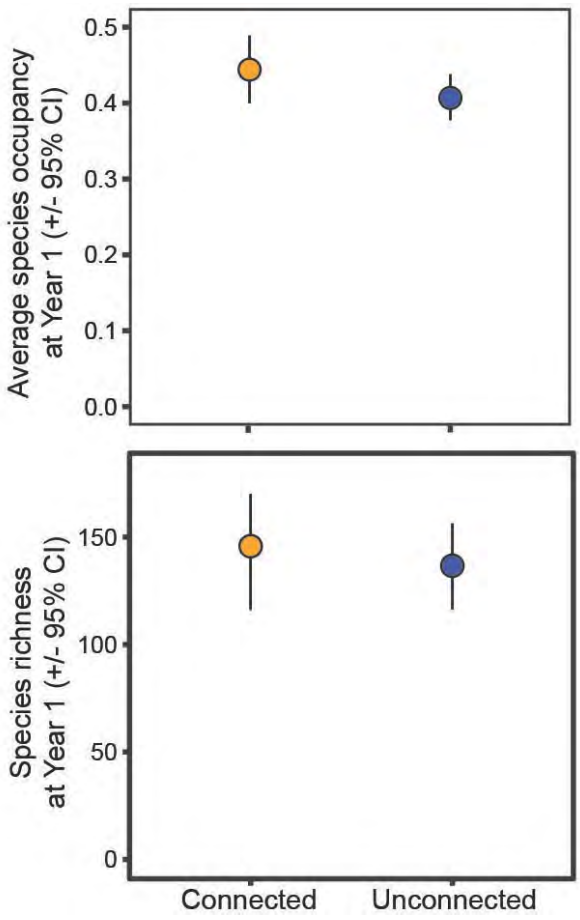

Fig. S1. Starting conditions did not vary by treatment. Initial probability of **(A)** species occurrence and **(B)** species richness did not differ by fragment type.

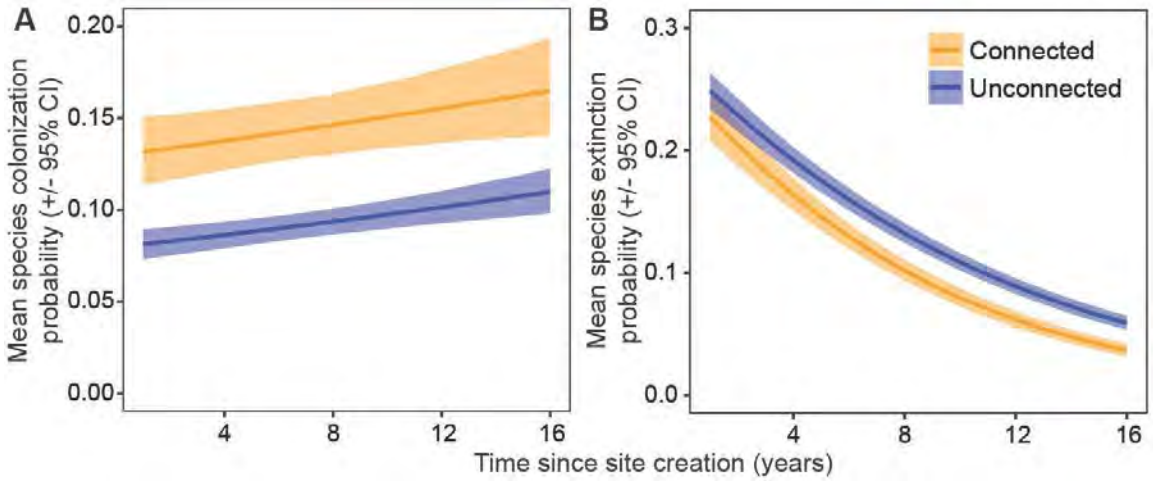

Fig. S2. (A) Colonization and (B) extinction rates over time for connected and unconnected fragments. The difference in these rates were used to produce Fig. 2A.

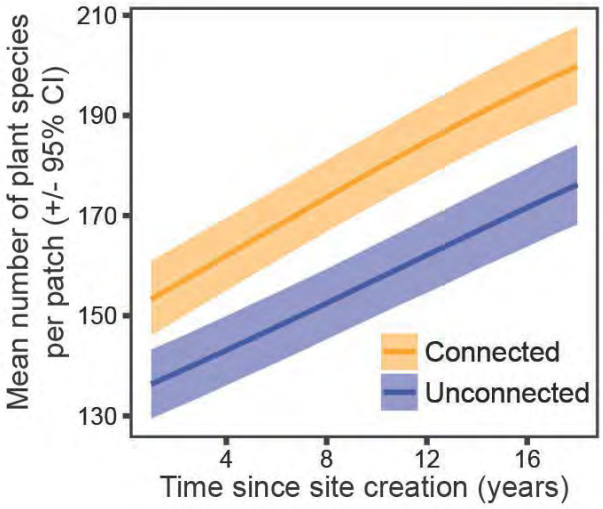

Fig. S3. Estimated species richness over time in connected and unconnected fragments. In the last time point (Year 18), on average there are 24 more species in connected than unconnected fragments (200 vs 176 species, respectively). The difference in these rates were used to produce Fig. 2B.

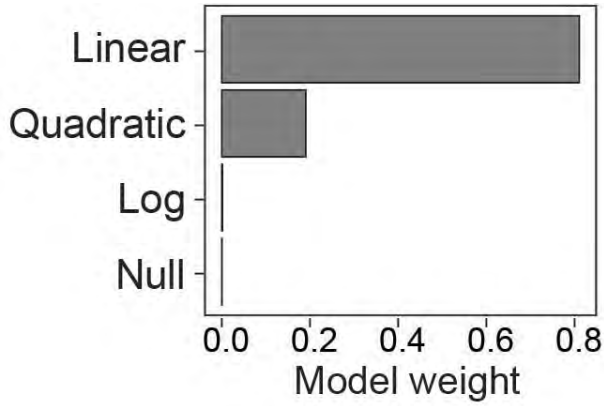

Fig. S4. A linear model is the best fit for the difference in species richness between connected and unconnected fragments over time. Model weights represent AIC model weights taken from negative binomial regressions that included the main and interactive effects of treatment and time since site creation (treated as either a linear, log-linear, or quadratic effect of time, in contrast to no effect of time represented as 'Null'. Higher model weight signifies greater support for a model relative to the other models considered, with a value of 1 indicating full support. Consequently, these weights suggest overwhelming support of a linear effect of treatments over time relative to potential non-linear (log time, quadratic time) effects of time.

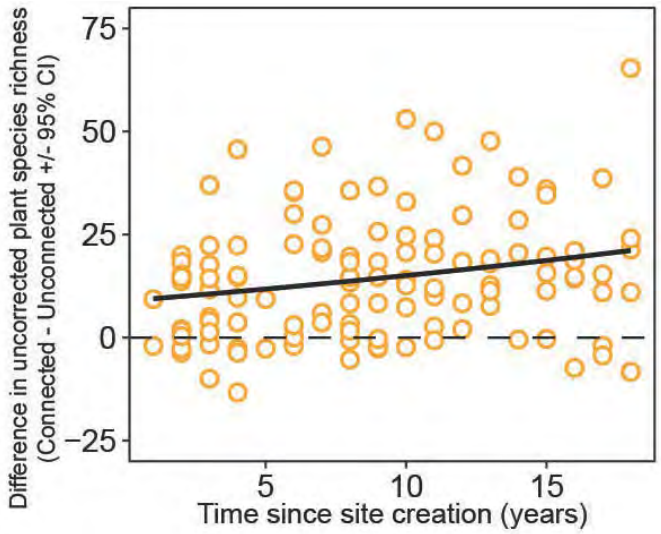

Fig. S5. The linear increase over time is evident in the difference in uncorrected, raw plant species richness over time between connected and unconnected fragments. Predicted line comes from the linear model (Fig. S4).

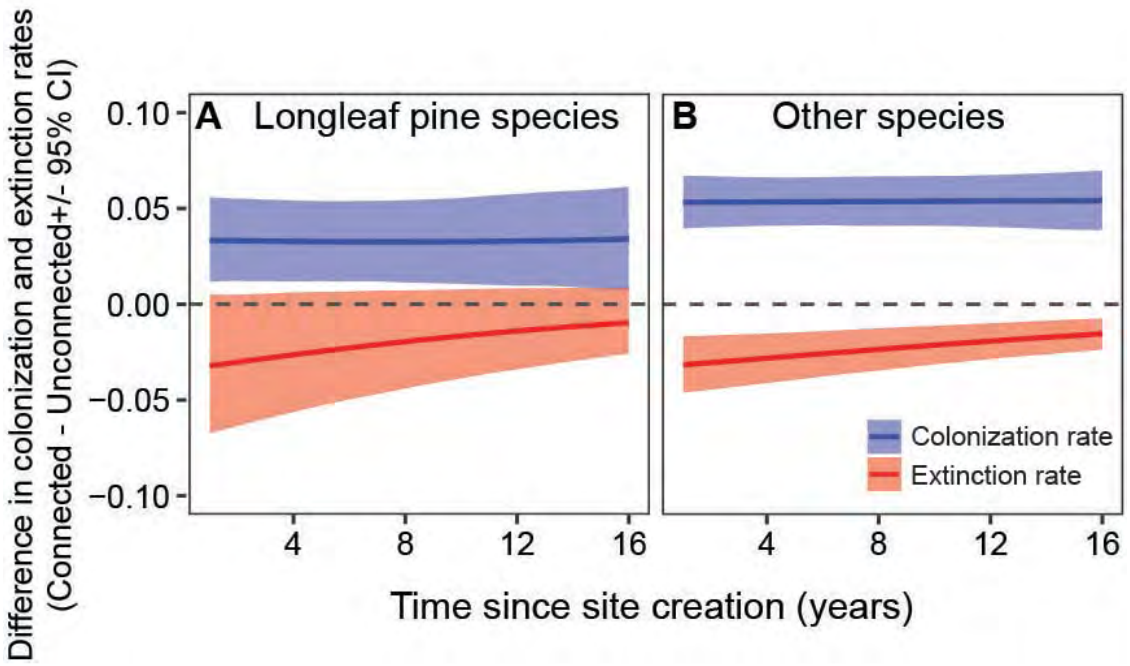

Fig. S6. Plant species (A) associated with longleaf pine habitat and (B) other species respond similarly to connectivity over time, although uncertainty is greater for species associated with longleaf pine habitat due to a smaller number of species**.** The difference between connected and unconnected fragments for colonization and extinction probabilities is shown for both groups.

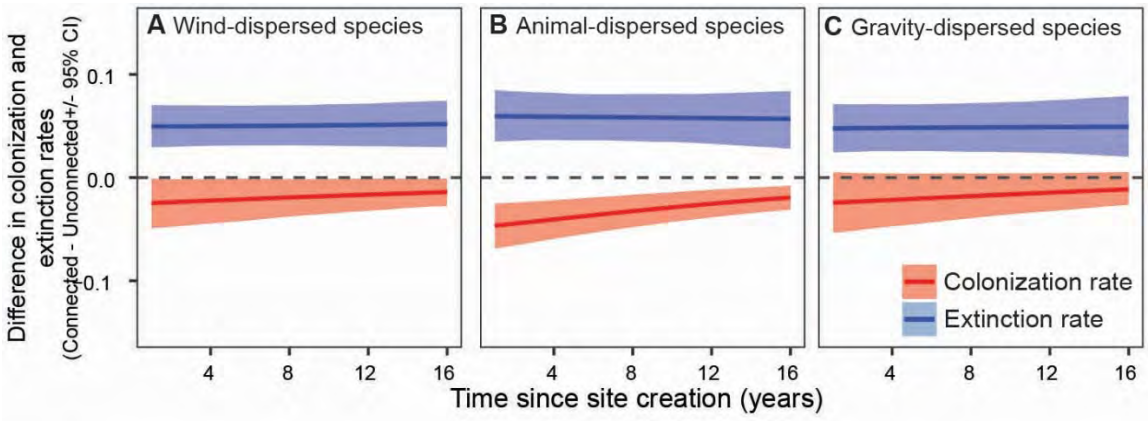

Fig. S7. Plant species respond similarly to connectivity over time across seed dispersal modes. The difference between connected and unconnected fragments for colonization and extinction probabilities of **(A)** wind-dispersed, **(B)** animal-dispersed, and **(C)** gravity-dispersed plant species over time.

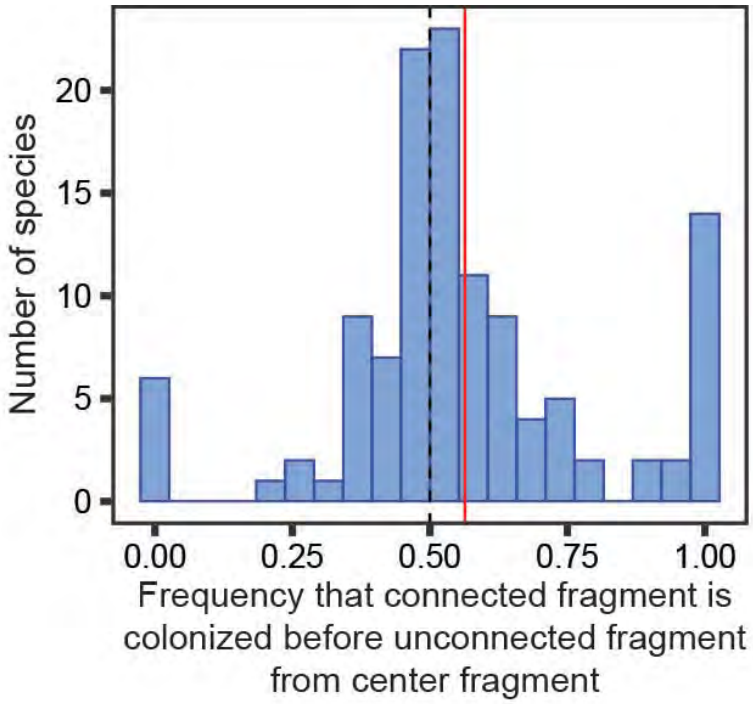

Fig. S8. Colonization events from the center fragment reach connected fragments sooner than unconnected fragments. When species arrived for the first time in an experimental block in the center fragment, connected fragments were colonized sooner than unconnected fragments for 60% of the species (out of 120 species for which this situation occurred; mean frequency = 0.56). The distribution was highly skewed providing some evidence of corridors facilitating colonization of species from center fragments.

Table S1. Summary of parameter estimates (on the logit scale) from multi-species occupancy model used to derive species richness over time. We show average estimates across species because this model estimates a parameter for each species (K = 309) regarding species detectability, treatment intercepts and rates of change over time. Estimates are provided for connected, unconnected rectangular, and unconnected winged fragments. LCL and UCL are lower and upper confidence limits, respectively.

Parameter	Estimate	95% LCL	95% UCL
Species mean detectability	-2.123	-2.466	-1.773
Species mean occupancy			
Connected intercept	0.447	0.294	0.607
Rectangular intercept	-0.220	-0.379	-0.065
Winged intercept	0.251	0.098	0.407
Connected time effect	0.672	0.574	0.768
Rectangular time effect	0.491	0.404	0.578
Winged time effect	0.553	0.467	0.672

Supplementary Code. The code used to estimate occupancy, species richness, and colonization-extinction dynamics over time is provided as a separate supplementary file.

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A Rapid, Strong, and Convergent Genetic Response to Urban Habitat Fragmentation in Four Divergent and Widespread Vertebrates

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Abstract

Background: Urbanization is a major cause of habitat fragmentation worldwide. Ecological and conservation theory predicts many potential impacts of habitat fragmentation on natural populations, including genetic impacts. Habitat fragmentation by urbanization causes populations of animals and plants to be isolated in patches of suitable habitat that are surrounded by non-native vegetation or severely altered vegetation, asphalt, concrete, and human structures. This can lead to genetic divergence between patches and in turn to decreased genetic diversity within patches through genetic drift and inbreeding.

Methodology/Principal Findings: We examined population genetic patterns using microsatellites in four common vertebrate species, three lizards and one bird, in highly fragmented urban southern California. Despite significant phylogenetic, ecological, and mobility differences between these species, all four showed similar and significant reductions in gene flow over relatively short geographic and temporal scales. For all four species, the greatest genetic divergence was found where development was oldest and most intensive. All four animals also showed significant reduction in gene flow associated with intervening roads and freeways, the degree of patch isolation, and the time since isolation.

Conclusions/Significance: Despite wide acceptance of the idea in principle, evidence of significant population genetic changes associated with fragmentation at small spatial and temporal scales has been rare, even in smaller terrestrial vertebrates, and especially for birds. Given the striking pattern of similar and rapid effects across four common and widespread species, including a volant bird, intense urbanization may represent the most severe form of fragmentation, with minimal effective movement through the urban matrix.

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Introduction

Habitat loss and the resulting fragmentation can have many impacts on wildlife populations. However, the effects of fragmentation may vary based on many factors including the size, configuration, and age of habitat patches, the vagility of the species in question, and the characteristics of the matrix between patches. Urban development may represent a particularly intense form of fragmentation for many animals. Species that are particularly sensitive to urban development may be quickly lost from urban areas [1,2,3]. For species that remain widely distributed across fragmented landscapes, connectivity and gene flow between populations may be reduced, leading to longer-term problems such as inbreeding, loss of genetic diversity, and even local extinction [4,5,6,7]. If local extinction occurs, then more isolated patches will be harder to re-colonize [4]. In addition, the loss of genetic diversity within isolated patches can lead to a decrease in a species' ability to adapt to environmental change [8,9].

An increasing number of studies of the genetic effects of fragmentation have occurred in the past decade or so, although 30–40% of these have not shown significant effects and many are in non-urban landscapes such as fragmented forests [10]. Urbanization is a common cause of fragmentation, and conservation efforts point to the extreme land use changes associated with urbanization as one of the largest threats to biodiversity [11]. However, to date, fine-scale (within 5–10 km) genetic effects of urban fragmentation have been documented for few species [12,13,14,15,16,17], and many studies find little effect [18,19,20]. Moreover, studies of the genetic effects of fragmentation are overwhelmingly on a single species, and we know of no studies

where genetic patterns were compared in the same urban landscape for species from different broad taxa, such as reptiles (Class *Reptilia*) and birds (Class *Aves*), and with radically different means of locomotion, such as flying and crawling.

We investigated the genetic effects of urban fragmentation on three lizards, the side-blotched lizard (*Uta stansburiana*), western skink (*Plestiodon skiltonianus*) and western fence lizard (*Sceloporus occidentalis*), and one bird, the wrentit (*Chamaea fasciata*) in Santa Monica Mountains National Recreation Area (SMMNRA), a national park near Los Angeles. The three lizard species have widespread distributions in California [21], are small in size, are still relatively common and widespread in natural habitat throughout the area [22], and have low dispersal capabilities [23,24,25,26,27]. Side-blotched lizards and fence lizards are both in the family *Iguanidae*, but side-blotched lizards are considerably smaller and prefer more open habitat. Western skinks are in a distantly-related different family (*Scincidae*) and locally prefer grassland habitat, although all three species are broadly sympatric in the region.

Wrentits are small birds (approximately 15 g) with a distribution that is limited to the west coast of North America and follows the scrub and chaparral habitat that they prefer[28]. Wrentits are monogamous, hold small (1–2.5 acres), year-round multi-purpose territories [28], and have short dispersal distances [29]. Wrentits are obviously very different phylogenetically and ecologically from the lizards and also have the ability to fly, which could potentially increase their movement across the landscape. A bird isolated in a habitat fragment could presumably simply fly over urban areas to disperse to other suitable habitats, thereby preventing genetic divergence between patches. However, because wrentits have short dispersal distances, small territories, and relatively specific habitat requirements, it is possible that wrentits could be affected by habitat fragmentation.

The landscape of southern California continues to be rapidly altered by urbanization and the resulting habitat loss and fragmentation, even though it is part of the California Floristic Province and is one of Conservation International's world biodiversity hotspots ([30,31], www.biodiversityhotspots.org). Because it is in the Los Angeles area, SMMNRA is under intense development pressure and urbanization might increase to as much as 47% of the area by 2050, whereas only 11% was urbanized in 2000 [32]. Given the low vagility of these four focal species, it is possible that movement out of suitable habitat across a highly urbanized landscape is rare. This isolation could increase the genetic divergence between populations living in fragments and also decrease genetic variability within fragments. If urbanization is not an impenetrable barrier to movement, migration between patches by individuals could mitigate negative genetic effects [4,33,34]. Understanding plant and animal responses to habitat destruction and fragmentation will be important for maintenance of this important biodiversity hotspot, especially in the face of unknown consequences of global climate change.

Results

We attempted to genotype approximately 20 individuals from each species for each sample site (Fig. 1a, Table 1), although for some locations fewer than 20 were captured. Microsatellite loci in lizards did not significantly deviate from HWE, however three loci in wrentits did (Ase48, Ase64, Ase50). We didn't find an excess of homozygotes, which could indicate the presence of null alleles, at any of the three loci; so analyses were done using all loci. All microsatellite loci were in linkage equilibrium for all 4 species, except that in western skinks 2 pairs of loci were significantly linked ($p = 0.05$; Eufa1×Elo34, Elo34×Eufa27).

Genetic Divergence

Pairwise F_{ST} values indicated many significant genetic differences between patches for all four species (84% of comparisons were significant for side-blotched lizards, 89% for fence lizards, 87% for skinks, and 71% for wrentits; Table S1). Average pairwise F_{ST} between patches was highest in the wrentit at 0.095 (range 0.012–0.299). Among lizards, the level of differentiation was highest for side-blotched lizards, with an average pairwise F_{ST} of 0.073 (range −0.006–0.200), and very similar for western skinks (mean $F_{ST} = 0.040$, range 0.003–0.104) and western fence lizards (mean $F_{ST} = 0.040$, range 0.003–0.095). As a baseline comparison from continuous habitat, when we computed genetic distances between the sampling arrays within large and core patches and between several other sites outside of our urban study area (but within the park, see Methods), we found lower average F_{ST} for all three lizard species (side-blotched lizards, 0.02; western fence lizard, 0.016; western skinks, 0.013), and fewer significant pairwise F_{ST} (side-blotched lizards, 12.5%; western fence lizards, 16.7%; western skinks, 30%; Table S2). For wrentits, genetic samples were also collected from two coastal canyons outside of our study area, and the F_{ST} between these two sites was non-significant ($F_{ST} = 0.026$). Significant genetic distances between patches could also be caused by isolation by geographic distance. We found no significant correlations between genetic distance (F_{ST}) and geographic distance in any of the four species, suggesting no pattern of isolation by distance (Table 2). However, partial Mantel tests showed that genetic distances for all four species were significantly correlated with highway presence, roads presence, and time since isolation (patch age) when geographic distance was held constant (Table 2).

Alleles in Space allows for visualization of genetic divergence over geographic space. We found that the largest area of genetic divergence for all four species was located in the area surrounding and including Highway 23 (Fig. 1b). There was also an area of higher divergence in the eastern part of the study area for two of the four species (wrentits, Fig. 1c; and western skinks, Fig. 1e).

Genetic clustering analysis revealed that the most likely number of genetic groups for all four species was between three and five (Table S3, Fig. 2). For wrentits (Fig. 2a) there were three most likely clusters, with the main genetic break again located across the developed areas surrounding and including Highway 23. For side-blotched lizards (Fig. 2b) and skinks (Fig. 2d) the most likely number of clusters was five, and for western fence lizards (Fig. 2c) it was four.

Genetic Diversity

Mean heterozygosity (H_e) and the mean number of effective alleles (N_A) were not significantly lower in smaller patches for any of the four species (Table S4). However, relatedness was higher in small patches for all three lizard species (side-blotched lizard difference = 0.03, $t = 4.1$, $p = 0.003$, d.f. = 6.2; fence lizard difference = 0.02, $t = 4.5$, $p = 0.001$, d.f. = 7; skink difference = 0.02, $t = 2.25$, $p = 0.03$, d.f. = 6). Rarefaction analysis indicated that the number of loci used produced consistent average relatedness results for all species and that the addition of the last locus added a 0.5% (fence lizards), 0.8% (side-blotched lizards), 1.4% (western skinks), and 0.1% (wrentits) change in relatedness estimates.

We tested the relationship between genetic diversity and the degree of isolation of each habitat patch and found that for wrentits, H_e was lower in more isolated patches ($R^2 = 0.498$, $p = 0.051$,

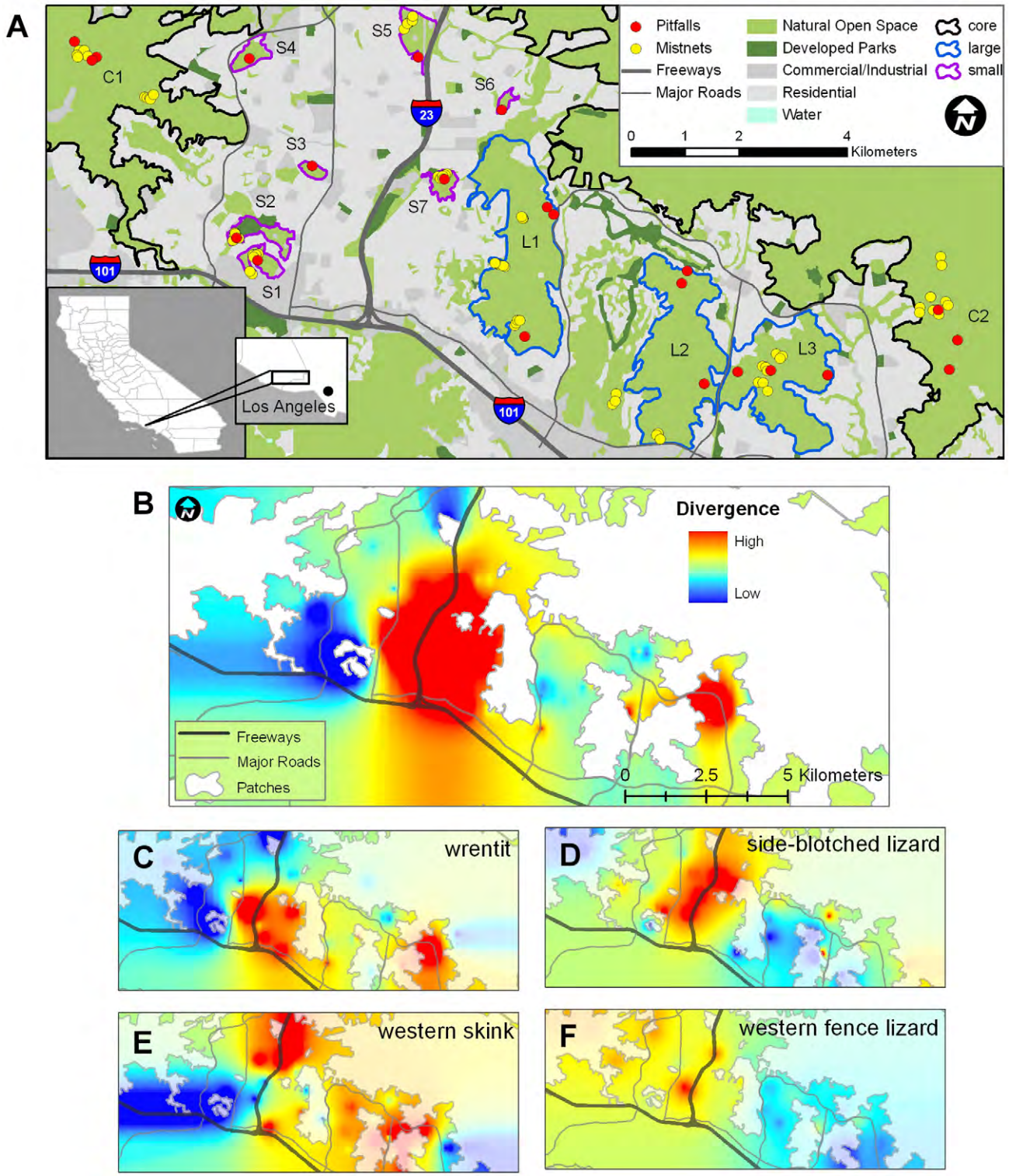

Figure 1. Study area and genetic divergence. A. Sampling sites (mist-net and pitfall locations), roads, and habitat patches (S = small, L = large, C = core) within the study area (Sample sizes are shown in Table 1). B. Mean genetic divergence mapped on the Simi Hills landscape for all four species, and separately for C. wrentits, D. side-blotched lizards, E. western skinks, and F. western fence lizards.
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d.f. = 7), as was N_A ($R^2 = 0.55$, $p = 0.035$, d.f. = 7; Fig. 3a). Relatedness was higher in more isolated patches for all three lizard species (side-blotched lizard $R^2 = 0.4$, $p = 0.03$, d.f. = 10; fence lizards $R^2 = 0.52$, $p = 0.002$, d.f. = 8; western skink $R^2 = 0.33$, $p = 0.05$, d.f. = 9; Fig. 3b). There were no correlations between genetic diversity and patch age for any of the four species (Table S5).

Table 1. Patch metrics (area, isolation, and age) and the number of samples genotyped by species.

Patch metrics					Number of samples genotyped			
Patch type	Sample site/patch	Area (ha)	Isolation (PROX)[a]	Age (years)[b]	Wrentit	Side-blotched lizard	Western fence lizard	Western skink
Small	S1	267.2	119.3	13	0	14	14	16
	S2	376.6	115.4	13	3	15	18	17
	S3	104.8	52.8	33	0	18	0	18
	S4	254.8	6404.8	23	0	17	0	0
	S5	450.2	195.9	33	5	14	18	5
	S6	78.2	747.4	13	0	17	0	20
	S7	206.5	133.1	43	8	15	16	10
Large	L1	4445.4	18428.1	28	7	0	18	28
	L2	3905.7	1598.1	23	8	22	17	29
	L3	3276.1	30121.0	18	12	18	17	18
Core	C1	25453.6	6368.9	23	11	7	15	0
	C2	121014.2	10718.8	13	15	24	14	18

[a]Patch isolation values (PROX) decrease with increasing isolation of patches.
[b]Patch age was calculated as the number of years since the patch was 100% isolated from other open natural space.
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Discussion

Loss of genetic connectivity

Using three different methods, traditional pair-wise genetic distance analysis (F_{ST}; Table S1), landscape genetic analysis (Fig. 1b), and Bayesian genetic clustering (Fig. 2), we found significant genetic differences between sample locations in all four species. Moreover, the three methods showed strikingly similar and strong genetic effects of fragmentation. All four species exhibited the largest genetic divergence over the oldest (based on building dates, see Methods) and widest expanse of urban areas surrounding and including Highway 23 (Fig. 1b).

Pairwise F_{ST} between habitat patches showed that the genetic divergence was significant, especially given the short amount of time that the habitat fragments have been isolated from each other and from core areas. For all four species, average F_{ST} values within continuous habitat were 2.5 to 3.6 times lower than in fragmented habitat, and the majority of comparisons were non-significant (Table S2). This suggests that microsatellite allele frequencies within and between habitat patches are changing on a very short time scale. Several other reptile and amphibian studies have found similar genetic divergences on similar time scales. For example, genetic divergence between fragmented populations of two gecko species in Australia was higher than divergence between samples in un-fragmented landscapes [35]. In that study, forested habitat patches were fragmented beginning around 1900 by wheat fields, which can be dry and barren during the non-growing season. In our study, however, the intervening landscape is concrete, asphalt, buildings, or urban yard landscaping, and although fragmentation began in the 1940s, many patches were only 50–75% isolated until 1980, making the isolation more recent. The long-lived tuatara (*Sphenodon punctatus*) was shown to have small yet significant genetic structuring (overall $R_{ST} = 0.012$) over less than 500 meters on a recently fragmented island [18]. Overall divergence was driven by one remnant forest fragment which was most isolated by island topography. Therefore, it was unclear that human activity, in this case pasture cleared for livestock grazing, was the cause of the genetic divergence. The eastern red-backed salamander (*Plethodon cinereus*), an even smaller and less mobile animal then the lizards we investigated, had pairwise F_{ST} between patches similar in value to the lizards in our study [14]. In that study, habitat fragmentation was also caused by 20th Century urbanization.

For birds, few studies have shown large pairwise F_{ST} between patches on such a small scale. For example, a study of the

Table 2. Mantel and partial Mantel tests with genetic distance and landscape features.

Mantel Tests	Wrentit		Side-blotched lizard		Western skink		Western fence lizard	
	r	*p*	r	*p*	r	*p*	r	*p*
F_{ST} and GD[a]	−0.015	0.500	−0.011	0.509	0.178	0.162	0.042	0.408
Partial test, HWY[b]	0.430	0.001	0.259	0.027	0.442	0.007	0.255	0.049
Partial test, RDS[b]	0.425	0.031	0.314	0.015	0.495	0.012	0.399	0.016
Partial test, AGE[b]	0.458	0.009	0.393	0.033	0.466	0.045	0.760	0.002

[a]Mantel test correlations between genetic distance (F_{ST}) and geographic distance (GD).
[b]Partial Mantel tests for partial correlations between the presence of Highway 23 only (HWY), the presence of major roads including Highway 23 (RDS), and the age of isolation between patches (patch age; AGE) while controlling for geographic distance.
doi:10.1371/journal.pone.0012767.t002

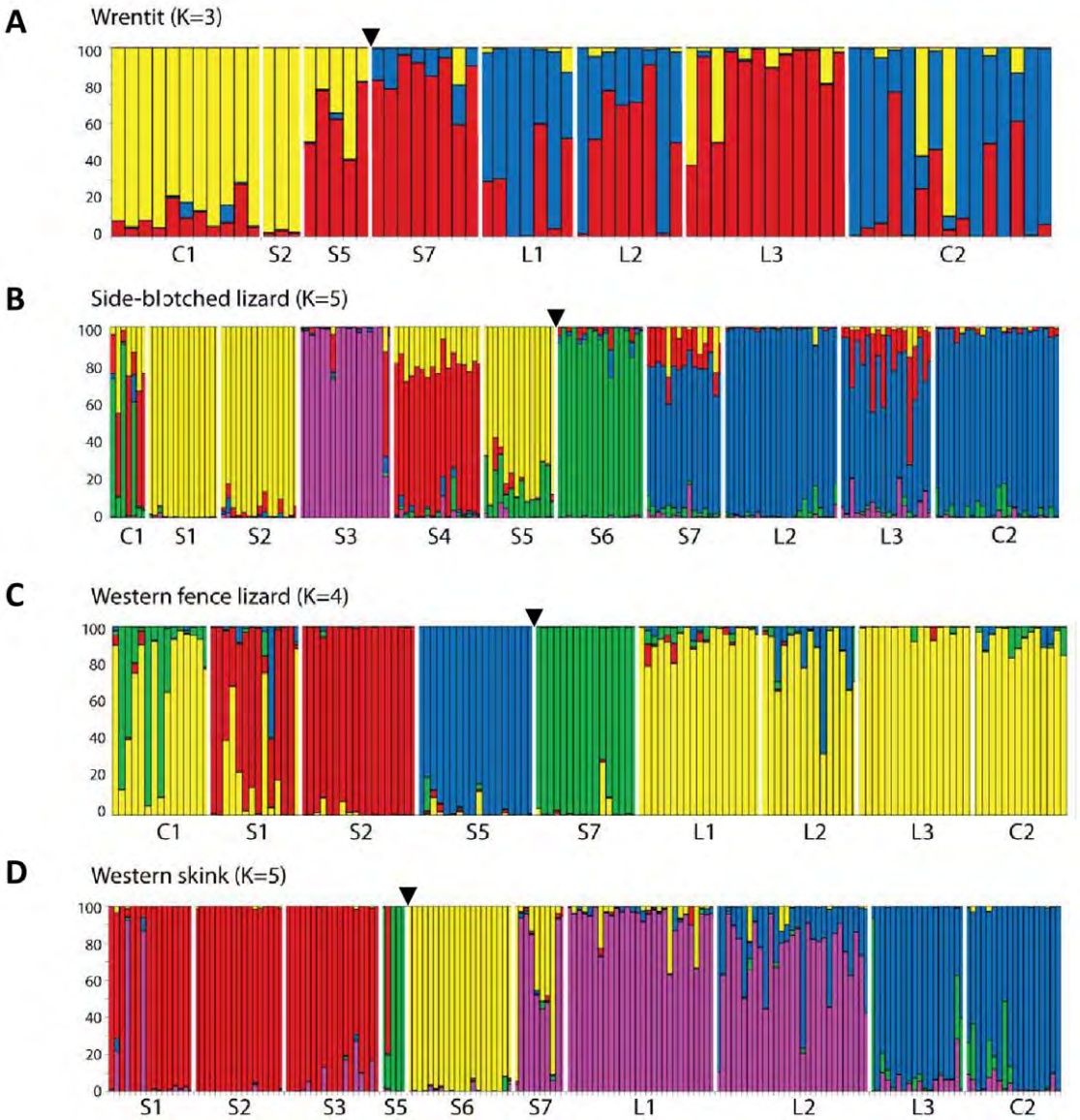

Figure 2. Genetic clustering analysis reveals the most likely K. Each column represents one individual and colors correspond to the percentage of assignment to each cluster. Patch names (Fig. 1a) are on the X-axis organized from west (left) to east (right). A black triangle indicates the location of the 23 freeway.
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capercaillie (*Tetrao urogallus*) in the Black Forest in Germany showed significant pairwise F_{ST} between sites, ranging from 0.007 to 0.036 [36]. In their study area, which was approximately 10 times the size of ours, suitable forest habitat was fragmented by other forest types and grassland, as opposed to by residential and commercial development. A study [37] of white-ruffed manikins (*Corapipo altera*) showed similar results to the capercaillie. There was some genetic structuring shown between remnant forest fragments, however all significant pairwise F_{ST} could be attributed to one forest fragment. In addition, pairwise F_{ST} between forest fragments ranged from 0.001 to 0.029 for manikins, whereas in our study the pairwise F_{ST} were approximately 10 times higher. Finally, a study of great tits (*Parus major*) in forest parks within the city of Barcelona found many significant pairwise F_{ST} between parks (average 0.067), but the parks actually had higher genetic diversity than the surrounding forest, and there was significant gene flow both between parks and from the parks to the forest [38]. Overall, there are few comparable studies of avian fine-scale genetic structure, particularly in urban landscapes, but wrentits in southern California appear to have the highest amount of genetic structure documented to date.

The Bayesian clustering analysis confirmed the loss of genetic connectivity for each species in our study area. Similar analyses in other bird studies have consistently shown that one genetic cluster is most likely [36,37,39,40], with only the great tit study finding two clusters [38]. For the lizards, in many of the small patches most or all individuals were given close to 100% assignment to that patch (e.g. S3 for side-blotched lizards, S5 and S7 for fence lizards, and S6 for skinks; Figure 2), which suggests a remarkable amount of genetic isolation within patches over relatively short geographic and temporal scales (Table S6). The short dispersal distances for all four species suggest that gene flow even within the natural landscape may be limited (for lizards, we did find a few significant F_{ST} values between sampling sites within continuous habitat), and therefore may be extremely restricted in a fragmented landscape.

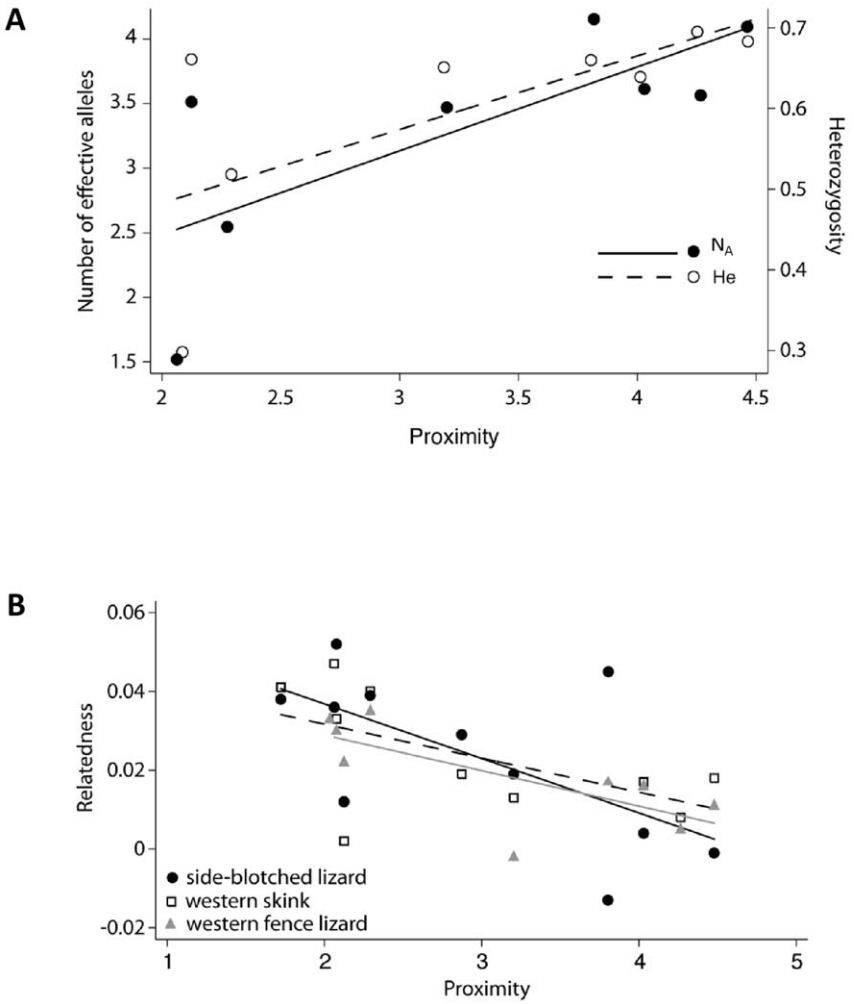

Figure 3. Relationship between genetic diversity (heterozygosity, number of effective alleles, and relatedness) and patch proximity[a] (log transformed). A. wrentits (H_e: $R^2 = 0.698$, $p = 0.051$, d.f. = 7; N_A: $R^2 = 0.55$, $p = 0.035$, d.f. = 7) and B. three lizard species (R_{LR}: side-blotched lizard $R^2 = 0.4$, $p = 0.03$, d.f. = 10; western skink $R^2 = 0.33$, $p = 0.05$, d.f. = 9; western fence lizard $R^2 = 0.52$, $p = 0.002$, d.f. = 8). [a] Patch proximity is the inverse of patch isolation.
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In one of the few other studies using Bayesian genetic clustering analysis, red-backed salamanders (*Plethodon cinereus*) were found to have two genetic clusters on either side of a large highway running through the urbanized study area [41]. Our genetic clustering results suggest that the intense fragmentation from urbanization may be a particularly strong barrier to animal movement and gene flow for all four species.

Along with significant divergence between patches, we also found significant correlations between specific causes (roads) and measures (patch age) of fragmentation and genetic divergence in all four species (Table 2). Further, our landscape genetic results revealed that the areas surrounding and including Highway 23 in the city of Thousand Oaks, which are the oldest and most densely urbanized, consistently had the highest peaks of differentiation, again for all four species (Fig. 1b). The concordance of these results for all four species is remarkable given their differences in mobility, ecology, and taxonomy. A second area of high genetic divergence in the eastern portion of our study area, also characterized by a major road surrounded by a wide swath of residential development, was shared by two species, wrentits and skinks. Other species have also shown fine-scale genetic changes related to roads and fragmentation in this region. Coyotes and bobcats exhibited significant genetic differentiation across Highway 101, the largest highway in the study area [42]. It is unknown if the species in our study would cross such a large barrier, but with short dispersal distances and small home range sizes, those events would likely be rare. Similarly, in smaller and less mobile species, a loss of genetic connectivity and diversity was found in two Jerusalem crickets (*Stenopelmatus 'santa monica'* and *Stenopelmatus 'mahogani'*) across the same region [16,43]. Genetic divergence in Jerusalem crickets was significantly associated with urban development and the presence of highways within the Simi Hills.

The significant genetic divergence and loss of genetic diversity over short geographic and temporal scales in these four vertebrates suggest that the urban matrix is relatively impenetrable for these animals. Anecdotal observations suggest that *S. occidentalis*, but not *P. skiltonianus* or *U. stansburiana*, will move through or persist in the residential areas of the urban matrix (RNF personal observation). However, reliable data on the urban movement and habitat use of these species does not exist. In fact, knowledge about use of the urban matrix by native animal species is extremely limited in general, but would be very valuable for understanding the

conservation and management implications of urbanization. Urbanized areas may be dangerous places for these small vertebrates. Residential neighborhoods often introduce predators such as domestic cats, which may regularly prey on native vertebrates [44]. Of course residential areas also include roads, which lizards and birds may actively avoid, or which may be a significant source of mortality [45,46,47].

Loss of genetic diversity

When the landscape is fragmented and gene flow is restricted, as we have shown for these four species, genetic diversity may be reduced in populations within smaller or more isolated habitat patches. Although we found no relationships between patch age and genetic diversity, we found significant relationships between genetic diversity measures and patch size or isolation for all four species. All three lizards had increased relatedness in smaller patches and with increasing patch isolation (Fig. 3b). Other reptile species have shown increased relatedness within habitat patches that were fragmented by agriculture [48,49,50]. In wrentits, although we did not find increased within-patch relatedness, we found lowered heterozygosity (H_e) and fewer alleles (N_A) in smaller patches (Fig. 3a). Decreased gene flow can result in decreased H_e and N_A in small patches as alleles are lost over the generations. This effect tends to be gradual and may not threaten populations in the short term, however, inbreeding within habitat patches tends to happen quickly and can lead to inbreeding depression [51]. Lizard relatedness values suggest that inbreeding is occurring within smaller and more isolated patches. The difference between taxa may be attributed to the increased effective isolation of lizards on suitable habitat patches as a result of more restricted dispersal ability compared to wrentits. Our results suggest that populations within smaller and more isolated patches may have an increased risk of harmful genetic effects and, over the long-term, even extirpation. In fact, the absence of individuals from certain study patches (e.g. skinks and fence lizards absent from S4; Table 1) suggests that populations that were presumably present at the time of patch isolation may have been extirpated.

In a relatively short time, we have documented significant genetic divergence between isolated patches and decreased genetic diversity in all four species. However, although time since isolation (patch age) was strongly correlated with genetic divergence between patches, the effects on genetic diversity in these animals were significantly related to patch size and degree of patch isolation, but not to patch age. This would suggest that the habitat is still relatively suitable in habitat fragments, resulting in relatively stable populations that are not going through bottlenecks, such that more time since isolation is not as important a factor. But patches that are smaller from the outset simply cannot support as large a population, and therefore are more subject to the deleterious effects of genetic drift, specifically the loss of genetic diversity. Patches that are more isolated may in turn be less likely to receive new dispersers, i.e. they would benefit less from the ''rescue effect'' that could offset reductions in genetic diversity [52]. Presumably patches that were both small and isolated would suffer the most ill effects.

Conservation implications

The extreme urbanization within the Simi Hills area has had a significant effect on lizard and bird population genetics. Unlike some other studies of landscape level genetic changes where a species' habitat is naturally patchy, this study examined genetic responses to species living in habitat that was likely once relatively continuous [42]. While these species are still widely distributed and relatively abundant throughout the study area, genetic effects of fragmentation have been manifested in a relatively short period of 40 years or less. This may be the most profound and potentially disturbing result of our study: the vulnerability even of species that are perceived to be common and thereby likely less affected by habitat fragmentation. This may be particularly true for low-vagility organisms, and for those with more specific habitat requirements. As a chaparral and coastal sage scrub requiring species, wrentits are likely rare in developed areas and have been shown to go extinct in habitat patches as urbanization progresses [2,53,54].

For rarer species in the region, such as horned lizards (*Phrynosoma coronatum*) and whiptail lizards (*Aspidoscelis tigris*), whose distributions have already been reduced by urban development [55], the genetic effects of fragmentation may be even more profound. Many endangered species in southern California are declining because of habitat loss, and many of these species also have low dispersal abilities along with more specific habitat requirements (e.g. light-footed clapper rail, *Rallus longirostris obsoletus*; Belding's savannah sparrow, *Passerculus sandwichensis beldingi*; red-legged frog, *Rana draytonii*; least bell's vireo, *Vireo bellii pusillus*). It is also unknown how stressors, such as increasing local or global temperature and urbanization, might affect species in southern California. A recent study of *Sceloporus* lizards in Mexico found that 12% of local populations have gone extinct since 1975 [56]. Sites where these common lizards were extirpated were too hot for too many hours of the day, presumably due to increasing global temperatures, which caused lizards to seek refuge from the heat instead of spending time foraging. In addition, our results have implications for endangered species such as the California gnatcatcher, where lack of differentiation at certain loci (e.g. mtDNA; [57]) may not reflect important genetic differentiation detectable with other markers such as microsatellites.

Materials and Methods

Study Area

Southern California is characterized by a Mediterranean climate with cool, wet winters and hot, dry summers. Vegetation consisted of coastal sage scrub, chaparral, riparian habitat, and oak woodlands. Our study site is within SMMNRA, the USA's largest urban national park (154,095 acres or 623.6 km^2; www.nps.gov/samo/parkmgmt/statistics.htm), which is located in Los Angeles and Ventura counties, California, USA (Fig. 1a). Approximately half of the land within the park boundary is privately owned, although some public acquisitions continue. Habitat patches within our study area were within 12.5 kilometers (km) of each other but were separated by roads of all sizes, housing, and commercial development (Fig. 1a). Most building started in the middle of the 20th Century, and none of the habitat patches have been completely isolated for longer than 43 years (Table 1; [58]). Two major freeways (101 and 23) and many busy four-lane roads run through the study area (Fig. 1a). The peak average daily traffic in this area is approximately 180,000 cars per day for the 101 Freeway and 90,000 cars per day for Highway 23 (Caltrans, www.ca.dot.gov). Both freeways are mostly surrounded by commercial and residential development. Within the study area there are large core areas of relatively undisturbed habitat, although some low-impact human recreation does occur. Within the urban mosaic, habitat patches were surrounded by high- or low-density housing, highways and other roads, golf courses and other landscaped areas.

We collected samples from habitat fragments which we characterized as ''small'' (75–450 ha) or ''large'' (3200–4400 ha) and from larger areas of continuous habitat which we called

"core" areas (Fig. 1a). There were 7 small patches (S1-S7), 3 large patches (L1-L3) and 2 core areas (C1 and C2). Patch area (m^2) and degree of isolation (PROX) were calculated using FRAGSTATS [59]. PROX is the sum of patch area divided by the nearest edge-to-edge distance squared between all of the patches within a defined search radius and the focal patch. PROX approaches 0 if the patch has no neighbors within the search radius (a 20 km radius encompassed our entire study site) specified in FRAGSTATS, therefore patches with smaller PROX numbers are more isolated. Building dates for roads, housing developments, and commercial areas were used to calculate the ages (in years) at which patches were 100% isolated up to the time of trapping for this study (patch age; Table 1). Patches were considered 100% isolated when they were completely surrounded on all edges by either commercial buildings, housing, or roads or a combination of these. We also made a matrix of patch ages (for pair wise comparisons) by calculating the number of years that each patch was separated from each other patch.

Field sampling

To capture lizards we used arrays of pitfall traps and drift fencing. All samples for this study were collected between October 2000 and September 2005. Each array had seven 19-liter buckets buried in the ground with the lip of the bucket flush with the ground to act as a pitfall trap [55,60]. Buckets were arranged in a "Y" configuration and buried approximately 7.5 m apart. Between the buckets, short drift fencing (0.5 m tall) consisting of erosion cloth acted to intercept reptiles moving through the habitat and directed them towards the buckets. Shade and moisture were provided for each bucket to maximize the chance of survival for reptiles, amphibians, or small mammals that were trapped. Pitfall traps were checked daily for a week at one-month intervals [22]. Each reptile was identified to species and snout to vent length was measured in mm. Each individual was assigned a unique number, was permanently marked by toe clipping [61,62] and a small sample from the tip of the tail was taken. Toes and tail tips were stored in 70% ethanol at 4°C or −80°C depending on storage space.

To capture birds, we used mist-nets. Trapping occurred from August 2004 to May 2006. Generally, we would open mist-nets (9–12 m long, 30 cm mesh) at sunrise and close them as the temperature increased to a potentially unsafe level in mid-morning. We targeted wrentits by playing male territorial songs with portable speakers placed at the base of the net. Once a bird was caught in the net, it was immediately removed and a U.S. Fish and Wildlife Service band was placed on its leg. We also took measurements of culmen length (mm), culmen width (mm), unflattened wing chord length (cm), tail length (cm), tarsus length (cm) and mass (g). Culmen length was taken from the anterior end of the nares to the tip of the beak using calipers. For genetic samples, we punctured the brachial vein on the wing of each bird with a small gauge needle and collected the blood that pooled there with a small capillary tube. Bleeding usually stopped after 10 seconds which yielded approximately 100 µl of blood. Blood was then placed in avian blood buffer [63].

All samples used in this study came from animals that were captured, handled, and released according to relevant national and international scientific guidelines. We used common field and handling methods that minimize stress and long-term effects of capture. We also researched methods alternative to toe-clipping of reptiles and determined that there were no less harmful yet permanent ways of marking individuals [62]. We obtained approval for our animal capture protocol from the UCLA Office of the Protection of Animals (OPRS).

We extracted genomic DNA with the Qiagen DNA mini kit (Qiagen Inc.). DNA samples were stored in TE buffer (10 mM Tris-Cl pH 8.0, 1 mM EDTA pH 8.0) at −20°C. We used six to eight microsatellite markers for each species (Table S6, J. Archie, Pers. Comm.; [64,65,66,67]). We used flourescently-labeled forward microsatellite primers when available. Alternatively, we used a three-primer genotyping protocol, where the forward microsatellite primer had an M13 sequence attached to the 5′ end (5′-GTAAAACGACGGCCAG-3′) and a third primer with the complementary M13 sequence was dye-labeled [68,69]. The forward, reverse and M13-dye primers were then used in a three-primer PCR protocol using Multiplex Mix (Qiagen Inc.) and 0.01% Bovine Serum Albumin (BSA) to generate microsatellite alleles which are flourescently labeled. Genotypes were run on an ABI 3700 sequencer and alleles were visualized using GENEMAPPER (Applied Biosystems, Inc.).

Genetic Analysis

We used the computer program CONVERT to translate our microsatellite genotype files into the correct input format for various analysis programs [70]. We used FSTAT 2.9.3 [71] to test for deviations from Hardy-Weinberg equilibrium (HWE) within samples using 1000 permutations. We also used FSTAT to test for linkage disequilibrium (LD) between loci. P-values were adjusted for multiple tests using a sequential Bonferonni correction [72]. For HWE and LD, all samples for each species were assumed to be a single population.

Genetic divergence. We used the program ARLEQUIN to estimate pair-wise F_{ST} values between patches using the infinite-allele model and 1000 permutations for significance [73,74]. We also calculated pair-wise F_{ST} between arrays within large and core patches with ARLEQUIN to show genetic divergence between sampling sites that were located within a patch of continuous habitat. For this calculation we also included some sampling sites from core areas of continuous habitat that were outside of the Simi Hills (our study area), but within SMMNRA, with an average of 4.28 km (range 1.8–6.6 km) separating these sites.

To examine patterns of sample clustering based on genetic similarity, we used the program STRUCTURE v. 2.3.1 [75]. We chose the LOCPRIOR model [76], assumed populations were not admixed and that allele frequencies were correlated between populations, and ran 100,000 MCMC chains with a 10,000 burn-in. We ran seven runs each of K = 1 to K = number of sample sites (Fig. 1a) for each species. We compiled results from our STRUCTURE runs with the program STRUCTURE HARVESTER (Dent Earl, http://taylor0.biology.ucla.edu/struct_harvest/). To determine the most likely K, we calculated the posterior probabilities of the mean of seven runs at each K (Table S3; [75]).

Isolation by distance, as revealed by a correlation between pairwise genetic and geographic (Euclidean) distances using a Mantel test, was performed using IBDWS 3.14 [77]. IBDWS uses a Reduced Major Axis (RMA) regression to estimate the slope and intercept of the isolation by distance relationship.

To test for the effect of major roads, highways, and patch age on genetic divergence, we performed partial Mantel tests [78] in IBDWS 3.14. Partial Mantel tests determined correlations of roads presence (RDS), highway presence (HWY), and patch age of isolation (AGE) on a genetic divergence matrix, while holding geographic distance constant. Tests were performed separately, one for each of these three variables, and all animals that were captured within a patch were used to calculate a patch average genetic divergence (F_{ST}; as calculated in ARLEQUIN, see above). The presence of major roads and the presence of Highway 23 were used separately in the analysis because the highway in our

study area is larger and has more traffic than other roads. Also, several habitat fragments are only separated by major roads. Age of isolation was chosen because this measure incorporates not only when roads and freeways were built, but also when residential and commercial developments were erected.

We mapped genetic distance on the landscape using Alleles in Space (AIS) and the landscape shape interpolation [79]. We used a Delaunay triangulation-based connectivity network to identify midpoints between our sample sites, then the raw genetic distance (D_{ij}) at each midpoint was calculated [79]. This genetic distance measure is similar to Nei's standard genetic distance (D_s; [80]), where D_{ij} is 0 if individuals are completely genetically identical, and D_{ij} is 1 if individuals are completely genetically dissimilar. We did not calculate the residual genetic distance, because we did not find a significant isolation by distance effect in the Simi Hills samples for any species (see Results). By this method, a landscape of genetic distances between sampling sites are expressed as "surface heights" and are displayed as a 3-dimensional graph. To better visualize the AIS height output, we imported the output file into ArcGIS 9.3 (ESRI Corporation, Redlands, CA) and created a 2-dimensional color hot-spot map overlaid on the geographic study area. Colors correspond to "heights" of genetic distance between points (e. g. Fig. 1b).

Genetic diversity. We used the program GENALEX [81] to calculate the genetic diversity indices of within-patch expected heterozygosity (H_e), observed heterozygosity (H_o), number of effective alleles (N_A), and relatedness (R_{LR}) [82]. We used the Lynch & Ritland (1999) estimator of relatedness because it has been shown to perform well in simulations for a wide range of marker data and population structure [83]. We performed a rarefaction analysis using the web-based program RERAT [84] which uses multiple simulations to determine the change in relatedness values as additional microsatellite loci are added. In RERAT, we performed 100 simulations and used the Lynch and Ritland (1999) relatedness analysis for each of the four species. For lizards, cores and large patches had three pitfall trap arrays while small patches had one (Fig. 1a). To reduce bias because of array clustering, we calculated pair wise relatedness of all individuals caught in the same array, and then used the mean of those within-array measures to calculate within patch relatedness.

We used the program STATA 9 (StataCorp, College Station, TX) to transform variables until they approached normal distributions and then to examine the relationship between the indices of genetic diversity and the size, degree of isolation, and age of the habitat patches. We used unpaired t-tests (with unequal variance when necessary) and Bonferroni corrections to compare genetic diversity measures between small and large/core habitat patches. Degrees of freedom for t-tests were calculated using the Satterthwaite (1946) method [85]. We lumped large patches and core areas for this analysis because, for these small species, population size is likely equivalently large in the large patches and the core areas, and because the numbers of sites were relatively small for core areas ($n = 2$) and large patches ($n = 3$). To test for a relationship between patch isolation and genetic diversity, we used linear regression to examine the relationship of the genetic diversity indices with the size, pair wise age of isolation, and proximity (PROX) of the habitat patches, where the degree of isolation of a patch is the inverse of proximity. Spearman's rank correlations were used to test for significant associations between patch age and genetic diversity.

Supporting Information

Table S1 F_{ST} between sample sites for 4 species. Significant pairwise F_{ST} values are in bold (see Fig. 1a for sample site locations).
Found at: doi:10.1371/journal.pone.0012767.s001 (0.22 MB DOC)

Table S2 Pairwise F_{ST} and the number of significant comparisons between patches in and continuous habitat.
Found at: doi:10.1371/journal.pone.0012767.s002 (0.05 MB DOC)

Table S3 Estimated posterior probabilities for K. Most likely number of genetic clusters (K) identified with the program Structure is shown in bold.
Found at: doi:10.1371/journal.pone.0012767.s003 (0.07 MB DOC)

Table S4 Mean genetic diversity measurements within patches (number of effective alleles, N_A; relatedness, R_{LR}; heterozygosity, H_e).
Found at: doi:10.1371/journal.pone.0012767.s004 (0.12 MB DOC)

Table S5 Spearman's Rho correlation coefficients. The number of individuals genotyped (N), the number of alleles (A), expected (H_e) and observed (H_o) heterozygosity.
Found at: doi:10.1371/journal.pone.0012767.s005 (0.04 MB DOC)

Table S6 Microsatellite primers used for each species. The number of individuals genotyped (N), the number of alleles (A), expected (H_e) and observed (H_o) heterozygosity.
Found at: doi:10.1371/journal.pone.0012767.s006 (0.14 MB DOC)

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Author Contributions

Conceived and designed the experiments: KSD SPDR RNF. Performed the experiments: KSD. Analyzed the data: KSD. Contributed reagents/materials/analysis tools: KSD SPDR. Wrote the paper: KSD SPDR.

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HOME-RANGE AND HABITAT SELECTION BY ADULT COUGARS IN SOUTHERN CALIFORNIA

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Abstract: Understanding the impact of habitat fragmentation, roads, and other anthropogenic influences on cougars (*Puma concolor*) requires quantitative assessment of habitat selection at multiple scales. We calculated annual and multiyear home ranges using a fixed-kernel (FK) estimator of home range for 13 adult female and 2 adult male radiotagged cougars that were monitored October 1986 through December 1992 in the Santa Ana Mountain Range of southern California, USA. Using compositional analysis, we assessed diurnal use of vegetation types and areas near roads at 2 orders of selection (second- and third-order; Johnson 1980). Mean annual and multiyear 85% FK home ranges for males were larger than those reported by previous studies in California. Mean wet-season 85% FK home ranges were significantly larger than those of the dry season. At both scales of selection and across seasons, cougars preferred riparian habitats and avoided human-dominated habitats. Grasslands were the most avoided natural vegetation type at both scales of selection. Although cougar home ranges tended to be located away from high- and low-speed 2-lane paved roads (second-order avoidance), cougars did not avoid roads within their home range, especially when roads were in preferred riparian areas. Protection of habitat mosaics that include unroaded riparian areas is critical to the conservation of this cougar population.

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Key words: California, compositional analysis, cougar, fixed-kernel home range, habitat selection, home range, *Puma concolor*, riparian, roads, scale, vegetation.

Persecution of North American cougars, overexploitation of their prey, and habitat loss across most of their historic range have relegated this species to habitats in the western states and southern Florida (Anderson 1983). Cougars persist in a wide range of ecosystems, including the hammock and swamp forests of southern Florida (Belden et al. 1988, Maehr and Cox 1995), the high deserts of southern New Mexico (Logan et al. 1996), and the northern Rocky Mountains (Williams et al. 1995). The vegetation and structural characteristics of these landscapes provide habitat for prey and cover for cub rearing, hunting, and stalking prey (Logan and Irwin 1985, Laing 1988, Koehler and Hornocker 1991, Beier et al. 1995, Williams et al. 1995). In California, an understanding of cougar distribution and habitat selection is relevant to managing the impact of hunting and trapping on cougars (Torres et al. 1996), cougar attacks on humans (Beier 1991), and habitat fragmentation (Beier 1993). Habitat fragmentation and road building are occurring at a rapid pace in the Santa Ana Mountains of southern California (Beier 1993).

Although some aspects of cougar ecology previously have been studied in California (Sitton and Wallen 1976, Neal et al. 1987, Hopkins 1989, Padley 1990, Beier and Barrett 1993, Pierce et al. 1999), these researchers did not quantitatively assess habitat selection. Only 4 previous studies have made quantitative assessments of cougar habitat use in the West (Logan and Irwin 1985, Laing 1988, Koehler and Hornocker 1991, Williams et al. 1995).

We used data from radiotagged cougars to quantify how adult cougars in the Santa Ana Mountains of southern California selected among vegetation types, topographic settings, and habitats with roads. We followed the framework developed by Johnson (1980) and Aebischer et al. (1993), in which animals make decisions about resource use at hierarchical stages, namely selection of a home range within a study area (second-order selection) and selection of patches within a home range (third-order selection). First-order selection (selection of a species' geographic range) was beyond the scope of this study. These orders of selection reflect a sequential process on the part of an individual animal. In locating its home range within 1 part rather than some other part of the Santa Ana Mountain Range, a cougar evaluates the resources (e.g., prey, ambush cover, water) and hazards (e.g., roads, human disturbance, other cougars) of various parts of the mountain range. Once this selection has occurred, the animal's day-to-day selection of sites within its home range is constrained by its

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previous selection of a home-range area. Important aspects of habitat selection could be masked by a study confined to only 1 level. For instance, an animal might spend 20% of its time in a habitat that composes 40% of its home range; a third-order study would interpret this as aversion to that habitat. However, the animal may have chosen that home range precisely for the high abundance of that habitat type; a second-order study would detect such selection. Conversely, a cougar might locate its home range away from areas of high density of paved roads (second-order aversion), but nonetheless suffer high risk of mortality if it does not avoid the few paved roads within its home range (third-order indifference). Although calculating home-range size was not our primary objective, delineation of home ranges is an integral part of the analysis of habitat selection and therefore became an important component of this study.

Our objectives were to (1) identify the seasonal, annual, and multiyear home-range characteristics for individual cougars; and (2) quantify habitat preferences at 2 orders of selection with respect to vegetation types, topography, and paved roads.

STUDY AREA

At the time of the study, the Santa Ana Mountain Range study area (SAMR) contained approximately 2,060 km^2 of nonurban land. These wildlands included portions of Orange (38% of study area), Riverside (28%), and San Diego (34%) counties; over 1 million people lived in the cities and communities surrounding the SAMR (Beier 1993). Much of the potential cougar habitat in the area was protected within the Cleveland National Forest, Camp Pendleton Marine Corps Base, Fallbrook Naval Weapons Station, Caspers Regional Park, and several smaller reserves (Padley 1990, Beier and Barrett 1993). We delineated the study-area boundaries where potential cougar habitat met a major interstate highway, abutted coastline, or where human dwellings exceeded 4 residences per hectare. We assumed these landscape features to be effective barriers to selection by cougars beyond the core wildlands of the SAMR. Beier (1993, 1995) provides maps of the study area.

Common California plant communities present on the study area included chaparral, oak woodlands (*Quercus engelmannii* and *Q. agrifolia*), coastal scrub, annual grasses, and coniferous woodlands at higher elevations (Barbour and Major 1995). Citrus and avocado orchards and other nonnative vegetation types occurred in parts of the area. While much of the study area remained undeveloped, human influence was widespread and included cattle grazing, orchards and agriculture, military training facilities, and public recreation areas. Maximum average daily temperature was 24 °C, and mean annual precipitation was 33 cm at lower elevations (Santa Ana Fire Station, Santa Ana, California; 1948–2000), with somewhat cooler and more mesic conditions at higher elevations. Precipitation in the form of fog drip was common during dry and wet seasons, and light snow accumulation was possible in winter at the higher elevations (Barbour and Major 1995). Elevations within the study area ranged from sea level at the coast to 1,717 m on Santiago Peak. The topography was rugged. Perennial streamflow was intermittent (Beier and Barrett 1993); however, springs, seeps, and other water sources were present and relatively common throughout the study area.

Other common carnivores included coyotes (*Canis latrans*), gray foxes (*Urocyon cinereoargenteus*), bobcats (*Lynx rufus*), raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*). Mule deer (*Odocoileus hemionus*) were common throughout the study area and were the most important prey species for cougars (Beier and Barrett 1993). Other prey included opossum (*Didelphis virginiana*), coyote, and raccoon (Beier and Barrett 1993).

METHODS

Radiotelemetry

Between October 1986 and December 1992, 13 adult (≥2 years old) female cougars and 2 adult male cougars were captured, radiocollared, and monitored on the SAMR study area (Padley 1990, Beier and Barrett 1993). Eighty-one percent of radiolocations were from ground-based triangulation conducted every 1 to 4 days, usually (85%) during daylight hours. Radiolocations were obtained from the ground using standard triangulation techniques (Mech 1983) conducted by a single observer. Because only a single observer was used and no network of precisely located receiving stations was available, we could not compute meaningful error polygons (White and Garrott 1990). Location errors were minimized by using only azimuths that differed by 60–120° and by getting close to the animal (White and Garrott 1990). Observers attempted to stay >100 m from the focal animal to avoid influencing its movement and <500 m away to obtain accurate locations; 76% of locations were determined

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from within 500 m of the focal animal, and 87% were from within 1 km. The remaining 19% of locations were obtained by aerial homing from fixed-wing aircraft from flights conducted approximately once every 10 days, always during daylight. All locations were recorded as Universal Transverse Mercator (UTM) points and exported into a vector-based geographic information system (GIS; ArcView® 3.2a [ESRI, Redlands, California, USA]).

Home-Range Delineation

We calculated home-range sizes separately for the dry season (May–Oct), the wet season (Nov–Apr), and annual periods (seasons combined). We use the term "multiyear" to indicate a home range or analysis using data pooled across >1 year of observation; thus, a multiyear dry-season home range includes locations for ≥2 dry seasons for a particular animal. Using an animal movement analysis extension (Hooge and Eichenlaub 1997) in ArcView, we calculated annual 50%, 85%, and 95% FK home ranges (Worton 1989) with a level of smoothing selected by least-squares cross-validation (Worton 1995, Seaman and Powell 1996, Seaman et al. 1999) and a grid cell size of 30 m × 30 m. All home-range contours were clipped at the study-area boundary before subsequent analyses.

Nonparametric kernel estimators can estimate densities of any shape (Seaman and Powell 1996) and are not influenced by effects of grid size or placement (Silverman 1986). We report the 50% home range as an area of core utilization and the 85% home range as an area of ecological importance to a cougar. We report the 95% home range as a commonly referenced contour, but agree with Seaman et al. (1999) that it is of little biological significance and unreliable, regardless of the home-range estimator used. Seasonal home ranges were calculated only for individual adult cougars that were monitored for >91 days of a 182-day season and that yielded >50 locations in a season. We tested for differences in seasonal 85% home-range sizes using a Wilcoxon signed-rank test (T = test statistic).

Compositional Analysis of Habitat Selection

We use the term "habitat composition" to refer to a vector of proportions of habitat classes (as defined by vegetation type and other classifying factors) used by or available to an animal; each habitat composition necessarily sums to 100%. Rettie and McLoughlin (1999) demonstrated that the use of point data (e.g., ignoring location error) increases the risk of drawing erroneous conclusions about relative preference because of the bias associated with assigning a point to a specific patch of habitat. To account for error in assigning an individual radiolocation to a particular class (e.g., vegetation type), our analysis assumed that a cougar used all classes within a 200-m radius of a radiolocation in proportion to the area of that class within the circle. We chose a 200-m-radius buffer to encompass triangulation error in estimating animal locations (Beier et al. 1995) and to encompass errors inherent in the digital coverages used to analyze selection. Equally important, this buffer allows our analysis to detect the potential importance of habitat mosaics in the selection process (see Rettie and McLoughlin 1999). To evaluate second-order selection, we compared the habitat composition of the study area to the averaged habitat compositions of individual cougar radiolocations. For third-order selection, we compared the habitat composition of an individual's multiyear 85% home range to the averaged habitat composition of the radiolocations of that individual captured in that multiyear 85% home range.

At both scales of selection, we used compositional analysis to develop a ranking of habitat preference (Aitchison 1986, Aebischer and Robertson 1992, Aebischer et al. 1993). Compositional analysis correctly uses the individual animal, not the radiolocation, as the sampling unit and avoids statistical problems arising from nonindependence of proportions within a habitat composition (Aebischer et al. 1993).

Because 6 animals are the minimum for statistical inferences from compositional analysis (Aebischer et al. 1993) and we had data for only 2 males, we pooled males and females. At both scales of analysis, we analyzed only those habitat classes available to all cougars.

Compositional analysis compares use of each habitat class to an arbitrary reference class k by the log-transformed ratio of habitat proportions for each animal (Aitchison 1986):

$$y_{ij} = \ln(x_{ij}/x_{ik}) \, (i = 1, \ldots, n; j = 1, \ldots, D; j \neq k),$$

where x_{ij} describes proportional use by an individual i of the jth of D habitat types, and n = number of individual animals. When an individual's proportional utilization of a habitat was 0, we replaced this value with a number less than 0.1 times the smallest observed value for that habitat (Aebischer et al. 1993). The differences between used and available habitat log-ratios for each indi-

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vidual formed a single row of a difference matrix with n rows and $D - 1$ columns. To test the null hypothesis that utilization was random (difference matrix = 0), we constructed a residual matrix from the matrix of log-ratio differences and computed the Wilks' lambda statistic:

$$\Lambda = \frac{|R1|}{|R2|},$$

where $R1$ is the matrix of mean corrected sums of squares and cross-products, and $R2$ is the matrix of raw sums of squares and cross-products. Following the procedure proposed by Aebischer et al. (1993), we transformed Λ into the test statistic:

$$-N \times \ln(\Lambda),$$

which approximates a chi-square distribution with $k - 1$ degrees of freedom, and where N is the number of individuals in the sample and k = the number of habitat classes. When habitat use was significantly nonrandom ($P < 0.05$), we calculated the mean and standard deviation for all log-ratio differences and constructed a matrix ranking habitat types in their order of use. To assess differences between ranks, we used a paired t-test to compare mean utilization between all pairs of habitats.

Vegetation Types

We obtained digital vegetation coverages from Orange, Riverside, and San Diego counties. Vegetation polygons available on the study area were identified by county personnel during 1990, 1992, 1993, and 1995 using Landsat Thematic Mapper and SPOT 2 satellite imagery, digital aerial photographs, and field vegetation mapping surveys (ground-based and aerial). County personnel digitized vegetation boundaries "on-screen" using the airphotos and satellite imagery as background layers and georeferenced the resulting polygons using terrain-corrected satellite data. These polygons were then digitally coded and projected into UTM zone 11 (North American Datum of 1927). These methods resulted in a mean spatial accuracy of approximately 25 m and a minimum mapping unit between 0.2 and 2.0 ha. In some cases, narrow riparian areas were more accurately delineated using the near infrared band of a SPOT image, which can detect greater leaf moisture content, or by using hydrographic data layers. All vegetation types were categorized and classified by the 3 counties based on modifications to the Holland classification system (R. F. Holland. 1986. Preliminary descriptions of the terrestrial natural communities of California. California Department of Fish and Game, Nongame Heritage Program, Sacramento, USA, unpublished report). Initially, we identified 16 broad vegetation types and interpolated these across the 3 counties. We further consolidated infrequent vegetation types into 9 more general vegetation types: scrub, chaparral, grassland, riparian, forest, woodland, agriculture, developed, and disturbed (Dickson 2001). Lakes, rivers, wetlands, vernal pools, beaches, and artificial watercourses (totaling 0.70% of the study area) were classified within the riparian vegetation type. Cliff and rock habitats (totaling 0.04%) were most often adjacent to chaparral vegetation types and so were reclassified as such. Coastal dunes (totaling 0.01%) often were associated with scrub vegetation and were grouped within this type.

Topography

Within the GIS, we merged 26 USGS 1:24,000 digital elevation models (DEMs) to describe elevation, slope, and aspect of the entire study area and individual 85% home ranges. The slope (in degrees) of a cell location was derived from the DEM by calculating the maximum rate of change between neighboring cells. The aspect (in degrees) of a cell location was derived from the DEM by calculating the steepest down-slope direction to its neighboring cells. We reclassified aspect into 4 cardinal direction categories: north (315°–45°), east (45°–135°), south (135°–225°), and west (225°–315°). We assessed cougar use of elevation, slope, and aspect by calculating the average of all 30 m × 30-m cell values captured within 200 m of an individual radiolocation. We used a z-test (z = Test Statistic) to test for significant differences between utilized and available calculations of elevation and slope. For each individual cougar, we calculated the proportion of radiolocations that fell into each of the 4 aspect categories.

Roads

To assess the response of cougars to roads on the SAMR, we obtained 1995 U.S. Bureau of the Census TIGER (Topologically Integrated Geographic Encoding and Referencing) digital data coverages for all roads on the 3 counties. We modified these coverages based on paper maps on which field crews had indicated accurate road location and condition (e.g., paved, dirt, unusable, absent) of mapped roads. We did not analyze cougar response to multi-lane freeways (because they occurred at the periphery of only 3

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Table 1. Mean multiyear home range areas (km^2) for 13 adult female (F1–F19) and 2 adult male (M2, M9) cougars in the Santa Ana Mountain Range, California, USA, 1986–1992, using a fixed-kernel estimator.

		Multiyear home range				Dry-season home range				Wet-season home range			
Animal ID	No. years	No. locations	50%	85%	95%	No. locations	50%	85%	95%	No. locations	50%	85%	95%
F1	3	433	20	80	158	211	14	68	122	222	19	74	157
F2	4	718	14	52	89	360	10	45	84	358	21	65	114
F3	2	590	7	42	82	306	7	33	67	284	16	58	96
F4	3	537	4	37	92	260	3	25	72	277	18	67	123
F5	4	251	51	151	264	147	41	146	252	104	70	195	334
F6	3	267	10	90	234	149	14	79	218	118	21	167	245
F9	2	213	16	52	95	84	11	43	78	129	17	58	96
F10	3	380	27	85	140	247	27	84	128	133	15	74	142
F11	5	357	7	75	147	171	7	48	120	186	26	128	201
F12	3	304	9	44	77	192	7	35	68	112	15	59	99
F15	1	131	17	77	139	77	9	43	105	54	25	145	265
F18	2	70	45	148	350	—	—	—	—	—	—	—	—
F19	1	130	33	114	225	88	24	88	186	—	—	—	—
Female mean	—	337	20	81	161	191	14	61	125	180	24	99	170
M2	2	290	51	412	671	115	59	291	543	175	105	544	735
M9	2	129	100	527	854	72	80	579	898	57	184	574	791
Male mean	—	210	75	470	763	94	69	435	721	116	144	559	763

home ranges) or dirt roads (because they were ubiquitous in all home ranges and because TIGER files provided inaccurate and incomplete coverage of these roads). We classified the remaining paved roads as either high-speed 2-lane paved roads (posted speed limits ≥80 km/hr) or low-speed 2-lane paved roads (posted speed limits ≤56 km/hr). We classified surrounding areas into 4 zones with respect to each road speed, namely <500 m; 500–1,000 m; 1,000–1,500 m; or >1,500 m from roads of that speed. We calculated the proportion of individual radiolocations captured within each zone and compared this to the proportion of available area in that zone. For second-order selection, we included all individuals, but for third-order selection, we included only those individuals whose multiyear 85% home range contained roads of the road speed being considered. Compositional analysis was used to develop a ranking of zone preference relative to the proportional availability of area in that zone. We calculated high-speed, low-speed, and total 2-lane paved road densities on the study area and on the individual multiyear 85% home range.

RESULTS

Home-Range Sizes

The annual 85% home range averaged 93 km^2 (SD = 50) for 12 adult female and 363 km^2 (SD = 63) for 2 adult male cougars. For both wet and dry seasons, males also had home ranges more than twice as large as those of females. Wet-season 85% home ranges were significantly larger than those of the dry season (for 7 females with data for both seasons, $T = 2.37$, $P = 0.02$).

Multiyear 85% home ranges averaged 81 km^2 (SD = 38) for 13 females and 470 km^2 (SD = 81) for 2 males (Table 1). Wet-season 85% home ranges were significantly larger than those of the dry season ($T = 2.90$, $P = 0.004$; $n = 13$ individuals).

Influence of Vegetation Type on Habitat Selection

Cougars selected riparian vegetation types and avoided human-dominated areas and grasslands at the second-order scale (e.g., radiolocations within the study area) and the third-order scale (e.g., radiolocations within a home range). At the second-order, proportional use of vegetation types on the study area was significantly different from habitat composition of the study area during the dry season ($-N\ln\Lambda = 56.68$, $P < 0.001$, df = 8; $n = 12$ females and 2 males), wet season ($-N\ln\Lambda = 51.18$, $P < 0.001$, df = 8; $n = 11$ females and 2 males), and across seasons ($-N\ln\Lambda = 61.99$, $P < 0.001$, df = 8; $n = 13$ females and 2 males; Fig. 1). Both within and across seasons, cougars consistently preferred riparian vegetation types. The rank order of vegetation types also was consistent

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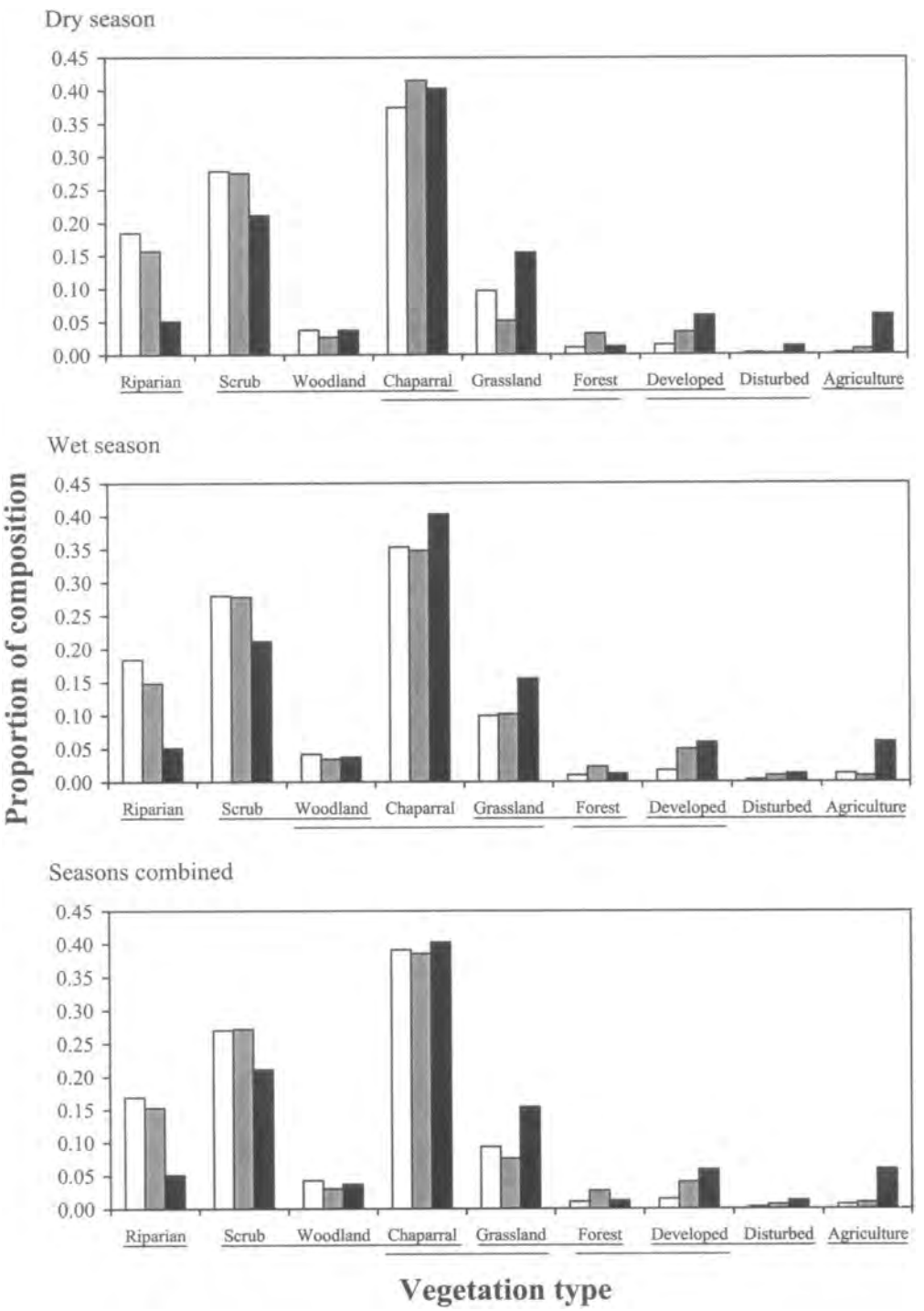

Fig. 1. Second-order selection (i.e., comparing habitat composition of individual buffered radiolocations to the habitat composition of the entire study area) by cougars in the Santa Ana Mountain Range, California, USA, 1986–1992. Vegetation types are arranged from most to least preferred for dry season, wet season, and seasons combined. White bars indicate mean female proportional utilization, gray bars indicate mean male proportional utilization, and black bars indicate habitat proportional availability. Underlining under names of vegetation types on the *x*-axis indicates vegetation types for which rankings are not significantly different.

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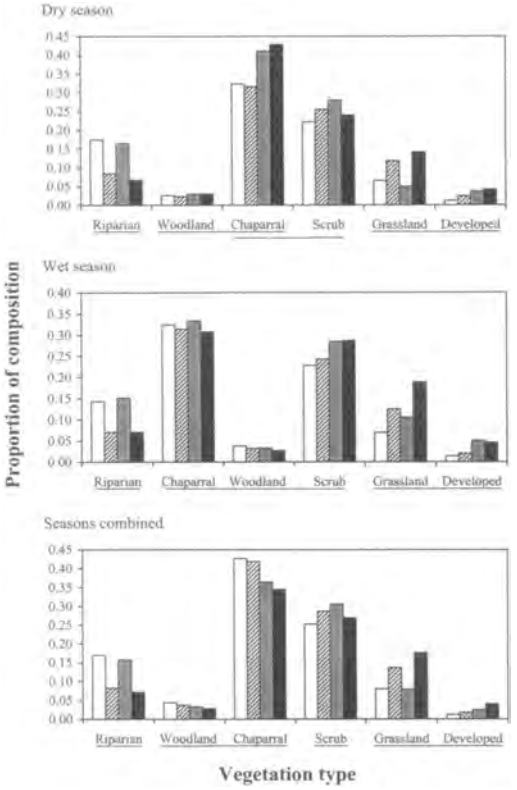

Fig. 2. Third-order selection (i.e., comparing habitat composition of individual buffered radiolocations to the habitat composition of the individual 85% home range) by cougars in the Santa Ana Mountain Range, California, USA, 1986–1992. Habitats are arranged from most to least preferred for dry season, wet season, and seasons combined. White bars indicate mean female proportional utilization, cross-hatched bars indicate mean habitat proportional availability for females, gray bars indicate mean male proportional utilization, and black bars indicate mean habitat proportional availability for males. Underlining under names of vegetation types on the *x*-axis indicates vegetation types for which rankings are not significantly different.

across seasons, although the statistical significance of pairwise contrasts varied slightly between seasons. Developed, disturbed, and agricultural vegetation types were consistently avoided.

In assessing third-order selection, we dropped forested, agricultural, and disturbed vegetation types from the compositional analysis because they were available to only a few individuals. Use of vegetation types on multiyear 85% home ranges was significantly different from availability during the dry season ($-N\ln\Lambda = 24.70$, $P < 0.001$, df = 5; n = 10 females and 2 males), wet season ($-N\ln\Lambda = 24.60$, $P < 0.001$, df = 5; n = 10 females and 2 males), and across seasons ($-N\ln\Lambda = 23.95$, $P < 0.001$, df = 5; n = 12 females and 2 males; Fig. 2). In all cases, riparian vegetation types were preferred, although significance of differences varied by season. When grassland and developed vegetation types occurred within a cougar's home range, they generally were used in lower proportion than their availability on that home range.

Influence of Topography on Habitat Selection

During both wet and dry seasons and at both second and third orders of selection, cougar locations tended to be lower in elevation and on gentler slopes than the average within the study area or home range, but differences were small and not statistically significant. Across years and seasons, locations of 13 female and 2 male cougars averaged about 275 m (SD = 146) in elevation and 12° (SD = 3) slope compared to an average elevation of 415 m (SD = 286) and 13° (SD = 9) slope on the entire study area (second-order $z = -1.79$, $P = 0.07$ for elevation and $z = -0.48$, $P = 0.63$ for slope) and an average elevation of 310 m (SD = 154) and 13° (SD = 3) slope within home ranges (third-order $z = -0.98$, $P = 0.32$ for elevation and $z = -1.50$, $P = 0.13$ for slope). These trends were similar for females and males. These small differences are consistent with selection for riparian areas (invariably slightly lower in elevation and gradient than the adjacent slopes). Cougars did not select habitats based on aspect at either the second- or third-order selection.

Influence of Paved Roads on Habitat Selection

At the second-order scale, cougars used areas in zones that were farther from both high-speed and low-speed paved roads than would be typical of the study area ($-N\ln\Lambda = 8.90$, $P < 0.05$, df = 3; n = 13 females and 2 males; Fig. 3). In general, use of areas increased with distance from paved roads.

These preferences were not evident at third-order selection. Although cougar locations were nonrandomly distributed with respect to high-speed paved roads ($-N\ln\Lambda = 11.88$, $P < 0.01$, df = 3; n = 8 females and 2 males), preference patterns were inconsistent, with cougars apparently preferring areas 500 to 1,000 m from high-speed roads to all other zones. Furthermore, cougar use of areas was random with respect to low-speed paved roads within their home range ($-N\ln\Lambda = 3.10$, $P > 0.05$, df = 3; n = 8 females and 2 males). Thus, although cougars tended to locate their home ranges away from paved roads, once they established a home range they did not avoid using areas close to those roads.

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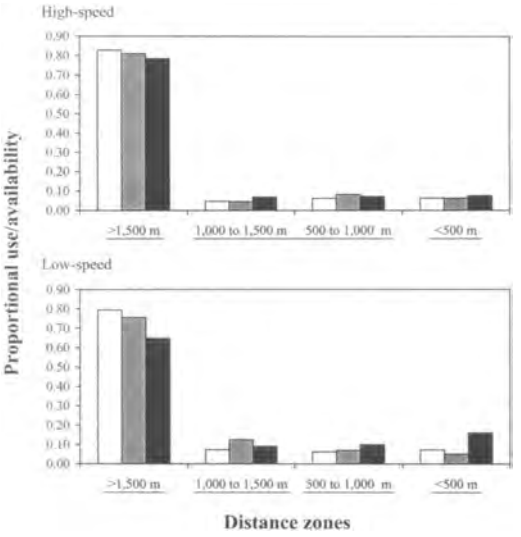

Fig. 3. Cougar use of areas at various distances from high- and low-speed 2-lane paved roads, compared to the proportion of area available in each zone on the study area, in the Santa Ana Mountain Range, California, USA, 1986–1992. Zones are arranged from most to least preferred. White bars indicate mean female proportional utilization, gray bars indicate mean male proportional utilization, and black bars indicate proportional availability. Underlining under names of zones on the *x*-axis indicates zones for which rankings are not significantly different.

A general avoidance of paved roads also was evidenced by the fact that density of low-speed paved (0.11 km/km^2, SD = 0.16 for females and 0.22 km/km^2, SD = 0.02 for males) and total paved roads (0.18 km/km^2, SD = 0.20 for females and 0.29 km/km^2, SD = 0.01 for males) in cougar home ranges was far lower than the density in the study area (0.40 km/km^2 for low-speed paved roads and 0.46 km/km^2 for total paved roads). Only 2 animals (F12, F15) had paved road densities in their home ranges that approached the densities for the study area.

DISCUSSION

Home-Range Size

Cougar home-range sizes reported in the literature are quite variable (see reviews in Anderson 1983 and Anderson et al. 1992), primarily due to both differences in estimation techniques and environments. Annual 85% home ranges for females in the SAMR were about 10% larger than those reported in the Diablo Range of northern California (Hopkins 1989; MCP estimator). Multiyear 85% home ranges for female cougars in the SAMR were about 38% smaller than those reported by Hopkins (1989; MCP estimator) for comparable periods, and about 54% larger than those reported on the central coast of California by Sitton and Wallen (1976; MCP estimator) in a study area similar to the SAMR. Annual 85% home ranges and multiyear 85% home ranges for male cougars in the SAMR were larger than those reported by Hopkins (1989) and Sitton and Wallen (1976). Female multiyear 85% home ranges in the SAMR were smaller than those reported in the Sierra Nevada Mountain Range by Neal et al. (1987) and Pierce et al. (1999), although male multiyear 85% home ranges were larger.

All previous studies in the West also have reported that home-range sizes of male cougars were larger than those of females (see reviews in Anderson 1983, Anderson et al. 1992, Logan et al. 1996, and Pittman et al. 2000). Males M2 and M9 probably were the only adult male residents in the southern half of the study area, and the large size of their home ranges may reflect limited competition from other males. These males covered 875 km^2 (42%) of the study area with their combined multiyear 85% home ranges (compared with 51% for 13 females), and each consorted with a number of females on the study area (Beier and Barrett 1993).

As did Hopkins (1989), we documented a decrease in most of the adult 85% home ranges during the dry season, perhaps because both cougars and prey concentrate near water sources during the dry season. Cover density and water sources were characteristics of areas heavily used by cougars in southern Utah (Laing 1988).

Vegetation Types

The strong concordance between rank orders for vegetation types at second- and third-order selection suggests that our results are not an artifact of factors operating at 1 scale (e.g., avoidance of conspecifics) distorting selection at another scale. At both scales of selection, and during both wet and dry seasons, riparian vegetation types were preferred to all other vegetation types. Previous studies have not documented selection for this vegetation type. Logan and Irwin (1985) reported statistically nonsignificant preference for riparian zones relative to their availability (3.6% vs. 1.3%) in north-central Wyoming. Without reporting riparian use, Laing (1988) stated that cougars used riparian zones proportional to their availability (8.9%) in southern Utah. Williams et al. (1995) reported the use (3.3%) of river and marsh habitats less than their

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availability (5.1%) in northern Montana. Some of these differences could be accounted for by methodological differences. For instance, Williams et al. (1995) documented selection for closed conifer vegetation, which included an unquantified amount of riparian areas. Riparian areas in the Santa Ana (and in much of the western United States) are narrow polygons relative to the average radiolocation error (White and Garrott 1990), so treating radiolocations as discrete points is likely to underestimate the importance of riparian areas. Thus, Logan and Irwin (1985) and Laing (1988), by treating locations as point data, may have had reduced ability to detect preference for riparian habitats. Poor representation of riparian areas on vegetation maps also could have skewed our results to indicate preference (if riparian areas are overmapped) or avoidance (if undermapped). An accuracy assessment (San Diego State University. 1993. Accuracy Assessment of MSCP GIS Vegetation Layer, San Diego, California, USA, unpublished report) on a 2,357-km^2 portion of the San Diego County vegetation map south of our study area suggests that such risks were low in our study, with riparian vegetation types correctly mapped 86% ± 4.6 (95% CI) of the time.

Logan and Irwin (1985), Laing (1988), Koehler and Hornocker (1991), and Williams et al. (1995) each emphasized the importance of cover characteristic of selected habitat types for stalking and feeding. Undoubtedly, riparian areas provide important stalking and feeding cover for the SAMR cougar population, as kill sites and caches were most often associated with this vegetation type (Beier et al. 1995). In northern California, Hopkins (1989) found 73% of all deer kill caches in creek bottoms. Preference for riparian habitats by nonmigratory mule deer in the West has been documented previously (Swenson et al. 1983, Carson and Peek 1987). Bowyer (1986) found that the seasonal distribution of mule deer does and fawns in San Diego County was regulated by proximity to water sources and succulent vegetation.

Logan and Irwin (1985) and Laing (1988) suggested that cougars use selected habitats adjacent to grassland habitats to stalk and kill prey. On the SAMR, riparian habitat patch perimeters did not often abut grassland patches (20% of total perimeter length) and were more often adjacent to chaparral and scrub vegetation types (36% and 27%, respectively). Environmental Science Associates (1992. Eastern Transportation Corridor Deer Telemetry Study, San Francisco, California, USA, unpublished report) noted that scrub habitats were preferred by mule deer in the Santa Ana Mountains. These scrub habitats provide little stalking cover (vegetation height typically <0.5 m), and adjacent riparian areas are thus likely ambush sites. Finally, riparian areas in major drainages provided important movement corridors for cougars on the study area and were often associated with travel paths (Beier and Barrett 1993, Beier 1995).

Across both scales of selection, grasslands were the only natural vegetation type that cougars avoided as strongly as they avoided developed areas. Our results support findings by Logan and Irwin (1985), Laing (1988), and Williams et al. (1995) that avoidance of grassland vegetation types by cougars is due to a lack of sufficient cover. Additionally, Laing (1988) reported an avoidance of agricultural/pasture lands by cougars in southern Utah due to a lack of adequate cover, and this is consistent with our findings. On the second-order scale, agricultural areas were consistently the most avoided vegetation type on the SAMR. Although the aversion to disturbed and developed habitat types is not surprising, this study is the first to document such avoidance.

Other researchers have documented differences in the seasonal selection patterns of cougars in winter versus nonwinter (Logan and Irwin 1985, Laing 1988, Williams et al. 1995), each noting that these differences likely were due to the seasonal shifts of mule deer herds. The relatively mild climate of our study area, as well as a nonmigratory prey base, did not produce seasonal habitat shifts.

Because compositional analysis requires a minimum sample size of 6 animals (Aebischer et al. 1993), we were unable to test for sex effects on habitat selection. Laing (1988) detected minimal to no difference between the habitat selection patterns of male and female cougars in southern Utah.

Although 88% of all radiolocations used in these analyses were obtained during the daylight hours, patterns of selection could differ during crepuscular and nocturnal hours when SAMR cougars exhibit peaks in movement activity (Beier et al. 1995).

Roads

We found that cougars avoided paved roads in placing a home range within the SAMR (second-order) but did not avoid zones nearest to paved roads within their home ranges (third-order). Similarly, cougar home ranges in northern Arizona and southern Utah contained road densities lower than those found on the respective study areas (Van Dyke et al. 1986) and cougars translo-

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cated into northern Florida established home ranges that contained road densities roughly 50% the density on that study area (Belden and Hagedorn 1993). Maehr and Cox (1995) assessed the influence of road-related variables on the distribution of cougars in Florida and suggested a pattern of second-order avoidance toward major highways. Hard-surface road densities on the SAMR study area were greater than in northern Florida (0.18 km/km^2; Belden and Hagedorn 1993), and greater than on 2 study areas in Arizona (0.02 km/km^2 and 0.04 km/km^2; Van Dyke et al. 1986). Van Dyke et al. (1986) reported an apparent pattern of third-order avoidance of hard-surfaced roads on 1 of 2 study areas in Arizona. The southeastern portion of the SAMR study area had the highest density of low-speed paved roads, which probably rendered it unsuitable for regular use as part of cougar home ranges.

Cougars did not avoid high-speed paved roads within their home ranges. These roads often were in highly preferred riparian areas. For example, of all cougars in this study, F15 showed the strongest apparent preference for areas close to high-speed paved roads. This almost certainly reflected the fact that such a road ran alongside the Santa Margarita River, which comprised the bulk of the riparian habitat in her home range. Where paved roads were not associated with riparian areas, cougars exhibited neither aversion nor avoidance of high-speed paved roads. Vehicle mortality on high-speed paved roads was the main source of mortality in this population (Beier and Barrett 1993). The combination of avoidance of paved roads in locating a home range and indifference toward paved roads within a home range means that roads have potentially severe impacts on both habitat suitability and mortality of cougars. Roads also have a third negative impact on cougars in that construction of a road into wild areas is often followed by a shift toward disturbed areas typically avoided by cougars.

MANAGEMENT IMPLICATIONS

California has lost over 95% of the riparian vegetation present prior to European settlement (Smith 1977, Katibah 1984). Habitat mosaics, including riparian areas, provide the survival and movement requisites of cougars. Protection of riparian areas from development, road building, and habitat alteration is crucially important to this population. Moreover, it is not sufficient to simply preserve riparian habitats alone. If these habitats are important because they offer ambush cover and cache sites adjacent to other habitats used by prey, it is important to maintain the relationships between riparian and other natural habitat types that support native prey.

Collisions with vehicles are the leading cause of mortality for this population, resulting in 10 (32%) deaths of radiotagged cougars and their offspring between 1988 and 1993 (Beier and Barrett 1993). Because cougars do not avoid paved roads within their home range, new paved roads should be located away from preferred cougar habitats such as riparian areas. Approximately 61 km (48%) of the total length of high-speed paved roads on the study area are within 200 m of riparian areas, and land within 200 m of a high-speed road encompasses 10% of the riparian vegetation types on the study area. Future transportation projects in the region must consider not only habitats directly lost to road building but also effects of roads on adjacent habitats.

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INFLUENCE OF VEGETATION, TOPOGRAPHY, AND ROADS ON COUGAR MOVEMENT IN SOUTHERN CALIFORNIA

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Abstract: Models of individual movement can help conserve wide-ranging carnivores on increasingly human-altered landscapes, and cannot be constructed solely by analyzing the daytime resting locations typically collected in carnivore studies. We examined the movements of 10 female and 7 male cougars (*Puma concolor*) at 15-min intervals during 44 nocturnal or diel periods of hunting or traveling in the Santa Ana Mountain Range of southern California, USA, between 1988 and 1992. Cougars tended to move in a meandering path (mean turning angle ~54°), and distance moved (mean and mode ~300 m) was not correlated with turning angle. Cougars used a broader range of habitats for nocturnal or diel movements than for previously described daybed locations for this same population. Riparian vegetation ranked highest in a compositional analysis of vegetation types selected during movement; grassland, woodland and urbanized sites were least selected. During periods of stasis (we presume many of these were stalking locations), patterns of selection were less marked. Cougars spent a disproportionate amount of time in highly ranked vegetation types, and traveled slowest through riparian habitats and fastest through human-dominated areas. Our results suggest that travel speed may provide an efficient index of habitat selection in concert with other types of analysis. Hunting or traveling individuals consistently used travel paths that were less rugged than their general surroundings. Traveling cougars avoided 2-lane paved roads, but dirt roads may have facilitated movement. Maintenance and restoration of corridors between large wildlands is essential to conserving cougars in southern California. Our results indicate that riparian vegetation, and other vegetation types that provide horizontal cover, are desirable features in such corridors, that dirt roads should not impede cougar use of corridors, and that corridors should lie along routes with relatively gentle topography. Our results suggest that cougars do not key in on highway-crossing structures in a way that creates a prey trap. Our empirical frequency distributions of distances and turning angles, along with cougar responses to vegetation, topography, and roads can help parameterize an individually-based movement model for cougars in human-altered landscapes.

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Key words: California, compositional analysis, cougar, habitat selection, movement, prey trap, *Puma concolor*, riparian, roads, scale, topography, travel speed, urbanized, vegetation.

Least-cost path analysis (Bunn et al. 2000, Paquet et al. 2001) and individual-based movement models (DeAngelis and Gross 1992, Bergman et al. 2000) for wide-ranging animals depend crucially on an understanding of how individuals move. These models, especially those built for terrestrial carnivores, can be used as tools for conservation planning and to assess, maintain, or improve habitat connectivity in human-dominated landscapes (Minta et al. 1999, Schadt et al. 2002). Animal movement probably depends on patterns of resource use relative to availability across multiple scales (Senft et al. 1987, Wiens 1989, Turchin 1998, Pace 2001), natural impediments in the landscape (With 1994), the animal's knowledge of its environment (including locations of conspecifics and primary prey), and human-induced habitat fragmentation and loss (Crooks 2002). A first step to modeling movement behavior is to study fine-scale movements and patterns of selection exhibited by individual animals (Wiens et al. 1993). If the broad-scale distribution patterns of individuals are the aggregate of fine-scaled movement behaviors (Turchin 1991, With 1994), then these behaviors may provide a mechanistic link to many ecological processes (Wiens et al. 1993).

Despite the increased use of wide-ranging nocturnal carnivores in conservation planning, little research has described their fine-scale movement patterns or factors influencing those movements. For instance, most studies of movement patterns of western cougars have described these patterns over weeks or months, based on ≤1 location per day, usually during daylight hours (Hemker et al. 1984, Anderson et al. 1992, Beier 1995, Ruth et al. 1998, Sweanor et al. 2000). Beier et al. (1995) described patterns in the distances cougars moved per 15-min interval as a function of time

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of day, sex, gross behavior state (e.g., hunting, feeding on previously-killed deer, raising cubs), but did not characterize cougar movements as a function of vegetation, topography, or other features in the animal's vicinity.

Cougar aversion to paved roads has been documented previously (Van Dyke et al. 1986, Belden and Hagedorn 1993, Sweanor et al. 2000, Dickson and Beier 2002), but all of these studies analyzed diurnal locations, presumably daybed locations in most cases, and no study has compared the observed number of paved road crossings with the number of crossings expected if cougars were indifferent to crossing. There has been increasing concern that highway crossing structures such as underpasses and culverts could funnel prey into areas where predators would exploit high prey density, creating a prey trap (Norman et al. 1998, Little et al. 2002), but there are no data supporting or refuting this possibility for cougars.

We attempted to address some of these information gaps by examining a subset of data collected and previously analyzed by Beier et al. (1995). Because cougar movement depends not only on habitat type and arrangement, but also on nonhabitat factors (e.g., location of a previously killed carcass, interactions with conspecifics), we attempted to isolate habitat factors by studying cougar movements during those periods when the focal animal was apparently not feeding on deer or interacting with other cougars. We studied animals during diel or nocturnal monitoring sessions to include periods of greatest daily movement. We also chose a time scale (movement during 15-min intervals) that minimized the risk that habitats traversed differed from those intersected by a line segment between consecutive locations, and we buffered these line segments to reflect the resolution of our measurements. Finally, we speculated that travel speed in a habitat might be a useful index of habitat selection. We reasoned that cougars would travel most quickly through habitats in which they are most uncomfortable (or that they perceive as less-profitable places to spend their time). If our data confirmed this pattern, travel speed could be used as a complement to more complex approaches such as compositional analysis.

Our objectives were to: (1) describe the travel path characteristics of individual cougars monitored during nocturnal or diel periods; (2) compare the vegetation, topography, and road density on paths used by and available to cougars during individual movement sessions; (3) investigate whether travel speed is correlated with habitat selection patterns; (4) identify landscape features that facilitated or inhibited cougar movements, with particular attention to cougar movements near 2-lane paved roads; and (5) describe the extent to which cougars might linger at road crossing structures to ambush prey.

STUDY AREA

The Santa Ana Mountain Range (SAMR) encompassed approximately 2,060 km^2 of nonurban wildlands and included portions of Orange (38% of study area), Riverside (28%), and San Diego (34%) counties; over 1 million people lived in the cities and communities surrounding the SAMR (Beier 1993). Our study area boundaries were delineated where the core of the study area met a major freeway or where human dwellings exceeded 4 residences per ha. The Cleveland National Forest, Camp Pendleton Marine Corps Base, Fallbrook Naval Weapons Station, Caspers Regional Park and several smaller reserves (Padley 1990, Beier and Barrett 1993) comprised most of the protected cougar habitat in the area. Beier (1993, 1995) and Dickson (2001) provide maps of the study area.

Plant communities on the study area included chaparral, oak woodlands (*Quercus engelmannii* and *Q. agrifolia*), coastal scrub, annual grasses, and coniferous forests at higher elevations (Barbour and Major 1995). Citrus and avocado orchards and other nonnative vegetation types occurred in parts of the area. Although human influence on the SAMR was widespread and included cattle grazing, agriculture, military training facilities, and public recreation areas, much of the study area remained undeveloped. Maximum average daily temperature was 24°C and mean annual precipitation was 33 cm in lower elevations (Santa Ana Fire Station, Santa Ana, California, USA, 1948–2000), with somewhat cooler and more mesic conditions at higher elevations. Precipitation in the form of fog drip was common throughout the year and light snow accumulation was possible in winter at the higher elevations (Barbour and Major 1995). Elevations within the study area ranged from sea level at the coast to 1,717 m on Santiago Peak. The topography was rugged. Although perennial streamflow was intermittent, springs, seeps, and other water sources were widely available throughout the study area (Beier and Barrett 1993).

Other carnivores common to the SAMR included coyotes (*Canis latrans*), gray foxes (*Urocyon*

cinereoargenteus), bobcats (*Lynx rufus*), raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*). Mule deer (*Odocoileus hemionus*) were common throughout the study area and were the most important prey species for this cougar population (Beier and Barrett 1993). Smaller prey included opossum (*Didelphis virginiana*), raccoon, and coyote (Beier and Barrett 1993).

METHODS

Radiotelemetry

Between May 1988 and December 1992, we captured, radiocollared, and monitored movements of cougars during distinct periods that ran from 1 hr before sunset until 1 hr after sunrise (nocturnal sessions) or for 24 hr (diel sessions, which always started and ended in the afternoon). During each session, we determined the location of a focal animal every 15 min using radiotelemetry. We obtained radiotelemetry locations from the ground using standard triangulation techniques (Mech 1983) conducted by a single observer using a vehicle. We attempted to track the focal animal at a distance >100 m to minimize influencing its movement and <500 m away to obtain accurate locations. To determine a single location, we took bearings within a span of 2–6 min. Because only a single observer was used and no network of precisely located receiving stations was available, we cannot compute meaningful error polygons (White and Garrott 1990). We minimized location errors by using only azimuths that differed by 60–120° and by getting close to the animal (White and Garrott 1990). We determined 85% and 96% of all locations from within 500 m and 1 km of the focal animal, respectively. We recorded these locations to the nearest 50 m of easting and northing; thus, movements ≤50 m in 15 min we typically recorded as stasis. We recorded each radiolocation as a Universal Transverse Mercator (UTM) point on a 1:24,000 U.S. Geological Survey (USGS) topographic map and then exported all points into a vector-based Geographic Information System (GIS; ArcView® 3.2a; Environmental Systems Research Institute, Redlands, California, USA).

By back-tracking movements with hounds on the day after a monitoring session to look for kills, tracks, and feces, and using other knowledge (such as vocalizations), Beier et al. (1995) classified the animal's behavior in each session into 1 of several categories. For this analysis, we used only sessions on adults (≥2 years old) and juveniles independent of their mother, excluding sessions involving copulation, raising cubs, feeding on a previously killed large mammal, or killing a large mammal. We assume that the focal animal was hunting or traveling during these sessions; cougars in these sessions traveled much farther, and for a much larger fraction of the night, than cougars in other behavior categories (Beier et al. 1995). We chose sessions with this pattern because it was the most common movement pattern and because this choice minimized the risk that cougar response to vegetation, topography, and roads would be obscured by other factors (presence of a kill, cub, or mate).

Analysis of Movement and Selection

Within the GIS, we developed an ArcView® extension (CGRMVMNT) using an object-oriented programming language (AVENUE; Environmental Systems Research Institute). Using this extension, we calculated whether the animal was moving or static during each 15-min period (interval, hereafter), the straight-line distance and rate of movement between consecutive locations, proportion of a movement segment (the straight line connecting consecutive locations) intersecting each vegetation type, deviation angles for consecutive movement segments, and the maximum slope encountered during a movement segment. Additionally, we used the CGRMVMNT extension to calculate the proportion of vegetation types and the maximum slope available to an individual (see below). Our approach assumed a constant rate of movement during a movement interval, and attributed that rate to movement in each vegetation type traversed during the interval.

We use the term "habitat composition" to refer to a vector of proportions of vegetation types used by or available to an animal and where total habitat composition adds up to 100%. To account for error in assigning an individual radio-location to a single vegetation type, which can seriously bias analyses of selection (Rettie and McLoughlin 1999), we assumed that a cougar used all types within a 100-m radius of a linear movement segment or a static location in proportion to the area of that type within the buffered region (Fig. 1). We chose a 100-m radius buffer partly to encompass triangulation error in estimating animal locations (Beier et al. 1995) and to encompass errors inherent in the digital coverages used to analyze selection. Additionally, this buffer allows our analysis to detect the potential importance of habitat mosaics in the selection process (see Rettie and McLoughlin 1999).

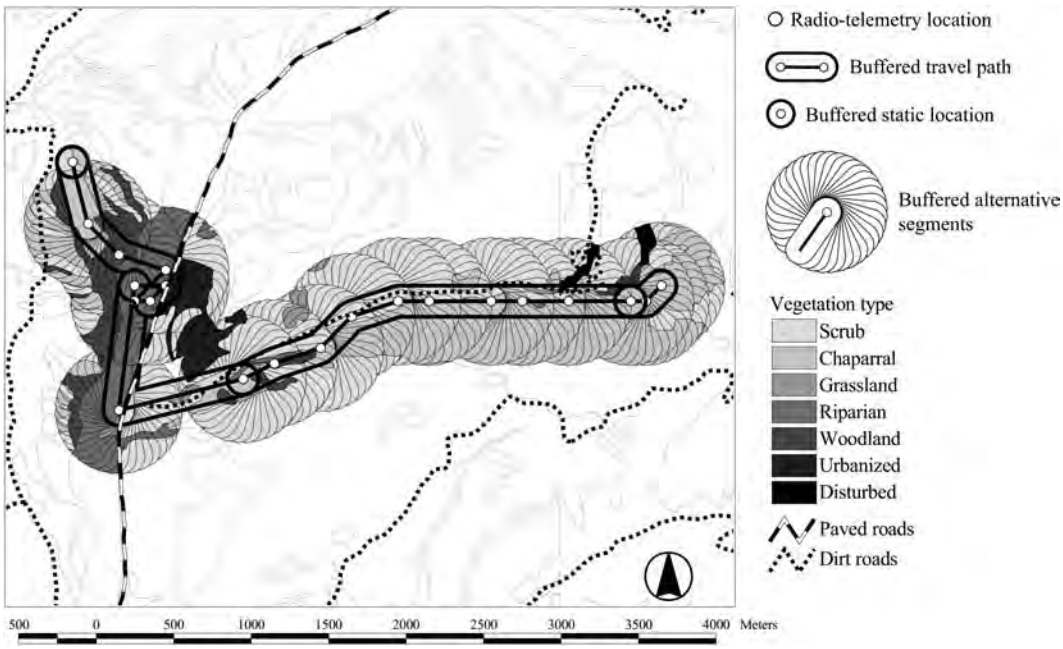

Fig. 1. Travel path through 7 vegetation types for female cougar F2 (session #100) monitored in the Santa Ana Mountain Range of southern California, USA, 1988–1992. This session began at 1800 hr, 6 Jul 1990 (eastern-most location) and ended at 0630 hr, 7 Jul 1990 (western-most location). Buffered static locations, travel path, and alternative segments generated by the CGRMVMNT extension are shown.

To evaluate selection for all movements during an individual session, we compared the average habitat composition of the buffered movement segments (used) to the average habitat composition of systematically assigned buffered movement segments (available). To estimate availability at each movement segment, we calculated the average proportion of each vegetation type captured within 35 alternative travel path segments (also buffered at 100 m) generated at 10° increments around the starting point of each movement segment and equal in length to the mean of all movement segments during that nocturnal or diel monitoring session (Fig. 1). To evaluate selection during static intervals within a session, we compared the average habitat composition of buffered radio-locations to the average habitat compositions of buffered movement segments during that session. For an individual monitored for >1 session, we first calculated used and available habitat compositions within a session, and then averaged across sessions so that each animal contributed only 1 composition to any inferential statistical analysis.

We used compositional analysis (Aitchison 1986, Aebischer and Robertson 1992, Aebischer et al. 1993) to rank cougar selection of habitats, with separate analyses for intervals of movement and stasis. Compositional analysis correctly uses the individual animal and not the radio-location as the sampling unit, thereby avoiding statistical problems arising from non-independence of proportions within a habitat composition (Aebischer et al. 1993). When cougar use of habitats was significantly nonrandom ($-N \ln\Lambda$ = test statistic, $\alpha < 0.05$), we used paired *t*-tests to compare mean utilization between all pairs of vegetation types ($\alpha < 0.05$). For each compositional analysis, we included only those habitat classes (e.g., vegetation types) available to all cougars, and included only those individual cougars using the same habitat classes. Because Aebischer et al. (1993) recommend a sample size ≥10 for compositional analyses, we pooled males and females together and did not test for sex effects on habitat selection.

For each movement session and individual cougar, we estimated the speed in each vegetation type,

$$S_v = \sum_{i=1}^{n} (s_i \times a_v) / \sum_{i=1}^{n} a_v,$$

where n = number of movement segments during the session, s_i = the average speed (km/h) during

each 15-min interval based on the straight-line distance between locations, and a_v = area of vegetation type v within each 100-m buffered segment, i. We used the unweighted average S_v across sessions for each cougar as an estimate of that animal's speed in a particular vegetation type. To determine whether the rankings of speeds in vegetation types were correlated with the ranking of selection for each vegetation type, we used Spearman's rank order correlation coefficient (r_s = test statistic, $\alpha < 0.05$). We also used a paired t-test to test for differences between male and female mean movement rates through each vegetation type (t = test statistic, $\alpha < 0.05$).

We calculated the angular deviation from a straight line for all consecutive movement segments for all cougars. To test whether the circular distribution of deviation angles during movements ≥100 m was nonuniform, we performed a Rao's (1976) spacing test of uniformity (U = test statistic, $\alpha < 0.05$). To determine whether mean movement distance was correlated with turning angle, we calculated an angular-linear correlation coefficient (Fisher 1993, Zar 1999; nr^2_{al} = test statistic, $\alpha < 0.05$).

We had an insufficient number of observations to investigate seasonal differences in patterns of selection during movements. Similarly, we had too few observations of daytime movement to compare nocturnal and daytime movements: we monitored all 17 individuals overnight, but only 5 cougars during diel sessions that included daylight hours.

Vegetation Types

Digital coverages of available vegetation types were acquired from Orange, Riverside, and San Diego counties. Vegetation polygons were identified by county personnel during 1990, 1992, 1993, and 1995 using LANDSAT Thematic Mapper and SPOT 2 satellite imagery, aerial photo interpretation, and field vegetation mapping surveys (ground-based and aerial). Although these data are nearly contemporaneous with our cougar locations, we checked all polygons classed as urban, disturbed, or agriculture in the vicinity of a session against field maps and notes, and made appropriate adjustments. We digitized and georeferenced all polygons using terrain-corrected satellite data and then digitally coded and projected these data as UTM coordinates (zone 11, North American Datum of 1927). These methods achieved a mean spatial accuracy of approximately 25 m and a minimum mapping unit between 0.2 and 2.0 ha. When possible, we more precisely delineated narrow riparian areas using the near infrared band of a SPOT image to detect greater leaf moisture content or by using hydrographic data layers. All vegetation types were categorized and classified by the 3 counties based on modifications to the Holland classification system (R. F. Holland. Preliminary Descriptions of the Terrestrial Natural Communities of California. California Department of Fish and Game, Nongame Heritage Program, Sacramento, California, USA, unpublished report). By consolidating infrequent vegetation types with similar types, our analyses used 9 general vegetation types: scrub, chaparral, grassland, riparian, forest, woodland, agriculture, urbanized (residential, industrial, or commercial developments), and disturbed (see Dickson 2001). We classified lakes, rivers, wetlands, vernal pools, beaches, and manmade watercourses (0.70% of the study area) within the riparian vegetation type. Cliff and rock habitats (0.04%) were most often adjacent to chaparral vegetation types, and so we reclassified these as such. Because coastal dunes (0.01%) were usually associated with scrub vegetation, we grouped these types together.

Topography

We merged 26 USGS 1:24,000 digital elevation models (DEMs) to describe elevation and slope of the study area. We derived the slope (in degrees) of a cell location from the DEM using the ArcView® Spatial Analyst extension (Environmental Systems Research Institute, Redlands, California, USA). On the scale of individual movements, we considered maximum slope to be the most appropriate measure of topographic roughness encountered by an individual cougar. To calculate the maximum slope encountered (used) by an individual during a movement segment, we generated 100 alternative segments (of length equal to the original and terminating at a randomly located point within 50 m of the start and end point of the original) within a movement segment buffer and intersected these alternative segments with the DEM to derive an average value of maximum slope. We assumed that the maximum slope available to an individual was the average maximum slope value for the 35 alternative segments intersected with the DEM. We used a paired t-test to assess topographic selection for slope during all movement sessions for all individuals ($\alpha < 0.05$). For each individual monitored for >1 session, we calculated the mean

maximum slope encountered during each session and then averaged across sessions so that each animal contributed only 1 value to the statistical analysis.

Roads

We obtained 1995 U.S. Bureau of the Census Topologically Integrated Geographic Encoding and Referencing (TIGER) digital data coverages for all roads on the 3 counties. We modified these maps based on paper maps on which field crews had indicated accurate road location and condition (paved, dirt, absent) of mapped roads. To assess whether roads affected cougar movements, we calculated total paved and dirt road densities (m/km^2) for all buffered movement (used) and alternative (available) paths. For each session, we calculated road densities at each used and available segment. To determine available densities, we averaged across the 35 alternative segments. We used a paired *t*-test to determine whether mean road densities for each session differed ($\alpha < 0.05$) between movements and alternative paths.

We analyzed road crossings by comparing the minimum number of crossings of 2-lane paved roads during a diel session to the number of crossings that would have occurred if the focal animal were indifferent to paved roads. We excluded freeway crossings from our analyses because 5 years of study documented only a single non-fatal freeway crossing (except via underpasses). To avoid having simulated paths cross paved driveways and residential roads, we restricted all simulations to a study area that was clipped to exclude residential areas within or abutting potential cougar habitat.

We inferred a single crossing for any movement segment that crossed a paved road. To estimate the expected number of crossings, we constructed a simple individual-based movement model, and we generated 50 simulated paths for each session, each with the same number of movement segments as the actual travel path. Each simulation started using the initial bearing of the actual movement path, giving each simulation a tendency to move in the direction that the focal animal moved. Each subsequent movement segment in the simulations used a circular deviation angle and displacement selected at random, with replacement, from the observed distributions (Fig. 2). If a simulated travel path encountered a study area boundary or residential area, we forced the contacting segment to reflect back into the study area at a random deviation angle. We used a paired *t*-test to determine whether the mean number of actual road crossings was less ($\alpha < 0.05$) than expected. For individuals monitored for >1 session, we calculated a mean for each session and then averaged across sessions so that each animal contributed only 1 value to the statistical analysis.

To examine whether cougars might exploit road crossing structures, such as underpasses or culverts, to trap prey, we examined the locations of all 5,562 daybed locations, 855 nocturnal static locations, and 145 cougar-killed prey carcasses in this study area during 1986–1992 (Beier and Barrett 1993, Beier 1995, Beier et al. 1995, Dickson and Beier 2002). We tallied the number of locations by type (daybed, static, carcass) that occurred within 300 m of a crossing structure under major roads (>2 lanes in each direction).

RESULTS

We analyzed 44 tracking sessions (29 nocturnal, 15 diel), including 22 sessions on 10 female cougars and 22 sessions on 7 male cougars (Table 1). Although most cougars were monitored for 3 or more sessions, 5 individuals were monitored for only 1 nocturnal or diel session. The behavior of these 5 animals was thus measured with relatively low precision. Imprecision in measurements decreases the power of statistical tests but does not increase risk of type I error (because these errors are subsumed in the residual sum of squares). Such risk is even lower for compositional analysis, which forced us to drop some of these animals from analyses when, for example, the individual did not use all vegetation types.

Movement Statistics

Total number of movement segments ≥50 m and static locations was 1,647 and 356, respectively. Following Beier et al. (1995) we assume that cougars were hunting during these sessions and that many static locations represented sites where cougars slowly stalked and attempted to ambush prey. Other static locations probably represented rest sites.

The mean number of movement segments per session was 36.4 (SD = 6.3) for females and 37.7 (SD = 7.7) for males. On average, tracking sessions lasted 19.9 hrs (SD = 5.1) for females and 17.3 hrs (SD = 1.9) for males. Total duration of movements during a session averaged 9.1 hrs (SD = 1.6) for females and 9.4 hrs (SD = 1.9) for males. During a session, female cougars traveled an average of 10.7 km (SD = 4.5) and males traveled 10.0

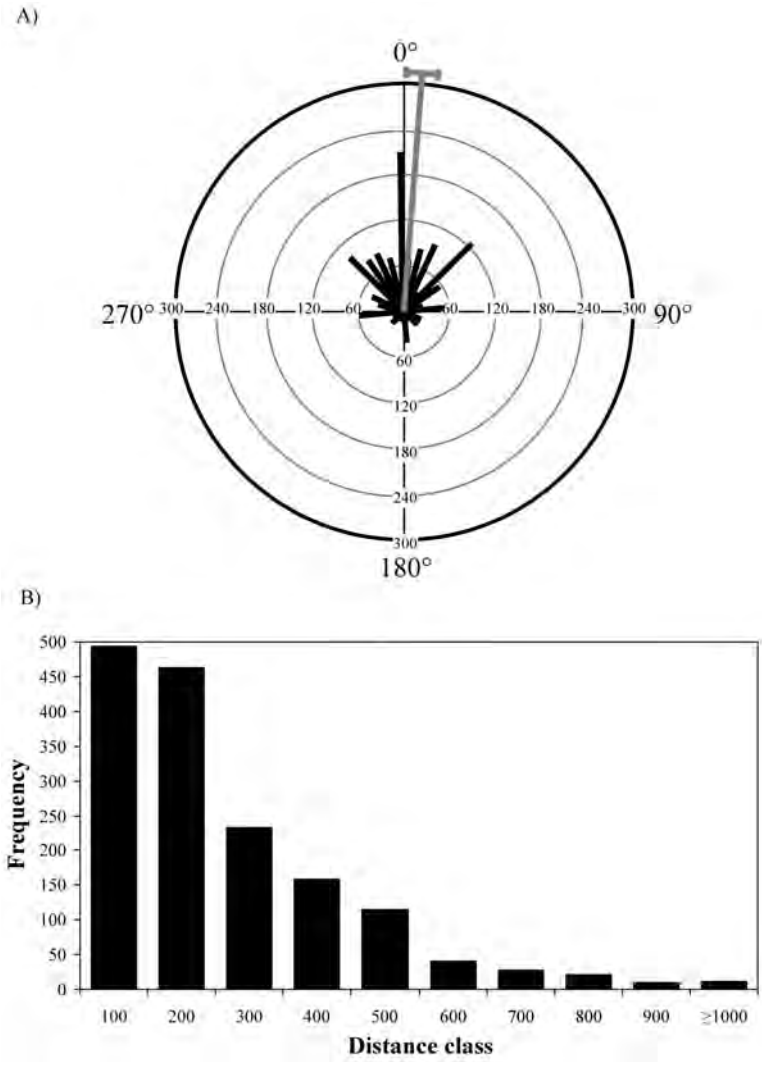

Fig. 2. (A) Frequency distribution of circular deviation angles for movements ≥100 m (n = 1,536) for 10 female and 7 male cougars during 44 radiotracking sessions in southern California, USA, 1988–1992. An angle of 0° indicates an animal did not deviate from a straight line. Mean deviation angle and +/– 95% confidence intervals are shown. (B) Frequency distribution of distance moved per 15 min; abscissa is lower bound of each 100-m distance class (n = 1,572).

km (SD = 3.0). Average time in static positions during a session was 10.8 hrs (SD = 5.1) for females and 7.9 hrs (SD = 3.5) for males, excluding the static intervals (of unknown duration) that occurred at the start and end of each session.

Movement segments between 50 and 100 m probably approached the resolution of triangulation. Because these short segments comprised only 0.4% of all movement segments, including these segments introduces little if any error to our analyses.

For 1,536 movement segments ≥100 m, cougars tended to move in a straight-line; the mean circular angle of deviation was 4.4° +/– 3.8 (95%CI; Fig. 2A), and the circular distribution of deviation angles was not uniform (U = 351.8, P < 0.001). During consecutive 15-min movement intervals, cougars often turned to the right or left; the average deviation angle during a session was 52.8° (SD = 47.8, n = 1,536). Distance traveled per 15 min (Fig. 2B) averaged 288 m (SD = 192, range = 100 – 2,059 m, n = 1,572), with 61% of movements <300 m. The distance moved was not correlated with turning angle (nr^2_{al} = 4.13, r = 0.34, P > 0.10, n = 36 angle classes of 10° each).

Influence of Vegetation Type

The habitat composition of travel paths used by cougars differed from the habitat composition of alternative segments ($-N\ln\Lambda$ = 15.00, P < 0.025, df = 5, n = 9 females and 7 males; Fig. 3). Because forested, agricultural, and disturbed vegetation types were not available to some individuals, these types were dropped from all compositional analyses. Although riparian types ranked highest in the compositional analysis of habitat use during movements, use was statistically significant only in contrast with urbanized types. Chaparral and scrub types also were ranked above urbanized types. However, other contrasts were more ambiguous and difficult to interpret.

During intervals of stasis, cougar use of vegetation types was not statistically different from the habitat composition through which they traveled

during movement intervals ($-N\ln\Lambda = 4.76$, $P > 0.25$, df = 4, $n = 8$ females and 7 males with ≥7 static locations). Urbanized vegetation types were available to only a few individuals and were excluded from this analysis. Although neither the omnibus test nor pairwise contrasts were significant ($P > 0.05$), chaparral (10%) and riparian vegetation types (27%) ranked higher than scrub, grassland, and woodland types during periods of stasis, and they were used as stopping points more often than they were encountered on travel paths.

Cougars moved slowest through riparian vegetation (grand mean = 1.07 km/hr), which was the type ranked highest in the compositional analysis of movements and fastest through urbanized types (1.49 km/hr), the lowest ranking type (Table 1; Fig. 4A). In all vegetation types, females moved faster than males ($t = 5.52$, $P < 0.001$, $n = 9$). There was a significant negative correlation between ranks for travel speed and selection for a vegetation type ($r_s = -0.89$, $P < 0.05$, $n = 6$; Fig. 4B).

Influence of Topography

During monitored intervals of movement, all cougars used maximum slopes that were more gentle than those available ($t = 7.38$, $P < 0.001$, $n = 17$). For indi-

Table 1. Mean travel speeds in 9 vegetation types for 10 female and 7 male cougars in the Santa Ana Mountain Range, California, USA, 1988–1992. "—" indicates vegetation type was not encountered on travel path.

Animal ID	Total no. of sessions monitored	Total no. of movement segments	Travel speed (km/hr)								Mean travel speed (+/– 1SD)
			Scrub	Chaparral	Grassland	Riparian	Woodland	Forest	Agriculture	Urbanized	Disturbed	
F1	4	164	1.17	1.33	1.30	1.22	1.29	2.42	1.30	1.43	1.85	1.48 (0.41)
F2	4	142	1.22	1.06	1.42	1.11	1.30	—	1.19	1.23	1.29	1.23 (0.12)
F3	4	146	1.05	1.04	0.98	0.92	1.04	1.10	—	3.50	1.60	1.40 (0.87)
F4	2	68	0.84	0.87	0.79	0.77	0.48	0.90	—	0.60	0.74	0.75 (0.14)
F8	1	34	1.23	0.98	1.86	0.72	2.58	2.01	—	—	—	1.56 (0.70)
F10	1	28	0.78	0.99	—	0.98	1.03	—	0.63	1.16	—	0.93 (0.19)
F11	1	27	1.55	0.71	1.33	1.38	0.83	—	—	—	—	1.16 (0.37)
F17	2	87	1.05	0.98	1.02	1.10	1.09	1.16	1.74	1.05	1.09	1.14 (0.23)
F18	1	47	1.47	1.67	2.04	1.19	2.12	—	1.67	1.79	—	1.71 (0.32)
F19	2	74	1.54	1.64	1.28	1.50	1.48	1.03	—	1.40	—	1.41 (0.20)
Female mean (+/- 1SD)	2	82	1.19 (0.27)	1.13 (0.32)	1.34 (0.40)	1.09 (0.25)	1.32 (0.62)	1.44 (0.63)	1.31 (0.45)	1.52 (0.87)	1.32 (0.43)	1.29 (0.14)
M2	5	154	1.29	1.45	1.25	1.14	1.20	2.54	2.13	1.83	1.44	1.59 (0.48)
M5	1	26	0.81	0.73	1.12	1.13	0.83	—	—	—	0.97	0.93 (0.17)
M6	3	126	0.87	0.96	1.09	1.02	0.79	—	0.80	1.34	0.75	0.95 (0.20)
M9	2	97	1.33	1.22	1.25	1.17	1.54	1.02	—	1.56	2.22	1.41 (0.37)
M10	4	140	0.77	0.90	0.79	0.64	0.44	0.44	0.50	0.58	0.40	0.61 (0.18)
M12	3	116	1.05	1.01	1.42	1.21	1.09	0.85	0.56	0.85	0.99	1.00 (0.24)
M13	4	171	0.96	0.94	0.99	1.01	1.18	1.17	—	2.47	1.28	1.25 (0.51)
Male mean (+/- 1SD)	3	119	1.01 (0.22)	1.03 (0.24)	1.13 (0.20)	1.04 (0.19)	1.01 (0.36)	1.20 (0.79)	1.00 (0.77)	1.44 (0.68)	1.15 (0.58)	1.11 (0.14)
Grand mean (+/- 1SD)	3	97	1.11 (0.26)	1.09 (0.28)	1.25 (0.45)	1.07 (0.22)	1.19 (0.53)	1.33 (0.68)	1.17 (0.59)	1.49 (0.77)	1.22 (0.51)	1.21 (0.31)

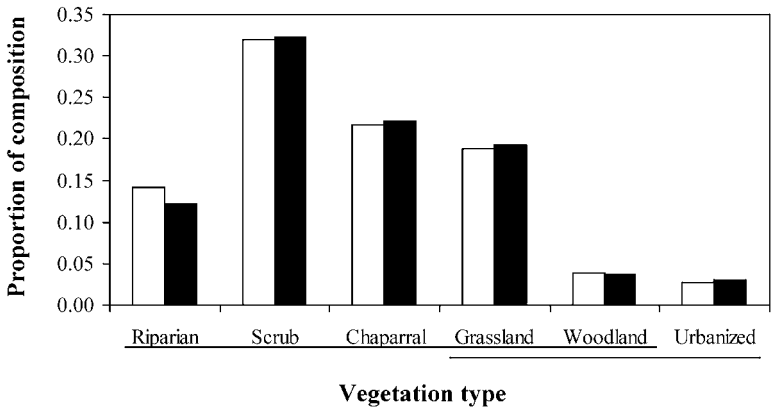

Fig. 3. Cougars (n = 9 females, 7 males) in the Santa Ana Mountain Range, California, USA, 1988–1992, tended to avoid human-dominated vegetation types and areas lacking understory woody plants during 15-min intervals when the animal moved ≥50 m. White bars indicate mean proportional utilization and black bars indicate mean proportional availability. Vegetation types are arranged from highest to lowest rank; underlining under names of vegetation types on the x-axis indicates vegetation types for which rankings are not significantly ($P > 0.05$) different.

vidual cougars, the mean available maximum slopes exceeded the used slopes by 0.71° to 3.54° (mean difference = 1.49°, SD = 0.81).

Influence of Roads

Total paved road density was about 21% lower on cougar travel paths (4.20 m/km^2, $\bar{x}$ = 0.10 +/– 0.20 m/km^2 [SD]) compared to available paths (5.30 m/km^2, $\bar{x}$ = 0.12 +/– 0.22 m/km^2; t = –2.16, P = 0.04, n = 44). Density of dirt roads was slightly higher on paths used by cougars (62.50 m/km^2, $\bar{x}$ = 1.42 +/– 1.04 m/km^2) compared to available paths (59.17 m/km^2, $\bar{x}$ = 1.34 +/– 0.78 m/km^2; t = 1.48, P = 0.15, n = 44). Buffered movement segments intersected dirt roads in all but 2 sessions, during which no dirt roads were available. All tracked individuals encountered or used dirt roads (368 occasions during 41 sessions).

Focal animals crossed 2-lane paved roads a total of 19 times; crossings involved 9 individual cougars and occurred during 11 of the 44 sessions, with a mean of 0.45 crossings per cougar per session (SD = 0.67, n = 17 individuals). In contrast, simulated paths had a mean of 1.29 crossings per cougar per session (SD = 1.37), a difference that was statistically significant (t = –2.50, P = 0.012). The simulated travel paths of all individuals crossed paved roads. Only 3 individuals (F2, F10, M10) crossed paved roads more often (1 crossing each) than expected (0.37, 0.12, 0.87, respectively), based on simulated paths.

Three of 5,562 daybed locations, 0 of 855 nocturnal static locations, 0 of 85 deer killed by cougars, and 2 of 60 small mammal kills (opossum, raccoon in these cases) were within 300 m of a crossing structure under a major highway. All 5 of these locations reflected the activities of a single female (F2) during the last days before her death, when she was apparently keying in on garbage-eating animals near a housing development, not on animals using the crossing structure. These numbers are lower than the 42 documented crossings via such structures (Beier and Barrett 1993, Beier 1995). Because we required cougar tracks or unambiguous radio signals to confirm a crossing, these 42 crossings underestimate the true frequency of these events.

DISCUSSION

Based on our observations, traveling cougars tended to continue moving in a consistent direction but often turned ~54° right or left, with few retrograde movements; movements averaged 288 m per 15-min interval and were not correlated with turning angle (Fig. 2). Our analysis of frequency of road crossings illustrates how these data can generate a null (random walk) model for hypothesis testing. These distributional data also can form the basis of more-sophisticated individually based movement models. Our results suggest that these advanced cougar movement models should reflect an aversion to paved roads and human-modified vegetation types, little differentiation among natural vegetation types, no aversion to dirt roads, and selection for gentle grades.

Our results support the assertion (Doak et al. 1992, Andren 1994, Dickson and Beier 2002) that habitat pattern has multi-scale impacts on the movement and distribution of animals. On the SAMR, Dickson and Beier (2002) identified strong patterns of selection by adult cougars for riparian areas at 2 spatial scales (based mostly on 1 static, diurnal location per animal per day). During the movement periods we analyzed here, riparian vegetation again ranked first, but several other natural vegetation types were statistically as

preferred as riparian vegetation. Additionally, grasslands ranked below riparian, scrub, and chaparral vegetation types for cougar movements, but not with the statistical significance Dickson and Beier (2002) observed for diurnal locations. Thus, traveling cougars monitored over nocturnal or diel periods used a broader range of habitats than used for diurnal locations alone (typically daybed sites; Beier et al. 1995). Our findings support the argument of Comiskey et al. (2002) that analysis of diurnal locations provides limited information about cougar patterns of selection during the times they are most active. We conclude that habitat use of cougars (and other nocturnal carnivores) estimated solely by analysis of diurnal locations may not accurately reflect habitat preferences of hunting and traveling animals. Movement studies of nocturnal carnivores should include data collected during those periods when the animal is most active.

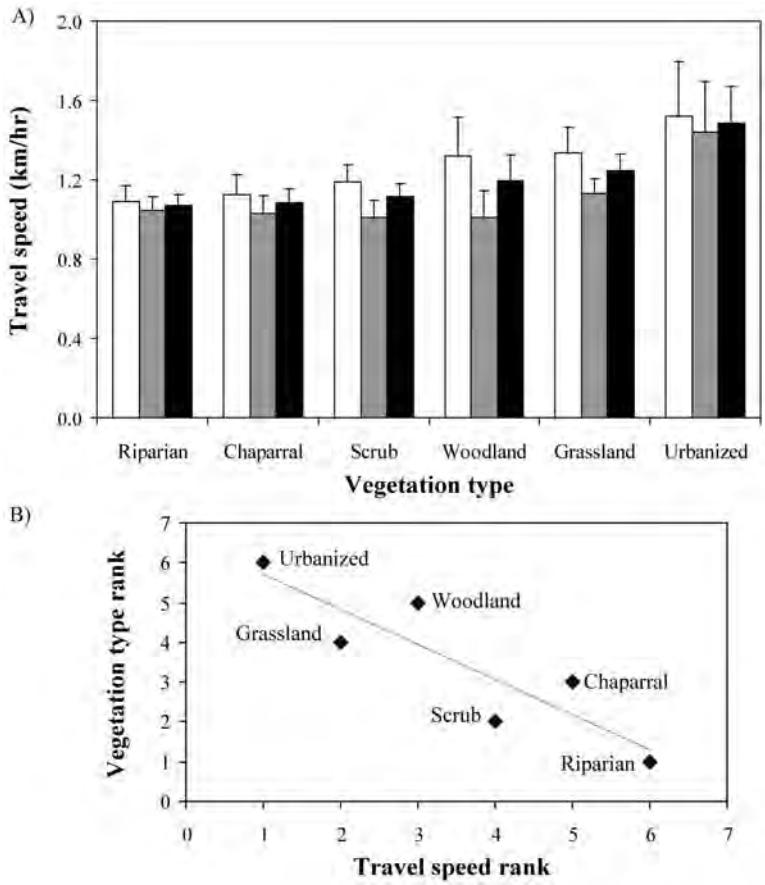

Fig. 4. Cougars in the Santa Ana Mountain Range tended to move more slowly through highly ranked vegetation types and more quickly through human-dominated types. (A) White bars indicate mean travel speed for females, gray bars indicate mean speed for males, and black bars indicate mean speed for the sexes combined. Error bars indicate +1 SE. Vegetation types are arranged from slowest to fastest based on the mean travel speed for the sexes combined. (B) The correlation between ranks for travel speed and vegetation type was statistically significant ($P < 0.05$).

Although previous research using diurnal locations suggested that cougars avoided grasslands due to lack of cover (Logan and Irwin 1985, Laing 1988, Williams et al. 1995, Dickson and Beier 2002), grasslands may play a more important role during cougar movement. Grassland vegetation constituted 19% of the composition of used movement segments. Perhaps grasslands provide cougars with the means to more readily permeate areas already known to them or to stalk and pursue prey. Grassland vegetation types were also a common (19%) characteristic of habitat mosaics used during intervals of stasis, which in some cases probably represented stalking or attempts to ambush prey (Beier et al. 1995).

If animals tend to move more rapidly through environments that make them uncomfortable or that offer few resources, our results on travel speed through various vegetation types is consistent with the rankings based on compositional analysis. An analysis of habitat selection based on travel speed, unlike other analyses of habitat use, does not require an estimate of habitat availability. Estimating habitat availability invariably requires making arbitrary assumptions. For instance, we made the reasonable assumption that habitat availability could be estimated by the average habitat composition in 35 buffered vectors with length equal to the average distance moved during a session. It would have been equally reasonable to estimate availability by buffered vectors with length equal to the actual distance moved in

a particular interval, or the average for all study animals. Our diligent search of the literature suggests that our study is the first attempt to make inferences about habitat use from travel speed for any terrestrial vertebrate, and we believe travel speed may offer an efficient tool for study of habitat selection patterns.

We found travel speed to be a useful complement to compositional analysis and other traditional methods of analyzing habitat selection. However, our single illustration of the method does not constitute a full exploration of its strengths and weaknesses. One important limitation of the travel speed method is that it cannot assess habitats the animal does not use at all. Similarly, travel speed cannot be used to assess animal response to fine-scale features such as paved roads.

Cougars consistently used travel paths that were less rugged than their general surroundings. This suggests that individuals consider the energetic cost of alternative paths and that they probably have a mental map of their surroundings. This is consistent with Beier's (1995) description of canyon bottoms and ridgelines as common travel routes for dispersing cougars. Hunting or traveling individuals minimize energetic expense by frequenting landscape features that cost the least.

The effectiveness of habitats to support cougars is reduced by human disturbance, particularly roads (Murphy et al. 1999). Our results indicate that 2-lane paved roads constrain cougar movement significantly but do not prevent movement. Indeed, vehicle collisions are the leading cause of mortality in this population, comprising 32% of all deaths of radiotagged cougars and their offspring (Beier and Barrett 1993). The problem is exacerbated by the placement of paved roads in preferred riparian habitats on the SAMR (Dickson and Beier 2002). Underpasses and other structures can facilitate cougar movements across paved roads (Beier 1993, Beier 1995, Foster and Humphrey 1995, Gloyne and Clevenger 2001), and we encourage efforts to construct or enhance crossing structures in preferred habitats.

Our data suggest that such structures are not exploited by predators in a way that creates a prey trap, supporting the conclusion of a recent review (Little et al. 2002). However, most crossings on our study area occurred where major roads crossed narrow, degraded habitat corridors, where cougars and their prey may not wish to linger. Cougars may behave differently where such crossing structures occur along roads passing through large blocks of intact habitat.

All individuals tracked during this study encountered or used dirt roads, and dirt road density was 8% higher on cougar travel paths than on available travel segments, suggesting that dirt roads do not inhibit, and may even promote, cougar movement. Back-tracking with hounds after our monitoring sessions confirmed that individuals frequently used dirt roads or trails to travel up to 2 km, especially in areas of dense scrub or chaparral (Beier 1995). In northern Florida, translocated cougars tended to cross light duty roads and trails in favor of all other road types (Belden and Hagedorn 1993). On study areas in northern Arizona and southern Utah, Van Dyke et al. (1986) reported that most cougars crossed most of the unimproved dirt roads within their home ranges. In addition to providing a path through dense scrub, dirt roads and trails may facilitate predator access to prey (James and Stuart-Smith 2000, Kinley and Apps 2001, Kerley et al. 2002). We believe that retaining or creating a dirt road or trail along the midline of a planned movement corridor would facilitate its use by cougars and minimize straying into adjacent human-dominated landscapes.

MANAGEMENT IMPLICATIONS

Our results suggest that riparian vegetation, and other vegetation types that provide horizontal cover, are desirable features in movement corridors, that dirt roads should not impede cougar use of corridors, that corridors should lie along routes with relatively gentle topography, and that cougars do not use road crossing structures to create prey traps. Managers and land-use planners are using these findings to design corridors to facilitate cougar movement in the South Coast ecoregion of California (Beier et al. 2005).

Because cougars will become extinct in even the largest core areas of this ecoregion if connectivity is severed (Beier 1996), cougars are an appropriate focal species for corridor design. However, because a corridor that serves cougars will not serve all species, we urge planners to consider a broad suite of focal species in designing landscape linkages (Beier et al. 2005).

Our frequency distributions of movement lengths and turning angles, in conjunction with the habitat preferences documented herein, are also being used to construct sophisticated individual-based movement models (in collaboration with J. Tracey and K. Crooks, Colorado State University). We hope these approaches can help quantify the influence of landscape features on

other, large carnivores used as umbrella species for conservation planning.

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Short communication

Vertebrate diversity benefiting from carrion provided by pumas and other subordinate, apex felids

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ABSTRACT

Carrion promotes biodiversity and ecosystem stability, and large carnivores provide this resource throughout the year. In particular, apex felids subordinate to other carnivores contribute more carrion to ecological communities than other predators. We measured vertebrate scavenger diversity at puma (*Puma concolor*) kills in the Greater Yellowstone Ecosystem, and utilized a model-comparison approach to determine what variables influenced scavenger diversity (Shannon's *H*) at carcasses. We documented the highest vertebrate scavenger diversity of any study to date (39 birds and mammals). Scavengers represented 10.9% of local birds and 28.3% of local mammals, emphasizing the diversity of food-web vectors supported by pumas, and the positive contributions of pumas and potentially other subordinate, apex felids to ecological stability. Scavenger diversity at carcasses was most influenced by the length of time the carcass was sampled, and the biological variables, *temperature* and prey *weight*. Nevertheless, diversity was relatively consistent across carcasses. We also identified six additional stalk-and-ambush carnivores weighing > 20 kg, that feed on prey larger than themselves, and are subordinate to other predators. Together with pumas, these seven felids may provide distinctive ecological functions through their disproportionate production of carrion and subsequent contributions to biodiversity. We urge conservation managers to increase support for these species, as a means of prioritizing resources to best ensure the persistence of carrion in natural systems.

1. Introduction

There is increasing recognition for the importance of carrion in supporting biodiversity and structuring ecosystems (Wilson and Wolkovich, 2011; Moleón and Sànchez-Zapata, 2015; Inger et al., 2016). Animals that eat carrion facilitate energy transfer between trophic levels and increase linkages in food webs, promoting ecosystem stability (DeVault et al., 2003; Wilson and Wolkovich, 2011; Moleón et al., 2014). Vertebrate scavengers, in particular, are essential vectors in spreading nutrients and other benefits of carrion across diverse terrestrial and aquatic ecosystems (Wilson and Wolkovich, 2011; Moleón and Sànchez-Zapata, 2015). Scavengers are also often predators themselves (Moleón et al., 2014), and competition over carrion and predator-prey dynamics near carcasses influences the heterogeneity of species assemblages across ecosystems (Cortés-Avizanda et al., 2009; Allen et al., 2015).

Carrion comes in all shapes and sizes, but large carcasses are particularly important, in that they support a greater diversity of scavengers (Selva et al., 2005; Moleón and Sànchez-Zapata, 2015), and therefore disproportionately contribute more to ecosystem function than smaller carcasses. Large carnivores that provide large carcasses, however, are in sharp decline (Ripple et al., 2014; Mateo-Tomás et al., 2015). Current human populations now produce exponentially more animal waste and carrion than native predators (Oro et al., 2013); carrion produced by people, however, generally occurs infrequently in pulses (e.g., hunters, Wilmers et al., 2003; Mateo-Tomás et al., 2015) or in limited areas (e.g., landfills, Oro et al., 2013; cities, Inger et al., 2016).

Research suggests that felids (Family Felidae) that are apex predators (Wallach et al., 2015) and subordinate to other carnivores in competition over resources, contribute more carrion to ecological communities than other top predators (cheetahs, *Acinonyx jubatus*, in central Africa, Hunter et al., 2006; pumas, *Puma concolor*, in Chilean Patagonia, Elbroch and Wittmer, 2012). Felids are stalk-and-ambush predators and expend less energy in obtaining prey than coursing predators, like wild dogs (*Lycaon pictus*) or wolves (*Canis lupus*) (Scantlebury et al., 2014). Therefore, felids do not suffer the energetic costs that coursing predators do when they lose their kills. Recent research suggests that subordinate, apex felids have adapted to contend with the costs of kleptoparatism by scavengers. Cheetahs, for example,

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are an apex predator found across Africa and Iran that can withstand losses of 25–35% of their kills with little need for compensatory killing (Scantlebury et al., 2014).

The puma is a widespread, apex predator found throughout the Americas and a species subordinate to a range of predators across its range (Ruth and Murphy, 2010). Pumas kill 10.10 ± 4.10 SD kg of prey/day and abandon 3.9 ± 2.6 kg of prey/day (Elbroch et al., 2014); based upon an average density of 1.7 resident pumas per 100 km^2 (Beausoleil et al., 2013), pumas conservatively contribute 1,507,348 kg of meat per day across their 22,735,268 km^2 range in North and South America (IUCN, 2015). Pumas lose or abandon on average 39% of their prey to competitors and scavengers (Elbroch et al., 2014), and like cheetahs, are likely tolerant of some level of kleptoparatism of their kills. In fact, pumas tolerate scavengers even while they are still feeding, and the presence of a puma at a carcass increases opportunities for smaller carnivores to feed as compared with other large carnivores that exclude them (Allen et al., 2015).

Here, we measured vertebrate scavenger diversity at puma kills in the Greater Yellowstone Ecosystem (GYE) with motion-triggered video cameras. As a specific test of how subordinate, apex predators might support biodiversity through carrion production, we compared mammalian and avian scavenger diversity documented at kills to local species assemblages to see what proportion of resident vertebrates benefited from puma kills. Based upon previous research (Selva et al., 2005; Hunter et al., 2006), we hypothesized that scavenger diversity recorded at puma kills would vary with temperature, carcass size, and canopy cover. We also assessed the global distributions of subordinate, apex felids as a means of assessing the potential contributions of ecologically-similar species to pumas around the world. Solitary felids > 20 kg that feed on prey larger than themselves (Carbone et al., 2007) and are subordinate to other predators may provide distinctive ecological functions through their disproportionate production of carrion and subsequent contributions to ecosystem stability (e.g., cheetahs, Hunter et al., 2006; Eurasian lynx, *Lynx lynx*, Krofel et al., 2012).

2. Methods

2.1. Study area

Our puma study spanned 2300 km^2 of the GYE north of Jackson, Wyoming (Fig. 2). Elevations ranged from 1800 m to > 3600 m. The area was characterized by short, cool summers during which prey were widely dispersed and long winters with frequent snowstorms during which elk (*Cervus elaphus*) formed large aggregations at lower elevations. Further details about the study area, including plant communities and mammal assemblages, are found in Elbroch et al. (2013).

2.2. Puma capture and collar programming

We captured pumas during winter months from 2012 to 2015, when we employed trailing hounds to force pumas to retreat to a tree where we could safely capture them. Pumas were fitted with a GPS collar (Lotek Globalstar S or Iridium M, Newmarket, Ontario; Vectronics Globalstar GPS Plus, Berlin, Germany). Our capture protocols adhered to the guidelines outlined by the American Society of Mammalogists (Sikes et al., 2011) and were reviewed by the Jackson Institutional Animal Care and Use Committee (Protocol 027-10EGDBS-060210); additional capture details can be found in Elbroch et al. (2013). GPS collars were programmed to acquire location data every two hours.

2.3. Locating and monitoring puma kills

GPS data acquired by puma collars were uploaded to Globalstar satellites six times per day or once per day to Iridium satellites. Upon retrieval, we displayed location data in ArcGIS 10.0. (ESRI, Redlands, CA), and following protocols for studying puma foraging (Elbroch et al., 2014), identified aggregated GPS points in which ≥ 2 locations spanning ≥ 4 h of time were within 150 m of each other. Researchers transferred puma location data to handheld GPS units to guide them in the field, and we systematically searched aggregated locations to locate prey remains. The state of prey remains, presence and location of bite marks, hemorrhaging at wound sites, and body parts consumed were used to determine whether the puma had killed the animal or was scavenging. If we judged that there was sufficient meat remaining to draw scavengers (e.g., the carcass was cached by the puma, indicating it would likely return, or there was enough meat to cover the long bones of the legs), we placed paired motion-triggered video cameras (Bushnell Outdoor Products, Overland Park, KS) to document scavenger diversity at the carcass; we programmed cameras to record 60s videos with 30s delay between triggers, and only included those species that clearly fed from the carcass as scavengers in our analyses, or in the case of passerines, that may have fed upon insects upon the carcass (it was sometimes difficult to differentiate whether they were eating meat or something on the meat); we did not include species that were recorded by cameras but did not feed from the carcass. Cameras monitored carcasses for variable lengths of time, primarily dependent upon animal activity that could quickly fill the camera's memory, or in winter, extreme temperatures that limited battery life.

2.4. Scavenger diversity

We compared mammal and avian scavengers detected at carcasses with species known to inhabit the area. Then we quantified the percent of local mammals and birds that scavenged puma kills, which were descriptive statistics that we could directly compare to scavenger studies compiled and reported in Mateo-Tomás et al. (2015). We included 201 of 304 bird species listed in the "Birds of Jackson Hole" (Raynes, 2014) (Appendix A), which presented species occurrence in four seasons (spring, summer, fall, winter) and five categories: abundant, common, occasional, rare (defined as "not occurring every year; unexpected as to season or range"), and accidental (defined as "rarely seen"); we did not include 103 birds because they were listed as rare or accidental in all four seasons (e.g., a species was included if it were rare in 1–3 seasons, but at least occasional in one season). We included all 60 mammal species listed for Grand Teton National Park (Wiki, 2016).

Using generalized linear and generalized linear mixed models, and a Poisson distribution, we built and tested 12 simple a priori models (Table 1) to test what biological factors best fit our selection parameter, scavenger biodiversity at kills (Shannon's Diversity Index *H*; Krebs, 1999), and to mitigate the inclusion of uninformative parameters (Arnold, 2010). Based upon previous research (Selva et al., 2005; Hunter et al., 2006) we included three biological variables that influence scavenger diversity at carrion resources: *Temperature*, which we defined as the mean temperature during sampling by cameras at each carcass, as quantified with hourly temperatures recorded by SNOTEL

Table 1
Model comparisons ranked from best fit to worth, AICc values, ΔAICc, Model likelihood, and Akaike weights (w_i).

Model	AICc	ΔAIC	Likelihood	w_i
CamDays + Weight	504.795	0	1.000	0.433
CamDays + Temp	504.906	0.111	0.946	0.410
CamDays + Temp + Weight	506.833	2.038	0.361	0.156
PumaID (Rnd) + Weight + CamDays	529.897	25.102	0.000	0.000
PumaID (Rnd) + Weight	534.495	29.700	0.000	0.000
PumaID (Rnd) + Temp	534.878	30.083	0.000	0.000
PumaID (Rnd) + Temp + Weight	536.694	31.899	0.000	0.000
PumaID (Rnd) + Canopy	546.253	41.458	0.000	0.000
PumaID (Rnd) + Canopy + Weight	547.876	43.081	0.000	0.000
PumaID (Rnd) + Canopy + Temp + Weight	548.686	43.891	0.000	0.000
PumaID (Rnd) + Canopy + Temp	550.59	45.795	0.000	0.000

weather station 506 in the north of our study area. We believed *temperature* would capture potential variation in scavenging activity due to season, snow cover, and other annual weather patterns; *CanopyCover* (4 categories: 0–25%, 26–50%, 51–75%, 76–100%), measured with a spherical densitometer directly above carcasses, to capture variation across habitat cover classes that might influence the detectability of carcasses by avian scavengers; *Weight* (carcass size in kg) to capture variation in the number of scavengers due to competition over limited resources. We also included *CameraDays*, which we defined as the number of days a carcass was sampled by cameras, to test for variation due to different sampling periods across kills, and individual *PumaID* as a random effect, to account for spatial autocorrelation between kills that might capture localized scavenger communities on the landscape, and thus bias results.

Before model building, we tested for multi-collinearity among covariates; all covariates were correlated at $r < |0.5|$, and all variables were included in our analyses. We calculated Akaike's Information Criterion adjusted for small sample size (AICc), ΔAICc, and Akaike weights (w_i) for each model (Burnham and Anderson, 2002). We assessed top model performance with R^2 values, and reported parameter estimates (± SE) for covariates in top models.

3. Results

3.1. Pumas and scavengers

Between April 2012 and December 31, 2015, we marked 15 independent pumas (5 male, 10 female), documented 1022 prey killed by pumas, and deployed motion-triggered cameras at 242 kills of prey weighing on average 135 (± 93 SD) kg to assess vertebrate scavenger diversity. We set cameras within 43 (± 38 SD) hrs of when kills were made, and recorded scavenger activity for on average 7.0 (± 3.7 SD) days. We detected 39 scavenger species (Appendix A; Fig. 1), plus domestic dogs which we did not include in our biodiversity analyses. Red foxes (*Vulpes vulpes*) and black-billed magpies (*Pica hudsonia*) were by far recorded at the most carcasses (Fig. 1). Scavengers represented 10.9% of local birds, 28.3% of local mammals, and 14.9% of all birds and mammals (Appendix A).

3.2. Scavenger diversity

Mean Shannon's Diversity Index *H* was 0.83 (± 0.58 SD) across all carcasses. We identified two top models that best fit our data, *H*, and which explained 84% of the AIC weight (Table 1). Neither top model, however, performed well as determined with R^2 values. Our model *CameraDays* + *Weight* explained 10% of the variation in the data; parameter estimates for *CameraDays* was 0.0538 (± 0.0177 SE), and for *Weight*, 0.0003 (± 0.0008 SE). Our second top model *CameraDays* + *Temperature* explained 9% of the variation in the data; parameter estimates for *CameraDays* was 0.0546 (± 0.0176 SE), and for *Temperature*, 0.0002 (± 0.0084 SE).

4. Discussion

We documented the highest vertebrate scavenger diversity of any study to date, emphasizing 1) the ecological importance of pumas, and potentially other subordinate, apex felids in the production of carrion, 2) the diversity of food-web vectors supported by pumas, and 3) the positive contributions of pumas to ecological stability through predation and their adapted tolerance for kleptoparatism by diverse scavengers. For example, we documented both higher numbers of species and higher representative percentages of local birds and mammals than nine studies of scavengers at hunter offal around the globe (Mateo-Tomás et al., 2015). We also documented > 3 times the scavenger species recorded at wolf and hunter kills in the same ecosystem just north of our study area (Wilmers et al., 2003), however, it remains possible that our results differed due to methods rather than reflected differences in diversity.

Overall, our analyses indicated scavenger biodiversity was relatively consistent across a range of temperatures, carcass sizes and canopy cover. Scavenger biodiversity was most influenced by the duration of sampling, emphasizing the need for longer sampling periods at carcasses in the future, as well as further research to determine the length of time needed to capture potential biodiversity, much like detection probabilities in camera-trap surveys for rare species (Long et al., 2012). In support for our hypotheses, temperature and carcass weight did influence scavenger diversity, but only minimally. Our sampling, however, was biased towards large carcasses over small, as large carcasses persisted long enough to visit and set up a camera to record scavengers. Therefore, we believe we did not adequately test for the potential effect of carcass size on scavenger diversity. In the case of temperature, our results suggested that there were a similar number of species scavenging puma carcasses across seasons; however, an important next step is to test for species turnover at carcasses to test for differences in scavenger assemblages. Some scavengers exhibit migrations, and others enter periods of dormancy during the coldest months, affecting their presence at carcasses (Fig. 1). Last, we did not find support for our hypothesis that canopy cover would influence species richness, but again, this may be due to an equal number of different species utilizing carcasses under different canopies, rather than identical scavenger assemblages across the landscape.

Carcasses produced by predators are greater utilized by scavengers than other sources of carrion (Selva et al., 2005; Moleón and Sànchez-Zapata, 2015), and evidence suggests that subordinate, apex felids that kill prey larger than themselves play disproportionate roles in providing carrion to natural systems (Hunter et al., 2006; Elbroch and Wittmer, 2012). Thus, we identified six additional felids ecologically-similar to pumas (e.g., stalk-and-ambush, apex predators that weigh > 20 kg, kill prey larger than themselves, and are subordinate to other sympatric predators in competition scenarios) that may also disproportionately provision carrion to their ecological communities: cheetah, clouded leopard (*Neofelis nebulosa*), Eurasian lynx, leopard (*Panthera pardus*), snow leopard (*Panthera uncia*), and sunda clouded leopard (*Neofelis diardi*). As determined with International Union for Conservation of Nature (IUCN) maps (Gerngross, 2016; Iberlince and EU LIFE Programme, 2015; International Snow Leopard Trust and WCS, 2010; IUCN, 2015; IUCN, 2016), the global distribution for all seven functionally-similar species is 57,975,188 km^2, or 43.0% of terrestrial lands except Antarctica (Fig. 2). According to the IUCN, the snow leopard is endangered, and the leopard, cheetah, sunda clouded leopard, and clouded leopard are vulnerable. The cheetah inhabits just 9% (Durant et al., 2017) and the leopard, 25–37%, (Jacobson et al., 2016) of their historic ranges, due to intense persecution. Yet even following centuries of exploitation, these seven species still cover an area almost half the land mass north of Antarctica; their wide-spread distributions are not only evidence of their ecological plasticity, but may also indicate their importance in diverse ecosystems around the globe. We urge conservation scientists and managers to prioritize the support of functioning populations of subordinate, apex felids, for example through reduced hunting quotas and livestock conflict mitigation measures, as a means of focusing resources to best ensure the production of carrion that promotes biodiversity and ecosystem stability.

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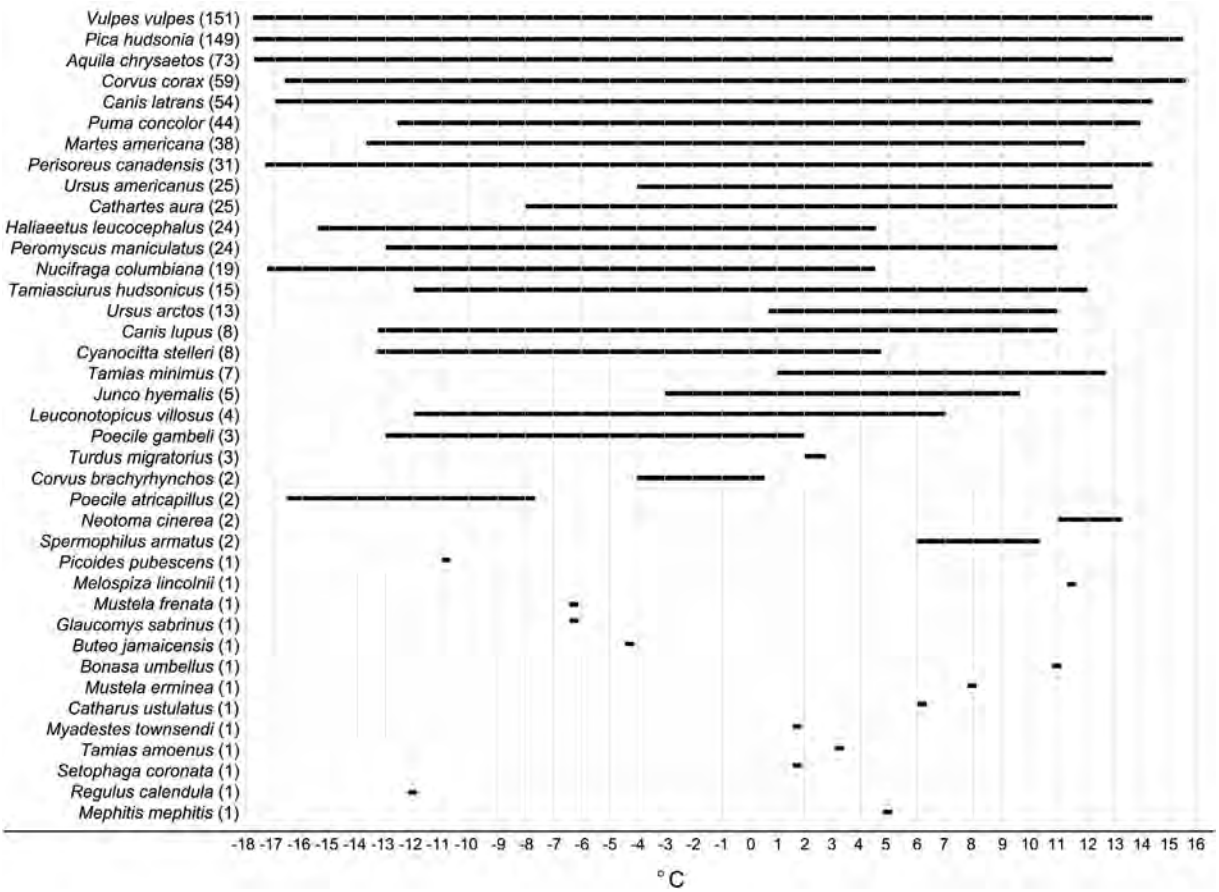

Fig. 1. Species recorded at puma kills in the Greater Yellowstone Ecosystem, ranked in order by the frequency of kills at which they were detected (*n*), and followed by a visual representation of the temperature range for kills at which they were detected (°C).



Fig. 2. The combined global distribution of seven functionally-similar subordinate, apex felids that hunt prey larger than themselves. a: puma (*Puma concolor*), b: cheetah (*Acinonyx jubatus)* compliments of Tobi87, c: leopard (*Panthera pardus*) compliments of Ninara, d: Eurasian lynx (*Lynx lynx*) compliments of Böhringer Friedrich, e: snow leopard (*Panthera uncia*) compliments of Bernard Landgraf, f: clouded leopard (*Neofelis nebulosa*) compliments of Ltshears, g: sunda clouded leopard (*Neofelis diardi*) compliments of Heiko Wittmer and Andrew Marshall. The star denotes the location of our puma study in North America.

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Appendix A. Appendix A

	Detected at puma kills
Mammals (Source: Wiki, 2016. https://en.wikipedia.org/wiki/Mammals_of_Grand_Teton_National_Park. Viewed 1 January 2017.)	
Black bear, *Ursus americanus*	1
Grizzly bear, Ursos arctos	1
Coyote, *Canis latrans*	1
Gray wolf, *Canis lupus*	1
Red fox, *Vulpes vulpes*	1
Bobcat, *Felis rufus*	
Cougar, *Felis concolor*	1
Raccoon, *Procyon lotor*	
American badger, *Taxidea taxus*	
American marten, *Martes americana*	1
American mink, *Neovison vison*, riparian forests	
North American river otter, *Lontra canadensis*	
Least weasel, *Mustela nivalis*	
Long-tailed weasel, *Mustela frenata*	1
Short-tailed weasel, *Mustela erminea*	1
Wolverine, *Gulo gulo*, alpine	
Striped skunk, *Mephitis mephitis*	1
Elk (wapiti), *Cervus elaphus*	
Mule deer, *Odocoileus hemionus*	
White-tailed deer, *Odocoileus virginianus*	
Moose, *Alces alces*	
Pronghorn, *Antilocapra americana*	
Bison, *Bison bison*	
Mountain goat, *Oreamnos americanus*	
Bighorn sheep, *Ovis canadensis*	
Snowshoe hare, *Lepus americanus*	
White-tailed jackrabbit, *Lepus townsendii*	
American pika, *Ochotona princeps*	
Masked shrew, *Sorex cinereus*	
American water shrew, *Sorex palustris*	
Dwarf shrew, *Sorex nanus*	
Vagrant shrew, *Sorex vagrans*	
Beaver, *Castor canadensis*	
Least chipmunk, *Tamias minimus*	1
Uinta chipmunk, *Tamias umbrinus*	
Yellow-pine chipmunk, *Tamias amoenus*	1
Yellow-bellied marmot, *Marmota flaviventris*	
Golden-mantled ground squirrel, *Spermophilus lateralis*	
Northern flying squirrel, *Glaucomys sabrinus*	1
American red squirrel, *Tamiasciurus hudsonicus*	1
Uinta ground squirrel, *Spermophilus armatus*	1
Northern pocket gopher, *Thomomys talpoides*	
Deer mouse, *Peromyscus maniculatus*	1
Western jumping mouse, *Zapus princeps*	
Muskrat, *Ondatra zibethicus*	
Western heather vole, *Phenacomys intermedius*	
Long-tailed vole, *Microtus longicaudus*	
Meadow vole, *Microtus pennsylvanicus*	
Montane vole, *Microtus montanus*	
Sagebrush vole, *Lemmiscus curtatus*	
Southern red-backed vole, Myodes gapperi	
Water vole, *Microtus richardsoni*	
Bushy-tailed woodrat, *Neotoma cinerea*	1
North American porcupine, *Erethizon dorsatum*	
Big brown bat, *Eptesicus fuscus*	

Hoary bat, *Lasiurus cinereus*		
Little brown bat, *Myotis lucifugus*		
Long-eared bat, *Myotis evotis*		
Long-legged bat, *Myotis volans*		
Silver-haired bat, *Lasionycteris noctivagans*		
60 mammals	Total	17
Percent		0.283333333
Birds (Source: Raynes, 2014. Birds of Jackson Hole. Jackosn WY: Grand Teton Association, Wyoming Game and Fish Department.)		
Snow goose		
Canada goose		
Trumpeter swan		
Tundra swan		
Wood duck		
Gadwall		
American wigeon		
Mallard		
Blue-winged teal		
Cinnamon teal		
Northern shoveler		
Northern pintail		
Green-winged teal		
Canvasback		
Redhead		
Ring-necked duck		
Lesser scaup		
Harlequin duck		
Bufflehead		
Common goldeneye		
Barrow's goldeneye		
Hooded merganser		
Red-breasted merganser		
Common merganser		
Ruddy duck		
Gray partridge		
Ruffed grouse		1
Greater sage-grouse		
Dusky grouse		
Sharp-tailed grouse		
Common loon		
Pied-billed grebe		
Eared grebe		
Western grebe		
Clark's grebe		
American white pelican		
Double-crested cormorant		
Great blue heron		
Great egret		
Snowy egret		
White-faced ibis		
Turkey vulture		1
Osprey		
Bald eagle		1
Northern harrier		
Sharp-shinned hawk		
Cooper's hawk		
Northern goshawk		
Swainson's hawk		
Red-tailed hawk		1
Ferruginous hawk		
Rough-legged hawk		
Golden eagle		1
American kestrel		
Merlin		
Peregrine falcon		
Prairie falcon		

Virginia rail	
Sora	
American coot	
Sandhill crane	
Semipalmated plover	
Killdeer	
American avocet	
Spotted sandpiper	
Solitary sandpiper	
Greater yellowlegs	
Willet	
Lesser yellowlegs	
Long-billed curlew	
Semipalmated sandpiper	
Western sandpiper	
Least sandpiper	
Baird's sandpiper	
Long-billed dowitcher	
Wilson's snipe	
Wilson's phalarope	
Franklin's gull	
Ring-billed gull	
California gull	
Caspian tern	
Common tern	
Forster's tern	
Rock dove	
Eurasian collared-dove	
Mourning dove	
Great horned owl	
Northern pygmy-owl	
Great gray owl	
Long-eared owl	
Short-eared owl	
Boreal owl	
Northern saw-whet owl	
Common nighthawk	
White-throated swift	
Black-chinned hummingbird	
Calliope hummingbird	
Broad-tailed hummingbird	
Rufous hummingbird	
Belted kingfisher	
Lewis' woodpecker	
Williamson's sapsucker	
Red-naped sapsucker	
Downy woodpecker	1
Hairy woodpecker	1
American three-toed woodpecker	
Black-backed woodpecker	
Northern flicker	
Olive-sided flycatcher	
Western wood-pewee	
Willow flycatcher	
Least flycatcher	
Hammond's flycatcher	
Dusky flycatcher	
Cordilleran flycatcher	
Eastern kingbird	
Loggerhead shrike	
Northern shrike	
Plumbeous vireo	
Warbling vireo	
Gray jay	1
Steller's jay	1
Clark's nutcracker	1

Black-billed magpie	1
American row	1
Common raven	1
Horned lark	
Tree swallow	
Violet-green swallow	
Northern rough-winged swallow	
Bank swallow	
Cliff swallow	
Barn swallow	
Black-capped chickadee	1
Mountain chickadee	1
Red-breasted nuthatch	
White-breasted nuthatch	
Brown creeper	
Rock wren	
House wren	
Marsh wren	
American dipper	
Golden-crowned kinglet	
Ruby-crowned kinglet	1
Mountain bluebird	
Townsend's solitaire	1
Swainson's thrush	1
Hermit thrush	
American robin	1
Gray catbird	
Sage thrasher	
European starling	
American pipit	
Bohemian waxwing	
Cedar waxwing	
Orange-crowned warbler	
Yellow warbler	
Yellow-rumped warbler	1
Townsend's warbler	
American redstart	
Northern waterthrush	
MacGillivray's warbler	
Common yellowthroat	
Wilson's warbler	
Western tanager	
Green-tailed towhee	
Spotted towhee	
American tree sparrow	
Chipping sparrow	
Clay-colored sparrow	
Brewer's sparrow	
Vesper sparrow	
Savannah sparrow	
Fox sparrow	
Song sparrow	
Lincoln's sparrow	1
White-crowned sparrow	
Dark-eyed junco	1
Snow bunting	
Black-headed grosbeak	
Lazuli bunting	
Bobolink	
Red-winged blackbird	
Western meadowlark	
Yellow-headed blackbird	
Brewer's blackbird	
Common grackle	
Brown-headed cowbird	
Bullock's oriole	

Gray-crowned rosy-finch		
Black rosy-finch		
Pine grosbeak		
Cassin's finch		
House finch		
Red crossbill		
White-winged crossbill		
Common redpoll		
Pine siskin		
American goldfinch		
Evening grosbeak		
House sparrow		
201 mammals	Total	22
Percent		0.109452736
Total percent		0.14942529

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Fractured Genetic Connectivity Threatens a Southern California Puma (*Puma concolor*) Population

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Abstract

Pumas (*Puma concolor;* also known as mountain lions and cougars) in southern California live among a burgeoning human population of roughly 20 million people. Yet little is known of the consequences of attendant habitat loss and fragmentation, and human-caused puma mortality to puma population viability and genetic diversity. We examined genetic status of pumas in coastal mountains within the Peninsular Ranges south of Los Angeles, in San Diego, Riverside, and Orange counties. The Santa Ana Mountains are bounded by urbanization to the west, north, and east, and are separated from the eastern Peninsular Ranges to the southeast by a ten lane interstate highway (I-15). We analyzed DNA samples from 97 pumas sampled between 2001 and 2012. Genotypic data for forty-six microsatellite loci revealed that pumas sampled in the Santa Ana Mountains (n = 42) displayed lower genetic diversity than pumas from nearly every other region in California tested (n = 257), including those living in the Peninsular Ranges immediately to the east across I-15 (n = 55). Santa Ana Mountains pumas had high average pairwise relatedness, high individual internal relatedness, a low estimated effective population size, and strong evidence of a bottleneck and isolation from other populations in California. These and ecological findings provide clear evidence that Santa Ana Mountains pumas have been experiencing genetic impacts related to barriers to gene flow, and are a warning signal to wildlife managers and land use planners that mitigation efforts will be needed to stem further genetic and demographic decay in the Santa Ana Mountains puma population.

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Introduction

Genetic diversity, demography, and abundance – biological characteristics that influence population viability – can vary across a species' distribution. Species that are generally perceived as wide-ranging and abundant are sometimes relegated to status as "least conservation concern", in spite of indicators signaling concern and frequently, lack of data. Pumas (*Puma concolor*; also known as mountain lion, cougar, and in Florida, panther) epitomize this dilemma. Although pumas in California have not been subjected to hunting since 1972, and were designated as a Specially Protected Mammal in 1990 [1], there is minimal active management and little scientifically validated data on statewide or regional population numbers. Pumas in southern California have one of the lowest annual survival rates among any population in North America, on par with rates seen in hunted populations (unpublished data). They are under increasing threats from habitat loss and fragmentation, and mortality from vehicle strikes, depredation permits, poaching, public safety kills, wildfire, and poisoning [2,3]. Timely evaluation of potential threats to population viability is imperative in order to prioritize conservation activities to prevent collapse of some populations.

The human population of southern California is over 20 million [4] and expected to exceed 30 million by 2060 [5]. This increasing population will likely result in further loss, fragmentation, and degradation of natural habitats in the region. Habitat fragmentation south of greater Los Angeles has effectively turned the Santa Ana Mountain range in mostly Orange and Riverside counties into a 'mega-fragment' of habitat, surrounded to the west, north, and east by dense urban land uses. The only remaining montane and foothill habitat linkage connecting the Santa Ana Mountain range to other mountains of the Peninsular Range is a southeasterly swath of habitat bisected by a very heavily traveled 10-lane highway, Interstate 15 (I-15) (Figure 1).

Population viability of pumas in the Santa Ana Mountains (a geography henceforth referred to as distinct from the broader Peninsular Ranges to the east) has been of conservation concern



Figure 1. Topographic map depicting location of Santa Ana Mountains, eastern Peninsular Ranges in southern California, and adjacent regions. Inset shows location in the state of California.
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for decades. Population monitoring and modeling in the 1980s highlighted that urbanization and highways were fragmenting puma habitat (e.g., [6]), and that in turn motivated efforts to protect habitat connectivity in the region (e.g., [7,8]). As part of a statewide assessment of puma genetic diversity and population structure, Ernest et al. [9] employed an 11-locus microsatellite panel and found that, for a limited sample size (n = 14) Santa Ana pumas had lower genetic diversity than other populations in California. Since 2001, pumas in the region have been the subject of an ongoing study by the Karen C. Drayer Wildlife Health Center of the University of California, Davis (UCD) School of Veterinary Medicine. Telemetry data from 74 pumas in the UCD study has confirmed that minimal connectivity (only one GPS-collared puma over ten years was documented to transit successfully; unpublished data) exists between the Santa Ana Mountains and the eastern Peninsular Ranges across I-15, confirming that previous connectivity concerns were warranted.

We conducted a detailed appraisal of the genetic diversity, relatedness, and population structure of southern California puma populations. Using 97 samples collected over 12 years as part of the UCD study, and a 46-locus microsatellite panel, we evaluated levels of genetic diversity, estimated effective population sizes and tested whether genetic data supported a hypothesis of recent bottleneck in the populations. We assessed whether genetics reflected our telemetry observations of infrequent puma crossings of I-15 between the Santa Ana Mountains and the Peninsular Ranges to the east. Additionally we explored inter-population gene flow at multiple time scales by employing methods that reflect recent (a few generations) and more historical (tens or more generations). Finally, we tested our hypothesis that the Santa Ana population had lower genetic diversity than those sampled from other regions in California.

Materials and Methods

Samples

We obtained blood or tissue samples for analysis of nuclear DNA from pumas captured for telemetry studies, and from those found dead or killed by state authorities for livestock depredation or public safety in San Diego, Orange, Riverside, and San Bernardino counties of southern California (n = 97) during 2001–2012 (Figure 2). Pumas captured for telemetry were captured and sampled as detailed in [10]. Forty-two samples were collected to the west of I-15 in the Santa Ana Mountains, and 55 samples were collected in the Peninsular Ranges to the east of I-15. A small number of additional samples were collected from deceased animals in San Bernardino County just to the north of the Peninsular Range across Interstate Highway 10. For population genetic comparisons with pumas sampled elsewhere throughout California, a 257 sample subset of our statewide puma DNA data archive was employed (regions and sample sizes detailed in Table 1 and depicted in Figure 1 in [9])

Ethics Statement

Animal handling was carried out in strict accordance with the recommendations and approved Protocol 10950/PHS, Animal

Table 1. Genetic diversity summary statistics for southern California pumas (n = 97) relative to other populations in California (n = 257).

Sampling Region	Abbrev.		N	Na	AR	Ho	He	I	%P
North Coast	**NC**	**Mean**	29	3.6	2.0	0.41	0.44	0.80	98%
		SE		0.2	0.1	0.03	0.03	0.05	
Modoc Plateau & Eastern Sierra Nevada	**MP-ESN**	**Mean**	51	4.2	2.4	0.52	0.54	0.98	100%
		SE		0.3	0.1	0.03	0.03	0.05	
Western Sierra Nevada	**WSN**	**Mean**	47	4.2	2.4	0.47	0.51	0.95	98%
		SE		0.2	0.2	0.03	0.03	0.06	
Central Coast: north	**CC-N**	**Mean**	83	3.2	1.9	0.41	0.41	0.70	98%
		SE		0.2	0.1	0.03	0.03	0.06	
Central Coast: central	**CC-C**	**Mean**	21	3.4	2.1	0.43	0.46	0.81	96%
		SE		0.2	0.1	0.03	0.03	0.05	
Santa Monica Mountains	**CC-S**	**Mean**		2.2	1.7	0.38	0.33	0.53	76%
Central Coast: South		**SE**	26	0.1	0.1	0.04	0.03	0.05	
Peninsular Range-East	**PR-E**	**Mean**	55	3.1	2.0	0.43	0.41	0.74	87%
		SE		0.2	0.2	0.04	0.04	0.07	
Santa Ana Mountains	**SAM**	**Mean**	42	2.3	1.6	0.33	0.32	0.54	80%
		SE		0.2	0.1	0.03	0.03	0.05	

Abbrev. = region abbreviations used in Tables and Figures. Mean with standard error (SE). N = sample size. Na = average number of different alleles per locus. AR = allelic richness, standardized to sample size. Ho = observed heterozygosity. He = expected heterozygosity. I = Shannon's information index (Sherwin et al 2006). %P = percent of polymorphic loci. Regions are detailed further in text and generally follow California Bioregions designations. (http://biodiversity.ca.gov/bioregions.html).

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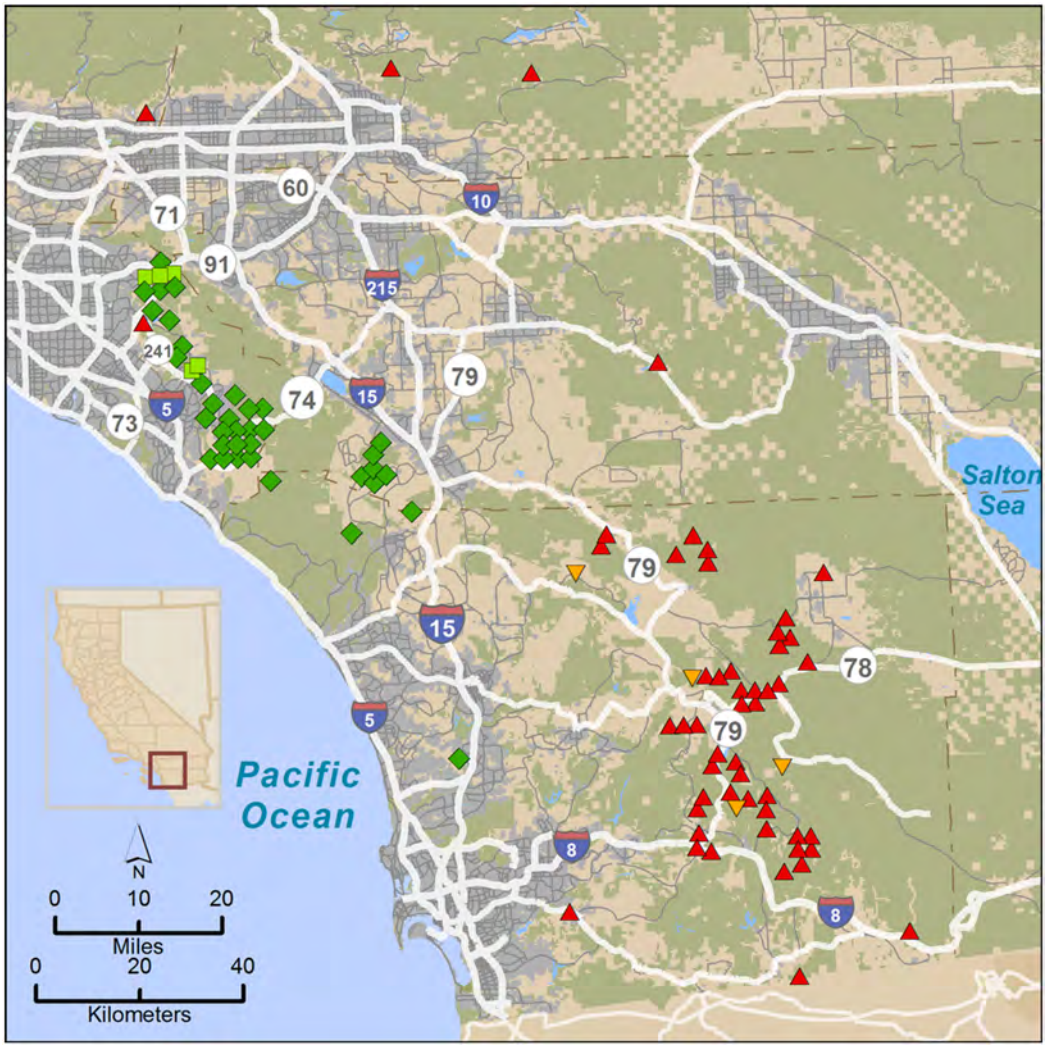

Figure 2. Map of puma capture locations in the Santa Ana Mountains and eastern Peninsular Ranges of southern California. Colors of symbols represent genetic group assignment inferred from Bayesian clustering analysis (STRUCTURE analysis, see Figure 4). Genetic group A-1 = green diamonds; A-2 = red triangles (apex at top). One male puma (M86) captured in the Santa Ana Mountains had predominant genetic assignment to the A-2 (red) genetic group. Five individuals (light green squares) captured in the Santa Ana Mountains had partial assignment to the A-2 group (M91, F92, M93, M97 and F102). Molecular kinship analysis showed that M86 and a female (F89) captured in the Santa Ana Mountains were parents of pumas M91, F92, and M93 (captured in the Santa Ana Mountains). Puma M97 assigned in parentage to M86 and F61, while F102 had unknown parentage (no parentage assignments; due possibly to her death early in project prior to collection of most of the samples). Three individuals (orange triangles, apex at bottom), had partial assignment (however, less than 20%) to A-1.
doi:10.1371/journal.pone.0107985.g002

Welfare Assurance number A3433-01, with capture and sampling procedures approved by the Animal Care and Use Committee at the University of California, Davis (Protocol #17233), and Memoranda of Understanding and Scientific Collecting Permits from the California Department of Fish and Wildlife (CDFW). Permits and permissions for access to conserved lands at puma capture and sampling sites were obtained from CDFW, California Department of Parks and Recreation, The Nature Conservancy, United States (US) Fish and Wildlife Service, US Forest Service, US Bureau of Land Management, US Navy/Marine Corps, Orange County Parks Department, San Diego County Parks Department, San Diego State University, Vista Irrigation District, Rancho Mission Viejo/San Juan Company, Sweetwater Authority, California Department of Transportation (CalTrans), and the City of San Diego Water Department.

DNA Extraction and Microsatellite DNA data collection

Whole genomic DNA was extracted using the DNeasy Blood & Tissue Kit (QIAGEN, Valencia, CA, USA). Fifty microsatellite DNA primers were initially screened for this project. Forty-six loci that performed well in multiplex PCR (using the QIAGEN Multiplex PCR kit; QIAGEN) and conformed to expectations for Hardy-Weinberg and linkage equilibria were selected for ultimate analysis [11,12,13]. One sex-identification locus (Amelogenin) was used to confirm sex in samples from degraded puma carcasses [14].

PCR products were separated with an ABI PRISM 3730 DNA Analyzer (Applied Biosystems Inc., Foster City, CA, USA) with each capillary containing 1 μL of a 1:10 dilution of PCR product and deionized water, 0.05 μL GeneScan-500 LIZ Size Standard and 9.95 μL of HiDi formamide (both products Applied Biosystems Inc.) that was denatured at 95°C for 3 min. Products

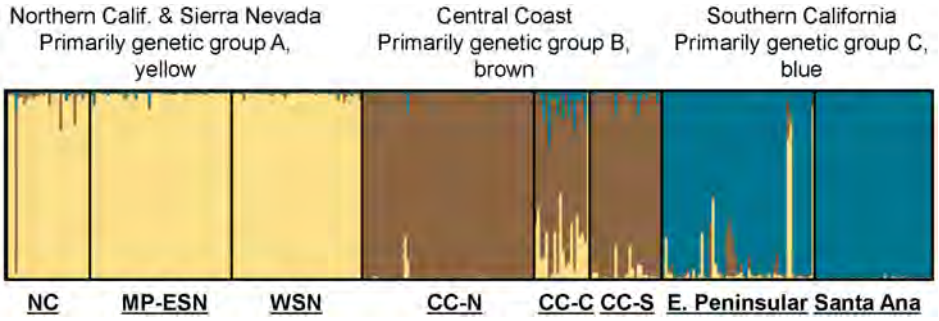

Figure 3. California puma population genetic structure. STRUCTURE bar plot displaying the genetic clustering relationship of southern California pumas relative to others in California. Three major genetic groups, A (blue, on right), B (brown, in center), and C (yellow, on left), are evident for analysis of 354 individuals sampled throughout California. Abbreviations: NC = North Coast, MP-ESN = Modoc Plateau & Eastern Sierra Nevada, WSN = Western Sierra Nevada, CC-N = Central Coast: north, CC-C = Central Coast: central, CC-S = Central Coast: South (Santa Monica Mountains), PR-E = Peninsular Range-East, SAM = Santa Ana Mountains. The plot is organized by grouping individuals in order of their geographic region sampling source. Proportional genetic assignment for each puma is represented by a vertical bar, most easily visualized for pumas that genetically assigned to a group different from most others sampled in its region (for example one individual with over 80% brown and 8% blue near far left of group A). Pumas primarily from the Sierra Nevada Range and northern California are represented by group A (yellow), group B (brown) includes primarily Central Coast pumas and group C (blue) represents primarily southern California pumas (Santa Ana Mountains and eastern Peninsular Ranges).
doi:10.1371/journal.pone.0107985.g003

were visualized with STRand version 2.3.69 [15]. Negative controls (all reagents except DNA) and positive controls (well-characterized puma DNA) were included with each PCR run. Samples were run in PCR at each locus at least twice to assure accuracy of genotype reads and minimize risk of non-amplifying alleles. For >90% samples, loci that were heterozygous were run at least twice and homozygous loci were run at least three times.

Genetic diversity

The number of alleles (Na), allelic richness (AR; incorporates correction for sample size), observed heterozygosity (Ho), expected heterozygosity (He), Shannon's information index [16], and tests for deviations from Hardy-Weinberg equilibrium were calculated using software GenAlEx version 6.5 [17,18]. Shannon's information index provides an alternative method of quantifying genetic diversity and incorporates allele numbers and frequencies. Testing for deviations from expectations of linkage equilibrium was conducted using Genepop 4.2.1 [19], and we tested for the presence of null alleles using the program ML RELATE [20]. We assessed significance for calculations at alpha = 0.05 and used sequential Bonferroni corrections for multiple tests [21] in tests for Hardy-Weinberg and linkage equilibria.

The average probability of identity (PID) was calculated two ways using GenAlEx: 1) assuming random mating (PID_{RM}) without close relatives in a population [22], and 2) assuming that siblings with similar genotypes occur in a population (PID_{SIBS}) [23]. Probability of identity is the likelihood that two individuals will have the same genetic profile (genotype) for the DNA markers used. PID_{SIBS} is considered conservative since it probably conveys a higher likelihood; however, we recognized that siblings occurred in these populations.

Assessing population structure and genetic isolation

We used a Bayesian genetic clustering algorithm (STRUCTURE version 2.3.4 [24,25]) to determine the likely number of population groups (K; genetic clusters) and to probabilistically group individuals without using the known geographic location of sample collection. We used the population admixture model with a flat prior and assumed that allele frequencies were correlated among populations, and ran 50,000 Markov chain Monte Carlo repetitions following a burnin period of 10,000 repetitions. First,

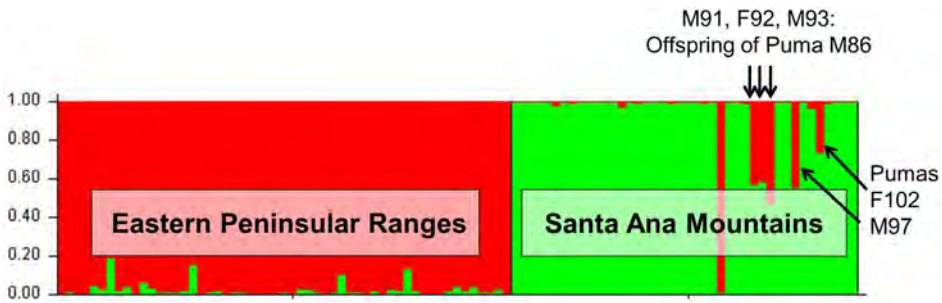

Figure 4. Southern California puma population genetic structure. Bar Plot displaying results of STRUCTURE analysis focused on genotypic data from 97 southern California pumas (the blue block from Figure 3). With removal of the strong genetic signal from northern California and Central Coast samples (see Figure 3), two distinct southern California groupings were inferred, C-1 (green, on right) and C-2 (red, on left). These reflect the two regions: Santa Ana Mountains to the west of I-15 (predominantly genetic group C-1) and eastern Peninsular Ranges to the east of I-15 (predominantly genetic group C-2). Genetic clustering is dependent on genetic variance among samples included in the analysis. One male puma (M86) captured in the Santa Ana Mountains has predominant genetic assignment to the C-2 (red) genetic group (the predominant genetic cluster for PR-E), and five others had partial assignment to the C-2 group (M91, F92, M93, M97 and F102). Molecular kinship analysis showed that M86 and a female (F89) assigning to the C-1 genetic group were parents of pumas M91, F92, and M93 (all were captured in the Santa Ana Mountains).
doi:10.1371/journal.pone.0107985.g004

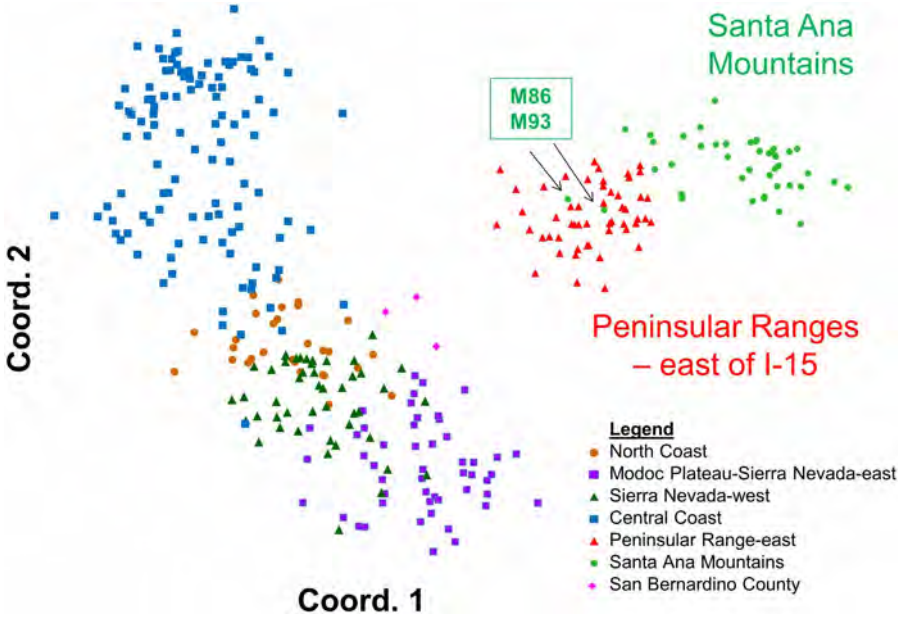

Figure 5. Principal Coordinates analyses (PCoA) constructed using genetic covariance matrices (GenAlEx) for 354 California puma genetic profiles including 97 from southern California. Patterns displayed for first two axes of variation within the genetic data set. Each point, color-coded to its sampling region, represents an individual puma. Note that colors in PCoA diagrams reflect geographic source of samples and not STRUCTURE genetic cluster assignment. Abbreviations and sample sizes per Table 1. Arrows denote pumas described in Figure 4.
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an analysis including 354 statewide puma genotypes (97 from southern California and 257 from other regions) was run to estimate the probability of one through 10 genetic clusters (K), with each run iterated three times. Second, given the output of the statewide run, we ran an analysis using only the 97 southern California puma genotypes to estimate the probability of one through five K, with each run iterated three times. Employing STRUCTURE HARVESTER [26] we averaged log probability

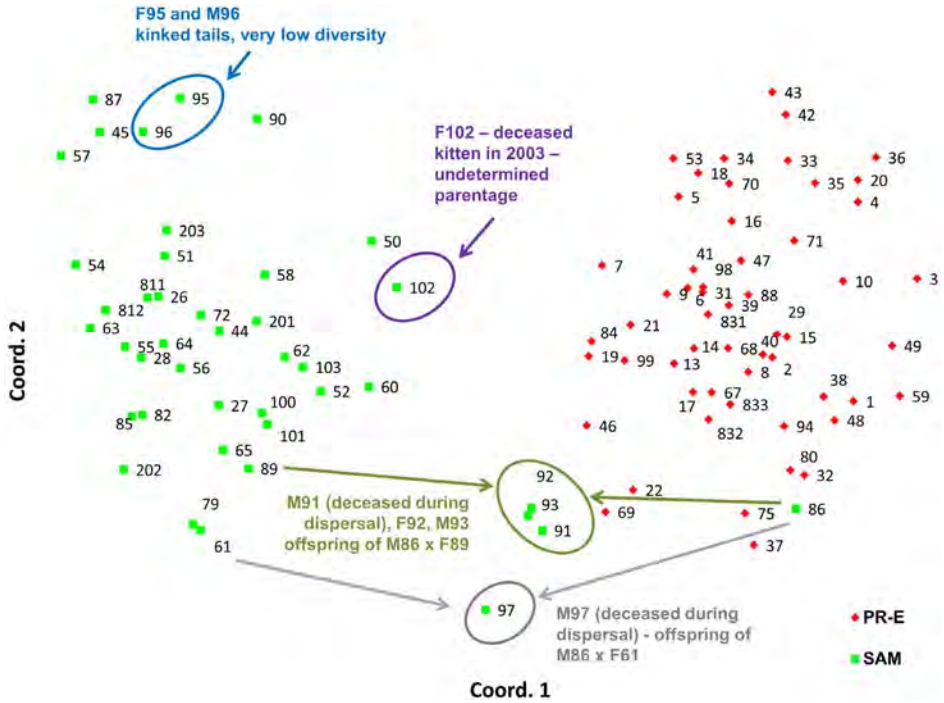

Figure 6. Principal Coordinates analyses (PCoA) via covariance matrices for 97 southern California puma genetic profiles as conducted in GenAlEx. Patterns displayed for first two axes of variation within the genetic data set. Each point represents an individual puma, and has sample identification number and color-coding to sampling region. Note that colors in PCoA diagrams reflect geographic source of samples and not STRUCTURE genetic cluster assignment. Abbreviations and sample sizes per Table 1.
doi:10.1371/journal.pone.0107985.g006

Table 2. Wright's F_{ST} values indicate that southern California mountain lion populations are genetically distinct from other populations in California.

	NC	MP-ESN	WSN	CC-N	CC-C	CC-S	PR-E	SAM
North Coast (NC)	0							
Modoc Plateau & Eastern Sierra Nevada (MP-ESN)	0.09	0						
Western Sierra Nevada (WSN)	0.05	0.03	0					
Central Coast: north (CC-N)	0.13	0.14	0.12	0				
Central Coast: central (CC-C)	0.08	0.09	0.06	0.07	0			
Santa Monica Mountains (CC-S)	0.17	0.15	0.12	0.14	0.10	0		
Peninsular Range-East (PR-E)	0.13	0.08	0.09	0.12	0.09	0.16	0	
Santa Ana Mountains (SAM)	0.18	0.16	0.17	0.19	0.17	0.27	0.07	0

Note that one of the geographically closest puma populations, Santa Monica Mountains, has highest F_{ST} with the Santa Ana population, evidence of high genetic isolation for both regions. Probability, P(random>= data) based on 9999 permutations for all values are <0.001. Abbreviation definitions and sample sizes are included in Table 1.

doi:10.1371/journal.pone.0107985.t002

of the data given K, log Pr(X|K), statistics across the multiple runs for each of the K estimates. In each case (statewide and southern California), we selected the K value of highest probability by identifying the set of values where the log Pr(X|K) value was maximized and subsequently selected the minimum value for K that did not sacrifice explanatory ability [27,28,29]. We defined membership to a cluster based upon the highest proportion of ancestry to each inferred cluster.

To further assess and visualize genetic relationships among regions and individuals, we performed principal coordinates analyses (PCoA) via covariance matrices with data standardization [30] using GenAlEx. This is a technique that allowed us to explore and plot the major patterns within the data sets. The PCoA process located major axes of variation within our multidimensional genotype data set. Because each successive axis explains proportionately less of the total genetic variation, the first two axes were used to reveal the major separation among individuals. Employing Genalex software, a pairwise, individual-by-individual genetic distance matrix was generated and then used to create the PCoA.

Wright's F-statistic, $F_{ST,}$ was calculated to appraise how genetic diversity was partitioned between populations. As implemented in GenAlEx, we used Nei's [31] formula, with statistical testing options offered through 9999 random permutations and bootstraps.

Detecting migrants

We used GENECLASS2 version 2.0.h [32] to identify first-generation migrants, i.e. individuals born in a population other than the one in which they were sampled. Genetic clusters identified during STRUCTURE analysis were treated as putative populations. GENECLASS2 provides different likelihood-based test statistics to identify migrant individuals, the efficacy of which depends on whether all potential source populations have been sampled. We first calculated the likelihood of finding a given individual in the population in which it was sampled, L_h, assuming all populations had not been sampled. We then calculated L_h/L_{max}, the ratio of L_h to the greatest likelihood among the populations [33], which has greater power when all potential source populations have been sampled. The critical value of the test statistic (L_h or L_h/L_{max}) was determined using the Bayesian approach of Rannala and Mountain [34] in combination with the resampling method of Paetkau et al. [33]; i.e., Monte Carlo simulations carried out on 10,000 individuals with the significance level set to 0.01.

Testing for bottlenecks and inferring effective population size

We tested for evidence of recent population size reductions in Santa Ana Mountains and eastern Peninsular Range regions with one-tailed Wilcoxon sign-rank tests for heterozygote excess in the program BOTTLENECK version 1.2.02 [35]. The program evaluates whether the reduction of allele numbers occurred at a rate faster than reduction of heterozygosity, a characteristic of populations which have experienced a recent reduction of their effective population size (Ne) [35,36]. This bottleneck genetic signature is detectable by this test for a finite time, estimated to be less than 4 times Ne generations [37]. These tests were performed using the two-phase (TPM, 70% step-wise mutation model and 30% IAM) model of microsatellite evolution and 10,000 iterations.

We then estimated contemporary Ne for each of the two regions based on gametic disequilibrium with sampling bias correction [38] using LDNE version 1.31 [39]. Ne is formally defined as the size of the ideal population that would experience the same

Table 3. Effective population size estimations and indications of recent genetic bottlenecks in southern California pumas.

	Mode	TPM	Ne (P-CI; JK-CI)
Santa Ana Mtns	Shifted mode	0.009	5.1 (3.3–6.7; 3.3–6.6)
Peninsular Range, East	Normal L	0.19	24.3 (21.7–27.3; 20.6–28.8)

Listed by column are p-values for population bottleneck tests (Wilcoxon sign-rank test; BOTTLENECK) assuming the two-phase (TPM) model of microsatellite evolution. Effective size (Ne) estimations (95% CI) based on data from 42 microsatellite loci. The Santa Ana Mountains population exhibited clear evidence of a population bottleneck. Effective population size estimate using the point estimate linkage disequilibrium method of (LDNE, Waples 2006) with 95% confidence intervals (CI) for both parametric (P) and jackknifed (JK) estimates.
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amount of genetic drift as the observed population [40]. These analyses excluded alleles occurring at frequencies ≤ 0.05, and we used the jackknife method to determine 95% confidence intervals [38].

Relatedness analyses: pairwise coefficient and internal

Molecular kinship analysis was conducted using a number of software packages. Pairwise relatedness among individuals was evaluated using the algorithm of Lynch and Ritland [41], with reference allele frequencies calculated and relatedness values averaged within each southern California population, as implemented in GenAlEx. Partial molecular kinship reconstruction was conducted using a consensus of outputs from the GenAlEx pairwise relatedness calculator, ML Relate [20], CERVUS version 3.0.3 [42], and Colony version 2.0.3.1 [43,44]. Individual genetic diversity (also called internal relatedness) was assessed using Rhh [45] as implemented in R statistical software [46]. This is a measure of genetic diversity within each individual (an estimate of parental relatedness [47], and we averaged over individuals for each of the two regions of southern California. Significance of differences between means was evaluated using t tests.

Results

Forty-two of the 46 loci that we employed were polymorphic in southern California and selected for the subsequent analyses. The average probabilities of identity with assumptions of either random mating (PID_{RM}) or mating among sibs (PID_{SIBS}) across the 42 loci for the eastern Peninsular Ranges were (PID_{RM}) 6.3×10^{-22} and (PID_{SIBS}) 3.1×10^{-10}, and for the Santa Ana Mountains were (PID_{RM}) 2.8×10^{-15} and (PID_{SIBS}) 1.1×10^{-7} respectively. These very small values indicate that the panel of genetic markers provided very high resolution to distinguish individuals. For example, given this data the probability of seeing the same multi-locus genotype in more than one puma was less than one in nine million for Santa Ana Mountains pumas.

Genetic diversity

Measures of genetic variation including allelic diversity, heterozygosity, Shannon's information index, and polymorphism, were lower for Santa Ana pumas than most of those tested from other regions of California (Table 1). Such low genetic diversity indicators were approached only by pumas in the Santa Monica Mountains (Ventura and Los Angeles Counties), a neighboring remnant puma population in the north Los Angeles basin (Figure 1).

Population Structure

Bayesian clustering analysis (STRUCTURE; Figure 3 of statewide puma genetic profiles (n = 354), including 97 from southern California, also support genetic distinctiveness of Santa Ana Mountains and eastern Peninsular Range pumas from other populations in the state. Three main genetic groups (A, B, and C) were evident in the analysis (Figure 3) The 97 pumas sampled in southern California (right-hand set of bars in Figure 3, with samples from Santa Ana and eastern Peninsular Range pumas labeled) predominantly cluster within genetic group C. The Santa Ana pumas assign very tightly to group C (0.996 average probability assignment), while pumas of the eastern Peninsular Ranges showed more variable assignment (0.93 average probability assignment), with 9 individuals (16%) having less than 0.90 assignment. Pumas sampled in the Central Coast of California (which included Santa Monica Mountains pumas) make up the central set of bands, and those individuals predominantly assign to the genetic group B. Pumas sampled in the other regions of California (North Coast Ranges, Modoc Plateau, western Sierra

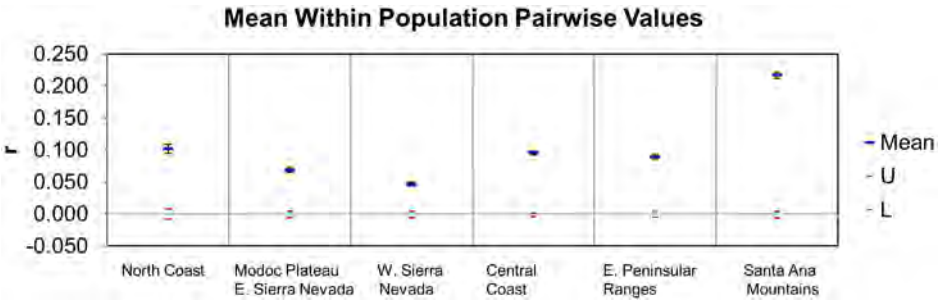

Figure 7. Average pairwise relatedness (r; blue bars with confidence intervals) for pumas sampled in southern California relative to other regions in California. Algorithm of Lynch and Ritland (1999) as implemented in GenAlEx. Expected range for "unrelated" is shown as red bars with confidence intervals. The average relatedness of Santa Ana Mountain pumas is higher than those sampled in Peninsular Ranges east of I-15 and for any other region tested in California. Relatedness in the Santa Ana Mountains pumas approaches second order family relationship (half sibs, niece-aunt, grandparent-grandchild, etc.). Abbreviations listed in Table 1.
doi:10.1371/journal.pone.0107985.g007

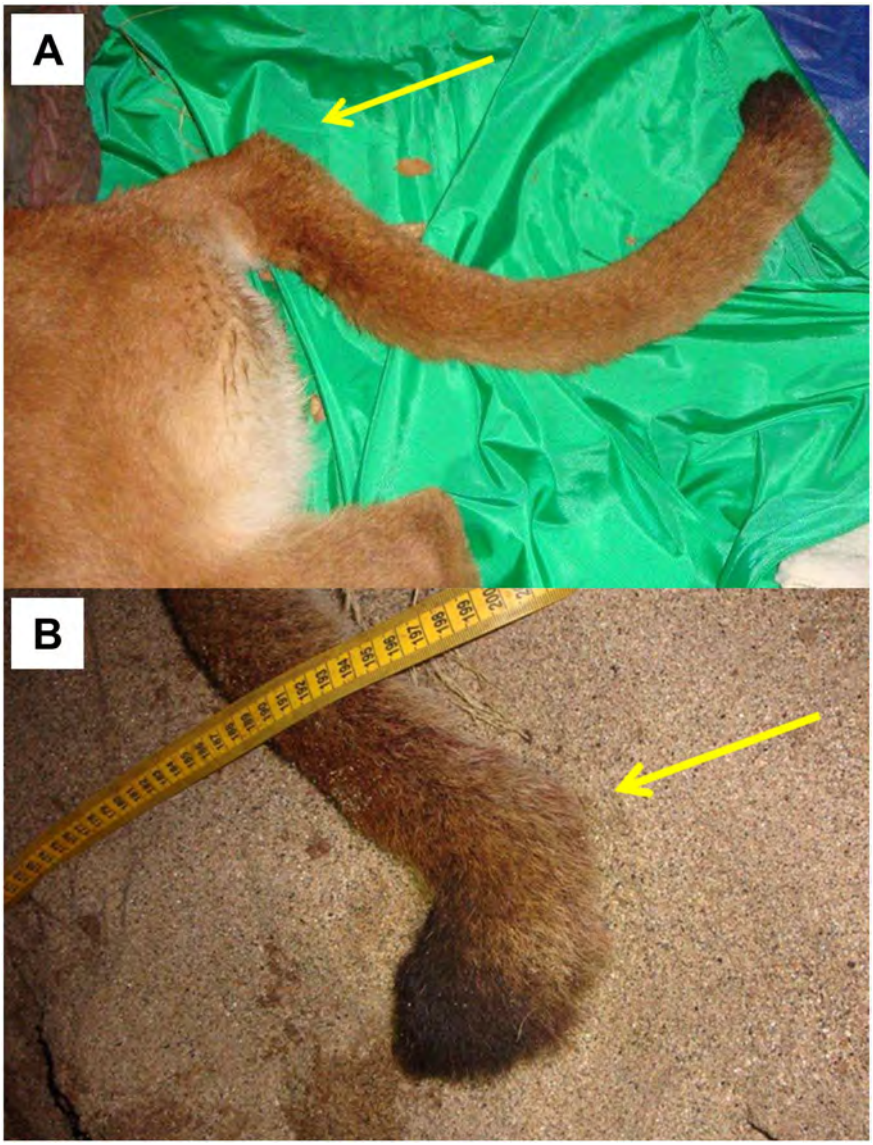

Figure 8. Photographs of kinked tails of pumas F95 (a) and M96 (b). Arrows indicate kink sites. Puma F95 had tail kink at base of tail and Puma M96 had tail kink near distal tip of tail. These two pumas had among the lowest genetic diversity measured in this study.
doi:10.1371/journal.pone.0107985.g008

Nevada, and eastern Sierra Nevada) predominantly cluster with the genetic group A. Notably, there are individuals sampled in each geographic area which cluster with a genetic group that is not the dominant one in that area, suggesting dispersal events and/or genetic exchange that have occurred to varying degrees in each region.

A STRUCTURE analysis focused only on genetic data from the 97 southern California pumas indicated two distinct genetic groups (C-1 and C-2 shown in Figure 4). Pumas sampled in the eastern Peninsular Range region east of I-15 group primarily with C-2 and those of the Santa Ana Mountain region on the west side of I-15 group with C-1. An exception to the consistent genetic clustering was an adult male (M) puma (M86), that was captured in the Santa Ana Mountains but clustered with pumas from the eastern Peninsular Ranges (primarily genetic group C-2). Five other pumas captured in the Santa Ana Mountains had a 30–50% assignment to the C-2 group (M91, F92, M93, M97 and F102). Molecular kinship analysis showed that M86 and a female (F89) captured in the Santa Ana Mountains and assigned to the C-1 genetic group were the likely parents of three of these pumas (M91, F92, and M93) (results of relatedness and kinship analyses). M86 also was the likely parent of another puma in the group (M97), an offspring of another female (F61) that was sampled in Santa Ana Mountains and clustered with the C-1 genetic group. F102 was a <1 year old female killed by a vehicle in 2003 prior to collection of the majority of samples from adults in the Santa Ana Mountains.

Principal coordinates analysis of statewide puma genetic profiles ($n = 354$) (PCoA; Figure 5) allowed graphical examination of the first two major axes of multivariate genetic variation, and confirmed and added detail to the genetic distinctiveness of southern California pumas relative to others in California. The PCoA also reinforced the distinctiveness of pumas sampled in the Santa Ana Mountains from those sampled in the eastern Peninsular Ranges. Most pumas sampled in the Santa Ana Mountains align in a cloud of data points distinct from the eastern

Peninsular Range pumas, and were the most genetically distant from all other pumas tested in California (Figure 5). The analysis also confirms the STRUCTURE findings that M86 who was sampled in the Santa Ana Mountains genetically aligns with the pumas sampled in the Peninsular Ranges, as does one of his offspring, M93 (see Figure 6 for additional detail). The PCoA position of data points for three pumas sampled in the San Bernardino Mountains north of Peninsular Ranges (pink diamonds in Figure 5) illustrates an intermediate genetic relationship between pumas from the rest of California and pumas sampled in the eastern Peninsular Ranges and Santa Ana Mountains, and suggests that they may represent transitional gene flow signature between southern California and regions to the north and east.

PCoA analysis of only the samples collected in the Santa Ana and Peninsular Ranges (Figure 6) confirms the findings from the STRUCTURE analysis indicating genetic distinctiveness of these two populations despite geographic proximity. Siblings M91, F92, and M93 (offspring of F89 and M86 according to our kinship reconstructions) as well as M97 (likely offspring of a female puma captured in the Santa Ana Mountains, F61, and M86, according to kinship reconstructions) are located graphically midway between their parents' PCoA locations.

Genetic isolation

Wright's F_{ST} calculations (Table 2) indicate that Santa Ana Mountains pumas are the most isolated of those tested throughout California ($p = 0.0001$). Despite the short distance (as short as the distance across the I-15 Freeway) between the Santa Ana Mountains and the eastern Peninsular Range region, F_{ST} was surprisingly high (0.07) given the very close proximity of the two regions (separated only by an interstate highway). The Santa Monica Mountains pumas and Santa Ana Mountains pumas had the highest F_{ST} (0.27; lowest gene flow) of all pairwise comparisons in the state, demonstrating a high level of genetic isolation between these regions.The Santa Monica Mountains and Santa Ana Mountains are less than 100 km direct distance apart, through the center of Los Angeles. However the more likely distance for puma travel between these two mountain ranges, avoiding urban areas and maximizing upland habitat, would likely exceed 300 km (estimated using coarse measurements on Google Earth, Google, Inc.).

Detection of migrants

GENECLASS2 identified four individuals as first-generation migrants ($P<0.01$), four with the L_h method (pumas F75, M80, M86, and M99), and one with the L_h/L_{max} ratio (M86, which was detected using both likelihood methods). Pumas F75, M80, and M99 were all captured from the San Bernardino Mountains (Figure 2) at the northern extent of the study region, yet clustered with individuals from the Eastern Peninsular Range during STRUCTURE analysis. Their migrant designation may suggest immigration from populations north of Los Angeles and/or a distinct genetic population within the San Bernardino region. Puma M86 was captured in the Santa Ana Mountains, but assigned strongly to the eastern Peninsular Range genetic cluster, indicating a seemingly clear population of origin. This individual assignment is in accord with the clustering results from STRUCTURE (Figure 4).

Evidence of genetic bottlenecks

The Santa Ana Mountains population exhibited clear evidence of a population bottleneck (Table 3; Wilcoxon sign-rank test for heterozygote excess, and detection of a shift in the allele frequency distribution mode [36]; BOTTLENECK software). The eastern Peninsular Range mountain lions did not show a strong signature of a bottleneck.

Effective population size

Effective population size (Ne) estimations using the linkage disequilibrium method (LDNe program) were 5.1 for the Santa Ana Mountains population and 24.3 for mountain lions in the eastern Peninsular Ranges. Statistical confidence intervals for both regions, given the genetic data, were tight (Table 3).

Relatedness: pairwise coefficient and internal

The average pairwise coefficient of relatedness (r, Figure 7) was highest in Santa Ana Mountains pumas relative to all others tested in California (0.22; 95% confidence interval of 0.22–0.23), a level that approaches second order kinship relatedness (half-sibs, grantparent/grandchild, aunt-niece, etc). The value for the eastern Peninsular Ranges was 0.10 (confidence interval of 0.09–0.10), less than that of third order relatives (first cousins, great-grandparent/great grandchild). Other regions of California averaged similar or lower values to those of eastern Peninsular Ranges (Figure 7).

Among pumas sampled in the Santa Ana Mountains, the population average (0.14) for internal relatedness as implemented in rHH software was significantly higher (t test; $p = 5.8\times10^{-6}$) than for those sampled in the eastern Peninsular Ranges (0.001). Of a group of six pumas which clustered near one another in PCoA (Figure 6), five have among the lowest individual genetic diversity measured in southern California (Puma ID [Internal Relatedness value: F45 [0.37], F51 [0.37], M87 [0.28], F90 [0.21], F95 [0.38], and M96 [0.33]). Notably, pumas F95 and M96 (highest internal relatedness) were observed with kinked tails at capture in the Santa Ana Mountains (Figure 8).

Discussion

Pumas of the Santa Ana Mountains are genetically depauperate, isolated, and display signs of a recent and significant bottleneck. In general, coastal California puma populations have less genetic diversity and less gene flow from other populations than those farther inland [9] (Table 1). This study showed that two coastal populations (Santa Ana Mountains and Santa Monica Mountains) had particularly low genetic variation and gene flow from other regions. Lack of gene flow is likely due in part to natural barriers to puma movement: geography and habitat (Pacific Ocean to the west; less hospitable desert habitat bounding certain regions, etc.). However, our data suggest that anthropogenic developments on the landscape are playing a large role in genetic decay in the Santa Ana Mountains puma population. As large solitary carnivores with sizable habitat requirements, pumas are extremely sensitive to habitat loss and fragmentation [48,49].

The genetic bottleneck in the Santa Ana Mountains pumas is estimated at less than about 80 years, depending on definitions of effective population size (Ne) and puma generation time. Luikhart and Cornuet [37] state that the bottleneck signatures decay after "4 times Ne [here estimated to be 5.1] generations". Logan and Sweanor [50] estimated generation time for their New Mexico population of pumas to be 29 months (2.4 years) for females. If an allowance of 2.4–4.0 years is made for generation times (unknown) in the Santa Ana Mountains population, the maximum estimated time since a bottleneck would be about 40–80 years. This was a period of tremendous urban development and multi-lane highway construction in southern California, particularly I-15 [51]. It is likely that the potential for connectivity between the Santa Ana Mountains and the Peninsular Range-East region will continue to be eroded by ongoing increases in traffic volumes on I-15, and

conversion of unconserved lands along the I-15 corridor by development and agriculture [8,48,52].

An isolated population of pumas in the Santa Monica Mountains to the north of the Santa Ana Mountains also exhibit low values relative to other western North American populations (see Table 2 in [53]. Santa Monica pumas are isolated by urbanization of a megacity and busy wide freeways (Ventura county, including greater Los Angeles region [53]. Multiple instances of intraspecific predation, multiple consanguineous matings (father to daughter, etc.), and lack of successful dispersal highlight a suite of anthropogenic processes also occurring in the Santa Ana Mountains. Our collective findings of kinked tails *and* very low genetic diversity in Santa Ana pumas F95 and M96 may portend manifestations of genetic inbreeding depression similar to those seen in Florida panthers [54,55]; however recognizing that kinked tails can have non-genetic etiologies.

Our analyses suggest that the Santa Ana Mountains puma population is highly challenged in terms of genetic connectivity and genetic diversity, a result hinted at in Ernest et al. [9] and now confirmed to be an ongoing negative process for this population. This compounds the demographic challenges of low survival rates and scant evidence of physical connectivity to the Peninsular Ranges east of I-15 (unpublished data). Beier [6] documented these same challenges during the 1990's, and data from the ongoing UCD study suggest the trends have accelerated. Substantial habitat loss and fragmentation has occurred and is continuing to occur; Burdett et al. [10] estimated that by 2030, approximately 17% of puma habitat that was still available in 1970 in southern California will have been lost to development, and fragmentation will have rendered the remainder more hazardous for pumas to utilize. Riley et al [53] document a natural "genetic rescue" event: the 2009 immigration and subsequent breeding success of a single male to the Santa Monica Mountains. This introduction of new genetic material into the population was paramount to raising the critically low level of genetic diversity, as also exemplified by the human-mediated genetic augmentation of Florida Panthers with Texas puma stock [56].

These findings raise concerns about the current status of the Santa Ana Mountains puma population, and the longer-term outlook for pumas across southern California. In particular, they highlight the urgency to maintain – and enhance – what connectivity remains for pumas (and presumably numerous other species) across I-15. Despite warnings [6,9] about potential serious impacts to the Santa Ana Mountains puma population if concerted conservation action was not taken, habitat connectivity to the Peninsular Ranges has continued to erode. We are hopeful that these new genetic results will motivate greater focus on connectivity conservation in this region. Indeed, the Santa Ana Mountains pumas may well serve as harbingers of potential consequences throughout California and the western United States if more attention is not paid to maintaining connectivity for wildlife as development progresses.

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Author Contributions

Conceived and designed the experiments: HBE TWV WMB. Performed the experiments: HBE TWV MRB WMB. Analyzed the data: HBE TWV MRB. Contributed reagents/materials/analysis tools: HBE TWV SAM WMB. Contributed to the writing of the manuscript: HBE TWV SAM MRB WMB.

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Small-scale habitat fragmentation effects on pollinator behaviour: experimental evidence from the bumblebee *Bombus veteranus* on calcareous grasslands

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Abstract

We examined visiting patterns of pollinators of *Betonica officinalis* L. (Lamiaceae) in experimentally fragmented calcareous grasslands and corresponding control plots at two study sites (Movelier and Nenzlingen) in the north-western Swiss Jura mountains. Fragments (1.5×1.5 m) were isolated by a 5-m wide strip of frequently mown vegetation while the control plots were situated in the adjacent undisturbed vegetation. The most common pollinator, the bumblebee *Bombus veteranus* (Apidae), visited fragments 53.7% less frequently than control plots. Furthermore, a change in foraging behaviour of *Bombus veteranus* was observed. In fragments the bumblebees visited more inflorescences, flew longer total visiting distances and the visiting time per patch tended to be higher than in control plots. The distribution of angles between arrival and departure direction (turning angles) differed from a uniform distribution in fragments but not in control plots. The increased directionality of bumblebee flight might be due to a decrease in floral rewards. Our results show that small-scale habitat fragmentation can affect plant pollination at two levels both relevant for plant fitness. First, lower visitation rates indicate a limitation of pollinators which might result in reduced seed set of the pollinated plant. Second, changes in pollinator behaviour might reduce pollen dispersal among flowers, increase inbreeding and hence reduce genetic variability in populations of this bumblebee pollinated plant. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: *Betonica officinalis*; *Bombus veteranus*; Bumblebee; Gene flow; Plant–pollination interaction

1. Introduction

Nutrient-poor, calcareous grasslands are among the habitats with the highest species richness in western Europe (Zoller, 1954; Ellenberg, 1982; Willems, 1982). However, industrialisation and changes in agricultural land use since the 1950s caused a dramatic decline of this once common type of grassland, and the remaining remnants are often small, fragmented and isolated (e.g. Willems, 1982; Zoller et al., 1986; Fischer and Stöcklin, 1997). Fragmentation of these natural habitats has especially negative biological consequences for ecosystem functions (Saunders et al., 1991; Kearns et al., 1998), such as plant–pollinator interactions, the subject of the present study.

The ecological importance of pollinators in their communities is crucial (Kearns et al., 1998). The entire structure of biotic communities will be dramatically changed when keystone plant species lose their pollinators. A cascade of changes including a decline in biodiversity may follow (Allen-Wardell et al., 1998; Kearns et al., 1998). Habitat fragmentation can affect pollinator behaviour, population size of animals and plants, and even pollinator morphology (Phillips, 1997; Berwaerts et al., 1998; Thomas et al., 1998; VanDyck and Matthysen, 1999). These chances might in turn influence community structure, population dynamics, trophic levels and genetic diversity in natural ecosystems. Plants experience lower fitness if pollinators are missing or reduced in numbers (e.g. Jennersten, 1988; Pavlik et al., 1993; Fischer and Matthies, 1997; Robertson et al., 1999). Furthermore, habitat fragmentation can change the spatial distribution of plants, which in turn changes foraging patterns of pollinators (Cresswell, 1997). If the distance between plants to be pollinated is too large, pollination is limited (Schmitt, 1983; Klinkhamer et al., 1989) and plant fitness may be reduced due to inbreeding and/or outbreeding depression caused by increased genetic drift (Waser and Price, 1983; Van Teuren et al., 1991; Holsinger, 1993; Percy and Cronk, 1997; Gigord et al., 1999). Thus, a change in pollinator behaviour might strongly affect plant reproductive success and plant fitness.

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There is empirical evidence that habitat fragmentation can influence pollinator populations directly or indirectly, and may cause declines of pollinators (Allen-Wardell et al., 1998). However, little attention has been given to the effect of fragmentation on pollinator behaviour. The aim of this study was to investigate under natural conditions the influence of experimental small-scale fragmentation on the pollinator behaviour of *Bombus veteranus* (Apidae), the most common pollinator of *Betonica officinalis* L. (Lamiaceae), a typical perennial forb in calcareous grasslands of the Swiss Jura mountains.

2. Methods

2.1. Fragmentation experiment and sampling

The study was carried out from 22 July to 7 August 1998 in the experimental habitat fragmentation study site of the University of Basel in the Swiss Jura mountains (Baur and Erhardt, 1995; Baur et al., 1996). The original design, established in spring 1993, consists of three field sites with a total of 12 blocks (Fig. 1) on nutrient-poor, dry calcareous grasslands belonging to the Teucrio-Mesobrometum type (Ellenberg, 1988). In the present study the medium-sized fragments (1.5×1.5 m) and control plots of equal size from six blocks at two sites were used (three blocks at Movelier and three blocks at Nenzlingen). These field sites are situated near Nenzlingen (10 km south of Basel) and near Movelier (5 km north of Delémont).

In each block, fragments were separated by a 5-m wide strip of frequently mown vegetation (6–12 times per year). Corresponding control plots of equal size were mirror-symmetrically arranged and surrounded by undisturbed vegetation (Fig. 1). Because the original control plots varied largely in occurrence of *Betonica officinalis*, we placed control plots in the undisturbed vegetation so as to contain approximately the same number of *Betonica officinalis* inflorescences as in the fragments. Thus, in the surroundings of the control plots numerous other *Betonica officinalis* inflorescences were present, whereas those in the fragments were separated by at least 5 m from other *Betonica officinalis* inflorescences.

In each patch (fragment or control plot) all *Betonica officinalis* inflorescences and open flowers were counted. The positions of all flowering *Betonica officinalis* inflorescences were mapped in 36 cells measuring 25×25 cm. Pollinators were observed in each patch for 20 min on three separate days. We recorded the visitation pattern of every flower visitor entering the plot during the survey. We measured for each insect the visiting distances between successively visited inflorescences, the total flying distance in the patch and the turning angles. Flower visitors that were already in the patch at the beginning

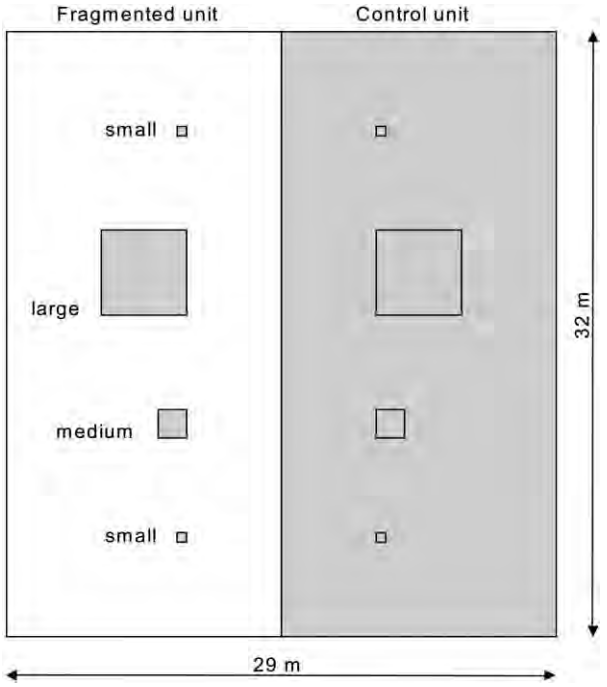

Fig. 1. Experimental layout for one of 12 experimental blocks of 29×32 m established in spring 1993. Each unit contained one large (4.5×4.5 m), one medium (1.5×1.5 m) and two small fragments (0.5×0.5 m), all of them separated by a 5-m wide strip of mown vegetation (white area), as well as the corresponding control plots, which were mirror-symmetrically arranged and surrounded by undisturbed vegetation (grey area).

of the survey were not considered. Additionally, the duration of the visit in the plot of each flower visitor was assessed using a DAT-recorder. Observations were performed between 10:00 and 16:00 in sunny and warm weather. To avoid any time effect the order of surveys in fragments and their control plots were randomised on each observation day. Fragments and control plots of each site were surveyed on three different days (Nenzlingen on 22 and 30 July and on 8 August 1998, Movelier on 24 July and on 6 and 7 August 1998).

The distance between nesting sites of *Bombus veteranus*, the most frequent visitor, and the experimental patches could potentially have affected our observations. However, the fact that bumblebees can forage several hundred metres away from their nesting sites (Osborne et al., 1999), and the design of our experiment (random distribution of fragments and control plots) suggest that positions of nesting sites do not affect the results of the present study.

2.2. Data analyses

To compare the number of visits between fragments and control plots a chi-square goodness of fit test with a hypothesised ratio of 1:1 was used for each site (Zar, 1999). We used pooled data from the three survey days for each fragment and control plot.

To prevent spatial pseudoreplication, data from visiting patterns were averaged per fragment or control plot, respectively, for each survey day. To prevent temporal pseudoreplication we used the average of the three survey days per site, thus, resulting in 12 independent replications (six fragments and six control plots). Three-way analyses of variance (ANOVA, type III model, using JMP 3.1, SAS, 1995) with the fixed factors site and treatment and the random factor block nested by site were used to examine effects on the following parameters (patches refer to fragments or control plots):

Percent of visited inflorescences

$$= \frac{\text{Mean of visited inflorescences per bumblebee}}{\text{Total number of inflorescences in patch}}$$

Visiting time per patch related to inflorescence number (= "Visiting time per patch")

$$= \frac{\text{Mean time spent in patch per bumblebee}}{\text{Total number of inflorescences in patch}}$$

Ratio of mean visiting distances

$$= \frac{\text{Mean distance flown between two successively visited inflorescences}}{\text{Mean nearest neighbour distance between inflorescences}}$$

Ratio of total visiting distances

$$= \frac{\text{Total distances between visited inflorescences in patch per bumblebee}}{\text{Total nearest neighbour distances between inflorescences in patch}}$$

As a measure of the pollinators' flight directionality, turning angles between the arrival and departure directions were assessed from visiting patterns of single bumblebees. For data analysis angles were assigned to 18 classes each of 20°. The distributions of angles recorded in fragments and those from the control plots were compared with a uniform distribution using chi-square goodness of fit test (Zar, 1999). Furthermore, a 2×18 contingency table (G-test) was used to compare the distribution of angles in fragments with those in control plots (Zar, 1999).

3. Results

The number of inflorescences per patch as well as the number of open flowers were not affected by the experimental fragmentation but differed between sites (Table 1). Furthermore, the number of open flowers per inflorescence did not differ between sites ($F_{1,4}=0.44$, n.s.) or treatments ($F_{1,5}=0.17$, n.s.).

In total, the visiting pattern of 314 flower visitors was recorded. Among them, 218 belonged to the most common species, *Bombus veteranus*. The remaining flower visitors were other Hymenoptera (34), *Zygaena* spp. (42), other Lepidoptera (12) and Diptera (eight). Individuals of *Bombus veteranus* visited the fragments less frequently (69 individuals) than the control plots (149 individuals; Fig. 2) which means 53.7% fewer visits in the fragments.

Fragmentation significantly influenced the behaviour of the pollinator *Bombus veteranus* (Fig. 3). The percentage of visited inflorescences and the ratio of total visiting distances was significantly higher in fragments than in control plots (Fig. 3A,D). Thus, flying longer distances and especially visiting more inflorescences within a fragment indicate more near-neighbour pollination, which may result in increased inbreeding in pollinated plants in the fragments. Furthermore, the "visiting time per patch" tended to be longer in fragments than in control plots (Fig. 3B), while the ratio of mean visiting distances did not differ between fragments and control plots (Fig. 3C). A significant site effect on

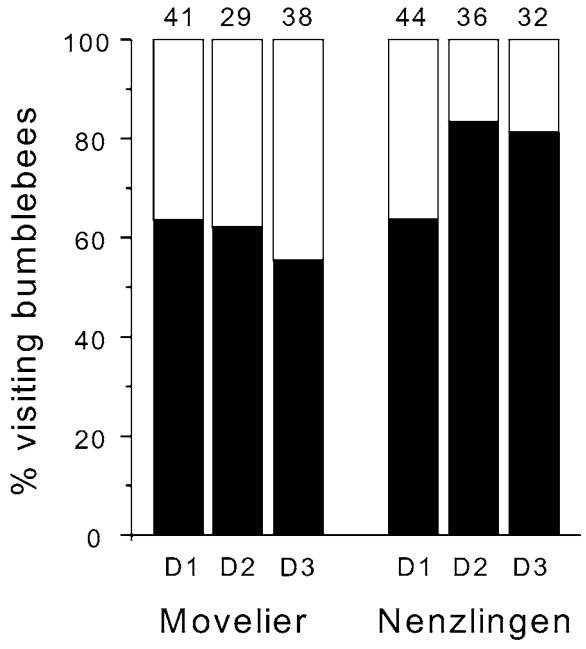

Fig. 2. Percentage of visits of *Bombus veteranus* in fragments (open bars) and corresponding control plots (black bars) at the two different sites, separated per day (D1, D2, D3 = first, second and third observation day, respectively). The numbers above the bar indicate the total number of observed bumblebees at this day. The difference between fragments and control plots was significant for both sites (Movelier: $\chi^2=4.48$, d.f. = 1, $P=0.034$; Nenzlingen: $\chi^2=28.00$, d.f. = 1, $P<0.001$).

Table 1
(a) Mean number (±1 S.E.) of inflorescences and open flowers of *Betonica officinalis* in fragments ($n=3$) and control plots ($n=3$) at the two study sites in Movelier and Nenzlingen. (b) Three-way analyses of variance (ANOVA) for effects of site and fragmentation treatment

(a)

Site	Treatment	Number of inflorescences per patch (2.25 m^2)	Number of open flowers per patch (2.25 m^2)
Movelier	Fragments	9.9±3.3	85.8±36.7
	Control plots	7.4±1.7	64.2±24.5
Nenzlingen	Fragments	22.9±1.3	146.0±8.4
	Control plots	21.7±0.5	176.8±14.5

(b)

	d.f.	SS	*F*	*P*	d.f.	SS	*F*	*P*
Site	1	630.18	35.58	0.004	1	30959.51	15.40	0.017
Treatment	1	17.17	3.87	0.11	1	163.33	0.12	0.75
Block (site)	4	70.84	3.99	0.08	4	8041.43	1.43	0.35
Error	5	22.20			5	7036.28		

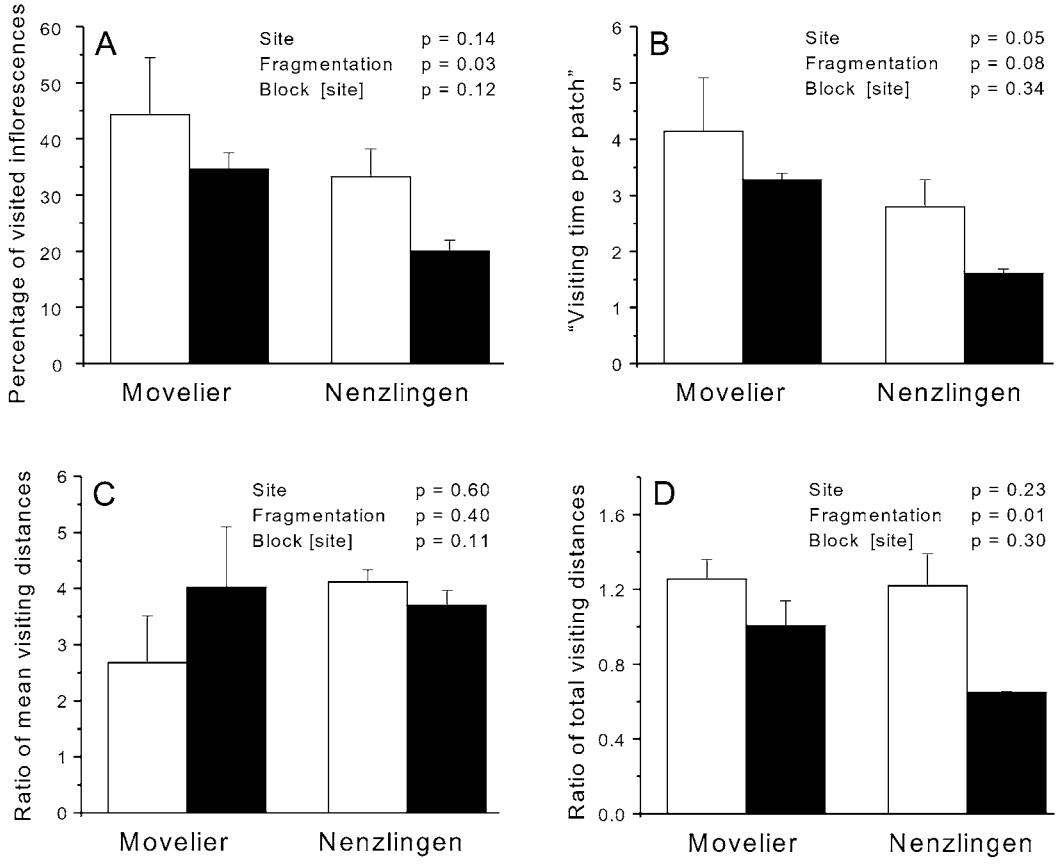

Fig. 3. Effect of habitat fragmentation on the behaviour of the pollinator *Bombus veteranus* visiting *Betonica officinalis* (mean±1 S.E.; open bars = fragments, black bar = control plots) at the sites Movelier and Nenzlingen. (A) percentage of visited inflorescences, (B) visiting time per patch related to inflorescence number ("visiting time per patch"), (C) ratio of mean visiting distances, and (D) ratio of total visiting distances.

the behaviour of *Bombus veteranus* was only found in "visiting time per patch" (Fig. 3B).

The distribution of turning angles of foraging *Bombus veteranus* differed significantly from a uniform distribution in fragments (Fig. 4, $\chi^2=48.28$, d.f. = 17, $P<0.001$), but not in the control plots (Fig. 4, $\chi^2=23.79$, d.f. = 17, $P=0.12$). There is thus a stronger tendency towards directionality in fragments than in control plots. However, a direct comparison of the distributions of turning angles in fragments and control plots revealed no significant difference ($G=14.14$, d.f. = 17, $P=0.66$).

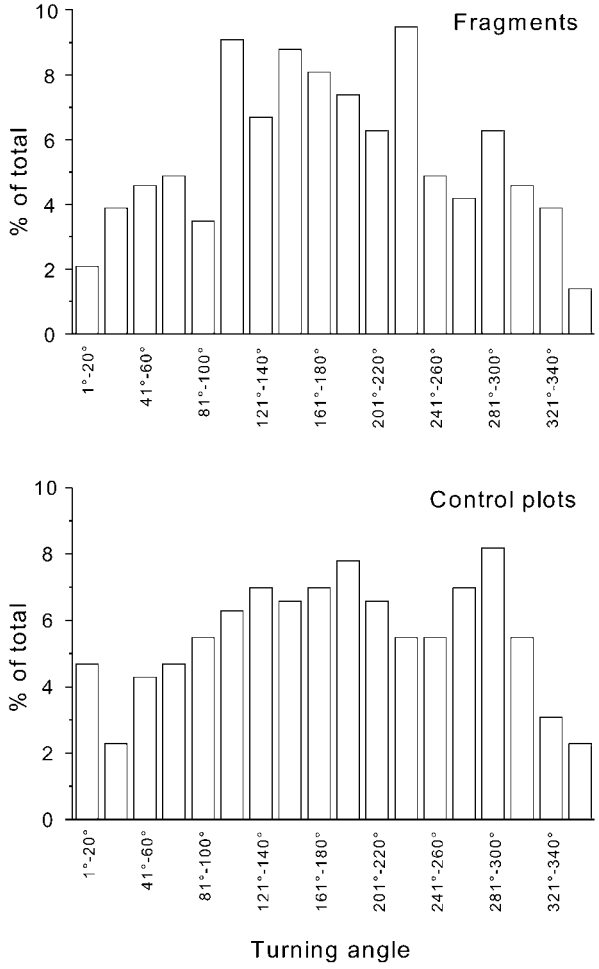

Fig. 4. Distribution of turning angles for *Bombus veteranus* visiting *Betonica officinalis* inflorescences in fragments ($n=285$) and control plots ($n=256$).

4. Discussion

The present study shows that the behaviour of the most common pollinator of *Betonica officinalis*, the bumblebee *Bombus veteranus*, was altered by small-scale fragmentation of calcareous grasslands. Bumblebees visited more inflorescences, flew longer total distances and tended to stay longer in fragments than in control plots (Fig. 3A,B,D). Thus, *Bombus veteranus* preferred to stay within the fragment rather than flying a long distance to reach the next inflorescence outside the fragment. Rasmussen and Brodsgaard (1992) examined visiting patterns of *Bombus lapidarius* in *Lotus corniculatus* patches, which were of different sizes and interspersed with dry areas dominated by mosses, lichens and short grass. Most flights of *Bombus lapidarius* were restricted to single patches (97.4%), although the animals had no difficulty to cross the distance of 10–40 m between patches. Since long distance flying is energetically expensive, the higher visitation rate within patches can be explained by the attempt of pollinators to optimise net energetic gain during foraging (Zimmerman, 1982; Price, 1997). In the present study, fragments were 53.7% less frequently visited than control plots. As a consequence, nectar rewards of inflorescences in fragments might be higher and pollinators might probe more thoroughly because movement decisions are based on the amounts of nectar encountered in flowers (Heinrich, 1979; Cresswell, 1990). However, measurements of nectar samples of *Betonica officinalis* did not support this assumption. The nectar quantity was smaller in fragments than in control plots, whereas the nectar concentration was higher in fragments than in control plots (H.-P. Rusterholz, unpublished data). These differences could be a result of lower soil moisture in fragments than in control plots resulting from frequent mowing of the surroundings (H.-P. Rusterholz, personal communication). In spite of this, bumblebees visiting fragments could have a more economic net energetic gain if they properly probe all available inflorescences in fragments.

The bumblebees' attempt to achieve the highest net energetic gain is confirmed by the observed difference in "visiting time per patch" between the two study sites (Fig. 3B). At Movelier, where there were fewer inflorescences per patch, bumblebees spent more time in a particular patch relatively to the total number of inflorescences, i.e. they visited more intensively all available inflorescences. This finding is supported by other studies in which bumblebees probed fewer flowers per plant and bypassed more plants with increased plant aggregation (e.g. Zimmerman, 1982; Cresswell, 1997). Furthermore, the directionality of foraging movement of bumblebees decreases with increasing plant aggregation (Cresswell, 1997). Additionally, edge plants in isolated patches provoke more reversals of flight than plants in the centre of patches (Rasmussen and Brodsgaard, 1992). Therefore, we assumed that foraging pollinators show less distinct directionality in their flights in fragments, while in the control plots pollinators would rather pass through the patch and, consequently show a directionality in their flight. Directionality in foraging flight decreases revisitation and results in decreased self-pollination, which in turn may affect the genetic structure of the plant population (Cartar and Real, 1997). In the present study bumblebees tended to fly more directly in fragments than in control plots (Fig. 4). A possible explanation could be an adjusted behaviour pattern of foraging strategy. The directionality of flights between inflorescences is random when rewards are high but approaches 180° when rewards are intermediate or poor (Heinrich, 1979; Richards, 1997). Thus, the lower nectar volume of flowers in fragments mentioned earlier might explain the observed tendency towards directionality in fragments.

Most relevant for plant fitness are the lower visitation rates in fragments and the tendency of bumblebees to

remain in isolated patches. Pollinator limitation may reduce seed set while the frequent neighbour visits may reduce the exchange of pollen between distant plants. Thus, gene flow is reduced between fragments which may decrease the probability of outcrossing. Indeed, genetic investigations conducted in the same fragmentation experiment revealed that offspring of *Betonica officinalis* had a lower genetic diversity and an increased self-fertilisation rate in fragments (H.P. Rusterholz, personal communication). These findings illustrate general processes in fragmented landscapes, which in turn might lead to an Allee effect followed by the extinction of small plant populations (Allee et al., 1949; Courchamp et al., 1999).

We showed that experimental small-scale fragmentation reduced flower visitation and changed the behaviour of a common pollinator. Other pollinator species might be affected in a similar way. The reproductive success of pollinated plants might be reduced in fragments due to higher geitonogamy and increased rate of inbreeding. However, any extrapolation of the findings to large-scale fragmentation should be made with caution.

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RESEARCH ARTICLE

Genetic source–sink dynamics among naturally structured and anthropogenically fragmented puma populations

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Abstract

Fragmentation of wildlife populations is increasing on a global scale and understanding current population genetic structure, genetic diversity, and genetic connectivity is key to informing wildlife management and conservation. We genotyped 992 pumas (*Puma concolor*) at 42 previously developed microsatellite loci and identified 10 genetic populations throughout the states of California and Nevada, USA. Although some genetic populations had large effective population sizes, others were small and inbred. Genetic diversity was extremely variable (heterozygosity, uHe = 0.33–0.53), with some populations nearly as low as an endangered subspecies, the Florida Panther (*P. c. coryi*, uHe = 0.24). Specifically, pumas in the Sierra Nevada were genetically diverse and formed the largest genetic source population in the region. In contrast, coastal and southern populations surrounded by urbanization had low genetic diversity, fragmented gene flow, and tended to be genetic sinks. The strong population genetic structuring of pumas across California (F_{ST} = 0.05–0.39) is vastly different than other genetic studies in less-urbanized states, including our analysis in Nevada, where pumas had few barriers to gene flow and weak population differentiation. Our results have far-reaching conservation and management implications for pumas and indicate large-scale fragmentation in one of North America's most biodiverse and rapidly-urbanizing regions.

Keywords Mountain lion · Cougar · *Puma concolor* · Population genetics · Genetic structure

Introduction

Fragmentation of wildlife habitat and resultant impacts to populations are increasing worldwide and urbanization is one of the primary contributors (Crooks et al. 2017; Fahrig 2003; Haddad et al. 2015; Newbold et al. 2016). Unlike

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natural barriers that have impacts over a geological timescale (Albert et al. 2016), urbanization can have more immediate effects on gene flow among populations (Balkenhol and Waits 2009; Karlson et al. 2014). Gene flow is critically important to individual fitness and to the evolutionary potential of populations because successful migrants can diversify gene combinations (i.e., increase heterozygosity) and introduce new genetic material (i.e., increase allelic richness) (Caballero and García-Dorado 2013; Chapman et al. 2009; Frankham 2015). Without receiving gene flow, small populations are especially subject to inbreeding, genetic drift, and increased extinction risk (Carlson et al. 2014; Wootton and Pfister 2015).

Population fragmentation is increasingly evident for species located in the urbanized western United States (Buchalski et al. 2016; Delaney et al. 2010; Fisher and Shaffer 1996; Tuma et al. 2016), including the puma (*Puma concolor*) (Beier 1995; Gray et al. 2016), which is becoming a model for studying genetics of isolated populations (Ernest et al. 2014; Gustafson et al. 2017; Johnson et al. 2010; Riley et al. 2014). Despite the long-distance dispersal ability of pumas (Hawley et al. 2016; Newby et al. 2013; Pierce et al. 1999; Thompson and Jenks 2005), gene flow among adjacent puma populations has been nearly negated by freeways in densely populated Southern California (Ernest et al. 2014; Gustafson et al. 2017; Riley et al. 2014). Consequently, some California puma populations have become functionally isolated and have experienced rapid population divergence and inbreeding (Ernest et al. 2014; Gustafson et al. 2017; Riley et al. 2014; Vickers et al. 2015) with concerns for extinction (Benson et al. 2016). Given that *P. concolor* and other wide-ranging species serve as umbrella species (Carroll et al. 2001; Maehr et al. 2002; Thorne et al. 2006)—the conservation of which indirectly provides protection for many other species (Roberge and Angelstam 2004)—the low genetic diversity of puma populations in human-fragmented habitats suggests that a large-scale ecological problem may be occurring in some of the most biologically-diverse regions of North America (Calsbeek et al. 2003; Dobson et al. 1997).

During the late Pleistocene, pumas were extirpated from North America and repopulated by migrants from South America (Culver et al. 2000). As a result, pumas in North America compose a single phylogenetic group (based on mtDNA) and exhibit founder effects (i.e., reduced population genetic diversity based on mtDNA and microsatellites) compared to pumas in South America and Central America (Culver et al. 2000). Therefore, it is critical to understand effects of fragmentation on populations from this North American lineage. A previous genetic analysis along the west coast of the United States indicated that pumas in California did not exist as a single population and suggested urbanization may have led to genetically-depauperate, fragmented populations (Ernest et al. 2003). In addition, a population genetic analysis in Nevada indicated there were asymmetric migration rates between the two states, and that pumas from Nevada were a genetic source for genetic-sink populations in California (Andreasen et al. 2012). However, these previous reports relied on a limited number of genetic loci ($\leq$13 microsatellites) and investigators did not sample across the two states. In this study, we attempted to address these limitations and provide a more comprehensive view of puma genetic diversity and gene flow within and among California and Nevada.

Our aim was to identify the number and spatial structure of puma populations across California and Nevada and the extent of gene flow among the populations. In doing so, we were able to identify genetic source and sink populations as well as isolated populations with limited gene flow. We expected pumas would exhibit genetic structure associated with both natural geographic features and anthropogenic development. Given the complex structure of ecoregions and large human population in California (> 39 million people; 92.5/km^2; US Census Bureau 2016), we hypothesized pumas in California would exhibit more population divergence and less interpopulation gene flow relative to pumas in Nevada, which have access to more contiguous ecoregions with fewer humans (< 3 million people; 10.3/km^2; US Census Bureau 2016). To address these hypotheses, we genotyped 992 pumas at 42 microsatellite loci across California and Nevada. We then identified regional populations using population assignment models and evaluated functional connectedness of puma populations by modeling population divergence and computing bi-directional migration rate estimates.

Materials and methods

Sampling and extractions

We obtained tissue or blood samples from 992 pumas captured alive, found dead, or legally killed by authorized agencies for livestock depredation, public safety, or sport hunting (Nevada only) during 1992–2016 (Fig. 1). Approximately 49% of individuals sampled were legally killed, 31% were from captures, 11% were hit by vehicles, and the rest were found dead of other causes. We isolated genomic DNA using QIAGEN DNeasy Blood & Tissue kits (QIAGEN Inc., Valencia, CA, USA).

Genotyping

We genotyped each individual puma at 42 previously developed microsatellite loci, plus a single sex-linked locus (Ernest et al. 2003, 2014; Riley et al. 2014) and ran polymerase chain reactions on ABI 2720 thermocyclers (Life Technologies, Carlsbad, CA, USA) using QIAGEN

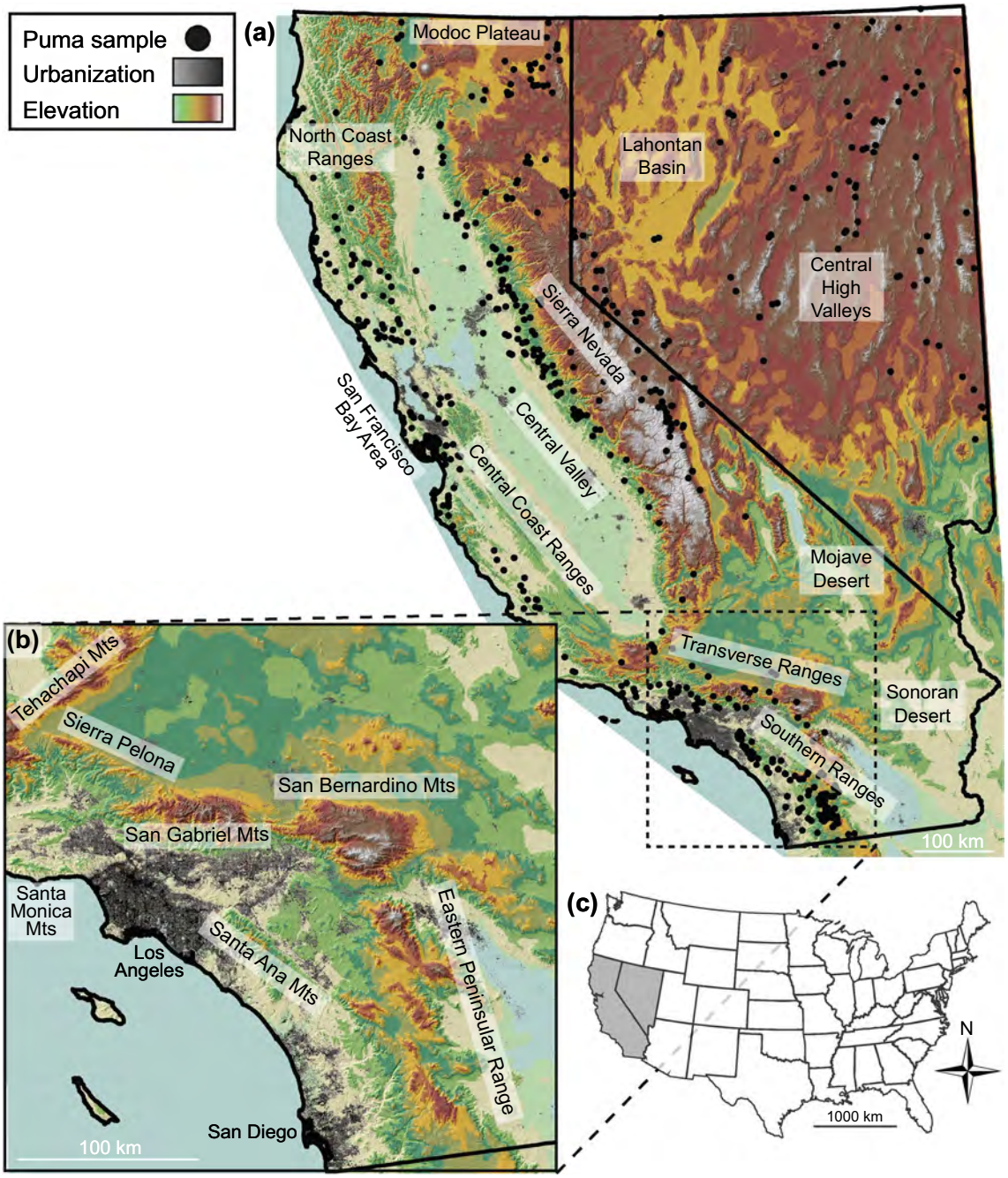

Fig. 1 Map of our study system, including **a** sampling locations of 992 pumas and ecoregions, **b** specific mountain ranges within the Transverse and Southern Ranges, and **c** an inset map of the United States of America showing the locations of California and Nevada. Elevation data source: USGS national elevation dataset (http://nationalmap.gov). Dark circles indicate locations where pumas were sampled, the gray to black scale indicates low to high urbanization, and the blue to white scale indicates 0 m elevation (sea level) to 4,421 m elevation

Multiplex PCR kits with Q solution (Table S1) following the protocols of Gustafson et al. (2017). We included negative and positive controls in each PCR run and visualized fragments with STRand version 2.3.69 (Toonen and Hughes 2001). For each locus, we confirmed heterozygous genotypes at least twice and homozygous genotypes at least three times.

Population genetic structure

The spatial arrangement of sample locations can confound population genetic analyses (Meirmans 2012; Schwartz and McKelvey 2009). Thus, we used spatially-explicit hierarchical Bayesian clustering programs TESS 2.3 (Durand et al. 2009a) and GENELAND 4.0 (Guillot et al. 2005b). We tested for consistency among programs because TESS has been shown to identify finer-scale hierarchical puma population genetic structure compared to GENELAND (Gustafson et al. 2017). In general, TESS outperforms GENELAND in the presence of isolation-by-distance (Safner et al. 2011) whereas GENELAND outperforms TESS at detecting genetic barriers to dispersal (Blair et al. 2012; Safner et al. 2011).

In TESS, the number of populations (K) must be specified and tested over a range of possible values. Model selection must be used to determine the K with the best fit to the data. We followed developer instructions for determining K and population assignments. First, we ran 10 non-admixture models for each K from 2 to 20. For model comparisons, TESS computes a deviance information criterion (DIC). We ran 10 spatially-conditional auto-regressive admixture models for each K to the DIC plateau of non-admixture models (Figs. S1, S2). All models included pairwise great circle geographic distances for weighting the Voronoi neighborhood, 100,000 iterations, and a 25,000 iteration burn-in period. We retained 20% of the models exhibiting the lowest DIC scores and used CLUMPP 1.1.2 to perform model-averaging (Jakobsson and Rosenberg 2007).

In GENELAND, K is optimized by the model. We followed developer recommendations for determining K and individual population assignments (Guillot et al. 2005a). First, we identified a distribution of K from initial models, and then we ran correlated allele frequency models allowing K to vary within its distribution from the initial models (Fig. S1). Finally, we ran 5 spatial, correlated allele frequency models with K fixed at the mode and selected the model with the highest negative log-likelihood value for further inference. Each run included an uncertainty on GPS coordinates of 0.1 decimal degrees (~ 11 km), 1,000,000 iterations, a thinning interval of 10,000, and a 25% burn-in period prior to extracting model output. We assigned individuals to populations based on their highest assignment probability. To visualize the probability of population membership across the study area, we used package POPSutilities 1.0 in R 3.3.0, which interpolates admixture coefficients using geospatial kriging (Jay et al. 2012).

Temporal variation in sampling can bias spatial population genetic analyses; however, spatially-explicit Bayesian clustering models should account for most temporal variation (Durand et al. 2009b; François and Durand 2010). Populations did not group based on sampling date in TESS or GENELAND. Additionally, isolation-by-distance was significant across our study area ($R^2 = 0.15$, $P < 0.001$). Although TESS and GENELAND showed nearly identical results, we used TESS admixture models for analyses and inferences because TESS outperforms GENELAND in the presence of isolation-by-distance.

Genetic diversity

We tested for linkage disequilibrium, deviations from Hardy–Weinberg proportions, and null alleles in GENEPOP 4.5.1 (Rousset 2008). For each identified population, we calculated standard measures of genetic diversity and used 1000 permutations to test for significant genetic isolation-by-distance in GenAlEx 6.502 (Peakall and Smouse 2006, 2012). To measure the number of alleles, we calculated allelic richness using rarefaction methods which correct for sample size in FSTAT 2.9.3.2 (Goudet 1995). To assess inbreeding, we calculated internal relatedness using package Rhh 1.0.2 in Program R 3.3.0 (Alho et al. 2010). We calculated effective population size (N_e) for each population using NeEstimator 2.01 using the linkage disequilibrium method assuming random mating (Do et al. 2014). Because the inclusion of low-frequency alleles can upwardly bias estimates of N_e (Waples and Do 2010), we ran two separate models including alleles with frequencies $\geq 5\%$ or $\geq 1\%$. To test for evidence of recent reductions in N_e (i.e., genetic bottlenecks), we used program BOTTLENECK 1.2.02 to determine if a population exhibited a significant number of loci with heterozygote excess (Piry et al. 1999). For each population identified by assignment models, we performed bottleneck analyses using two-phase (70:30 step-wise:infinite-alleles) microsatellite mutation models for 100,000 iterations.

We used biotools 3.1 (da Silva et al. 2017) in R to obtain spatial unbiased genetic diversity estimates [uHe: unbiased expected heterozygosity; (Nei 1978)] based on the interpolation of individual estimates (Manel et al. 2007). We minimized spatial extrapolation by using a radius of 500 m and reduced bias by setting the neighborhood size (i.e., minimum number of individuals used to calculate uHe) to 2. The mean size of each neighborhood was 14.6 and 42.5% of the neighborhoods contained at least 10 individuals.

Population differentiation and genetic source–sink dynamics

We used three complementary approaches to assess functional population connectivity, including a discriminant analysis of principal components (DAPC), pairwise estimates of population divergence (F_{ST}), and pairwise estimates of bi-directional migration rates (m). The DAPC uses linear combinations of alleles to maximize between-population genetic variation and provides a graphical representation

of functional connectivity among genetic clusters (Jombart et al. 2010).

We implemented the DAPC in program R using package adegenet 2.0.1 (Jombart 2008). The identified number of genetic clusters in adegenet agreed with TESS and GENELAND (Fig. S3). Because the algorithm for individual assignments in adegenet is not as powerful as Bayesian population assignment algorithms (Jombart et al. 2010), we defined populations in the DAPC using results from the Bayesian population assignments. Because we were not assigning individual membership probabilities in the DAPC, we retained all information (i.e., 344 PCA axes and all 9 discriminant functions) in the analysis. Our results from retaining all information did not differ from results when only retaining an estimated optimal number of PCA axes using the α-score method. Pairwise population divergence estimates (F_{ST}) were calculated in GenAlEx using 999 permutation tests for significance. To conform to the expectations of genetic isolation-by-distance, rather than an island model, we also calculated Rousset's $F_{ST}/(1-F_{ST})$ (Rousset 1997).

We used program BayesAss 3.0 to estimate migration rates (*m*) among populations identified by population assignment models (Wilson and Rannala 2003). We used 10 randomly-seeded runs each with 5,000,000 iterations, a burnin of 1,000,000, and thinning interval of 1000. Posterior mean parameter estimates were nearly identical among runs, and all trace files indicated convergence of model parameters (Meirmans 2014). We tested the hypothesis of Andreasen et al. (2012) that Nevada pumas were a genetic source for California pumas by summing emigration rates and subtracting the sum of immigration rates for each population (Andreasen et al. 2012). Positive numbers indicate the population was a genetic source whereas negative numbers indicate a sink. We used package circlize 0.3.7 in program R to visualize bi-directional migration rates estimated in BayesAss (Gu et al. 2014).

Results

Population genetic structure and diversity

Our analyses revealed that pumas in California exhibited strong population genetic structure and some California populations had extremely low levels of genetic diversity. We identified nine genetic clusters in California and one genetic cluster in Nevada (Figs. 2, S1, S2, S4). We classified these 10 genetic clusters as genetic populations, including the Nevada (NV), Eastern Sierra Nevada (ESN), Western Sierra Nevada (WSN), North Coast (NC), Northern section of the Central Coast (CC-N), Central section of the Central Coast (CC-C), Southern section of the Central Coast (CC-S), San Gabriel/San Bernardino (SGSB), Santa Ana (SA), and Eastern Peninsular Range (EP) populations (Fig. 2).

The genetic diversity of California puma populations exhibited a large amount of variation with some populations having estimates similar to other large populations and some exhibiting estimates nearly as low as the endangered Florida Panther. The NV, ESN, and WSN populations had the highest estimates of genetic diversity compared to other populations (Table 1). Regionally, the Modoc Plateau and Sierra Nevada contained individuals that had consistently high genetic diversity (Fig. 3). Although the NV population had high genetic diversity, the individual-based analysis indicated spatially-heterogenous genetic diversity across Nevada with low levels occurring near the Lahontan Basin (Fig. 3). The CC-C population had relatively intermediate levels of genetic diversity (Table 1). The SA population had the lowest genetic diversity observed across all estimates, followed by the SGSB, NC, CC-S, and CC-N populations. SA also had the highest measure of internal relatedness. WSN had the largest effective population size (N_e), followed by NV, NC, and CC-C (Table 2). All other populations had an N_e of < 50 (often given as a desirable minimum from a conservation genetics point of view; Frankham 1995; Mace et al. 2008), and CC-S and SGSB had extremely low effective population sizes (≤ 5). All populations except NV and NC exhibited evidence of a prior genetic bottleneck (Table 2).

Population differentiation and genetic source–sink dynamics

Our discriminant analysis of principal components (DAPC) revealed that puma populations in California had low connectivity compared to pumas in Nevada which were composed of a single genetic population that exhibited high connectivity with several California populations. The first axis (x-axis; 33.3% of total variation) of the DAPC broadly corresponded to a latitudinal population separation with north to the left and south to the right (Fig. 4a). The second axis (y-axis; 24.4%) separated populations longitudinally and primarily separated central coast populations from southern populations (Fig. 4a). The NV, ESN, WSN, and NC populations grouped together, as did the CC-N, CC-C, and CC-S populations. The SA and EP populations grouped slightly but were separated from all other populations (Fig. 4a). Lastly, the SGSB was intermediate relative to all other populations, but was most closely-related to the WSN population (Fig. 4a).

Bi-directional migration rate models indicated there were 5 genetic source populations (i.e., ESN, WSN, CC-N, CC-C, EP) and 5 genetic sink populations (i.e., NV, NC, CC-S, SGSB, SA), however, there was only weak evidence indicating CC-N and NC were source and sink populations, respectively. Bi-directional migration

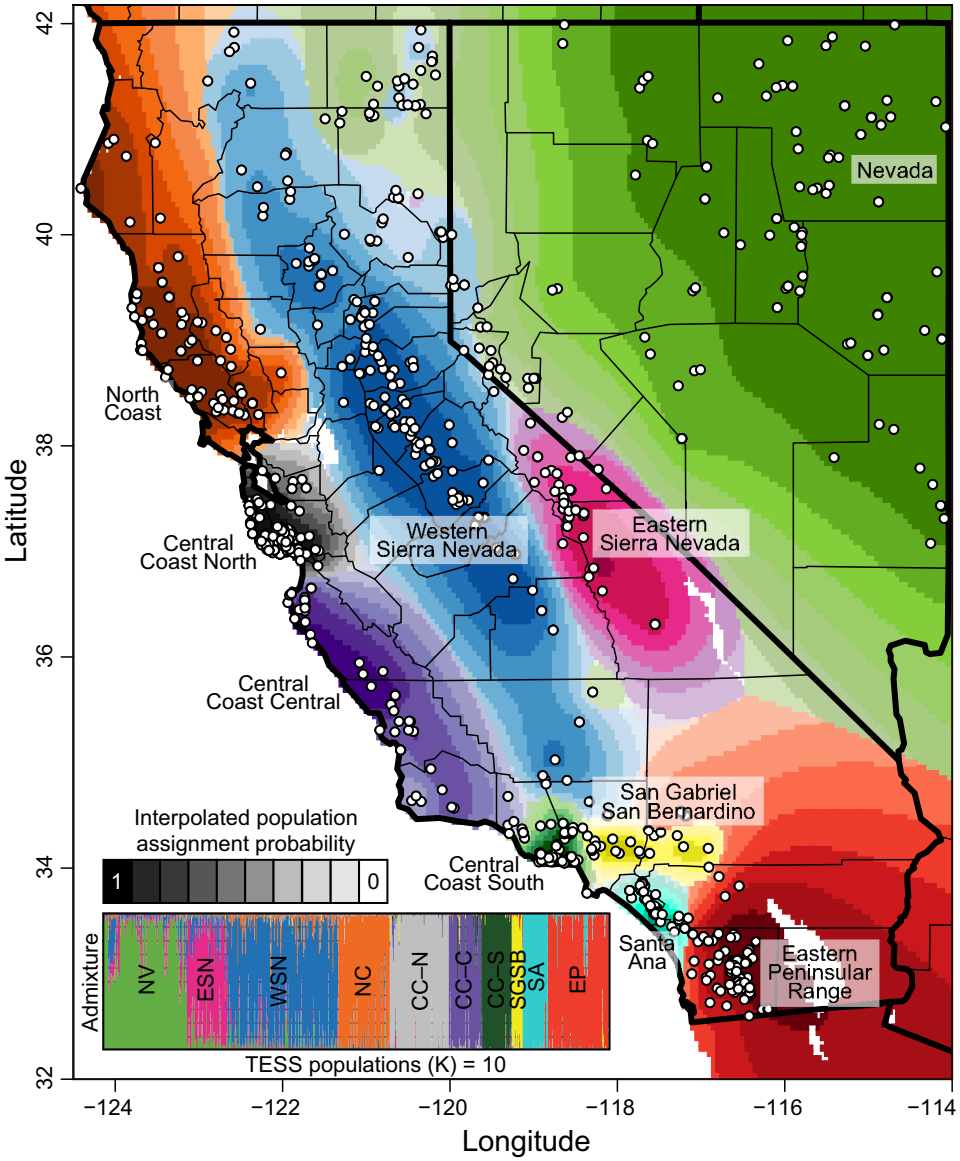

Fig. 2 Population genetic structure of pumas across California and Nevada. Individual admixture proportions from TESS (inset barplot) were spatially-interpolated. Each color represents a genetic population. The decay in color intensity on the map represents lower probabilities of population assignment and indicates areas with admixture between populations. State and county borders are displayed for reference. *NV* Nevada, *ESN* Eastern Sierra Nevada, *WSN* Western Sierra Nevada, *NC* North Coast, *CC-N* Northern section of the Central Coast, *CC-C* Central section of the Central Coast, *CC-S* Southern section of the Central Coast, *SGSB* San Gabriel/San Bernardino, *SA* Santa Ana, *EP* Eastern Peninsular Range

rate estimates showed connectivity patterns similar to the DAPC (Fig. 4). Although there was gene flow among the NV, ESN, and WSN populations based on bi-directional migration rates, the NC population primarily exchanged migrants with the ESN and WSN populations (Fig. 4b). The populations in the Sierra Nevada (ESN, WSN) were the greatest genetic source populations but exhibited limited gene flow with the populations along the central coast of California (CC-N, CC-C, CC-S), and neither NV nor NC exhibited appreciable gene flow with central coast populations (Fig. 4b; Table S2). The SA population exhibited gene flow only with the EP population, and the EP population had low connectivity with the SGSB population (Fig. 4b). The puma population in the Transverse Ranges (SGSB) was the largest genetic sink but exchanged some genetic material with the WSN, CC-C, and EP populations (Fig. 4b). Populations in the Southern Ranges (SA, EP) were largely disconnected from all other populations (Fig. 4b).

Table 1 Allelic and genetic diversity of puma populations, including sample-size corrected allelic richness, the number of private alleles, the percent of polymorphic loci, observed heterozygosity, unbiased expected heterozygosity, and average internal relatedness (a measure of inbreeding)

Population	N	Allelic richness	Private alleles	Polymorphic Loci (%)	Observed heterozygosity	Expected heterozygosity	Internal relatedness
NV	166	3.47 (0.09)	9	100	0.50 (0.03)	0.52 (0.03)	0.15 (0.01)
ESN	79	3.46 (0.13)	5	100	0.52 (0.03)	0.53 (0.03)	0.11 (0.01)
WSN	217	3.63 (0.08)	5	100	0.51 (0.03)	0.52 (0.03)	0.09 (0.01)
NC	101	3.06 (0.10)	5	97.6	0.40 (0.03)	0.41 (0.03)	0.28 (0.01)
CC-N	116	2.62 (0.08)	1	97.6	0.41 (0.03)	0.42 (0.03)	0.27 (0.01)
CC-C	63	3.00 (0.12)	1	95.2	0.45 (0.03)	0.46 (0.03)	0.19 (0.02)
CC-S	60	2.63 (0.13)	1	92.9	0.41 (0.04)	0.41 (0.03)	0.27 (0.02)
SGSB	22	2.75 (0.17)	0	95.2	0.40 (0.03)	0.42 (0.03)	0.29 (0.03)
SA	48	2.27 (0.12)	0	85.7	0.34 (0.03)	0.33 (0.03)	0.39 (0.02)
EP	120	3.07 (0.11)	3	100	0.44 (0.03)	0.44 (0.03)	0.21 (0.01)

NV Nevada, *ESN* Eastern Sierra Nevada, *WSN* Western Sierra Nevada, *NC* North Coast, *CC-N* Northern section of the Central Coast, *CC-C* Central section of the Central Coast, *CC-S* Southern section of the Central Coast, *SGSB* San Gabriel/San Bernardino, *SA* Santa Ana, *EP* Eastern Peninsular Range. Standard errors are presented in parentheses

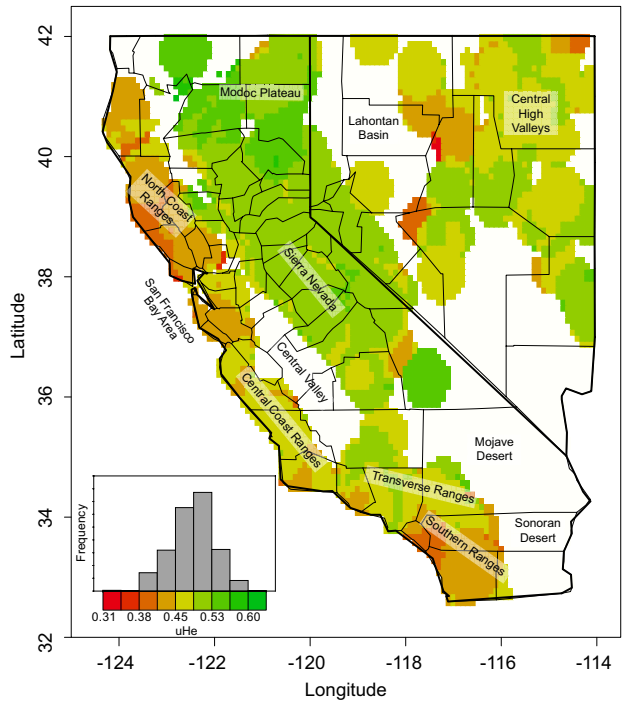

Fig. 3 Gene diversity (uHe: unbiased expected heterozygosity) heat map of pumas in California and Nevada. Neighborhood size was not significantly related to uHe ($R^2 = 0.005$, $P < 0.001$)

Discussion

We identified 10 genetically-distinct puma populations within California and Nevada that varied considerably in genetic diversity (uHe range 0.33–0.53) and effective population size (N_e range 5–157). Some of our previous analyses identified family-level genetic structure which was not observed here (Ernest et al. 2014; Gustafson et al. 2017; Riley et al. 2014), indicating these genetic populations are not the result of sampling related individuals. The large number of populations (N = 9) and the strong genetic differences among neighboring puma populations in California differed from other studies at similar spatial scales (Anderson et al. 2004; Holbrook et al. 2012; Loxterman 2011; McRae et al. 2005), including Nevada (Andreasen et al. 2012). Most state-wide studies have been conducted in less-developed locations with more continuous habitat and showed that geographic distance and natural landscape components were the most common factors associated with the broad-scale genetic structure of puma populations (Anderson et al. 2004; Holbrook et al. 2012; Loxterman 2011; McRae et al. 2005; Wright 1943). In contrast, mountain ranges in California are variable in size and arrangement and there are vast areas of inter-mountain anthropogenic development throughout the state. Previous local studies in California have identified individual roadways and associated human development as major barriers to puma movements (Ernest et al. 2014; Gustafson et al. 2017; Riley et al. 2014; Vickers et al. 2015), and our study confirms, on a broad geographic scale, strong population structure among adjacent puma populations. The considerable variation in genetic diversity and effective population size among California and Nevada populations is likely attributable to the variation in the amount of suitable habitat and their degree of isolation. The Western Sierra Nevada population had the largest effective size and was closely related (i.e., lowest F_{ST} values) to every population except for the Northern Central Coast population and populations south of Los Angeles (Santa Ana, Eastern Peninsular Range), suggesting puma populations form a

Table 2 Summary of effective population size and bottleneck analyses for each population

Population	Sample size	Effective population size (N_e) N_e with AFs ≥ 0.05	Bottleneck N_e with AFs ≥ 0.01	P-value
NV	166	92.2 (84.2–101.4)	107.2 (98.5–117.1)	0.123
ESN	79	22.6 (20.8–24.5)	26.5 (24.7–28.5)	< **0.001**
WSN	217	157.5 (141.2–176.8)	180.6 (164.1–199.7)	**0.038**
NC	101	82.5 (71.3–96.8)	66 (59.3–73.9)	0.256
CC-N	116	16.6 (15.1–18.2)	15.5 (14.2–16.8)	**0.001**
CC-C	63	56.6 (47.4–69.0)	63 (53.3–75.8)	**0.018**
CC-S	60	2.7 (2.5–2.9)	3.6 (3.4–3.9)	**0.008**
SGSB	22	5 (3.3–6.4)	7.5 (6.2–9.1)	**0.046**
SA	48	15.6 (13–18.7)	21.7 (18–26.4)	**0.007**
EP	120	31.6 (29.1–34.4)	37.4 (34.5–40.5)	**0.021**

AF allele frequencies, *NV* Nevada, *ESN* Eastern Sierra Nevada, *WSN* Western Sierra Nevada, *NC* North Coast, *CC-N* Northern section of the Central Coast, *CC-C* Central section of the Central Coast, *CC-S* Southern section of the Central Coast, *SGSB* San Gabriel/San Bernardino, *SA* Santa Ana, *EP* Eastern Peninsular Range. Parametric 95% confidence intervals are presented in parentheses. Bottleneck P-values from standardized differences tests are presented

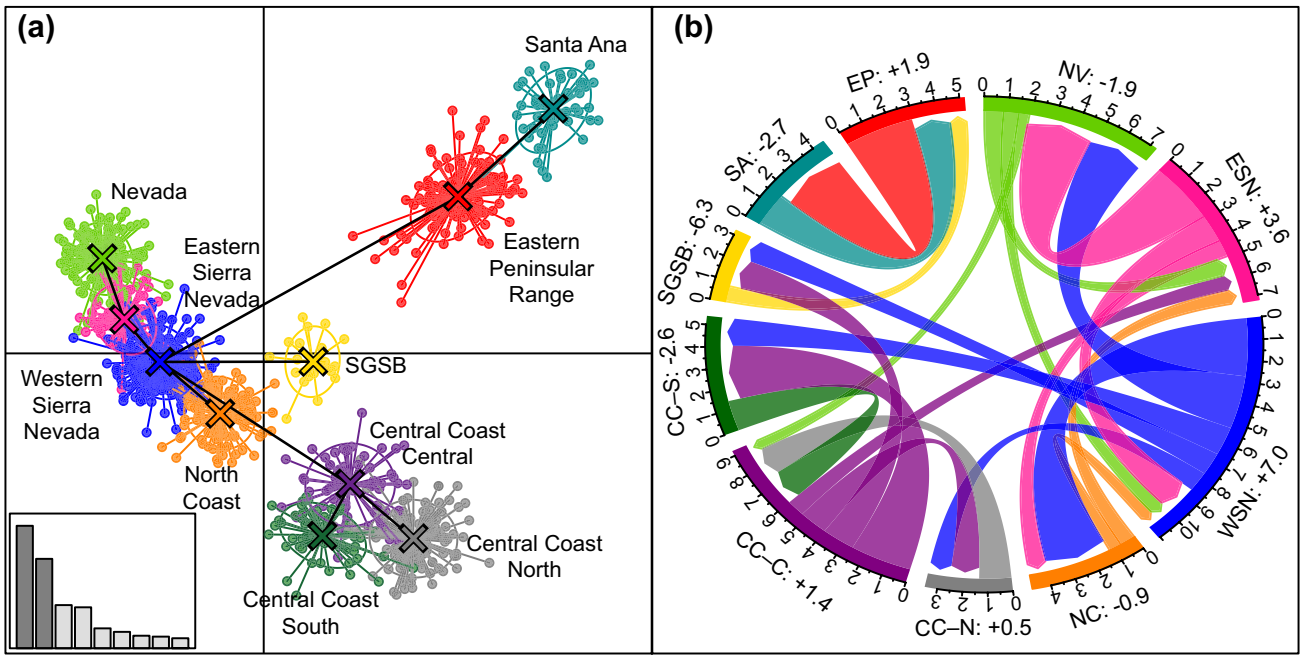

Fig. 4 Functional connectedness of puma populations, based on **a** a discriminant analysis of principal components and **b** bi-directional migration rate estimates (multiplied by 100 for visualization). Each dot represents an individual (**a**). Each color **a, b** represents a population. Black lines **a** indicate the most closely-related population based on genetic dissimilarities. The inset barplot **a** shows which axes are being displayed (i.e., discriminant functions 1 and 2) and the relative proportion of variation explained by each of the 9 discriminant functions. Two-thirds of the individuals in each population are contained within the corresponding ellipsoid. For a biologically meaningful interpretation, only estimates of interpopulation migration rates with 95% confidence intervals that do not cross 0 are presented (b; Table S2). Net genetic source–sink migration rates are presented next to population names with positive values indicating a net genetic source and negative values indicating a net genetic sink (e.g., WSN exported 9% of migrants and received 2%, so its net rate is +7.0). *NV* Nevada, *ESN* Eastern Sierra Nevada, *WSN* Western Sierra Nevada, *NC* North Coast, *CC-N* Northern section of the Central Coast, *CC-C* Central section of the Central Coast, *CC-S* Southern section of the Central Coast, *SGSB* San Gabriel/San Bernardino, *SA* Santa Ana, *EP* Eastern Peninsular Range

"horseshoe" network around the Central Valley with San Francisco Bay acting as a major barrier along the coast (Hooper 1944). The large National Parks and National Forests (e.g., Sequoia–Kings Canyon and Yosemite National Parks) in the Sierra Nevada provide contiguous habitat for pumas with minimal anthropogenic infrastructure (Ernest et al. 2000).

Our results are consistent with a previous report (Andreasen et al. 2012) indicating pumas from Nevada form a single genetic cluster and are distinct from pumas in the Sierra Nevada of California, but our results contrast with their suggestion that pumas from Nevada are a genetic source for pumas in California. There are several differences between the studies that could explain the inconsistencies. Andreasen et al. (2012) used considerably fewer genetic markers than the present study (9 microsatellites vs. 42). Because the number of loci used in bi-directional migration rate models has the largest effect on the accuracy of the estimates (Faubet and Gaggiotti 2008; Wilson and Rannala 2003), we expect the differences are driven by the different number of loci. Although we sampled fewer pumas from Nevada and more pumas from California, sample size differences generally only affect the variance and not the accuracy of the bi-directional migration rate estimates (Faubet and Gaggiotti 2008; Wilson and Rannala 2003). Further, sample size alone likely does not explain the contrasting results and the multiple lines of evidence supporting the Sierra Nevada populations as a genetic source for the surrounding populations, including Nevada.

Both our population-level and individual-based analyses clearly indicated that the Western Sierra Nevada population had the highest genetic diversity, which is likely being maintained by the large effective population size and not via migrants from the Nevada population, which had lower genetic diversity estimates. Further, instead of testing migration rates among the two populations (K = 2) which had the highest model support in their study, Andreasen et al. (2012) tested among five genetic clusters (K = 5) which had average within-cluster migration estimates of only 54% (and a large SD of 8.4%) compared to our within-population migration estimates of 94% (± 1.9%). Thus, their examination of genetic source–sink dynamics was based on significantly less distinct genetic units (F_{ST} = 0.05–0.09 compared to our study where Rousset's F_{ST} = 0.05–0.39), which is computationally problematic with a small number of loci (Faubet and Gaggiotti 2008; Wilson and Rannala 2003). Additionally, puma hunting is legal in Nevada but not California, and puma densities that have been reduced regionally from hunter harvest are known to be compensated by higher immigration rates from neighboring populations (Cooley et al. 2009; Robinson et al. 2008), which is biologically consistent with our observations.

The North Coast and inland populations (Nevada, Eastern Sierra Nevada, Western Sierra Nevada) appear to be large (i.e., high N_e), genetically diverse, and well-connected, and may form an evolutionary significant unit (ESU: a group of populations that have accumulated adaptive differences from other populations in part from reproductive isolation; Palsbøll et al. 2007). However, genome-wide data and gene–environment correlation studies will be needed to evaluate whether these population are exhibiting adaptations to specific habitats or ecoregions. Within this group of populations, we detected evidence for bottlenecks in the Eastern Sierra Nevada population and Western Sierra Nevada population. The bottleneck in the Eastern Sierra Nevada population is not surprising given that the puma abundance in this region may have been reduced by 50% after a severe decline in mule deer (Pierce and Bleich 2014; Pierce et al. 2000; Villepique et al. 2011). Besides the North Coast and Nevada populations, all of the other populations also exhibited evidence of genetic bottlenecks; however, we do not know if this was caused by urbanization, a decrease in prey abundance, or some other factor, because the demographic and genetic histories of these populations are not well-documented.

The Central population of the Central Coast exhibited intermediate levels of genetic diversity, and maintaining gene flow from this population to the genetically-depauperate Northern and Southern Central Coast populations is critically important for their long-term viability (Benson et al. 2016; Gray et al. 2016; Riley et al. 2014). A previous report examined the southern area of the central coast region specifically and observed extremely low genetic diversity in the Santa Monica Mountains, south of Highway 101 in the Los Angeles Area (Riley et al. 2014). At a statewide level, we found pumas in the Santa Monica Mountains to be part of a larger genetic population including pumas in the Simi Hills and Santa Susana Mountains; however, our larger sample from the Southern Central Coast population revealed only slightly higher estimates of genetic diversity than pumas sampled from the Santa Monica Mountains alone (Riley et al. 2014). Road-isolated pumas in the Santa Monica Mountains only receive rare migrants from the Simi Hills and Santa Susana Mountains and are at a high risk of extirpation from isolation and subsequent demographic and genetic stochasticity (Benson et al. 2016). These results emphasize the need to conserve within-population connectivity, specifically from the Coast Ranges and the Sierra Nevada through the Santa Susana Mountains and Simi Hills to the Santa Monica Mountains.

Despite being very close geographically, the puma populations around Los Angeles (Southern Central Coast, San Gabriel/San Bernardino, Santa Ana) are highly diverged. For example, the Santa Ana and Southern Central Coast population are among the closest populations geographically

(~ 100 km apart) but are among the most genetically distant populations we observed (Rousset's $F_{ST} = 0.32$). Additionally, the Southern Range populations (Santa Ana, Eastern Peninsular Range) are largely disconnected from all other populations in this study, including those just to the north of the Los Angeles Basin. These observations are consistent with the hypothesis of reduced connectivity from habitat fragmentation by human development (i.e., the Los Angeles metropolitan area), including major roads (i.e., I-10, I-15, I-210, etc.) (Ernest et al. 2003). The San Gabriel/San Bernardino population was most genetically similar to the Western Sierra Nevada, Central region of the Central Coast, and Eastern Peninsular Range populations, indicating it is an area of intersection between multiple populations. We suggest the small mountain ranges in this area (i.e., Tehachapi, Sierra Pelona, San Gabriel, and San Bernardino Mountains) are necessary for contiguous statewide genetic connectivity and that pumas occupying those ranges, and the wildlands habitat in those ranges, should be considered conservation priorities (Beier et al. 2009; Ernest et al. 2003; Wildlands 2008).

The Santa Ana population exhibited the lowest measures of genetic diversity and the highest measures of inbreeding among all populations, with levels nearing those of Florida panthers (most recent estimates of $He = 0.24$), which nearly went extinct from genetic factors prior to artificial genetic rescue (Johnson et al. 2010). It is important to note, however, that out of the 42 microsatellite loci used in this study, only 4 were shared with the 23 microsatellite loci used in the Florida panther study. A set of shared markers would be most appropriate for direct interpopulation comparisons (e.g., Culver et al. 2000). A single immigrant from the Eastern Peninsular Range recently enhanced the genetic diversity of Santa Ana pumas and is likely responsible for the higher effective population size than previously observed (Ernest et al. 2014). Nevertheless, genetic diversity of Santa Ana pumas will decline without additional immigration (Gustafson et al. 2017). The Eastern Peninsular Range population had the highest genetic diversity and effective size among the populations in the Los Angeles—San Diego area (Southern Central Coast, San Gabriel/San Bernardino, Santa Ana, Eastern Peninsular Range). Restoring connectivity with the Eastern Peninsular Range and reducing further impacts from development on gene flow among the adjacent populations, including pumas from Arizona and Mexico (Gustafson et al. 2017), are critically important to avoiding extirpation of genetically-depauperate populations (Benson et al. 2016).

By identifying puma populations and measuring gene flow among them, our analyses can help guide and inform puma conservation and management. Whenever possible, government agencies and other stakeholders should consider population connectivity and prevent further fragmentation by human development both within and among populations. In contrast to other studies in 7 western states that generally indicated weak puma genetic structure (Anderson et al. 2004; Holbrook et al. 2012; Loxterman 2011; McRae et al. 2005), our study showed strong genetic structure. Although puma habitat in California is aggregated and separated by valleys, it is unlikely these valleys would have been such strong barriers to gene flow pre-development given that pumas have been documented to move across the entire Central Valley post-development (Ernest et al. 2003; McClanahan et al. 2017). Further, similar geographic features, such as the Wyoming Basin, have not been reported to structure puma populations (Anderson et al. 2004). Instead, we hypothesize that human-associated infrastructure within the valleys are artificially isolating pumas beyond what they would naturally experience among ecoregions.

Population-level conservation strategies are needed to reintegrate fragmented, at-risk populations into a connected multi-state, multi-landscape population network (Zeller et al. 2017). Gene flow via maintenance of existing occupied habitat combined with improved and additional networks of wildlife corridors (Bennett 2017; Gloyne and Clevenger 2001; Johnson et al. 2010; Sawaya et al. 2013) will ultimately be necessary to promote the long-term persistence of isolated populations (Benson et al. 2016; Ernest et al. 2014; Gustafson et al. 2017; Riley et al. 2014). Without such measures, it is likely too late to expect a natural increase in genetic connectivity or selection for increased dispersal (Burdett et al. 2010; Cheptou et al. 2017), and assisted gene flow may be needed in perpetuity for several populations to remain viable (Benson et al. 2011, 2016; Ernest et al. 2014; Gustafson et al. 2017; Johnson et al. 2010; Vickers et al. 2015).

In some of these populations, individual migrants are of immediate conservation importance, and human-induced mortality should be avoided to the extent possible. The effects of fragmentation on multiple populations of this umbrella species are likely indicative of a larger ecological problem in one of the most biologically diverse regions of North America (Calsbeek et al. 2003; Dobson et al. 1997; Thorne et al. 2006). We strongly encourage land owners and managers to proactively consider broad-scale wildlife connectivity in future development proposals. However, in the absence of maintaining habitat of a spatial scale grand enough to ensure the persistence of prey and predator populations, the issue of connectivity will become a moot point.

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Data availability Through agreements with non-profit organizations, private landowners, and Native American Tribes, exact GPS locations of puma samples are not to be publicly shared. Thus, puma GPS locations are referenced to the nearest town or city. Sampling locations and microsatellite genotypes are available on Dryad: https://doi.org/10.5061/dryad.j76c4k4.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Permission to carry out fieldwork and necessary permits were obtained from CDFW, California Department of Parks and Recreation, The Nature Conservancy, United States (U.S.) Fish and Wildlife Service, U.S. Forest Service, U.S. Bureau of Land Management, U.S. Navy/Marine Corps, Orange County Parks Department, San Diego County Parks Department, Riverside County Parks Department, San Diego State University, University of California—Riverside, Audubon Starr Ranch, Vista Irrigation District, Rancho Mission Viejo/San Juan Company, Sweetwater Authority, California Department of Transportation, the City of San Diego Water Department and Parks Department, and the Irvine Ranch Conservancy.

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Review

Biodiversity management in the face of climate change: A review of 22 years of recommendations

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ABSTRACT

Climate change creates new challenges for biodiversity conservation. Species ranges and ecological dynamics are already responding to recent climate shifts, and current reserves will not continue to support all species they were designed to protect. These problems are exacerbated by other global changes. Scholarly articles recommending measures to adapt conservation to climate change have proliferated over the last 22 years. We systematically reviewed this literature to explore what potential solutions it has identified and what consensus and direction it provides to cope with climate change. Several consistent recommendations emerge for action at diverse spatial scales, requiring leadership by diverse actors. Broadly, adaptation requires improved regional institutional coordination, expanded spatial and temporal perspective, incorporation of climate change scenarios into all planning and action, and greater effort to address multiple threats and global change drivers simultaneously in ways that are responsive to and inclusive of human communities. However, in the case of many recommendations the how, by whom, and under what conditions they can be implemented is not specified. We synthesize recommendations with respect to three likely conservation pathways: regional planning; site-scale management; and modification of existing conservation plans. We identify major gaps, including the need for (1) more specific, operational examples of adaptation principles that are consistent with unavoidable uncertainty about the future; (2) a practical adaptation planning process to guide selection and integration of recommendations into existing policies and programs; and (3) greater integration of social science into an endeavor that, although dominated by ecology, increasingly recommends extension beyond reserves and into human-occupied landscapes.

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1. Introduction

Climate change poses major new challenges to biodiversity conservation. As atmospheric CO_2 increases over the next century, it is expected to become the first or second greatest driver of global biodiversity loss (Sala et al., 2000; Thomas et al., 2004). Global average temperatures have increased 0.2 °C per decade since the 1970s, and global average precipitation increased 2% in the last 100 years (IPCC, 2007a). Moreover, climate changes are spatially heterogeneous. Some locations, such as the Arctic, experience much larger changes than global means, while others are exposed to secondary effects like sea level rise (IPCC, 2007a). Climate change may have already resulted in several recent species extinctions (McLaughlin et al., 2002; Pounds et al., 2006). Many species ranges have moved poleward and upward in elevation in the last century (Parmesan and Yohe, 2003; Root et al., 2003) and will almost certainly continue to do so. Local communities are disaggregrating and shifting toward more warm-adapted species (Parmesan, 2005). Phenological changes in populations, such as earlier breeding or peak in biomass, are decoupling species interactions (Walther et al., 2002).

These changes raise concerns about the effectiveness of existing biodiversity protection strategies (Halpin, 1997; Hannah et al., 2002; Peters and Darling, 1985; Scott et al., 2002). Biodiversity conservation relies predominately on fixed systems of protected areas, and the mandated goals of many conservation agencies and institutions are to protect particular species assemblages and ecosystems within these systems (Lemieux and Scott, 2005; Scott et al., 2002). With the magnitude of climate change expected in the current century, many vegetation types and individual species are expected to lose representation in protected areas (Araujo et al., 2004; Burns et al., 2003; Lemieux and Scott, 2005; Scott et al., 2002). Reserves at high latitudes and high elevations, on low-elevation islands and the coast, and those with abrupt landuse boundaries are particularly vulnerable (Sala et al., 2000; Shafer, 1999). Landscapes outside of protected areas are hostile to the survival of many species due to human infrastructure and associated stressors, such as invasive species, hunting, cars, and environmental toxins. Such fragmentation directly limits species migration and gene flow. Projected rates of climate change are also faster than they were in the past – so rapid that in situ genetic adaptation of most populations to new climate conditions is not likely (Jump and Penuelas, 2005), nor is migration likely to be fast enough for many species (Davis and Shaw, 2001). Moreover, even if major global action reduced emissions significantly within the next years or capped them at year 2000 levels, the thermal inertia of the oceans will continue to drive climate change for decades and will require adaptive responses (Meehl et al., 2005; Wigley, 2005). A recent update of atmospheric CO_2 growth rate, which has more than doubled since the 1990s as global economic activity increases and becomes more carbon-intensive, makes clear that significant global emissions reductions are a distant goal at best (Canadell et al., 2007).

How should we modify our biodiversity protection strategies to deal with climate change? Here we focus on adaptation strategies. Adaptation is broadly defined as adjustment in human or natural systems, including structures, processes, and practices (IPCC, 2007b). Scientists have written about adaptation with increasing frequency over the last two decades, but developments in this area have progressed slowly. For years, emissions mitigation has largely been the only game in town, with little governmental or private support for climate change adaptation. For instance, the United States National Park Service (NPS) in collaboration with the Environmental Protection Agency (EPA) has created a 'Climate Friendly Park' program. It aims to reduce greenhouse gas emissions, but it does not include measures or incentives to park managers to build and test adaptation strategies to preserve biodiversity under climate change. In many ways, adaptation science has begun to develop only very recently in response to recent widespread acceptance by governments and private citizens of the certainty of climate change.

In this paper we review the growing, published literature specifically addressed at biodiversity management and adaptation in the face of climate change. We consider biodiversity to include all types of organisms at all scales, from genes to ecosystems. The genesis for our review was the 2006 annual meeting of the California Invasive Plant Council, where climate change was identified by both researchers and practitioners as a key issue for action. Discussions throughout the meeting, however, made clear that practitioners felt at a loss for practical steps to take. Managers working at local preserves were particularly uncertain about what, if anything, they could do to prepare for climate change. We use this review in order to highlight what actions and actors scientists have so far identified to address climate change, and to

explore how recommendations inform an adaptation planning process at various management scales. Scott and Lemieux (2005) reviewed a similar literature but focused on park management. Here we explore adaptation planning across scales and in both protected and unprotected areas.

2. Methods

We used Web of Science, including Science Citation Index Expanded, Social Science Citation Index, and Arts and Humanities Citation databases from 1975 to March 2007, to search for published journal articles on climate change and biodiversity management. We used the search terms "climate change", "global warming", "climatic change", "climate-change" and "changing climate" in all possible combinations with the search string "management OR biodiversity OR adaptation OR conservation OR restoration OR planning OR reserve design OR strategy OR land-use OR landuse OR landscape OR protected area OR park". Articles that discussed strategies for both biodiversity and related ecosystem services were included, but we excluded articles that only addressed ecosystem services such as management strategies for carbon stocks, human infrastructure, and food security. We also did not attempt to review studies that explore climate impacts on ecosystem components and processes without making explicit recommendations for biodiversity management. This literature is large and has been reviewed elsewhere (Kappelle et al., 1999; McCarty, 2001; Walther et al., 2002). From these searches, we identified and read 281 prospective articles, and from these culled those that provided explicit recommendations for management in the face of climate change. An additional four articles published after March 2007 were included, which were found through personal communication.

To analyze recommendations, we created a database in which we recorded every recommendation for action or information in the exact language used in the paper and answered a series of questions designed to synthesize recommendations and identify biases in the literature to date. We asked:

(1) *In what formal and informal contexts does action need to occur?* To answer this question, we categorized recommendations into broad spheres of activity: (1) policy reform, (2) science and technology effort and advances, (3) changes in conservation sector activity including restoration, or (4) changes in individual and community behavior, such as by farmers, ranchers, and other private landowners.

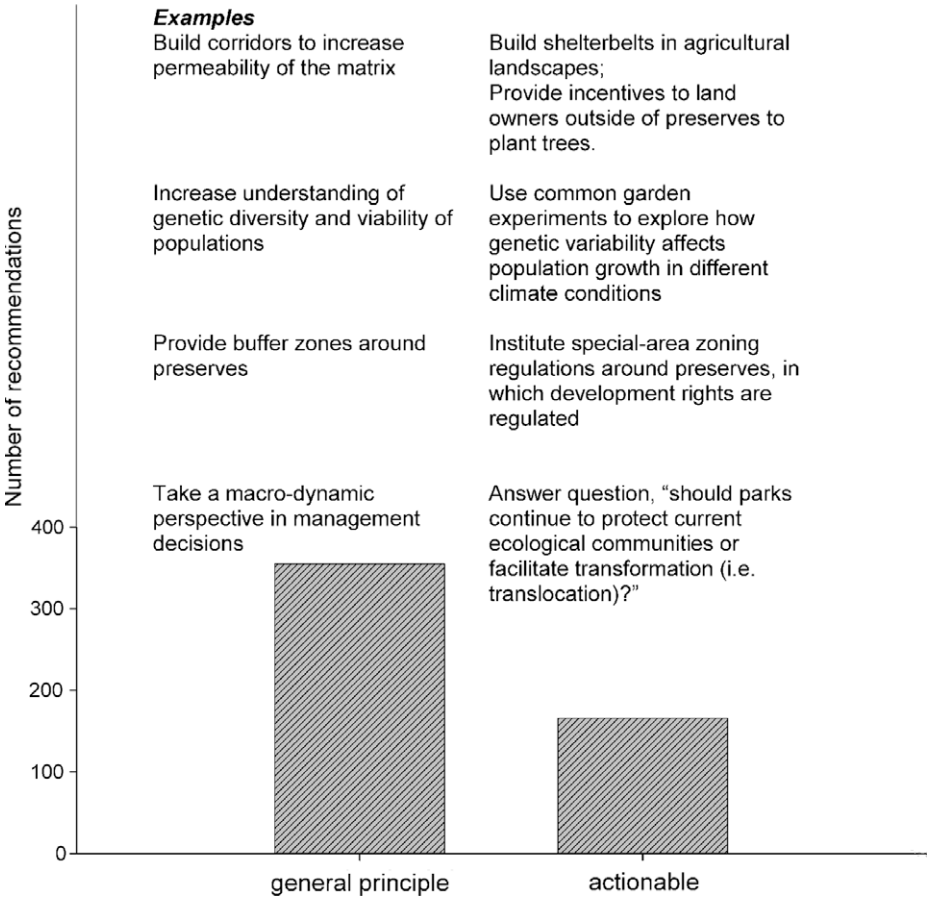

Fig. 1 – Examples and distribution of recommendations classified as "general principle" and "actionable". Most recommendations offer general principles for climate change adaptation but lack specificity needed for implementation.

(2) *What is the basis for the recommendation?* We recorded what information an author used to formulate their recommendation. Categories included empirical experimental data, simulation, literature review, case studies, interviews, or workshops. We also included the term 'ecological reasoning' to encompass studies based predominately on theory and opinion.
(3) *Is the recommendation a general principle or actionable?* A recommendation was considered a "general principle" if it provided a guiding concept, such as "build flexibility", but was generic open-ended and without example of who should act or what one should do (see Fig. 1). "Actionable" was given to those recommendations that identified a very clear who and what and often gave examples, such as, "[in restoration] use a broader range of species than prescribed solely on local basis to build system resilience (Harris et al., 2006)".
(4) *Is the recommendation for biodiversity or for biodiversity and related ecosystem services?*
(5) *Is there a geographic context for the recommendation?*
(6) *Does the article focus on a biome or ecosystem-type?*
(7) *Where in the landscape would the recommendation apply?* We categorized recommendations as applying to reserve (any public or private land-holding dedicated to biodiversity protection and maintenance, synonymous with protected area), or human-use lands (the matrix), or non-specific, meaning the recommendation could be enacted in either reserve or matrix land.
(8) *Does the recommendation describe an information need or a necessary action?* All recommendations for research were categorized as information needs, while the 'action' category included recommendations such as building corridors, reforming policy or buying more land.

To minimize variation in how articles were classified as a function of when they were read (i.e. the 1st paper entered compared to the 100th), records in the database were periodically shuffled by different criteria (i.e. year published or geographic context) and then re-classified. In addition, both authors coded a sub-sample of recommendations. After compiling the database, similar records were grouped into 'recommendation' categories. We tabulated the most common recommendations and ranked them by frequency cited overall.

3. Results and discussion

We recorded 524 recommendations from 113 papers, published in 57 different source journals and three books. Recommendations ranged from calls for specific types of modeling (e.g. inexact-fuzzy multiobjective programming (Huang et al., 1998) to broad shifts in governance structures (Tompkins and Adger, 2004) (Table 1). The number of papers published on this topic has increased dramatically in recent years (Fig. 2). Thirty-three percent of recommendations addressed biodiversity protection in conjunction with related ecosystem services, including forest products, fisheries and hunting, agriculture and grazing, and human health. Recommendations call for research, leadership and reform by a range of actors in several sectors; Emphasis in this set of literature is on science and nature conservation rather than on social or political adaptation measures (Fig. 3), with an emphasis somewhat more focused on reserve land over the matrix (Fig. 4a). Action is weighted more than information needs (Fig. 4b). When information needs were identified, they were overwhelmingly calls for more ecological rather than social scientific data (Fig. 4c). Recommendations are biased toward North America and Europe (Fig. 5a) and forests ecosystems (Fig. 5b).

Recommendations address various stages in an adaptation process, from research needs to methods for impact assessments to large-scale changes in policies by governmental, academic or non-governmental institutions (Table 1). About 70% of recommendations were classified as general principles under our classification scheme rather than specific, actionable strategies or tactics (Fig. 1). For example, seven authors suggest flexibility in management approaches, but only Millar et al. (2007) suggest flexibility and follow with a definition of what that means: willingness to change course, risk-taking including doing nothing, and capacity to reassess conditions frequently. Climate change adaptation work, at least in this literature, is still largely at the "idea" stage – it is based predominately on ecological reasoning rather than specific research, case studies, or empirical data (Fig. 5c), and it is largely nonspecific in the geographic areas or biome types that it targets (Fig. 5a and b). Many articles based on concrete modeling work or empirical studies of species responses to climate change tended either to not elaborate their results to management directives, or to present recommendations in vague terms such as, "restoration should be considered". Alternatively, very specific recommendations were proposed and not generalized for use outside of the target system. There appears to be a need for a happy medium between highly specific recommendations useful only in target areas and highly generalized recommendations that fail to inspire application (Halpin, 1997). This happy medium is likely to emerge rapidly as climate change adaptation science grows.

In the literature reviewed here, few recommendations suggested a process a manager could use to develop an adaptation plan and evaluate its usefulness (but see Hannah et al., 2002). More information on adaptation frameworks are developed in reports by Parks Canada (Welch, 2005), the NCEAS Conservation and Climate Change Working Group 2 (personal communication), and England's Department for Food Environment and Rural Affairs (http://www.defra.gov.uk/wildlife-countryside/resprog/findings/ebs-climate-change.pdf), which were not reviewed here. In practice, planners and managers could apply recommendations in at least three ways. At the broadest scale, long-term planning and policy formulation should tackle adaptation for whole landscapes and regions, with tools like reserve selection, ecosystem management, and landuse zoning schemes. Second, managers of individual reserves might want to know what they can do at their sites, individually or in concert with other sites. Third, rather than initially pursuing an idealized regional, landscape, or site-scale plan, the first practical step for many managers, conservation stakeholders and policymakers is to evaluate and adapt existing conservation plans. In the following

Table 1 – List of recommendations for climate change adaptation strategies for biodiversity management assembled from 112 scholarly articles. 524 records were condensed into 113 recommendation categories and are ranked by frequency of times cited in different articles.

Rank	Recommendation	No. articles	References
1	Increase connectivity (design corridors, remove barriers for dispersal, locate reserves close to each other, reforestation	24	Beatley (1991), Chambers et al. (2005), Collingham and Huntley (2000), Da Fonseca et al. (2005), de Dios et al. (2007), Dixon et al. (1999), Eeley et al. (1999), Franklin et al. (1992), Guo (2000), Halpin (1997), Hulme (2005), Lovejoy (2005), Millar et al. (2007), Morecroft et al. (2002), Noss (2001), Opdam and Wascher (2004), Rogers and McCarty (2000), Schwartz et al. (2001), Scott et al. (2002), Shafer (1999), Welch (2005), Wilby and Perry (2006) and Williams (2000)
2	Integrate climate change into planning exercises (reserve, pest outbreaks, harvest schedules, grazing limits, incentive programs	19	Araujo et al. (2004), Chambers et al. (2005), Christensen et al. (2004), Dale and Rauscher (1994), Donald and Evans (2006), Dyer (1994), Erasmus et al. (2002), Hulme (2005), LeHouerou (1999), McCarty (2001), Millar and Brubaker (2006), Peters and Darling (1985), Rounsevell et al. (2006), Scott and Lemieux (2005), Scott et al. (2002), Soto (2001), Staple and Wall (1999), Suffling and Scott (2002) and Welch (2005)
3	Mitigate other threats, i.e. invasive species, fragmentation, pollution	17	Bush (1999), Chambers et al. (2005), Chornesky et al. (2005), Da Fonseca et al. (2005), de Dios et al. (2007), Dixon et al. (1999), Halpin (1997), Hulme (2005), McCarty (2001), Noss (2001), Opdam and Wascher (2004), Peters and Darling (1985), Rogers and McCarty (2000), Shafer (1999), Soto (2001), Welch (2005) and Williams (2000)
4	Study response of species to climate change physiological, behavioral, demographic	15	Alongi (2002), Chambers et al. (2005), Crozier and Zabel (2006), Dyer (1994), Erasmus et al. (2002), Fukami and Wardle (2005), Gillson and Willis (2004), Honnay et al. (2002), Hulme (2005), Kappelle et al. (1999), McCarty (2001), Mulholland et al. (1997), Noss (2001), Peters and Darling (1985) and Swetnam et al. (1999)
	Practice intensive management to secure populations	15	Bartlein et al. (1997), Buckland et al. (2001), Chambers et al. (2005), Chornesky et al. (2005), Crozier and Zabel (2006), Dixon et al. (1999), Dyer (1994), Franklin et al. (1992), Hulme (2005), Morecroft et al. (2002), Peters and Darling (1985), Soto (2001), Thomas et al. (1999), Williams (2000) and Williams et al. (2005)
	Translocate species	15	Bartlein et al. (1997), Beatley (1991), Chambers et al. (2005), de Dios et al. (2007), Halpin (1997), Harris et al. (2006), Honnay et al. (2002), Hulme (2005), Millar et al. (2007), Morecroft et al. (2002), Pearson and Dawson (2005), Peters and Darling (1985), Rogers and McCarty (2000), Schwartz et al. (2001), Shafer (1999) and Williams et al. (2005)
5	Increase number of reserves	13	Burton et al. (1992), Dixon et al. (1999), Hannah et al. (2007), Hughes et al. 2003, LeHouerou (1999), Lovejoy (2005), Peters and Darling (1985), Pyke and Fischer (2005), Scott and Lemieux (2005) (2007), van Rensburg et al. (2004), Wilby and Perry (2006) and Williams et al. (2005)
6	Address scale problems match modeling, management, and experimental spatial scales for improved predictive capacity	12	Chornesky et al. (2005), Da Fonseca et al. (2005), Dale and Rauscher (1994), Ferrier and Guisan (2006), Guisan and Thuiller (2005), Huang (1997), Hughes et al. (2003), Kueppers et al. (2004), Kueppers et al. (2005), Mulholland et al. (1997), Noss (2001), Root and Schneider (1995) and Root and Schneider (2006)
	Improve inter-agency, regional coordination	12	Bartlein et al. (1997), Cumming and Spiesman (2006), Da Fonseca et al. (2005), Grumbine (1991), Hannah et al. (2002), Lemieux and Scott (2005), Rounsevell et al. (2006), Scott and Lemieux (2005), Soto (2001), Suffling and Scott (2002), Tompkins and Adger (2004) and Welch (2005)
7	Increase and maintain basic monitoring programs	11	Chambers et al. (2005), Cohen (1999), Huang (1997), Rogers and McCarty (2000), Root and Schneider (1995), Schwartz et al. (2001), Shafer (1999), Staple and Wall (1999), Suffling and Scott (2002), Wilby and Perry (2006) and Williams (2000)
	Practice adaptive management	11	Allison et al. (1998), Chambers et al. (2005), Hulme (2005), Lasch et al. (2002), Maciver and Wheaton (2005), Millar et al. (2007), Scott and Lemieux (2005), Staple and Wall (1999), Suffling and Scott (2002), Tompkins and Adger (2004) and Welch (2005)
	Protect large areas, increase reserve size	11	Beatley (1991), Bellwood and Hughes (2001), Burton et al. (1992), Bush (1999), Halpin (1997), Hulme (2005), Morecroft et al. (2002), Peters and Darling (1985), Shafer (1999), Soto (2001) and Watson (2005)

Table 1 – continued

Rank	Recommendation	No. articles	References
8	Create and manage buffer zones around reserves	10	Bush (1999), de Dios et al. (2007), Halpin (1997), Hannah et al. (2002), Hartig et al. (1997), Hughes et al. (2003), Millar et al. (2007), Noss (2001), Shafer (1999) and van Rensburg et al. (2004)
9	Create ecological reserve networks large reserves, connected by small reserves, stepping stones	8	Allison et al. (1998), Collingham and Huntley (2000), de Dios et al. (2007), Gaston et al. (2006), Opdam et al. (2006), Opdam and Wascher (2004), Shafer (1999) and Welch (2005)
	Develop improved modeling and analysis capacity i.e. more effective software, integration with GIS, integrate greater complexity	8	Chornesky et al. (2005), Ferrier and Guisan (2006), Guisan and Thuiller (2005), Guo (2000), Huang et al. 1998, Mulholland et al. (1997), Peters and Darling (1985) and Rounsevell et al. (2006)
	Do integrated study of multiple global change drivers	8	Dale and Rauscher (1994), Desanker and Justice (2001), Donald and Evans (2006), Halpin (1997), Hannah et al. (2002), McCarty (2001), Watson (2005) and Williams (2000)
	Improve techniques for and do more restoration wetlands, rivers, matrix	8	Da Fonseca et al. (2005), de Dios et al. (2007), Dyer (1994), Hartig et al. (1997), Lovejoy (2005), Millar et al. (2007), Mulholland et al. (1997) and Shafer (1999)
	Increase interdisciplinary collaboration	8	Gillson and Willis (2004), Guisan and Thuiller (2005), Hannah et al. (2002), Hulme (2005), Kappelle et al. (1999), Root and Schneider 1995, Soto (2001) and Williams (2000)
	Promote conservation policies that engage local users and promote healthy human communities	8	Chapin et al. (2006), Desanker and Justice (2001), Eeley et al. (1999), Lovejoy (2005), Opdam and Wascher (2004), Ramakrishnan (1998), Tompkins and Adger (2004) and McClanahan et al. (2008)
	Protect full range of bioclimatic variation	8	Bush (1999), Eeley et al. (1999), McCarty (2001), Noss (2001), Pyke et al. (2005), Pyke and Fischer (2005), Shafer (1999) and Thomas et al. (1999)
	Soften landuse practices in the matrix	8	Beatley (1991), Burton et al. (1992), Da Fonseca et al. (2005), Franklin et al. (1992), Hannah et al. (2002), Noss (2001), Williams (2000) and Woodwell (1991)
10	Adopt long-term and regional perspective in planning, modeling, and management	7	Eeley et al. (1999), Ferrier and Guisan (2006), Franklin et al. (1992), Guo (2000), Lovejoy (2005), Millar and Brubaker (2006), Opdam and Wascher (2004), Peters and Darling (1985), Peterson et al. (1997), Scott et al. (2002) and Welch (2005)
	Re-asses conservation goals (i.e. move away from concepts of natural, embrace processes over patterns	7	Franklin et al. (1992), Hulme (2005), Millar et al. (2007), Scott and Lemieux (2005) (2007), Scott et al. (2002) and Suffling and Scott (2002)
	Study species dispersal across landuse boundaries, gene flow, migration rates, historic flux	7	Guo (2000), Halpin (1997), Hughes et al. (2003), Kappelle et al. (1999), Lovejoy (2005), Opdam and Wascher (2004) and Rice and Emery (2003)
	Study species distributions current and historic	7	Da Fonseca et al. (2005), Eeley et al. (1999), Erasmus et al. (2002), Guo (2000), Hannah et al. (2002), Kappelle et al. (1999) and Millar and Brubaker (2006)
11	Broaden genetic and species diversity in restoration and forestry	6	Burton et al. (1992), de Dios et al. (2007), Harris et al. (2006), Maciver and Wheaton (2005), McCarty (2001), Millar et al. (2007), Rice and Emery (2003) and Staple and Wall (1999)
	Develop adaptation strategies now; early adaptation is encouraged	6	Huang et al. (1998), Hulme (2005), Lemieux and Scott (2005), Scott and Lemieux (2005) (2007) and Welch (2005)
	Do not implement CO_2 emission mitigation projects that negatively impact biodiversity	6	Chambers et al. (2005), Klooster and Masera (2000), Koziell and Swingland (2002), Kueppers et al. (2004) and Streck and Scholz (2006), Welch (2005)
	Manage for flexibility, use of portfolio of approaches, maintain options	6	Eeley et al. (1999), Hulme (2005), Kappelle et al. (1999), Lovejoy (2005), Millar et al. (2007) and Welch (2005)
	Validate model results with empirical data	6	Dale and Rauscher (1994), Guisan and Thuiller (2005), Hulme (2005), Malcom et al. (2006), Opdam and Wascher (2004) and Watson (2005)
12	Do regional impact assessments	5	Cohen (1999), Desanker and Justice (2001), Lasch et al. (2002), Lindner et al. (1997) and Suffling and Scott (2002)
	Identify indicator species	5	Chambers et al. (2005), Hulme (2005), Noss (2001), Underwood and Fisher (2006) and Welch (2005)
	Initiate long-term studies of species responses to climate	5	Mulholland et al. (1997), Noss (2001), Opdam and Wascher (2004), Peters and Darling (1985) and Root and Schneider (2006)
	Model species ranges in the future	5	Allison et al. (1998), Da Fonseca et al. (2005), Hannah et al. (2002), Kerr and Packer (1998) and Kriticos et al. (2003)
	Protect refugia current and predicted future	5	Bush (1999), Chambers et al. (2005), Eeley et al. (1999), Noss (2001) and Scott et al. (2002)
	Study adaptive genetic variation	5	Harris et al. (2006), Hughes et al. (2003), Jump and Penuelas (2005), Kappelle et al. (1999) and Rice and Emery (2003)

(continued on next page)

Table 1 – continued

Rank	Recommendation	No. articles	References
13	Leadership by those with power senior management, government agencies	4	Scott and Lemieux (2005) (2007), Tompkins and Adger (2004) and Welch (2005)
	Limit CO_2 emissions	4	Hannah et al. (2007), Hannah et al. (2005), Mayer and Rietkerk (2004) and Rogers and McCarty (2000)
	Predict effects of directional climate change on ecosystems, communities, populations	4	Allison et al. (1998), de Dios et al. (2007), Kappelle et al. (1999) and Root and Schneider (2006)
	Preserve genetic diversity in populations	4	Chambers et al. (2005), de Dios et al. (2007) and Lovejoy (2005), Noss (2001)
	Represent each species in more than one reserve	4	Halpin (1997), Millar et al. (2007), Peters and Darling (1985) and Shafer (1999)
14	Create culturally appropriate adaptation/ management options	3	Dixon et al. (1999), Huang (1997), Tompkins and Adger (2004)
	Create education programs for public about landuse practices and effects on and with climate	3	Bush (1999) and Welch (2005), Williams (2000)
	Develop best management practices for climate change scenarios	3	Mulholland et al. (1997), Rogers and McCarty (2000) and de Dios et al. (2007)
	Institute flexible zoning around reserves	3	Halpin (1997), Peters and Darling (1985) and Soto (2001)
	Increase investment in climate related research	3	Lemieux and Scott (2005), Lovejoy (2005) and Peters and Darling (1985)
	Increase communication of knowledge about climate change impacts to policymakers and stakeholders	3	Erasmus et al. (2002), Opdam and Wascher (2004) and Welch (2005)
	Initiate dialogue among stakeholders	3	McKenzie et al. (2004), Rogers and McCarty (2000) and Scott et al. (2002)
	Institute government reform (i.e. adaptive governance)	3	Chapin et al. (2006), Tompkins and Adger (2004) and Williams (2000)
	Locate reserves in areas of high heterogeneity, endemism	3	Halpin (1997), Opdam and Wascher (2004) and Peters and Darling (1985)
	Maintain natural disturbance dynamics of ecosystems	3	Halpin (1997), Noss (2001) and Shafer (1999)
	Practice proactive management of habitat to mitigate warming	3	Halpin (1997), Mulholland et al. (1997) and Wilby and Perry (2006)
	Secure boundaries of existing preserves	3	Hannah et al. (2007), van Rensburg et al. (2004) and Welch (2005)
	Start strategic zoning of landuse to minimize climate related impacts	3	Bush (1999), Solecki and Rosenzweig (2004) and Tompkins and Adger (2004)
	Study and monitor ecotones and gradients	3	Halpin (1997), Lovejoy (2005) and Stohlgren et al. (2000)
	Study effectiveness of corridors	3	Graham 1988, Halpin (1997) and Williams et al. (2005)
	Use predictive models to make decisions on where to situate new reserves	3	Bush (1999), Hannah et al. (2007) and Pearson and Dawson (2005)
15	Anticipate surprises and threshold effects i.e. major extinctions or invasions	2	Bartlein et al. (1997) and Millar et al. (2007)
	Design biological preserves for complex changes in time, not just directional change	2	Bartlein et al. (1997) and Graham (1988)
	Locate reserves at northern boundary of species' ranges	2	Peters and Darling (1985) and Shafer (1999)
	Manage the matrix	2	Eeley et al. (1999) and Lovejoy (2005)
	Practice proactive research on climate change	2	Harris et al. (2006) and Williams (2000)
	Protect many small reserves rather than single large	2	Opdam and Wascher (2004) and Pearson and Dawson (2005)
	Provide education opportunities and summaries of primary literature for management staff to learn and network about climate change	2	Grumbine (1991) and Welch (2005)
	Study and protect metapopulations	2	Crozier and Zabel (2006) and Opdam and Wascher (2004)
	Study processes of change at multiple spatial and temporal scales	2	Dale and Rauscher (1994) and Watson (2005)
	Use GIS to study species distributions and landscape patterns	2	Brown (2006) and Da Fonseca et al. (2005)

Table 1 – continued

Rank	Recommendation	No. articles	References
16	Action plans must be time-bound and measurable	1	Welch (2005)
	Adjust park boundaries to capture anticipated movement of critical habitats	1	Welch (2005)
	Create institutional flexibility	1	Millar et al. (2007)
	Create linear reserves oriented longitudinally	1	Pearson and Dawson (2005)
	Establish cross-national collaboration	1	Desanker and Justice (2001)
	Establish neo-native forests plant species where they were in the past, but are not found currently	1	Millar et al. (2007)
	Experiment with refugia	1	Millar et al. (2007)
	Focus protection on sensitive biomes	1	Scott et al. (2002)
	Focus on annual plants rather than perennials near climate boundaries	1	Buckland et al. (2001)
	Increase wetland protection	1	Hartig et al. (1997)
	Institutional capacity enhancement to address climate change	1	Lemieux and Scott (2005)
	Institute reform to improve support for interdisciplinary, multi-institutional research	1	Root and Schneider (1995)
	Locate reserves so major vegetation transitions are in core	1	Halpin (1997)
	Locate reserves at core of ranges	1	Araujo et al. (2004)
	Manage for landscape asynchrony	1	Millar et al. (2007)
	Manage human-wildlife conflict as change occurs	1	Wilby and Perry (2006)
	Manage populations to reduce temporal fluctuations in population sizes	1	Rice and Emery (2003)
	Develop guidelines for climate sensitive restoration and infrastructure development	1	Welch (2005)
	Need to increase social acceptance of shared resilience goals	1	Tompkins and Adger (2004)
	Promote personal action plans among employees to reduce emissions	1	Welch (2005)
	Protect endangered species ex situ	1	Noss (2001)
	Protect functional groups and keystone species	1	Noss (2001)
	Protect mountains	1	Peterson et al. (1997)
	Protect primary forests	1	Noss (2001)
	Protect urban green space	1	Wilby and Perry (2006)
	Quantify environmental susceptibility versus adaptive capacity to inform conservation planning	1	McClanahan et al. (2008)
	Schedule dam releases to protect stream temperatures	1	Rogers and McCarty (2000)
	Study changes in populations at rear of range rather than only range fronts	1	Willis and Birks (2006)
	Study response of undisturbed areas to climate change	1	Mulholland et al. (1997)
	Study social agency and human decision making	1	Desanker and Justice (2001)
	Study time-series data on species dynamics	1	Erasmus et al. (2002)
	Substitute space for time to study the responses of species to climate change	1	Millar and Brubaker (2006)
	Train more taxonomists	1	Huber and Langor (2004)
	Use caution in predictive modeling because the responses of some species are not well predicted	1	Willis and Birks (2006)
	Use simple decision rules for reserve planning	1	Meir et al. (2004)
	Use social networks for education about climate change	1	Huang (1997)
	Use triage in short-term to prioritize action	1	Millar et al. (2007)

sections, we discuss how recommendations in the literature to date inform these three scales of application.

4. Regional policy and planning

Species historically respond to changing climate with distributional shifts, and many species are expected to lose current habitat representation in the future. In light of this, many recommendations call for greater integration of species protection plans, natural resource management, research and development agendas across wider geographic areas, on longer time-scales, and involving more diverse actors than in current practice. (1) Long-term, regional perspective and (2) improved coordination among scientists, land managers, politicians and conservation organizations at regional scales are among the most frequently cited recommendations to protect biodiversity in the face of climate change (Rank 10 and 6 respectively, see references in Table 1 and for all ranks mentioned hereafter). Increased interdisciplinary collaboration (Rank 9) as well as regional-scale impact assessments are also frequently identified (Rank 12). Recommendations for adaptation to regional policy and planning focus on two comple-

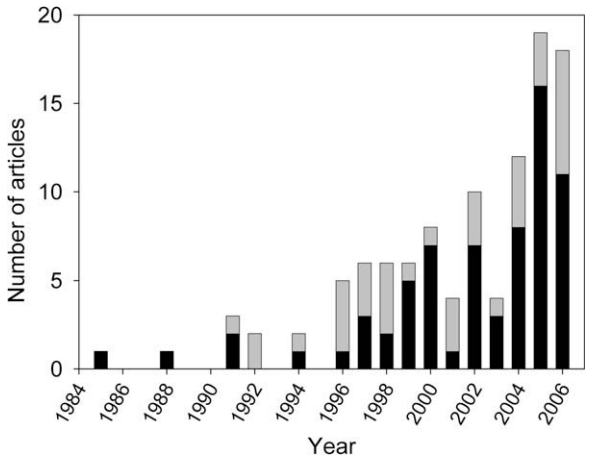

Fig. 2 – Frequency distribution by publication year of papers included in this review, including articles addressing biodiversity only (black) or biodiversity in conjunction with ecosystem services (grey). Records from 2007 were only partially covered in this review and not included.

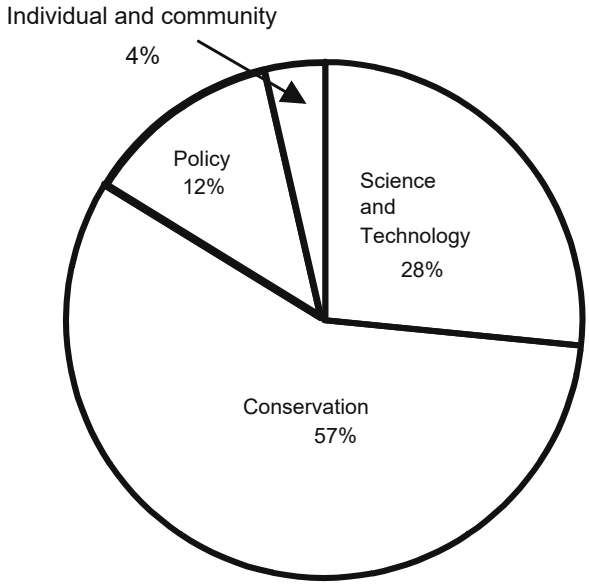

Fig. 3 – Distribution of recommendations calling for climate change adaptation among different activity sectors: conservation (e.g. reserve purchases, management, restoration and regional coordination), science and technology (e.g. research and modeling), policy (e.g. land-zoning, governance structure and institutional capacity), and individuals and communities (e.g. private landowner practices and grassroots action). Recommendations were counted in all applicable sectors.

mentary strategies: reserve planning and improving landscape connectivity. We discuss these issues further in the following two sections.

4.1. *Reserve planning*

Basing reserve acquisition priorities on predictions of future biome, community or individual species distributions under different climate scenarios is one method for climate change adaptation. The guiding principle is that reserves should be accumulated in areas predicted to be hotspots for biodiversity in the future or to provide habitat for species of high conservation value, warranting increased effort to model species distributions in the future (Rank 12). There are, however, several limitations to the accuracy and precision of simulation and analytical models of future species, biome or community distributions, leading some authors to recommend improved modeling capacity as the first step (Rank 9).

Model prediction error results from variation in model types, emissions, landuse and socio-economic scenarios. There are little-understood, but important, interactions between climate change and other global change drivers that could influence where species and habitats occur in the future (Rank 9). Insufficient data on species distributions (Rank 10) the effects of species interactions on distribution (Ferrier and Guisan, 2006; Kappelle et al., 1999), dispersal (Rank 10) and species, community or ecosystem responses to climate change (Rank 4) are also widely expressed concerns and lead authors to advocate for increased research in these areas before models are accepted. For example, bioclimatic envelope modeling uses current species distributions to predict future distributions as a function of climate. For many species such models can be productive, but in cases where species distributions are limited by factors other than climate, this extrapolation will prove misleading. Willis and Birks (2006) discuss the accuracy of bioclimatic models. Species-envelope model runs were conducted for backward predictions of species distributions and compared to paleo-ecological records. Many species distributions were predicted well, but some were largely inaccurate.

Problems of scaling also raise uncertainty (Rank 6), including scaling-down global climate models (GCMs) to fit management scales, or scaling-up empirical observations typically made at small spatial scales to predict larger scale processes (Root and Schneider, 1995). The scales of global climate models (GCM) and management activities simply do not match. Most reserves are smaller than a single grid cell in a GCM. Climate can vary sharply within this scale, and this variation often drives local patterns of species distribution and abundance – particularly in mountainous or coastal areas. Regional climate models, which are only available for small areas of the globe, are a more appropriate choice for management and planning (Dale and Rauscher, 1994; Guisan and Thuiller, 2005; Kueppers et al., 2005; Mulholland et al., 1997), though they remain limited by key uncertainties, assumptions and costs (Root and Schneider, 1995).

Not surprisingly, these inherent limitations of bioclimatic envelope models generate debate about whether and how to apply them to reserve selection. Some strongly advocate including climate change in reserve selection models and locating new reserves with expected changes in climate (Araujo et al., 2004; Bush, 1996; Dyer, 1994; Pearson and Dawson, 2005). Araujo et al. (2004) compare the ability of six existing reserve selection methods to secure European plant species in the context of climate change. They found species loss from protected reserves on the order of 6–11% of taxa for all models, and they conclude that new reserve-selection models specific to climate change are needed. Hannah et al. (2007)

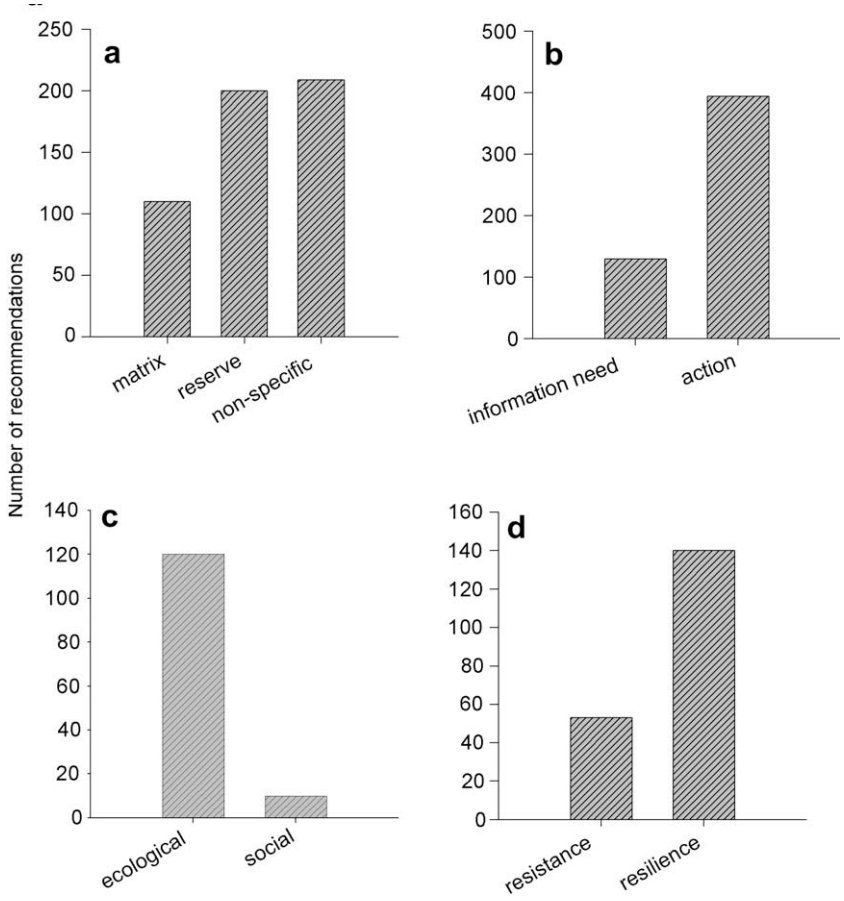

Fig. 4 – Distribution of recommendations among broad categories referring to (a) type of land targeted, (b) information need or action, (c) type of information need, and (d) management goal. Y-axis ranges vary across graphs because not all recommendations fit into every set of categories.

make a compelling case for not waiting to incorporate climate change forecasts into reserve selection models despite uncertainty. They use bioclimatic envelope models to explore the need for additional protected areas to achieve representation for thousands of species in three regions (Mexico, South Africa Cape, and Europe) in current and future climate and find that less land is needed in the long-term if planning models are designed to solve for both current and future conditions simultaneously.

Others argue, however, that given tremendous uncertainty, the priority should be to acquire new reserves in locations that minimize the spatial distances among new and existing reserves so that species can migrate (Allison et al., 1998; Collingham and Huntley, 2000; Halpin, 1997; Opdam and Wascher, 2004; Shafer, 1999). Williams et al. (2005) used a simulation model to estimate that 50% more protected land area in particular locations was needed to create reserve corridors to protect *Proteaceae* in the South African Cape region through 2050. Citing a number of sources of potential error in model results, however, they recommend that as much reserve area as possible be set aside. Such strategies do not require extensive modeling capacity and resources and instead focuse on rapid acquisition of land as it becomes available to create porous landscapes. Other authors reason that to facilitate migration and adaptation potential, reserves should be located with reference to focal species or community distributions, such as in their cores (Araujo et al., 2004; Halpin, 1997) or at their northern boundaries (Peters and Darling, 1985; Shafer, 1999). There seems to be little consensus or data to inform this debate. More research is needed about where in a species' range individuals are most likely to survive, migrate or adapt to rapid environmental change (Willis and Birks, 2006).

Debate also arises around the relative advantages of few large versus several small reserves in the context of climate change. The tension is whether large reserves will be large enough to allow species to track changing climate and remain inside reserve boundaries, and whether small preserves along latitudinal, elevational or other climate gradients will be close enough together for species to move between them. Eleven sources recommend protecting large areas (Beatley 1991; Bellwood and Hughes 2001; Burton et al. 1992; Bush 1996; Halpin 1997; Hulme 2005; Morecroft et al. 2002; Peters and Darling 1985; Shafer 1999; Soto 2001; Watson 2005), while two advocate focusing on many small areas (Opdam and Wascher, 2004; Pearson and Dawson, 2005). Eight suggest a compromise strategy of creating ecological networks of small and large reserves embedded within intermediate land uses (Allison et al., 1998; Collingham and Huntley, 2000; de Dios et al., 2007; Gaston et al., 2006; Opdam et al., 2006; Opdam and Wascher, 2004; Shafer, 1999; Welch, 2005).

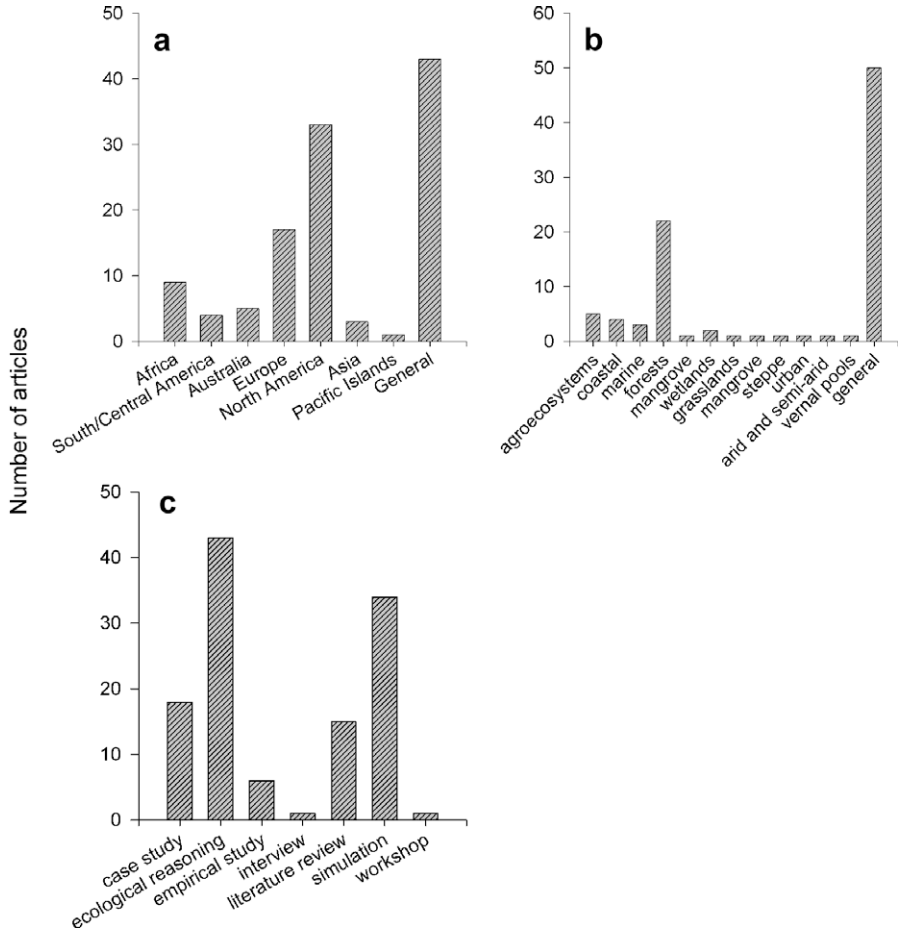

Fig. 5 – The (a) geographic focus, (b) biome focus, and (c) evidence basis for recommendations addressing climate change adaptation strategies for biodiversity management.

What all of the recommendations for reserve selection share is an urge to protect more land rapidly (Rank 5). This push will certainly help buffer biodiversity against climate change as well as other threats. However, climate change is likely to exacerbate existing tensions and tradeoffs between protecting areas and meeting basic human needs. Creating more new reserves might be feasible in some settings but must be guided by targeted, well-informed strategies likely to maximize effectiveness in the face of climate change. In most areas, action in lands outside of reserves must also be a part of climate change strategies for biodiversity conservation (Franklin et al., 1992; Lovejoy, 2005).

4.2. *Landscape connectivity*

To improve landscape connectivity, so that species can move, is the most frequent recommendation for climate change adaptation in the literature reviewed here (Rank 1). Authors recommend some form of corridor creation via the designation of new parks (de Dios et al., 2007; Halpin, 1997; Scott et al., 2002) oriented longitudinally (Eeley et al., 1999; Noss, 2001; Shafer, 1999), or through actions in non-reserve land, such as protecting riparian habitat and railway lines in cities (Wilby and Perry, 2006), or by planting trees and shrubs to create shelterbelts and hedgerows in farmlands (Donald and Evans, 2006; Guo, 2000; Schwartz et al., 2001). There was little guidance in this literature set for corridor implementation beyond common-sense reasoning, however. Illustrative examples of current corridor projects or elaboration of specific ecological or political tactics for corridor creation might help jump-start this process. For example, case studies of the Dutch Ecological Network and other similar national models to plan and link protected areas may be particularly informative at this stage of adaptation planning (Gaston et al., 2006). Further, despite widespread favor for ecological networks, assessment of their effectiveness remains in its infancy. Similarly, the field of corridor ecology, while recognized as integral to conservation practice in fragmented landscapes for years, is still young (see Hilty et al., 2006). Some authors warn of a significant need for more empirical data to support the effectiveness of corridors, optimize their spatial arrangement, and minimize risks of increased transmission of disease or invasive species before the conservation community embraces corridors uniformly as the tool to combat biodiversity loss in the face of global climate change (Graham, 1988; Halpin, 1997; Scott and Lemieux, 2005; Williams et al., 2005).

A second popular recommendation for improving landscape connectivity is to change how we manage the matrix

(Da Fonseca et al., 2005; Eeley et al., 1999; Lovejoy, 2005). Many authors advocate creating buffer zones around reserves (Rank 8) or flexible landuse zoning at reserve boundaries to allow for land swaps in the future as species distributions shift (Rank 14). Others recommend urban planning and zoning to avoid climate-related risks (Rank 14). In general, enlisting people and human communities to 'soften' landuse through sustainable or less damaging practices (e.g. low intensity forestry or alternatives to building sea walls) (Rank 9) and to restore habitat (Rank 9) will facilitate species movement and persistence in the future.

Despite wide acknowledgement, these connectivity strategies were among the most poorly developed recommendations, limited mainly to very general actions (e.g. "build flexibility", "manage the matrix", "modify landuse practices") without identification of kinds of actors that might need to be involved (e.g. reserve managers, policymakers, individuals) or information gaps. Landuse reform likely needs to bring together local governments, urban planners, community groups and conservation organizations and to involve high degrees of coordination across multiple jurisdictions to provide landscape cohesion (Press et al., 1995). Substantial work to flesh out this process, as well as to guide information acquisition, is needed before new forms of management across landuse types can be implemented.

Even with good landscape connectivity, some species will not be able to migrate. For these species – such as dispersal-limited species, those restricted to rare or confined habitat types, or those with life history traits like low reproductive rates – translocations from within their current range to locations suitable in the future are widely advocated (Rank 4). Translocations are a contentious issue because of the challenges associated with moving populations successfully and predicting suitable future habitats, as well as the potential for unintended consequences from introducing new species into existing communities (Lemieux and Scott, 2005; McLachlan et al., 2007). Empirical evidence suggests that animal translocations tend to be unsuccessful and costly (Fischer and Lindenmayer, 2000). Despite these real problems, we did not find discussion of the feasibility of such programs. Climate change adaptation strategies would likely necessitate moving at least some species outside of their current range, an action that has rarely been pursued thus far. To fully evaluate the feasibility of translocations would require stronger understanding of best available methods, potential risks, and policies for regional coordination to avoid situations in which different conservation objectives are put in conflict (McLachlan et al., 2007).

5. Site-scale action

Many land managers feel that there is little they can do about climate change beyond what they are already doing, such as trying to maintain basic ecosystem functioning and mitigate other threats like invasive species and pollution. To a certain extent, recommendations we reviewed validate this perspective. A number of "business as usual" recommendations rank high in their frequency in the literature, e.g. mitigating current threats, such as invasive species and habitat loss (Rank 2), increasing or continuing basic monitoring programs (Rank 7) or managing populations for natural disturbance dynamics (Halpin, 1997; Noss, 2001; Shafer, 1999). Franklin et al. (1992) describe how in forest ecosystems mature trees slow the effects of climate change because they tolerate a wide range of temperatures, while seedling establishment is far more sensitive. Under climate change, removal of long-lived trees will therefore act to intensify and speed-up the rate at which forest ecosystems change compared to intact forests. Restoration and greening efforts function as proactive management to mitigate local-scale warming (Halpin, 1997; Mulholland et al., 1997; Wilby and Perry, 2006). Mulholland et al. (1997) point out that restoration of riparian vegetation, needed to secure wildlife populations and ecosystem services now, will also function to decrease stream temperatures in the future. Wilby and Perry (2006) highlight how green building and landscaping techniques, such as planting green roofs, neighborhood trees, and water structures, will help to counter increasing problems of urban heat-island effects.

Other authors point out that business as usual is probably not enough in many cases. Peters and Darling (1985) suggest that managers consider rescue measures such as adding irrigation or drainage systems to secure sensitive populations. Buckland et al. (2001) anticipate that soil fertility in some grasslands may require manipulation to impede species invasions under warmer conditions. Advice to incorporate a broader range of species and genotypes in restoration and forestry than prescribed based on local provenance was common (Rank 11). This type of strategy would depart significantly from the preference for local genotypes prevailing in restoration and forestry practice to date (Millar and Brubaker, 2006; Millar et al., 2007; Scott and Lemieux, 2007) and warrants increased experimentation to better understand potential costs and benefits (Harris et al., 2006; Rice and Emery, 2003).

5.1. *Resilience versus resistance*

A first step for managers will be to wrestle with the question of whether and when they will attempt to resist biotic change, such as by adding irrigation if precipitation declines, rather than try to build resilience to change, such as by facilitating population adaptive capacity through introduction of a wider range of genotypes. In theory resistant strategies attempt to bolster a system's defenses to rapid environmental change, while resilience strategies attempt to bolster a system's ability to absorb rapid environmental change. More recommendations advocate resilience than resistance strategies (Fig. 4d). However, intensive management actions to protect historical species in their current distributions are widely advocated (Rank 4). The latter align best with a fixed-reserve approach focusing on local species precedence, an approach that will be increasingly costly and challenging to maintain as directional global changes accelerate.

For some species and systems, options other than intervention might not exist. Resistance approaches designed to maintain the status quo are nevertheless risky – they may leave systems vulnerable to total collapse if interventions are not maintained or compromise other system components (Harris et al., 2006; Walker et al., 2002). For example, the removal of invasive species has sometimes resulted in unpredicted and negative impacts to ecosystem structure and

function (Zavaleta et al., 2001). Managing for resilience (sensu Holling, 1973) on the other hand explicitly focuses on increasing the flexibility and ability of systems to adapt and self-organize in response to change. To build resilience to climate change into systems, however, may require radical shifts in perspective for many conservation stakeholders and re-evaluation of conservation goals (Rank 10). Land managers might need to view a broader range of ecosystem states as desirable, such as novel or dynamic local assemblages that maintain functioning and trophic complexity but not necessarily species identity (Hulme, 2005), or to re-evaluate operational definitions and guidelines, such as what constitutes an invasive species or when a species can be added to a risk list (Scott and Lemieux, 2005; Scott et al., 2002).

Examples of broad perspective shift are found in the restoration literature. Millar and Brubaker (2006) emphasize the use of paleo-ecological perspectives to guide restoration goals and interventions. They ask that managers and restoration practitioners "make friends with physical and climatic change," arguing for instance that which species are deemed 'natural' or 'invasive' depends on the spatial and temporal resolution of data used to inform perspective. For example, Monterey pines (*Pinus radiata*) are considered native to a small region of California in which they were found at the time of European colonization. The species has since naturalized widely in California from landscaping plantings and is targeted for removal as an unwanted exotic in these regions. Paleo-ecological records of *P. radiata* reveal strong climate-driven dynamics in range, with widespread distribution during favorable periods and retreat during unfavorable periods. Millar and Brubaker (2006) suggest that naturalized populations be restored rather than removed in locations where *P. radiata* thrived when the climate was similar to the present or predicted future. Pearsall (2005) describes an experimental landscape-scale project in North Carolina, USA designed to test a range of restoration options for combating peat-land loss as a result of rising sea level. Options include oyster bed formation, dune formation, native plant establishment, as well as nonnative plant establishment. The experiment is scheduled to run for 25 years with regular evaluation intervals. Bradley and Wilcove (in press) imagine a "transformative restoration" in which the plant species used to repopulate restoration sites are determined by future climate conditions rather than historical presence. For example, based on results of bioclimatic envelope models, areas in the Great Basin ecoregion of the Western US may be restored best with plants introduced from the Mojave Desert, a more arid, neighboring biome. These projects share a broad, long-term and pragmatic perspective on acceptable restoration outcomes, one that may be necessary to tackle climate change.

A key strategy for building the adaptive capacity of systems is to enhance diversity at various scales. Diverse populations tend to be more adaptable, placing a premium on protecting and managing for high genetic diversity (Rank 13). Capturing the full range of bioclimatic variability within preserves and across landscapes and designing high species, structural, and landscape diversity into constructed and managed systems are also recommended (Rank 9). Pockets of outlier vegetation, areas of high endemism, ecotones, and refugia that protected species during climate shifts in the past are anticipated to be important sources for species re-colonization and radiation in the future, as well as provide retreats for migrating or translocated species (Rank 12). Willis and Birks (2006) discuss methods that combine genetic and paleo-ecological evidence to identify sites with distinctive patterns of genetic diversity that resulted from past geological events and refugial isolation.

Resistance and resilience strategies are not mutually exclusive. Very special communities or organisms that are of high conservation value may warrant highly invasive, intense and costly management regimes to maintain them. Regimes for intensive management are likely to be implemented through existing threatened species management frameworks, such as recovery plans. For more widespread populations, communities and ecosystems, which often provide important ecosystem services, a focus on resilience might be most appropriate. At the site-scale, managers need to address a host of practical issues such as the cost and cost-effectiveness of adaptation options, their compatibility with existing regulatory and institutional constraints, and their likely effectiveness in the absence of coordination with adjoining private lands.

6. Adapting existing conservation plans

The existing literature does provide an array of actions for managers to build on and consider incorporating into existing conservation plans. A practical first step to climate change adaptation planning is to evaluate the likely outcomes for biodiversity of continuing current management and conservation directions. Most conservation policies and management plans do not yet explicitly consider climate change (Chambers et al., 2005; Groves et al., 2002; Hannah et al., 2002; Scott and Lemieux, 2007). A consistent theme in the literature is at the very least to immediately appraise current conservation and management practice in the context of climate change (Rank 2) with the goal of developing and adopting specific climate change adaptation policies in the near future (Rank 11). The literature here contained some suggestions for how to do this. A few articles emphasized the use of models to guide evaluation and adaptation of existing practices. For example, Christensen et al. (2004) used a simulation model to investigate a coupled system of plants and grazers in the Inner Mongolia Steppe under different climate scenarios. They determined that grasslands were likely to undergo a state-transition to shrublands if existing grazer densities are maintained, and they advocate reducing grazers in this area as well as in other semi-arid managed grassland systems. Hulme (2005) provided a general overview of how mathematical models can integrate long-term demographic and climate data to set climate change-appropriate harvest or stocking schedules or to forecast pest outbreaks.

Some authors highlight existing efforts that are well-suited to tackle climate change and warrant increased funding and research. Donald and Evans (2006) argue that agri-environment incentives and easement programs in the US and the EU, which are growing due to shifts in farm policies, warrant increased funding priority because of their potential to improve habitat availability and landscape connectivity across managed ecosystems. They discuss how these policies

could be modified to tackle climate change directly. Site-specific climate conditions and biotic responses could be mapped on to landscapes and used to prioritize locations for farm diversification. Similar gains could be made by targeting other private landowner biodiversity enrichment programs, like the USDA Forest Legacy Program (http://www.fs.fed.us/spf/coop/programs/loa/flp.shtml) or the National Wildlife Federation's Urban Backyard Wildlife Program (http://www.nwf.org/gardenforwildlife/).

6.1. *Holistic strategies*

Issues that currently challenge conservation practice may need to be addressed before the added stress of climate change complicates them further. Communities of local users are often in conflict with conservation objectives (Chan et al., 2007; Suffling and Scott, 2002). Identifying opportunities for reduced conflict and increased synergy between conservation and local communities will become more important as climate changes. A number of authors warn that conservation policies must create positive economic outcomes for local peoples to buffer them against potentially dramatic shifts in livelihoods that will accompany climate shifts (Rank 9). Adaptation requires community buy-in and participation (Chapin et al., 2006). To this end, conservation policies that foster learning and participation (Ramakrishnan, 1998) and provide options that are culturally and economically appropriate, such as those that honor traditional management systems and do not rely on expensive technologies, are more likely to be embraced and implemented (Rank 14). McClanahan et al. (2008) argue that climate-informed conservation planning necessitates site-specific understanding of environmental susceptibility and societal capacity to cope and adapt. They illustrate this process for five western Indian Ocean countries with respect to coral reef conservation. Locations with high environmental susceptibility and low adaptive capacity will be most difficult to secure effectively in the future, while those with low environmental susceptibility and high adaptive capacity will be easiest. Locations with low environmental susceptibility and low adaptive capacity are good candidates for biodiversity investment, but to be effective these locations also require investments in human infrastructure, livelihood diversification and social capital.

Climate change is acting in concert with multiple other drivers of biodiversity loss including habitat degradation, soil loss, nitrogen enrichment, and acidification. Strong policies must simultaneously address more than one issue (Watson, 2005) or risk exacerbating environmental problems in the process of trying to combat them. Emission reduction programs are a significant push for many governments, organizations and individuals. They warrant an important place in any climate change combat strategy (Rank 13). A number of authors in this review urge, however, that emissions reduction programs and the Clean Development Mechanisms (CDMs) in the Kyoto Protocol be implemented in ways that simultaneously address carbon sequestration, biodiversity conservation and human livelihoods, rather than carbon sequestration in isolation (Rank 11).

Finally, climate change provides a much-needed impetus to evaluate how conservation policies respond to change in general. Climate change is only one of several global environmental trends to which biodiversity and its conservation must respond. Uncertainty in the climate change arena and about the future in general should not limit action to strengthen existing conservation strategies, with a focus on enhancing the ability of ecosystems to absorb and recover from rapid and unpredictable change.

7. A complete strategy

Climate change challenges conservation practice with the need to respond to both rapid directional change and tremendous uncertainty. Climate change adaptation therefore requires implementation of a range of measures, from short- to long-term and from precautionary and robust to more risky or deterministic, but specifically anticipatory (Fig. 6). To cer-

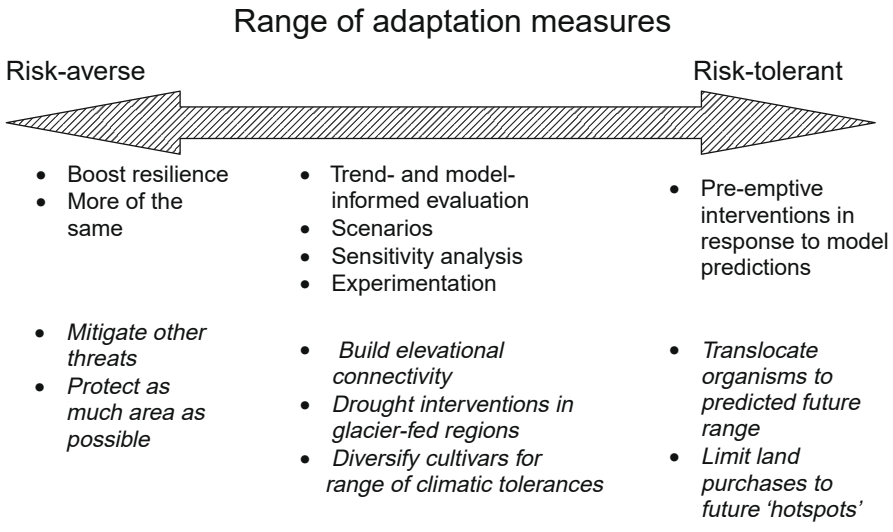

Fig. 6 – Adaptation measures classified along a risk continuum. Under each risk category are examples of general approaches followed by examples of specific adaptation measures. A complete strategy should span a risk continuum.

tain degree, risk tolerance of individual actors will guide strategy selection. Millar et al. (2007) discuss how managers must proactively decide whether to adopt deterministic or indeterministic approaches.

Each type of approach has benefits and drawbacks. Precautionary measures such as restoration, increased monitoring of species distribution, and increased investment in reserve protection do not necessarily require highly certain and precise climate change predictions, but such precautionary steps will help managers respond to current biodiversity threats as well as threats that emerge in the future. Precautionary measures alone, however, will not expand our ability to absorb and respond to rapid directional changes in climate, nor do they capitalize on available predictive information and efforts. In worst-case climate scenarios, over-reliance on bet-hedging measures may spread resources too thin or prove insufficient to help biodiversity weather the rapid changes underway. On the other hand, forecast-interventions bear significant risks if they are too deterministic, not robust to alternative futures or have negative unanticipated consequences (Suffling and Scott, 2002). They could also deliver great rewards and should be weighed with sensitivity analyses and scenarios, tested in pilot programs, and implemented initially at small scales (McLachlan et al., 2007). Scenario building – done in ways that are amenable to local data limitations and useable by policymakers and managers – is particularly apt for exploring the range of magnitudes and direction of possible futures and trends without commitment to specific forecasts (Brown, 2006; Millar et al., 2007).

While the range of recommendations in the literature is great, four consistent, broad themes emerge in this review for conservation stakeholders to apply to climate change planning and adaptation: (1) the need for regional institutional coordination for reserve planning and management and to improve landscape connectivity; (2) the need to broaden spatial and temporal perspective in management activities and practice, and to employ actions that build system resilience; (3) the need to incorporate climate change into all conservation planning and actions, which will require increased research and capacity to forecast future conditions and species responses and to deal effectively with unavoidable uncertainty; and (4) the need to address multiple threats and global change drivers simultaneously and in ways that are responsive to and inclusive of diverse human communities and cultures. Action along each of these fronts will involve difficult tradeoffs, barriers to implementation, and collaboration across diverse actors.

Action will also require an adaptation planning process or series of processes appropriate for various scales and applications. Most of the literature to date fails to distinguish adap-

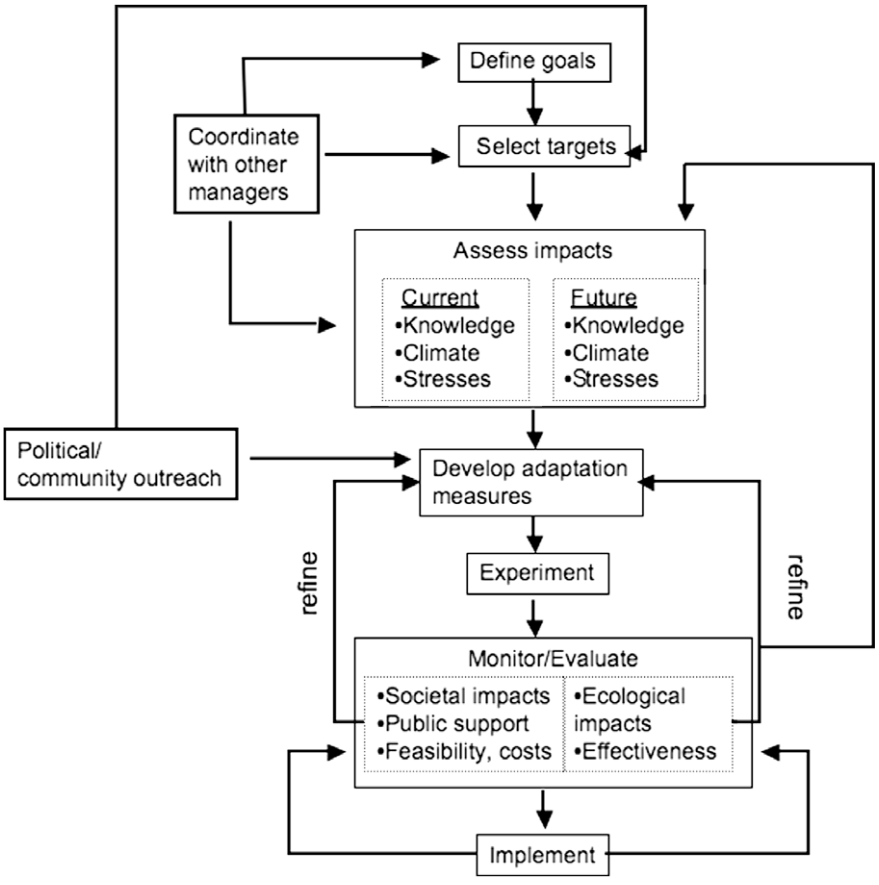

Fig. 7 – Adaptation planning involves at least a few key steps, each complex and requiring collaboration among actors such as land managers, the public, scientists, funders and lawmakers. Recommendations reviewed here address aspects of these steps, but without specifying where they fit in relation to one another.

tation from climate change impact assessment, or adaptation planning from implementation. These are distinct steps in an as-yet largely undefined process that the recommendations we survey could inform. We propose a series of general steps that should be modified, elaborated, and tailored to specific needs (Fig. 7). Key to any adaptation planning process will be to follow the principles of adaptive management (Rank 7), in which later steps inform earlier steps in an iterative and on going process.

8. Conclusions

Widespread calls exist for immediate action to adapt conservation practice to ongoing climate change in order to ensure the persistence of many species and related ecosystem services. However, the majority of recommendations in the published journal literature lack sufficient specificity to direct this action. Over the last 22 years, general recommendations have been reiterated frequently without the elaboration necessary to operationalize them. Greater effort to increase the availability and applicability of climate change adaptation options for conservation—through concrete strategies and case studies illustrating how and where to link research agendas, conservation programs and institutions—is badly needed.

Recommendations to date also largely neglect social science and are overwhelmingly focused on ecological data (Fig. 4c). This bias is alarming given the obvious importance of human behavior and preferences in determining conservation outcomes (Watson, 2005) and the increasingly important role of multi-use public and private lands in conservation practice. A holistic landscape approach to conservation, driven by a vision of humans and other species co-mingling across reserves and developed lands, has gradually gained prominence over the last 20 years. In their seminal paper, Peters and Darling (1985) provided a number of recommendations that continue to be widely advocated (Table 1), but they did not address the roles of conservation and restoration in human-dominated landscapes. These ideas emerge strongly in more recent literature highlighting a need to integrate ecology with other disciplines and approaches that explicitly address the roles of institutions, policy, politics and people in successful conservation strategies.

Finally, few resources or capacity exist to guide an adaptation planning process at any scale (Hannah et al., 2002; Scott and Lemieux, 2007; Welch, 2005). Such a process would place the sea of adaptation ideas and recommendations in framework and provide practitioners with tools, roles and a structure to evaluate what ideas might be useful and feasible for particular situations. Large-scale adaptation efforts that incorporate many of the recommendations found in this review are currently underway, including governmental efforts such as by Parks Canada or DEFRA in England, and by international non-governmental organizations such as The Nature Conservancy and the Wildlife Conservation Society. Well-documented case studies that focus not only on the outcome but also on the development process of adaptation plans are a promising avenue. These efforts can best enhance and encourage more widespread climate change adaptation, particularly at smaller scales, by capturing what they learn and disseminating it widely.

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Spatial risk assessment of eastern monarch butterfly road mortality during autumn migration within the southern corridor

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ABSTRACT

Road mortality may contribute to the population decline of eastern monarch butterflies (*Danaus plexippus* L.). We estimated autumn monarch roadkill rates within the primary Oklahoma to Mexico southern migration corridor (i.e., Central Funnel). Dead monarchs were surveyed along Texas roadsides during four weeks of autumn migration in 2016 and 2017. Roadkill averaged 3.4 monarchs per 100 m transect, reaching 66 per 100 m in a roadkill hotspot in southwestern Texas. Extrapolations of Central Funnel roadkill based on survey data and road types were 3.6 and 1.1 million in 2016 and 2017, respectively. Spatial distribution of roadkill across the Central Funnel was projected from Texas survey data using 30 m resolution MaxEnt niche models. Highest roadkill probability was linked to arid climate and low human population density. The latter variables may not be directly related to roadkill, but instead represent indirect correlates of increased densities of monarchs where the migration corridor narrows southwards. The higher roadkill projected in southwest Texas and Mexico by MaxEnt models agrees with previously reported monarch roadkill hotspots. MaxEnt-based 2016–2017 projections for annual roadkill rates throughout the Central Funnel averaged 2.1 million. This figure is similar to the result by simple extrapolation, and represents about 3% of the overwintering monarch population for these years. Mitigation at roadkill hotspots in the Central Funnel could reduce monarch roadkill mortality during migration and contribute towards conservation efforts for the monarch butterfly.

1. Introduction

Wildlife-vehicle collision is the most widely acknowledged impact of roads on wildlife, and can contribute to the decline of species of conservation concern (Tok et al., 2011; Visintin et al., 2016; Bennett, 2017), including globally declining pollinator insect species (Baxter-Gilbert et al., 2015). Roadkill can result in high mortality and lower abundance for species with large area requirements, pronounced migratory movements, small population sizes, and slow reproduction rates (Seiler and Helldin, 2006; Fahrig and Rytwinski, 2009). Wildlife-vehicle collisions are often spatially and temporally aggregated and substantial annual and inter-annual variation has been associated with environmental factors and traffic volume (Seiler and Helldin, 2006; Shilling and Waetjen, 2015). This tendency for high spatio-temporal variability in roadkill can be difficult to interpret based solely on the mapping of field survey data. Accordingly, there is a trend to use predictive spatial models to account for the variability in investigating the impacts of roads on wildlife mortality (Bennett, 2017). Typical roadkill niche models use a combination of environmental and anthropogenic variables and are often restricted to small areas (Visintin et al., 2016). Species distribution modeling has previously been used to project roadkill risk of mammals (Grilo et al., 2009; Roger and Ramp, 2009; Visintin et al., 2016, 2017) and owls (Gomes et al., 2009). Spatial models for insect roadkill have not yet been developed.

Only five out of 215 roadkill studies (2%) between 2011 and 2015 were specifically focused on invertebrates (Bennett, 2017). Despite this taxonomic bias in the literature, roadkill may be a substantial threat to certain insect populations. Baxter-Gilbert et al. (2015) projected that hundreds of billions of pollinating insects are lost annually to roadkill across North America. Although relatively few studies exist on butterfly road mortality, researchers have suggested that butterflies are one of the most common insect orders killed by vehicles (McKenna et al., 2001; Rao and Girish, 2007). Despite the high numbers of road-killed butterflies, the risk of Lepidopteran roadkill has been estimated as low to moderate (Baxter-Gilbert et al., 2015; Muñoz et al., 2015). Several studies have estimated butterfly roadkill numbers and examined

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contributing factors (Munguira and Thomas, 1992; McKenna et al., 2001; Ries et al., 2001; Rao and Girish, 2007; Skórka et al., 2013), but most of these studies concentrate on local, relatively sedentary butterfly populations and their utilization of roadside habitats rather than migratory butterflies. Migratory danaine butterflies (Nymphalidae: Danainae) may be especially susceptible to roadkill during migration (Her, 2008; Taiwan Environmental Protection Administration [EPA], 2010; Santhosh and Basavarajappa, 2014), including the monarch butterfly (*Danaus plexippus* L.) in the United States (McKenna et al., 2001) and Mexico (Correo Real, 2015).

Significant population decline of the eastern migratory monarch butterfly has been observed at the overwintering sites in Central Mexico during the past two decades (Vidal and Rendón-Salinas, 2014; Thogmartin et al., 2017). Consequently, the persistence of the migratory phenomenon of the eastern population may be endangered (Brower et al., 2012). The long-distance migration of monarchs is unique among butterflies. Mortality during the autumn migration (often referred to as fall migration) has been suggested as a contributing factor to the decline (Badgett and Davis, 2015; Ries et al., 2015a; Inamine et al., 2016; Agrawal and Inamine, 2018). Road mortality may significantly affect monarch survival during migration, especially where monarchs become highly concentrated as the migration narrows in Texas and northern Mexico (Badgett and Davis, 2015). Only McKenna et al. (2001) have previously evaluated monarch butterfly roadkill. They reported monarchs as the second-most killed butterfly species during six weeks of autumn in Illinois. They estimated that > 500,000 monarchs were killed statewide along interstate highways during one week in early September 1999 (McKenna et al., 2001). There are several unpublished citizen-science reports of locally high monarch roadkill occurrence in West Texas and northern Mexico during the autumn migration, with observed roadkill reaching 5.7 monarchs per meter near Monterrey, Mexico (Correo Real, 2015; Journey North, 2017). Incidences of high monarch road mortality in northern Mexico have led to the placement of road signs along portions of highways in to reduce speed in the presence of monarchs (Vangaurdia, 2016).

Monarch roadkill has yet to be quantified in relation to an overall population estimate. Seiler and Helldin (2006) point out that any sustained mortality factor, such as roadkill, can be especially damaging for species that are either approaching or are in an annual population decline, such as the monarch. The extent of monarch roadkill needs to be assessed to estimate its potential contribution to the population decline and support conservation planning. Our goal was to develop MaxEnt niche models for monarch road mortality during the autumn migration within the main migration pathway in Texas. The MaxEnt algorithm has been employed before to spatially investigate vehicle-animal collisions of birds and mammals (Ha and Shilling, 2017). The roadkill models were also projected throughout the Central Funnel, which is the identified main southern autumn migratory pathway within the Central Flyway for monarchs from Oklahoma to Mexico (Tracy, 2018; Tracy et al., 2018a). This study includes the first analysis of monarch roadkill data outside of Illinois, and the first development of a spatial roadkill model for an insect. Our specific objectives were to (1) conduct monarch roadkill field surveys within the Central Funnel in Texas, (2) develop MaxEnt niche models for roadkill within the Texas survey area, and project these models throughout the Central Funnel, (3) estimate monarch roadkill numbers within the survey area and the Central Funnel using both simple field survey-based and model-based extrapolation techniques, and (4) discuss the results in the context of monarch conservation and potential applications to other species of conservation concern.

2. Methods

2.1. Study species

The monarch autumn migration is uniquely accomplished by one generation. Adults begin migrating in late August to September from the summer breeding grounds, traveling to overwintering grounds in Central Mexico (Brower, 1995; Calvert and Wagner, 1999). Most migrants usually reach Oklahoma and North Texas in late September or early October (Calvert and Wagner, 1999; Monarch Watch, 2018a) and arrive at the overwintering grounds in November (Brower et al., 2006). There are two main migration routes, the Central Flyway and the Eastern or Coastal Flyway (Calvert and Wagner, 1999; Howard and Davis, 2009). The Central Flyway through the Great Plains is the most heavily traveled route (Howard and Davis, 2009), which narrows into the Central Funnel from Oklahoma southwards (Tracy, 2018; Tracy et al., 2018a).

Autumn migrants fly during the day and stop at night and during inclement weather to nectar and roost in trees and shrubs (Brower, 1996). These roosts may comprise a few individuals to several thousand individuals and may last one to several days (Davis and Garland, 2004; Howard and Davis, 2009). In the morning, roosting monarchs either resume migration or search for nectar. These behaviors are influenced by wind patterns or lipid levels (Brower, 1996; Davis and Garland, 2004). During unfavorable southerly winds, monarchs may roost for several days (Schmidt-Koenig, 1985). Migrating monarchs are observed to nectar in a variety of locations, including in right-of-ways (Brower et al., 2006), where they may be vulnerable to vehicle collisions. Brower et al. (2006) suggested that monarchs shift their behavior upon reaching Texas and spend more time nectaring to accumulate lipids for the winter and re-migration in the spring. Migrating monarchs regularly fly at high altitudes, around 300–500 m (Gibo and Pallett, 1979; Gibo, 1981, 1986), but may fly close to the ground, especially when facing headwinds or during overcast weather (Gibo, 1986; Brower, 1996), exposing them to road mortality. Citizen science observations also include reports of low flying fall migrating monarchs over roadways (Correo Real, 2015).

2.2. Monarch roadkill surveys and simple roadkill extrapolation

Monarch roadkill field surveys were conducted during the main autumn migration through the Central Funnel in Texas (Fig. 1). Four four-day surveys were conducted in each of the autumns of 2016 and 2017, between 10th October to 4th November and 3–27 October, respectively. The survey area was divided into four north to south sections, with surveys timed to generally occur after the dates of average peak migration (Journey North, 2017; Monarch Watch, 2018a) to allow time for the accumulation of road-killed monarchs. Observed monarch roadkill densities most likely represent accumulations of dead migrating monarchs over a period of one or two days to a few weeks during the main migration pulse through an area (Munguira and Thomas, 1992). Surveyed road types included (1) highways, (2) primary roads, and (3) secondary roads. Each survey location comprised at least a single 100 m by 1 m transect along the grassy edge of one side of the roadway. To assess if the side of the road surveyed influenced the number of dead monarchs, additional transects were surveyed across multiple edges of single and divided-lane highways at some sites. Transects were located using a handheld GPS device (accuracy up to ± 3 m). Roadkill transects were spaced according to travel and survey time constraints at about 30 to 100 km intervals along the primarily east to west pre-planned survey routes, with additional surveys in 2016 in the southwestern portion of the study area where high monarch roadkill was found (Fig. 1).

All dead monarchs or parts of monarchs were collected to estimate the total number and sex ratio of dead monarchs along transects. A similar spring monarch roadkill survey was conducted in Texas during April to May of 2017 (Fig. A.1; for details, see Appendix A, section 1.1). The boundary of the background evaluation extent for our roadkill study was defined by a 10 km buffer around a convex hull polygon formed using un-thinned 2016 to 2017 monarch roadkill survey data (Fig. 1). We extrapolated the mean roadkill counts for the three road

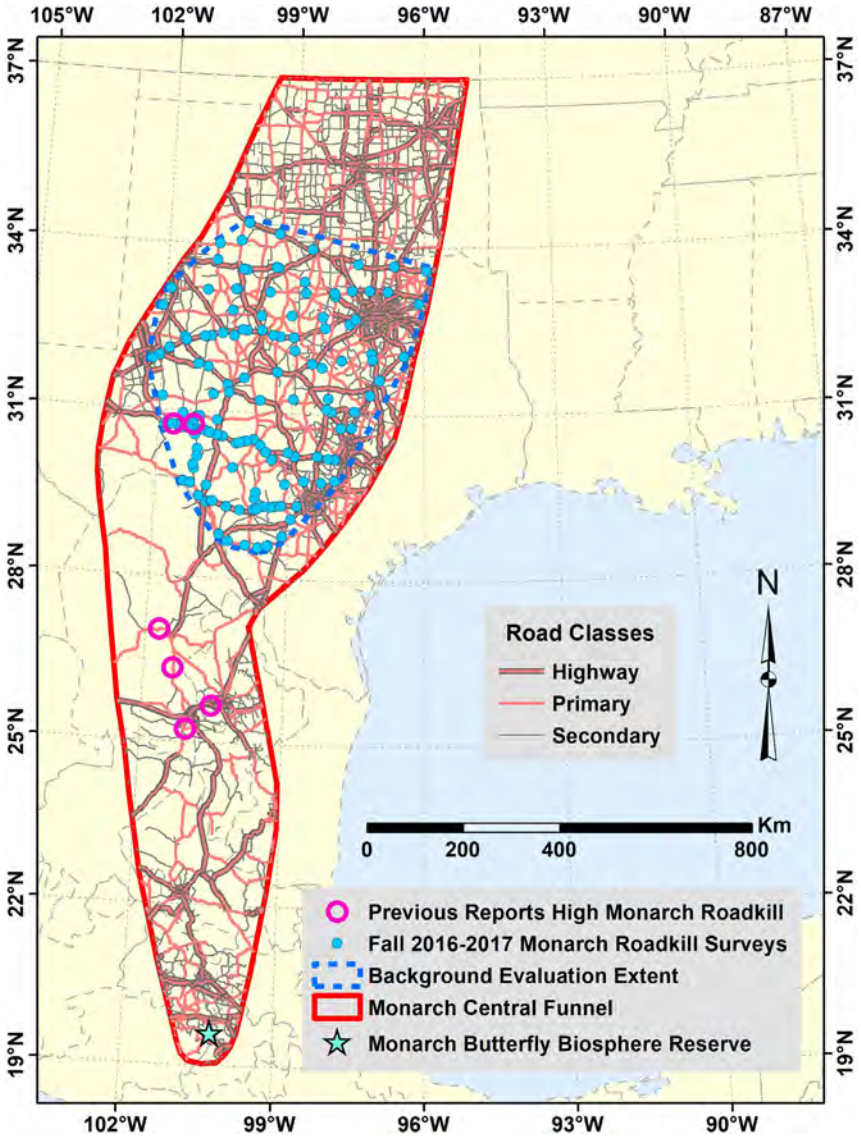

Fig. 1. Monarch roadkill survey 100 m transects for autumn 2016 and 2017 along three major road classes within the monarch Central Funnel in Texas.

types over the background evaluation extent and Central Funnel in a manner similar to that of McKenna et al. (2001). Roadkill rates in areas of locally high monarch roadkill (hotspots) can vary greatly between years and highly differ from other areas. Consequently, roadkill rates in hotspots can bias roadkill rates in larger areas if they are disproportionally represented in the sampling. Therefore, in some extrapolations, hotspot roadkill rates were considered separately for each year from non-hotspot locations. This separation allowed us to understand the importance of the roadkill hotspots within a year, and compare the hotspot differences between years. We also made roadkill extrapolations including hotspot roadkill rates with non-hotspot data and thinning the hotspot data in 2016 to be in proportion to the sample effort in non-hotpot locations (for details, see Appendix A, section 2.1).

2.3. Environmental variables

Thirty environmental variables were initially screened for use in the roadkill modeling (Table A.1, Fig. A.2). These variables were selected for their value in previous roadkill niche models and for their use in characterizing the environment of the study area. The variables consisted of nine topographic indices (including four stream indices), eight land cover indices, six road indices, three human population indices, and four climatic indices. All indices were either calculated at 30.8 m spatial resolution or resampled with bilinear interpolation to the 30.8 m resolution, to match the resolution of the base layer of 1 arc sec Shuttle Radar Topography Mission (SRTM) digital elevation model (DEM) data obtained from USGS Earth Explorer (https://earthexplorer.usgs.gov/). The high spatial resolution of 30.8 m facilitated modeling of roadkill along individual surveyed roadways over a broad area (see more details in Appendix A, section 7).

2.4. Monarch roadkill models

Preliminary MaxEnt model runs indicated that there was not enough data from 2017 to obtain good accuracy statistics for both single year models. Consequently, we combined 2016 and 2017 roadkill presence data, which were randomly spatially thinned to 2 km to reduce spatial autocorrelation. Ten thousand background points were randomly generated within the road mask evaluation area. We calculated background/presence versions of the area under the curve statistic (AUC_{bgp}) and true skill statistic (TSS_{bgp}) using R software (R Core Team, 2018) and the PresenceAbsence package (Freeman and Moisen, 2008). In the same manner, we calculated a presence/absence version of AUC (AUC_{pa}) and TSS (TSS_{pa}) using transects with no observed monarch

roadkill as absence data, although we acknowledge roadkill may have occurred in these absence locations as well. We adjusted the MaxEnt beta regularization value to two and used only quadratic and hinge features to reduce model complexity and overfitting for improving model generalization (Jiménez-Valverde et al., 2008; Warren and Seifert, 2011; Tracy et al., 2018b).

Roadway rasters served as a mask for analysis of environmental variables. The original set of 30 environmental variables was decreased to 20 variables. We dropped nine variables exhibiting zero or negative testing gain of AUC_{bgp} from a MaxEnt threefold jackknife run (Table A.1, Fig. A.3). We also dropped traffic volume because data were not readily available for Mexico. Traffic volume was utilized in preliminary niche models for the Texas background evaluation extent. Preliminary runs indicated that no substantial gain in model performance was achieved with > 10 of the 20 variables, and that employing fewer variables (three) substantially increased undesired high spatial variability in roadkill among models. Consequently, final MaxEnt roadkill models were developed from ten random sets of ten of the 20 variables to represent model variability due to variable selection. The absolute Spearman rank correlation of variables within random variable sets was limited to < 0.7 using the multiple randomized sequential forward selection procedure within the random subset feature selection algorithm (RSFSA) of Tracy et al. (2018b). The final MaxEnt models were calibrated to binary presence/absence format using a threshold of maximum TSS_{pa} (Liu et al., 2013) and combined using frequency consensus to form a feature subset ensemble. We also created presence/absence niche models for monarch roadkill using linear and quadratic binomial logistic regression with the R Glmnet package (Friedman et al., 2010) for the same ten random sets of ten of 20 variables. These presence/absence models produced lower AUC_{bgp} values and similar AUC_{pa} values compared to MaxEnt models, and these models were not investigated further (results not shown).

3. Results

3.1. Monarch roadkill survey and simple roadkill extrapolation

We surveyed 16.1 km of roadsides (161,100 m transects), 8.8 km in 2016 and 7.3 km in 2017. We found 581 dead monarchs in 59 locations (102 absence locations) for an average of 3.4 monarchs per transect. We found 546 dead monarchs in 2016 and 35 in 2017 (for raw survey count data, see Appendix A, section 3.1). Of the 546 monarchs in 2016, 499 (91%) were located along or near IH-10 between Sonora and Sheffield (23 of 95 transects) (Fig. 2). This area was defined as a single large 2016 hotspot area extending 95 km along Interstate Highway (IH) 10 from Sonora to 24 km east of the Pecos River. This hotspot included a portion of Texas state highway (SH) 163 extending from 7.6 km south of Ozona to 5 km north of Ozona and a 2 km section of SH-137 extending west from the junction with SH-163. The hotspot was bounded along IH-10 in the west and east by counts of 15 and 10 roadkill per 100 m, and included counts of 21 and 6 roadkill per 100 m on SH-137 and SH-163, respectively. About 93% (466/499) of the dead monarchs in the 2016 hotspot occurred in 14 transects ranging from 10 to 66 per 100 m (Fig. A.4). A total of 257 monarchs were sexed in 2016–2017, of which ca. 38% were female (n = 98). The portion of females was 41% in 2016 (132 males, 91 females) and 21% in 2017 (27 males, 7 females). After the 2 km spatial thinning for spatial modeling, the field survey data consisted of 151 transects (53 presence and 98 absence) and 249 individual dead monarchs. Only two road-killed male monarchs were found among 54 transects in our spring 2017 roadkill survey (Fig. A.1).

Southern edges of roadsides contained 43.8% (± 36% SD, n = 13) of the roadkill found in the northernmost edge for both single and divided-lane roads. This relationship was used to estimate roadkill across all two to four edges per roadway when extrapolating roadkill per km per year (for details, see Appendix A, section 5). Estimated roadkill per km ranged from 6.15 to 645 monarchs per km depending on year, road type, and location in relation to the hotspot area (Table 1). In 2016, mean estimated roadkill per km along highways was significantly higher within the Sonora-Sheffield hotspot (645.38; SD = 446.92; n = 15) compared to outside the hotspot (12.64; SD = 22.30; n = 22) (P = 0.00008; Welch *t*-test). Between years, the estimated roadkill per km generally varied widely among road types, and there was no evidence of any hotspot in 2017 (Table 1). Estimates of roadkill within the hotspot area in 2016 and 2017 ranged from about 74,000 to 5000, representing about 10% and 1% of the entire mortality within the Texas background evaluation extent. Using the field survey data from the whole area, including the randomly thinned hotspot data, the estimated roadkill for the Central Funnel in 2016 rose to over 3.5 million monarch butterflies (Table 1). The estimate for 2017 was 1.1 million road-killed monarchs. Combining the data from both of the years yielded an annual estimate of 2.1 million road-killed monarchs. When the hotspot data were separated from the survey data, total estimated annual roadkill rates in 2016 and 2017 were about 1.6 million and 1.0 million monarchs, respectively. In 2016, about 47%–49% of the roadkill within the Central Funnel was projected to occur within the Texas background evaluation extent, of which 5% was projected to occur in the Sonora-Sheffield hotspot area. In 2017, only about 0.3% of the roadkill within the Central Funnel was projected within the hotspot area, and the percent roadkill in the background area ranged from 31% when hotspot data were analyzed separately to 48% when data from the hotspot area were included (Table 1, Appendix A, section 2).

3.2. Monarch roadkill model

The feature subset ensemble of ten MaxEnt roadkill niche models provided excellent discrimination of roadkill presence locations from background locations within the background evaluation extent, with AUC_{bgp} values ranging from 0.82 to 0.88 (0.86 ± 0.02, mean ± SD). The models provided marginally poor discrimination of roadkill presences from absences observed in the field, with AUC_{pa} values ranging from 0.60 to 0.67 (0.64 ± 0.02, mean ± SD). Among the top eight variables with the highest permutation importance in the MaxEnt models (Table 2) were three human population density indices and two climatic indices. Other top ranked variables included elevation (m), road density over a 3 km radius (km/~28 km^2), and percent cover of artificial surfaces within a 500 m radius. Traffic volume (annual average daily traffic, AADT) ranked third in permutation importance in preliminary models but was not available for Mexico, precluding its use in our final models.

The MaxEnt response curves for population density indices all indicated that lower human population densities had higher association with monarch roadkill (Fig. 3A, E). The climatic indices indicated that roadkill was associated with more arid climates (Fig. 3B, C). Lower road densities and lower percent cover of artificial surface were also associated with higher monarch roadkill (Fig. 4F, G). The response curve for traffic volume, which was not used in the final models, indicated that the highest roadkill was associated with lower traffic volume. The traffic volume response curve was very similar to that of percent cover of artificial surface (Fig. 3G, H), with which it was moderately correlated (r_s = 0.58).

The proportion of MaxEnt models projecting monarch roadkill generally increased from northeast to southwest within both the background evaluation extent and Central Funnel (Fig. 4; see Appendix Section 5 for embedded zipped shapefile of MaxEnt consensus model). The highest number of models projected roadkill within much of southwest Texas and Mexico in the Central Funnel. None of the MaxEnt models projected monarch roadkill over most of the northeastern Central Funnel, including the Dallas/Fort Worth metroplex and most of eastern Oklahoma.

Roadkill extrapolations for each of the ten individual MaxEnt models were made across each year and both years combined.

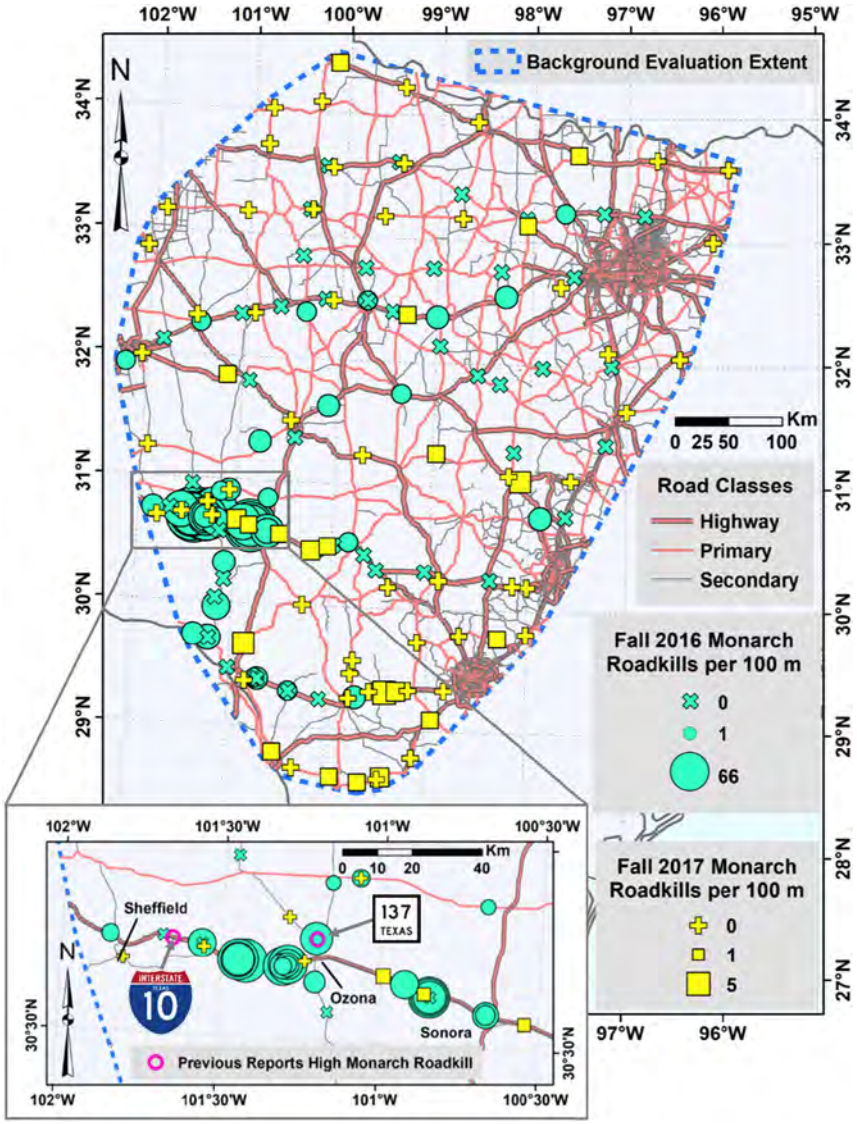

Fig. 2. Monarch roadkill autumn 2016 and 2017 survey results for 100 m transects along major road classes within the background evaluation extent in the monarch Central Funnel in Texas, including previously reported locations of high monarch roadkill.

Extrapolations were based upon roadkill rates per km for presence-only transects (no zero roadkill data) of each road type that were multiplied by the MaxEnt model predicted lengths of roadkill presence for the road type. Roadkill rate calculations for extrapolations included data from hotspot transects that were thinned for 2016 as done for simple extrapolations (for details, see Appendix A, sections 2.1, 5). Extrapolating roadkill rates across the Central Funnel, we estimated averages of 3.0 ± 0.7 and 1.1 ± 0.3 million (mean ± SD) road-killed monarchs for 2016 and 2017, respectively (Tables 1, A.2). Combining roadkill data across both years for the Central Funnel yielded annual roadkill rates of 2.1 ± 0.5 million. The mean projected percentage of road-killed monarchs in the Central Funnel that occurred within the Texas background evaluation extent ranged from 67% to 68% in 2016 and 2017 (Tables 1, A.4).

4. Discussion

4.1. Monarch roadkill survey

In our 2016 roadkill survey (but not 2017), we found a Sonora-Sheffield, Texas, monarch roadkill hotspot that corresponds to the only two previous citizen-science reports of monarch roadkill hotspots in the US (Fig. 2). It is unclear why hotspots have repeatedly occurred in this area. The hotspot location may be partly related to higher densities of migrating monarchs in more southern areas of the Central Funnel. In addition, local stochastic weather events probably influence the occurrence of roadkill hotspots, such as unfavorable winds that may induce lower monarch flight patterns or extended roosting and nectaring behavior close to the ground in the vicinity of roadways. More research is needed to evaluate how frequently roadkill hotspots occur in this region. It is possible that one or both years represent an outlier, and that hotspots may occur in additional areas.

The variation in roadkill rates observed between the two years of our survey was consistent with other roadkill studies (Seiler and Helldin, 2006). Our overall roadkill rates varied from 6 to 646 dead monarchs per km depending on year, road type, and location (Table 1). This range falls within previous reports for monarchs of from 1.3 to 11.9 butterflies per km per week in Illinois (McKenna et al., 2001) to a very high number of 115 road-killed monarchs within a 20 m stretch along toll highway 40D southwest of Monterrey, Mexico in October 2015 (Correo Real, 2015; see Appendix A, section 8 for data). Reported roadkill rates for other butterflies have ranged from 0.45 to 80 per km per day in North America, Asia, and Europe (Rao and Girish, 2007, De la Puente et al., 2008, Yamada et al., 2010, Skórka et al., 2013, Baxter-

Table 1
Monarch roadkill estimates per year for 2016 to 2017 over the Sonora-Sheffield roadkill hotspot, Texas background evaluation extent (BEE) and the Central Funnel (Figs. 1–2) from the field data by road type using simple extrapolation or MaxEnt model projections.

Year	Millions of monarch roadkill[a]						
	Simple extrapolation					MaxEnt model extrapolations $\bar{X} \pm$ SD (n = 10)[b]	
	Hotspot data separated			Hotspot data included		Hotspot data included	
	Sonora-Sheffield hotspot	Texas BEE	Central Funnel	Texas BEE	Central Funnel	Texas BEE	Central Funnel
2016							
Millions of dead	0.074	0.768	1.570	1.663	3.554	2.050 ± 0.760	3.041 ± 0.743
% Overwintering population[c]	0.09%	0.90%	1.82%	1.93%	4.03%	2.36 ± 0.86%	3.46 ± 0.82%
% Texas BEE mortality	9.58%						
% Central Funnel mortality	4.69%	48.95%		46.78%		66.48 ± 14.79%	
2017							
Millions of dead	0.005	0.492	1.042	0.533	1.131	0.738 ± 0.272	1.084 ± 0.258
% Overwintering population[c]	0.01%	0.79%	1.67%	0.86%	1.81%	1.19 ± 0.43%	1.73 ± 0.41%
% Texas BEE mortality	1.02%						
% Central Funnel mortality	0.32%	31.34%		47.16%		68.86 ± 14.18%	
2016–2017							
Millions of dead	0.058	0.561	1.138	0.995	2.118	1.460 ± 0.540	2.119 ± 0.510
% Overwintering population[c]	0.09%	0.91%	1.82%	1.59%	3.33%	1.96 ± 0.71%	2.82 ± 0.66%
% Texas BEE mortality	10.25%						
% Central Funnel mortality	3.66%	35.75%		27.99%		67.90 ± 15.08%	

[a] Mean roadkill rates (roadkill/km/year) (Table A.2) by road type for extrapolations are calculated from transects in the Texas BEE and incorporate estimates for all road edges. Roadkill rates are multiplied by length of road in various areas to obtain extrapolations (see Table A.3 for road lengths used in simple road type extrapolation) (for all calculations, see Appendix A, section 5).
[b] See Table A.4 for individual MaxEnt model estimates.
[c] Based on 84.61 (2016) and 61.4 (2017) million overwintering monarchs (Monarch Watch, 2018b). Estimated from 21 million monarchs per hectares overwintering (Thogmartin et al., 2017).

Gilbert et al., 2015).

The observed sex ratios of roadkill monarchs were also consistent with previous studies. About 38% of the dead monarchs in our autumn field surveys were females, ranging from 21% in 2017 to 41% in 2016. These figures generally match two separate citizen science observations on the percentage of female monarch roadkill in Mexico of 27% and 36% in October 2015 (Correo Real, 2015). They also are within the range reported from the other roadkill study (McKenna et al., 2001), as well as studies of sex ratios during migration (Borland et al., 2004) or on the overwintering grounds (Steffy, 2015). Davis and Rendón-Salinas (2010) found a decreasing trend (~10%) in percent female monarchs at the Mexican overwintering sites from 1976 to 2008, which they suggested could reflect female biased mortality due to the protozoan parasite *Ophryocystis elektroscirrha*.

While our estimates of monarch roadkill are likely conservative, carcass persistence is not likely to be a major source of bias. However, we did not evaluate persistence in our study, which could vary based on various factors, such as region, time of year, and weather conditions.

Munguira and Thomas (1992) placed butterfly specimens on roadsides and found that only one of their 50 specimens disappeared during

Table 2
MaxEnt model variable permutation importance for 19 variables used in ten random sets of ten of the 20 variables in monarch roadkill models.

Variable[a]	Abbreviation	Permutation importance[b], mean ± SD
Human population density per km^2 in 9 km radius (population/254.47 km^2)	*popden9kr*	44.2 ± 3.8 (3)
Autumn quarterly mean monthly actual evapotranspiration/potential evapotranspiration × 1000	*etrt_autq*	41.7 ± 23.3 (2)
Annual mean monthly rainfall (mm)	*prec_ann*	36.4 ± 15.6 (4)
Human population density per km^2 in 3 km radius (population/28.27 km^2)	*popden3kr*	30.1 ± 0.0 (1)
Elevation (m)	*elev*	27.9 ± 5.5 (4)
Distance to urban areas (areas with ≥300 humans per km^2) (km)	*urbdist*	27.1 ± 10.8 (4)
Road density, km road in 3 km radius (km/28.27 km^2)	*roadden3kr*	19.6 ± 2.4 (2)
Artificial surfaces % cover in 500 m radius	*artsur_500mr*	13.4 ± 3.2 (3)
Autumn quarterly mean monthly maximum temperature (°Celsius)	*tmax_autq*	10.5 ± 9.8 (3)
Distance to highways (m)	*hwydist*	10.4 ± 2.5 (7)
Latitude (decimal degrees)	*latitude*	6.4 ± 4.3 (3)
Grasslands % cover in 500 m radius	*grslnd_500mr*	5.6 ± 3.4 (9)
Autumn mean quarterly wind speed (m/s)	*wndsp_autq*	5.6 ± 5.4 (4)
Distance to secondary roads (m)	*secrddist*	5.1 ± 2.9 (8)
Shrublands % cover in 500 m radius	*shrub_500mr*	4.5 ± 3.4 (9)
Distance to primary roads (m)	*primrddist*	2.3 ± 3.0 (4)
Road density, km road in 500 m radius (km/0.79 km^2)	*roadden500mr*	2.2 ± 3.8 (5)
Distance to high flow accumulation areas (> 60,000 ~km^2 upslope grid cells) (m)	*strmhiflodist*	1.2 ± 1.0 (5)
Topographic Position Index (TPI), 3 km radius	*tpi3kr*	1.0 ± 0.2 (5)
Cultivated land % cover in 500 m radius[c]	*cult_500mr*	0.0 ± 0.0 (0)

[a] See Table S1 for sources of variables. Variables ordered from highest to lowest mean permutation importance.
[b] Permutation importance of the variable in the MaxEnt models, number of models in which the variable was used out of the 10 random models in parentheses.
[c] Cultivated land layer was initially included in all 10 random models, but it was not included by MaxEnt in calculating any of the models.

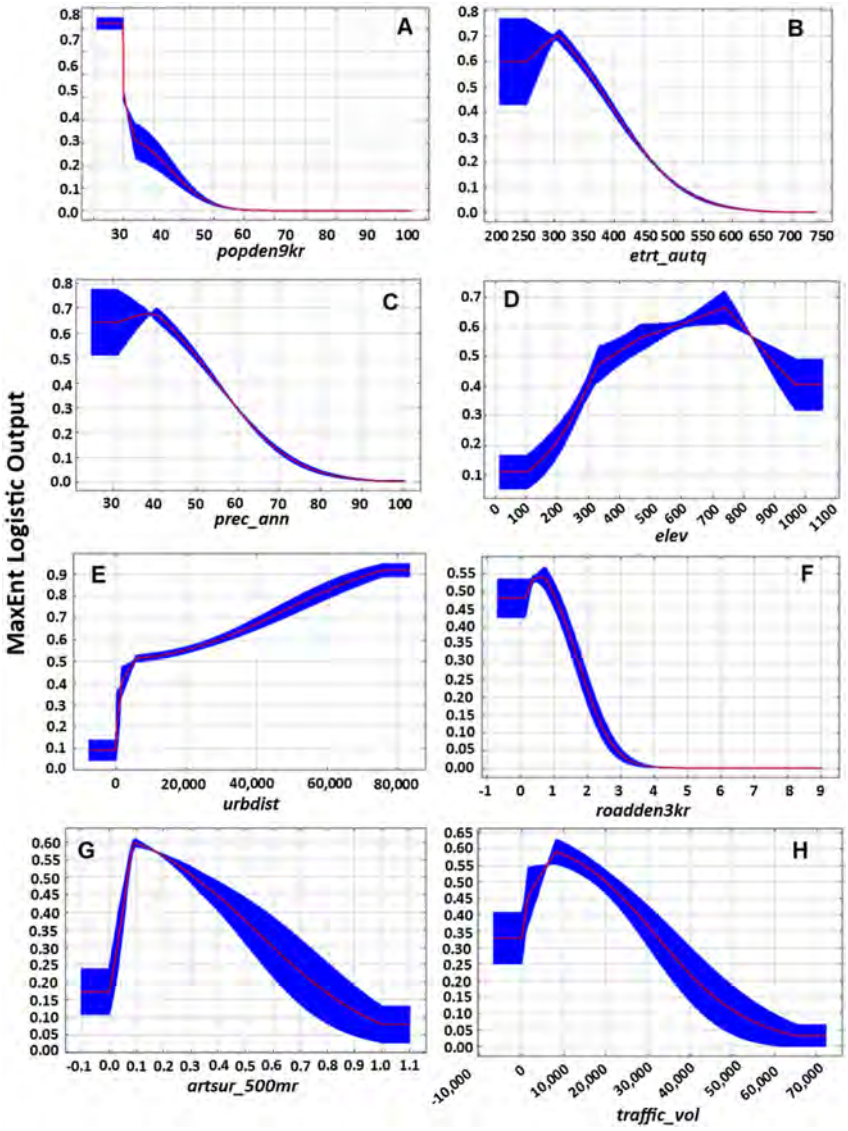

Fig. 3. MaxEnt variable response curves (logistic output probability of presence vs. variable) representative of the final ten models (A–G) and for a 30-variable model (H): (A) popden9kr, (B) etrt_autq, (C) prec_ann, (D) elev, (E) urbdist, (F) roadden3kr, (G) artsur_500mr, (H) traffic_vol (traffic volume for 2015) (see Table 2 for abbreviations and permutation importance).

two weeks (daily loss rate of 0.15%). Several factors contribute to the conservative nature of our estimates, including the difficulty in detection of dead monarchs, especially in taller vegetation, shredding of dead monarchs by roadside mowing, and a portion of the monarchs remaining attached to the colliding vehicles (McKenna et al., 2001; Seiler and Helldin, 2006). However, several studies indicate that road killed butterflies are mostly blown to the roadside edge, with individuals rarely trapped in car grills (Munguira and Thomas, 1992; Ries et al., 2001). The overall agreement of our roadkill results with previous studies in terms of the range of roadkill rate variability and sex ratios supports the reliability of the data for extrapolating monarch road mortality according to road types and spatial modeling.

4.2. Monarch roadkill models

4.2.1. Roadkill projections

Most of the MaxEnt models projected monarch roadkill from the southwestern portion of the Central Funnel from West Texas to Mexico (Fig. 4). Our MaxEnt consensus projection agrees with all seven of the previously known citizen science reports of monarch roadkill hotspots in North America (Fig. 4), including two hotspots in West Texas (Journey North, 2017) and five hotspots in northern Mexico (Correo Real, 2015; Rogelio Carrerra, Universidad Autonoma de Nuevo Leon, Nuevo Leon, Mexico, personal communication).

Our annual MaxEnt based roadkill estimates for monarch mortality throughout the Central Funnel was 3.0 to 1.1 million for 2016 and 2017, respectively. These MaxEnt roadkill estimates were similar to those based on simple roadkill extrapolation by road type when hotspot data were included (3.6 and 1.1 million, respectively). Most of the roadkill projected by MaxEnt models outside of the study area occurred in Mexico, indicating that more MaxEnt models are projecting roadkill along the sparser road network within the Central Funnel over northern and central Mexico than in the northern parts of the funnel (Fig. 4). As the autumn migration pathway narrows in the South, migrating monarchs become more concentrated in the Central Funnel. This higher concentration may contribute to higher roadkill densities in the southern parts of the Central Funnel in Mexico, where most previous reports of monarch roadkill hotspots originate (Fig. 4). Although our models project some increased southward mortality risk, additional data are needed to assess the extent of this risk in Mexico. The extrapolations including the hotspot data with other roadkill data and projecting higher annual roadkill of up to 3.6 million in the Central Funnel

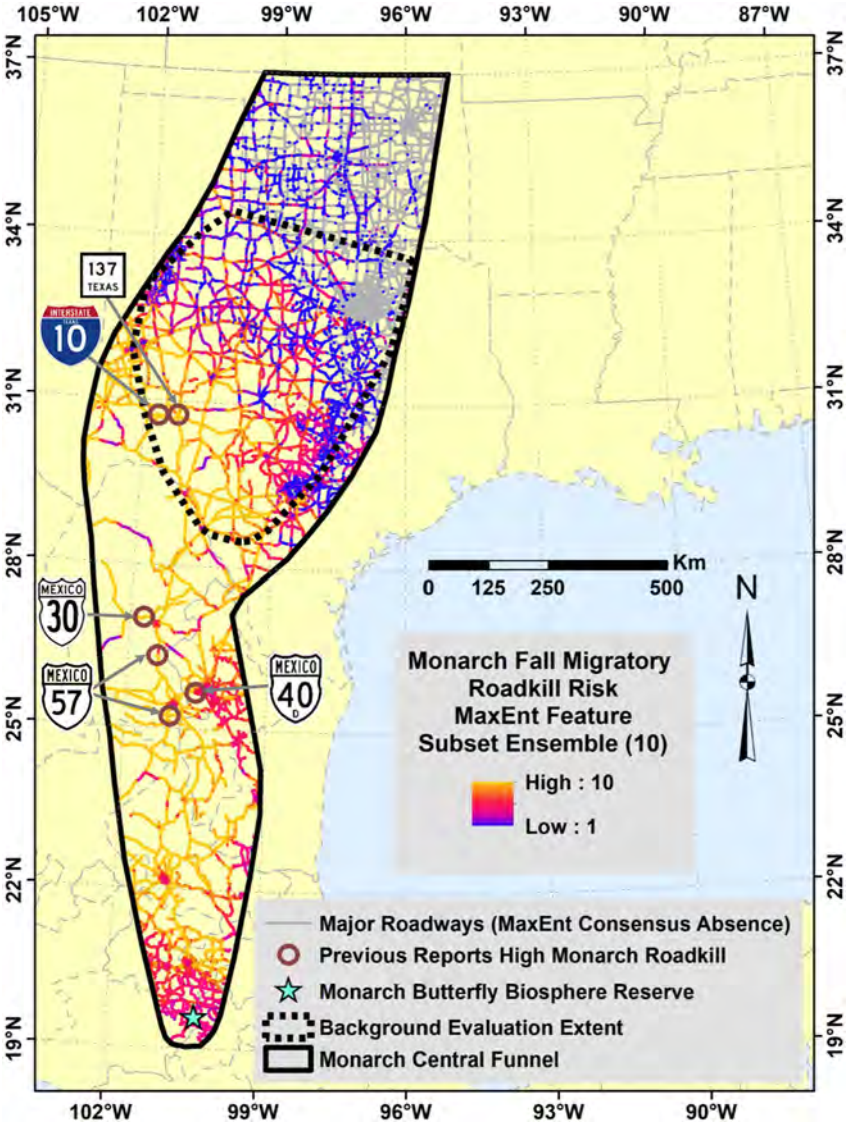

Fig. 4. MaxEnt frequency consensus for feature subset ensemble of ten models developed from random subsets of ten of 20 variables correlated < 0.7 (see Appendix Section 5 for embedded zipped shapefile of MaxEnt consensus model).

should be more realistic considering the occurrence of multiple roadkill hotspots in Mexico of higher density than seen in Texas. The MaxEnt models project little to no roadkill in the northeastern part of the funnel area, including the Dallas/Fort Worth area and eastern Oklahoma. However, some roadkill likely does occur in this area, but possibly at a lower rate than in the more southern areas of the Central Funnel. Further research and field surveys are needed to verify roadkill rates outside of our survey area in the southern and northern parts of the Central Funnel. Additional data may allow effective use of roadkill density models, rather than presence only MaxEnt models used in this study. Roadkill density models can better reveal regional roadkill patterns useful in refining projections, especially for northern Mexico where roadkill could be much higher than in Texas. Roadkill field surveys from other parts of the autumn migration pathways could improve estimates for the total impact of roadkill on the monarch population.

4.2.2. Factors affecting roadkill

MaxEnt projections of monarch roadkill within the Central Funnel were generally associated with more arid climate and less densely populated areas (Fig. 3). These conditions generally describe those for the seven previous monarch roadkill hotspots reported from Texas and Mexico, with the possible exception of the roadkill hotspot in the vicinity of Monterrey, Mexico (Fig. 4). This could be related to a variety of factors. For example, autumn migrating monarchs have been observed to spend additional time flying lower to the ground during the afternoon in desert areas, perhaps to seek shelter from the heat or find nectar (Journey North, 2018). Monarchs may need to spend more time searching for nectar in arid environments, although this has not been evaluated. Finally, the increased roadkill rates may simply reflect the increased number of monarchs in more southern areas of the Central Funnel. This southern locality factor cannot be associated with most of the predictors, with the exception of latitude, but it may have the highest influence. Local climate, weather patterns, and geography affect monarch movement and behavior, and they all are likely important contributors to road mortality. Wind patterns (direction, duration, and speed) may especially be more important than anthropogenic factors, but short-term weather events could not be incorporated in the models. Occurrence of these weather events is also highly variable and difficult to predict.

Traffic volume has been noted as one of the most important variables in previous roadkill studies (Bennett, 2017). Traffic volume ranked high in importance in our preliminary roadkill models, but we found that model accuracy (AUC) was not significantly affected by its

removal. Other variables that were correlated with traffic volume likely compensated for its absence, including human population density, artificial surface cover, distance to urban areas (km to population ≥ 300/km^2), and road density. In our models including traffic volume, the highest roadkill was associated with fairly low AADT values, similar to the study by McKenna et al. (2001). In general, higher roadkill has been associated with higher traffic volume due to increased probability of vehicle collisions (Seiler and Helldin, 2006; Skórka et al., 2013). Samways (1994) suggested that roads with high traffic volume serve as corridors for high butterfly mortality. In our study, low traffic volume, along with related anthropogenic variables, is correlated with locations of monarch roadkill hotspots, but may not be directly related to the roadkill mortality. As the human population grows, traffic volume should increase, including in the lower traffic volume monarch roadkill hotspot areas, likely leading to higher roadkill rates (Bennett, 2017).

4.2.3. Spatial and temporal variation

Over 70,000 monarch roadkill were estimated in the Sonora to Sheffield, Texas hotspot in 2016, compared to about 5000 in 2017. This illustrates the high spatio-temporal variability of roadkill and the potential contribution of hotspots to the monarch road mortality. The timing of our field surveys relative to the peak migration in those years may have varied among transect locations and years, which could have influenced our results. If peak migration occurred after our field surveys in one or both years, we may have underestimated roadkill numbers. For example, the autumn migration in 2017 was later than usual due to unusually hot summer (Agrawal and Inamine, 2018). Few other studies have identified roadkill hotspots for butterflies (but see Samways, 1994, Her, 2008). Monarch roadkill hotspots may vary from year to year and may be difficult to locate or may not occur in some years.

We observed much higher monarch road mortality during autumn migration than in the spring (Fig. A.1), indicating that seasonality is a factor contributing to monarch roadkill rates. However, the monarch spring migration is more spatio-temporally dispersed making comparisons difficult. Temporal variability can occur between years, within the migration phase, or even within a day. For example, monarch behavior, such as flying low in the mornings (McKenna et al., 2001), probably affects the risk of roadkill at different times of day. Temporal patterns affecting monarch roadkill should be investigated further. Other sampling methods may be effective in detecting additional roadkill hotspots, such as adaptive cluster sampling, which was developed for inventorying scattered and clustered phenomena (Thompson, 1990). More frequent samples in a given location can also be critical for detecting roadkill hotspots (Santos et al., 2015).

4.3. Implications and impacts in relation to monarch conservation

4.3.1. Autumn migration mortality

Butterfly roadkill is a density independent mortality factor (Rodewald and Gehrt, 2014) with the incidence of roadkill being subject to high variability. Consequently, roadkill percentage of the migrating population is very unpredictable in any given year. We estimated a conservative annual percentage of migrating monarchs subject to road mortality in the Central Funnel by dividing a roadkill estimate by the sum of overwintering populations and roadkill estimate (overwintering cohort). The size of the overwintering populations is calculated by multiplying the hectares of roosting monarchs at the Mexican overwintering sites from Rendón-Salinas et al. (2018) by the value of 21.1 million monarchs per ha suggested by Thogmartin et al. (2017). Based on these amounts, the estimated annual roadkill rates from our combined years of 2016–2017 MaxEnt models in the Central Funnel represent an average of 2.8% (2.1 million) of the overwintering cohort. In 2016, roadkill within the Central Funnel may have represented about 4.0% of the overwintering cohort (Table 1). The corresponding roadkill for 2017 ranges from 1.5% to 1.8% of the overwintering cohort. In contrast, the projection of 500,000 road-killed monarchs by McKenna et al. (2001) in Illinois during one week in 1999 represents only 0.26% of the overwintering cohort that year (191 million, 9.05 ha), indicating potentially lower roadkill rates for areas north of the Central Funnel in some years.

The actual monarch population decline within a given year can be much higher than the differences in overwintering cohort sizes from year to year, since it includes the unknown quantities of butterflies recruited, or not recruited due to habitat loss, during spring and summer breeding. Mortality at the Mexican overwintering sites due to occasional winter storms can produce very high mortality, estimated at around 75% in 2002 (Brower et al., 2004) and > 40% in 2016 (Brower et al., 2017). Average monarch overwintering mortality is around 36% ± 21% (n = 7; range 4–55%) based on data from Ries et al. (2015b; see their Fig. 24.7). Lowered recruitment due to loss of milkweed habitat has been identified as the primary factor in monarch population declines (Pleasants, 2017; Thogmartin et al., 2017), with losses of milkweed resources in Iowa estimated at 76% from 1999 to 2014 (Pleasants et al., 2017). Other studies place more importance on mortality during the autumn migration in the decline of monarchs (Badgett and Davis, 2015; Inamine et al., 2016; Agrawal and Inamine, 2018). Consequently, it is complex to evaluate the relative importance of roadkill to other factors in the monarch population decline, but it is probably lower compared to the factors of milkweed habitat loss and overwintering mortality. Northward expansion of the monarch summer breeding range is anticipated with climate change (Batalden et al., 2007; Lemoine, 2015), making the southward autumn migration route even longer, increasing both exposure to traffic and associated road mortality (Badgett and Davis, 2015). Monarch roadkill during autumn migration should be further evaluated in the context of other mortality factors along the migration path (Baxter-Gilbert et al., 2015).

Brower et al. (2012) fitted an exponential decline curve to the estimated monarch overwintering populations (ha) in Mexico from 1995 (winter 1994–1995) to 2011 (P = 0.015, R^2 = 0.336). Inclusion of seven additional years of data through 2018 (Vidal and Rendón-Salinas, 2014; Monarch Watch, 2018b) strengthens fit of an exponential curve ($y = ae^{bx}$ Fig. 5) (P = 0.0009; adjusted R^2 = 0.486; ZunZun.com, 2018). A concave exponential curve represents the most serious form of species population decline, indicating constant proportional negative pressure on the population (Di Fonzo et al., 2013). A standard geometric population growth curve, fit to the modeled exponential curve,

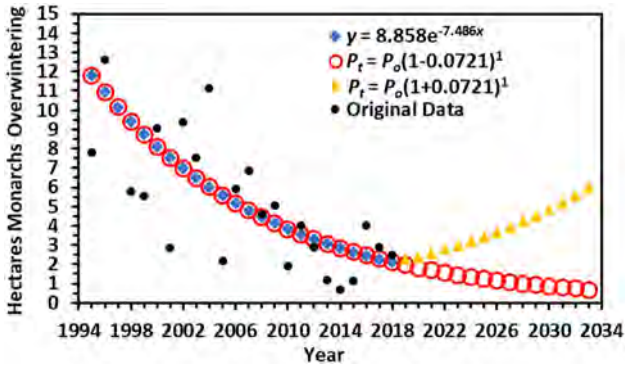

Fig. 5. Annual monarch population in hectares in Mexican overwintering sites from 1995 to 2018 (original data, black circles; Vidal and Rendón-Salinas, 2014; Monarch Watch, 2018b) with fitted exponential curve, $y = ae^{bx}$ (adjusted R^2 = 0.49; P = 0.00009; blue diamonds), and corresponding geometric population growth equation curve, $P_t = P_o(1 + r/n)^{nt}$, where P_t is the final hectares (2.11), P_o is the initial hectares (11.79), t is the number of years (23), n is the number of sub-periods (1), and r is the population growth (or declination) rate (derived population declination of 7.21% per year; open red circles). Fifteen years to restore 6 ha of overwintering monarchs based on totally reversing the current decline to 7.21% growth per year (gold triangles). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

reveals an average − 7.21% annual population decline over the last 23 years associated with an overall 82% population reduction (for details, see Appendix A, section 8). In comparison, a fitted exponential curve until 2011, as used by Brower et al. (2012), yielded a slightly lower annual decline rate of 6.46%. The updated results indicate that the decline rate may have increased or at least has not slowed down. Continuance of the 7.21% rate of decline would result in an average of 0.24 ha of overwintering monarchs occurring in 29 years (by 2046–2047), greatly increasing the chance of extirpation of eastern migrating monarchs by an extreme winter storm mortality event as the overwintering population crosses below the 0.25 ha quasi-extinction threshold (Semmens et al., 2016). A total reversal of the 7.21% annual monarch decline, coupled with an annual 7.21% population increase (net change 14.4%), would be needed to restore the size of the overwintering population to current conservations goal of six hectares (Thogmartin et al., 2017) over the next 15 years. A 0.5% annual reduction in migrating monarch mortality through roadkill mitigation could significantly contribute to a reversal in the long-term 7.2% annual exponential decline in monarch populations (Fig. 5).

4.3.2. Roadkill mitigation

While some major factors in the monarch decline are difficult to reduce, such as overwintering mortality, the opportunity for reducing road mortality is possible through roadkill mitigation (see Rytwinski et al. (2016) for a review on mammal roadkill mitigation). The potential ability to locate re-occurring monarch roadkill hotspots could facilitate more effective mitigation. Scattered and unpredictable monarch roadkill would be more difficult to mitigate. A variety of roadkill mitigation measures have been implemented for danaine migratory butterflies. In Taiwan, a four-meter high net was placed along a 400 m section of bridge on National Freeway 3 to successfully induce spring migrating purple crow butterflies (*Euploea* spp.) to fly over and above the traffic, reducing on site roadkill from around 2.5% to 0.5%. In addition, an outer traffic lane was closed when > 500 butterflies per minute were crossing (Her, 2008; Taiwan EPA, 2010). In response to heavy autumn migratory monarch roadkill observed in Coahuila state of Mexico, traffic signs were posted in 2015 limiting the maximum speed to 60 km per hour (37 mph) in the presence of monarchs (Miranda, 2015). Police have been observed slowing traffic in Nuevo Leon state in Mexico to reduce monarch mortality along a highway south of Monterrey (Dr. Orley R. Taylor, personal communication). Additional research is needed to test and assess the effectiveness of these types of butterfly roadkill mitigation strategies for monarch roadkill hotspots in west Texas and Mexico.

5. Conclusions

Our study represents a novel approach for projecting roadkill of a migratory insect through ecological niche modeling. Annual monarch roadkill rates during autumn migration varied substantially. We found close agreement between two methods of estimating monarch roadkill rates, simple extrapolation by road type and MaxEnt roadkill model projections. We project about 1.0 to 3.6 million road-killed monarchs per year during autumn migration over the Central Funnel, which could represent 2–4% of the Mexican monarch overwintering population. MaxEnt model roadkill projections also aligned with several previously known monarch roadkill hotspots, which suggests MaxEnt models could be used to identify additional monarch roadkill within the Central Funnel. Roadkill rates may differ throughout the Central Funnel compared to those observed in the Texas survey area, and should be further investigated. Monarch road mortality should also be investigated along the Coastal Funnel, especially from Texas to Mexico. We recommend more detailed investigation into the spatial and temporal variability in monarch road mortality in the Central Funnel, including how local and short-term weather events, especially related to wind, influence monarch roadkill hotspots. With the new information on monarch road mortality in the Central Funnel, conservation efforts could be implemented to mitigate mortality at monarch roadkill hotspots. Reducing roadkill rate over the Central Funnel for the eastern monarch population is as an important step towards reversing the continuing decline of this iconic butterfly.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.01.008.

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Historical patterns of wildfire ignition sources in California ecosystems

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Abstract. State and federal agencies have reported fire causes since the early 1900s, explicitly for the purpose of helping land managers design fire-prevention programs. We document fire-ignition patterns in five homogenous climate divisions in California over the past 98 years on state Cal Fire protected lands and 107 years on federal United States Forest Service lands. Throughout the state, fire frequency increased steadily until a peak *c.* 1980, followed by a marked drop to 2016. There was not a tight link between frequency of ignition sources and area burned by those sources and the relationships have changed over time. Natural lightning-ignited fires were consistently fewer from north to south and from high to low elevation. Throughout most of the state, human-caused fires dominated the record and were positively correlated with population density for the first two-thirds of the record, but this relationship reversed in recent decades. We propose a mechanistic multi-variate model of factors driving fire frequency, where the importance of different factors has changed over time. Although ignition sources have declined markedly in recent decades, one notable exception is powerline ignitions. One important avenue for future fire-hazard reduction will be consideration of solutions to reduce this source of dangerous fires.

Additional keywords: arson, debris burning, equipment, lightning, powerlines, smoking.

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Introduction

Increasing concern over wildfires has prompted a re-emphasis by the federal government to stop this trend (https://www.doi.gov/pressreleases/secretary-zinke-directs-interior-bureaus-take-aggressive-action-prevent-wildfires, accessed 1 April 2018; Bedard 2017). For many decades, the focus of fire management has been on fuel modification with success on certain landscapes (Kalies and Kent 2016) but limited improvement on others (Keeley and Safford 2016). Because humans are a dominant ignition source over the majority of North America (Balch *et al.* 2017; Syphard *et al.* 2017) there is reason to believe improvements in fire prevention may be a key to reducing fire impacts. Indeed, the United States Forest Service (USFS) has been reporting fire causes since it began collecting systematic data on fires in 1905, with the explicit purpose of helping land managers design fire prevention programs (Donoghue 1982*a*).

Effective fire-prevention requires a sound understanding of the patterns and causes of fire ignitions, which are closely aligned with both human and biophysical-landscape characteristics (Syphard *et al.* 2008). Prestemon *et al.* (2013) suggested a conceptual model that linked ignitions to changes in biophysical, societal, prevention and management variations that illustrates the complexities of ascertaining relationships between different sources and how they change over time.

An important characterisation of anthropogenic ignitions is that the most abundant ignition sources are not always associated with the greatest area burned (Syphard and Keeley 2016). Thus, a topic in need of further study is how to sort out those ignition sources that are most damaging, how those have changed over time, and in light of future needs, how climate change is likely to affect different ignition sources and losses. For example, it has been demonstrated for the state of Victoria, Australia, that some ignition sources, such as electrical distribution lines, may be limited in number but result in much more severe fire consequences (Miller *et al.* 2017). In addition, these fires are more likely during periods of elevated fire danger. If some ignition sources play a larger role in area burned, these might be targets for closer scrutiny and fire-management planning. This potential has been demonstrated for parts of southern California over recent decades, where powerlines have been shown to cause a substantial amount of area burned in both subregions in southern California (Syphard and Keeley 2015). Other important factors were arson in one subregion and equipment in another.

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The goal of the present research is to expand that approach to include the entire written history of fires in the state. Our focus was on the spatial and temporal patterns of different ignition sources and the relationship between type of ignition and area burned. We took a long-term historical approach utilising data from 1910 to 2016 for USFS lands and from 1919 to 2016 for state protected Cal Fire lands. First, we examine the spatial and temporal patterns of natural lightning-ignited fires *v.* human fires in the state, and their contribution to area burned. Next, we investigated which anthropogenic causes are most frequent, their distribution within the state, their change over time and their contribution to area burned. Based on a study of state-protected lands in California, Syphard *et al.* (2007) found that fires increased from 1931 to the 1980s, but then decreased over the subsequent decades. A similar pattern for the whole state was also reported by Keeley and Syphard (2017) on both Cal Fire and USFS lands. Thus, the present study contrasts fire-ignition patterns within climatically homogenous sub-regions for the period before 1980 and for the period 1980–2016.We also investigated the extent to which seasonal climate parameters could explain patterns of ignitions and area burned for each type of ignition source.

Methods

Fire-history data for numbers of fires and area burned, by cause, were analysed separately for state-protected Cal Fire and federal USFS lands. Data for counties, forests and climate divisions were all normalised by the area protected each year and within each unit and expressed as number of fires, or hectares burned, per million hectares.

Cal Fire data included 51 of the state's 58 counties (see Fig S1, available as Supplementary material to this paper) as 7 counties had limited fire activity or records. Fire statistics were from direct protection areas (DPA), which are mostly state-responsibility lands with smaller amounts of federal lands, and included the years 1919–2016, summarised by county. The term DPA was first used in 1986 and the area included was equivalent to what was called State Zone (1972–1985), Zones I and II (1945–1971) and Zones 1, 2, 3 (1919–1944). Cal Fire data from 1919 to 1930 are unpublished and were only available as typed reports at the California State Archives in Sacramento. Data from 1931 to 2016 were available in annual reports variously named, Forest Fire Summary, Fire Statistics, Fire Activity Statistics, and Wildfire Activity Statistics, often referred to as the *Redbook* series, available from research libraries or directly from the agency. Only 30 counties had complete data (excluding 1927 for nearly all counties and a few additional years in other counties) beginning in 1919, and an additional 21 counties had continuous data beginning in 1945 (or slightly later in a few cases) (see Table S1 for years of records for each county). Area protected has changed through this period of record and thus data were normalised to the hectares protected for that year presented with the annual reports. There was a period from 1941 to 1952 area where protected-area data were not included in annual reports and, as best we can determine, those data are no longer available, so we used the areas protected in 1940. In all cases, the changes between 1940 and 1953, when such data were again available, were minor.

USFS fire data covered 17 national forests (Fig S2) and included the years 1910–2016 (see Table S2, two forests were created after 1910 carved out of area from adjoining forests). Area protected has changed through this period of record and thus data were normalised to the hectares protected for that year. Data for USFS lands through the 1980s were from annual fire statistics reports for Region 5, available in the Forestry Library (most of which was transferred to the Bioscience Library) at the University of California, Berkeley. More-recent data, 1970 to 2016, were from the National Wildfire Coordinating Group (see http://fam.nwcg.gov/fam-web/weatherfirecd/state_data.htm, accessed 1 June 2017).

Most investigators are unfamiliar with these historical fire records and are sometimes sceptical of their accuracy. For example, Stephens (2005) contended that USFS data before 1940 were inaccurate, but cited a source (Mitchell 1947) that provided no evidence of this. Likely, the idea comes from Donoghue's (1982*b*) comment '1940 marked the modern era of fire reporting'. However, that comment was in reference to the fact that 'the report issued at this time was the first designed for automated data processing and easy readability' and was not in reference to reliability.

Historians have generally been confidant in these early California fire records (Brown 1945; Show 1945; Clar 1969; Cermak 2005). The first author, J. E. Keeley, examined all of the California fire-related materials stored at the state and federal archives and believes collectively they show managers have always been conscientious about reporting accuracy and completeness. For example, beginning in 1905, USFS record-keeping required 15 items of information on the fire reporting Form 944, including the specific cause (Donoghue 1982*b*). On state-protected lands there was an incentive in that the 1911 *Federal Weeks Law* provided fiscal aid to states based on statistics of fire protection (see http://www.calfire.ca.gov/about/about_calfire_history2, accessed 23 May 2018). In 1919, the California state legislature appropriated money for fire prevention and suppression, and records in the state archive show that, by 1920, there were more than 400 fire wardens distributed throughout the state who were charged with fire-fighting and fire reporting. In 1920, there were 800 flights of the Army's 9th Aero Squadron fire patrol that covered 426 500 km during the 5-month California fire season (Cermak 1991).

One complication in studying ignition sources is that reported categories have changed over time. Certain causes have persisted over the entire period of record, including lightning, smoking and camping, but other categories have changed their names. For example, arson fires are a relatively new category as intentionally set fires have, in the past, been labelled as 'incendiary', and seem to have been more rural than contemporary urban arson fires (Kuhlken 1999) and in this paper they are all recorded as arson fires. Other changes include the term 'brush burning' being changed to 'debris burning', and the categorisation of brush burning has been folded into debris burning. Causes that were unknown or represented minor categories have been included as miscellaneous fires (Donoghue 1982*a*), but are not addressed here.

Cal Fire data were spatially explicit at the level of the county and USFS data at the level of the individual forest. However, for analysis, these were grouped into climatically homogenous

areas as defined by the National Oceanic and Atmospheric Administration's (NOAA) National Climatic Data Center (NCDC) California Climate Divisions (Fig. 1), comprising the main fire-prone landscapes in the state (see http://www.ncdc.noaa.gov/temp-and-precip/time-series/index.php?parameter=pdsi&month=1&year=2008&filter=p12&state=4&div=5, accessed 15 June 2016). These include, from north to south, Division 1 (North Coast), 2 (North Interior), 5 (Sierra Nevada), 4 (Central Coast), and 6 (South Coast). Where boundaries did not match precisely, counties or forests were placed in the climate division comprising the majority of land area in that unit.

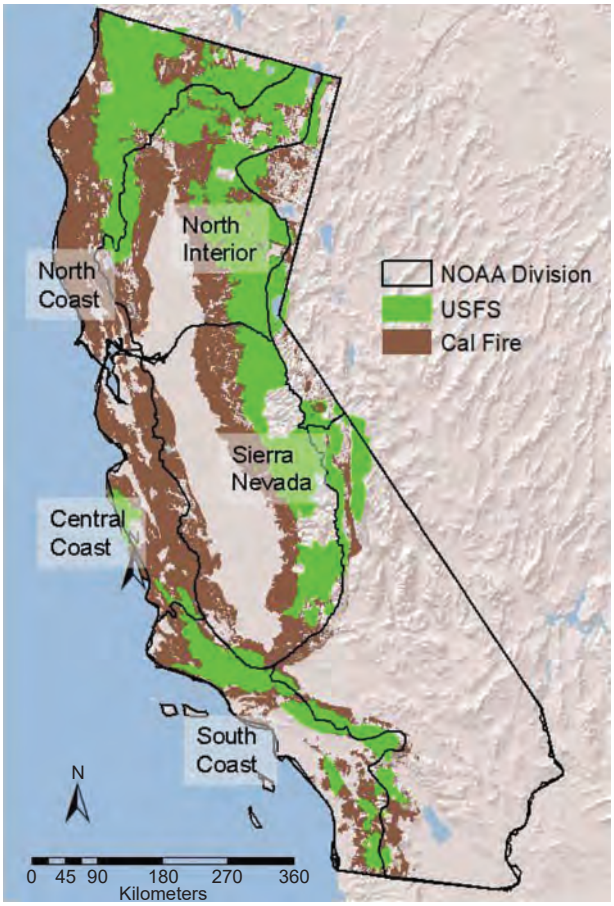

Fig. 1. NOAA climate divisions and Cal Fire protected and USFS protected lands in California for the five climate divisions with long-term fire history.

In 1919, Cal Fire-protected lands were 11.7×10^6 ha and increased to 12.5×10^6 ha in 2016. USFS lands comprised 9.8×10^6 ha in 1919 and decreased to 9.5×10^6 ha in 2016. Vegetation on state lands was dominated by grasslands and shrublands in the south and with significant woodlands and coniferous forests farther north (see Keeley and Syphard 2017 for more detailed vegetation data). USFS lands were dominated by coniferous forests, except in the southern part of the state where they were dominated by shrublands.

To evaluate climate impact on fire activity, we utilised PRISM climate for each county on Cal Fire-protected lands and each forest on USFS lands (Fig. 1). For every year in the analysis, we extracted 2.5 arc-minute PRISM data (PRISM Climate Group, Oregon State University, see http://prism.oregonstate.edu, accessed 15 February 2017) for areas within the boundaries of the Cal Fire and USFS lands. For each county and forest, we computed area-weighted averages of monthly mean precipitation and temperature, summarised by season – winter being December (prior year), January and February, spring being March, April and May, summer being June, July and August, and autumn being September, October and November.

Analysis was conducted with Systat software (ver. 11.0, Systat Software, Inc., San Jose, CA, http://www.systat.com/). For the climate analysis, we developed multiple regression models explaining area burned for USFS and Cal Fire based on seasonal temperature, precipitation and prior-season precipitation variables. To ensure multicollinearity would not be an issue, we calculated correlation coefficients among all potential explanatory variables and eliminated those that were strongly correlated ($P < 0.05$) with other variables in the model.

Results

Long-term averages show that on a per-unit-area basis fires were approximately twice as frequent or more on Cal Fire lands as on USFS lands in all five NOAA climate divisions (Table 1). However, the relationship between ignitions and area burned varied markedly between Cal Fire and USFS lands and between divisions. In the North Coast division, Cal Fire dealt with twice as many fires as the USFS but the average area burned was very similar. In contrast, in the interior from the Sierra Nevada northward, Cal Fire experienced approximately double the number of fires and nearly double the area burned. In the coastal

Table 1. Fire frequency and area burned on state and federal lands in California

NOAA division	Cal Fire (1919–2016)		USFS (1910–2016)	
	Fire frequency (n/year/10^6 ha)	Area burned (ha/year/10^6 ha)	Fire frequency (n/year/10^6 ha)	Area burned (ha/year/10^6 ha)
North Coast	317	7780	150	7559
North Interior	421	9642	207	5914
Sierra Nevada	356	8436	169	4709
Central Coast	277	5496	66	18860
South Coast	656	15278	369	24442

Table 2. Cal Fire counties total fires, percentage due to human ignitions and regression coefficients for population density *v.* number of fires (per year per million ha) for years 1919–2016

Division	County	Total	Percentage human	<1980		≥1980	
				r	*P*	*r*	*P*
North Coast	Del Norte	330	97	0.39	0.007	0.07	0.667
	Humboldt	219	93	0.31	0.018	−0.62	0.000
	Lake	446	98	0.72	0.000	−0.66	0.000
	Marin	1155	100	0.10	0.526	−0.07	0.699
	Mendocino	255	94	0.46	0.000	−0.46	0.004
	Napa	493	99	0.79	0.000	−0.83	0.000
	Siskiyou	256	63	0.44	0.000	−0.07	0.681
	Sonoma	488	99	0.90	0.000	−0.71	0.000
	Trinity	229	75	0.05	0.709	−0.27	0.102
North Interior	Butte	929	95	0.89	0.000	−0.51	0.001
	Colusa	115	95	0.44	0.003	−0.60	0.000
	Glenn	87	93	0.28	0.069	−0.64	0.000
	Lassen	178	50	0.55	0.000	−0.39	0.017
	Modoc	113	51	0.42	0.020	0.04	0.811
	Nevada	936	97	0.72	0.000	−0.80	0.000
	Placer	1645	98	0.88	0.000	−0.89	0.000
	Plumas	489	74	0.67	0.000	0.08	0.654
	Shasta	469	90	0.77	0.000	−0.38	0.020
	Solano	406	99	0.55	0.000	−0.54	0.000
	Tehama	196	93	0.90	0.000	−0.48	0.000
	Yolo	226	97	0.61	0.000	−0.32	0.051
	Yuba	723	97	0.49	0.000	−0.26	0.118
Sierra Nevada	Amador	507	99	0.60	0.000	−0.47	0.003
	Calaveras	337	99	0.59	0.000	−0.57	0.000
	El Dorado	213	98	0.77	0.000	−0.26	0.123
	Fresno	100	96	0.84	0.000	−0.69	0.000
	Inyo-Mono	255	98	0.67	0.002	−0.63	0.000
	Kern	804	99	0.84	0.000	−0.51	0.002
	Kings	321	99	0.29	0.146	−0.32	0.107
	Madera	823	99	0.65	0.000	−0.48	0.003
	Mariposa	617	97	0.70	0.000	−0.45	0.005
	Merced	602	95	0.21	0.180	−0.42	0.010
	San Joaquin	850	97	0.05	0.789	−0.46	0.005
	Stanislaus	237	95	0.35	0.024	−0.20	0.244
	Tulare	180	93	0.77	0.000	−0.33	0.048
	Tuolumne	280	93	0.89	0.000	−0.23	0.174
Central Coast	Alameda	117	98	0.65	0.000	−0.68	0.000
	Contra Costa	447	93	0.59	0.000	−0.21	0.213
	Monterey	306	93	0.84	0.000	−0.83	0.000
	San Benito	151	93	0.62	0.000	−0.81	0.000
	San Luis Obi	322	99	0.77	0.000	−0.64	0.000
	San Mateo	158	97	0.74	0.000	−0.08	0.055
	Santa Clara	242	93	0.38	0.002	−0.63	0.000
	Santa Cruz	814	97	0.80	0.000	−0.57	0.000
South Coast	Los Angeles	778	98	0.41	0.007	−0.53	0.001
	Orange	1198	100	0.85	0.000	−0.62	0.000
	Riverside	790	98	0.82	0.000	−0.82	0.000
	San Bernardi	791	96	0.73	0.000	−0.81	0.000
	San Diego	576	97	0.63	0.000	−0.60	0.000
	Santa Barbar	347	99	0.70	0.000	−0.64	0.000
	Ventura	713	99	0.84	0.000	−0.42	0.010

areas from San Francisco to San Diego, there were substantially more fires on Cal Fire-protected lands but the area burned was substantially greater on USFS lands.

For Cal Fire-protected landscapes, the area-based average number of fires per year (1919 to 2016) varied from 1645 in Placer County to 87 in Glenn County (Table 2). Humans were

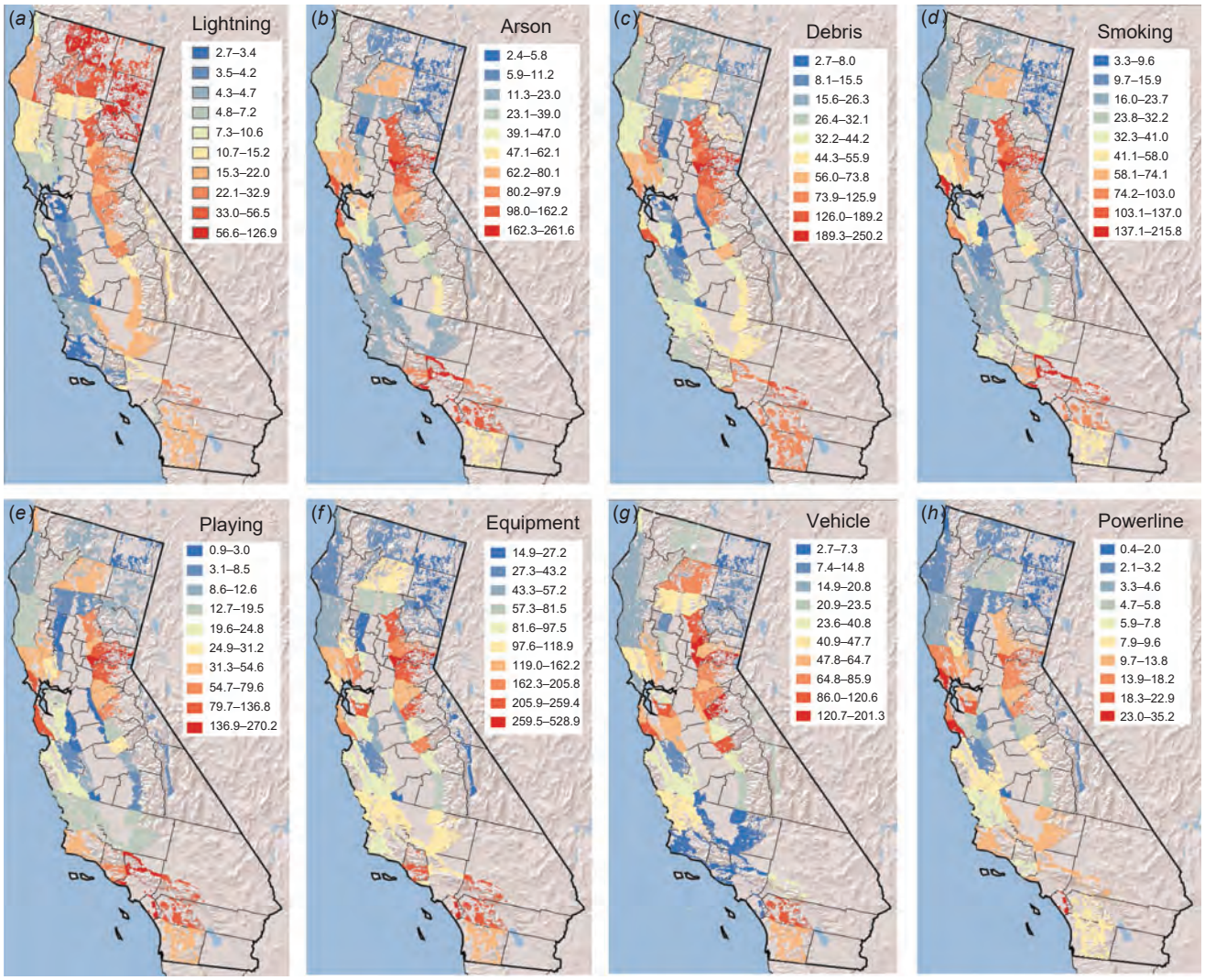

Fig. 2. Fire frequency for different ignition sources on Cal Fire protected lands in California for the years 1919–2016 (n/year/10^6 ha); note change in scales for each source.

responsible for most of fires, accounting for 95% or more of the ignitions in two-thirds of the counties. However, certain northern California counties stood out as notable exceptions, e.g. in Siskiyou, Trinity, Lassen, Modoc and Plumas counties lightning accounted for one-quarter to more than half of all ignitions, patterns illustrated in Fig. 2*a*. Regions with the lowest lightning-ignited fires extended through the coastal ranges from north of San Francisco to Santa Barbara. Area burned by lightning-ignited fires generally followed a similar pattern, although it was the source for significant burning in the San Bernardino County of southern California (Fig. 3*a*).

For USFS lands, the area-based average number of fires per year (1910 to 2016) varied from 478 in San Bernardino to 67 in Eldorado National Forest (Table 3). Humans accounted for far fewer fires than on Cal Fire lands. In the South Coast division, humans were responsible for 74–88%; however, in half of the other forests, humans accounted for less than 50% of the fires. As with Cal Fire landscapes, USFS lightning-ignited fires were most common in the north-east part of the state and declined markedly in coastal central and southern California (Fig. 4*a*). Area burned by lightning-ignited fires generally followed a similar pattern with the exception that parts of the North Coast and Central Coast, despite having few such ignitions, had substantial area burned by this source (Fig. 5*a*).

On both Cal Fire- and USFS-protected lands, humans played a substantial role in fire ignitions. During the first two-thirds of the 20th century there was a very strong positive relationship between population density and fire frequency in nearly 90% of the counties (Table 2) and more than 75% of the forests (Table 3). However, from 1980 to 2016, although population growth continued throughout the state, in most counties and forests, population density exhibited a highly negative relationship with fire frequency (Tables 2, 3).

On both Cal Fire- and USFS-protected lands, human-ignited fires derived from both intentional and accidental causes. The highest number of fires was from equipment, arson, debris

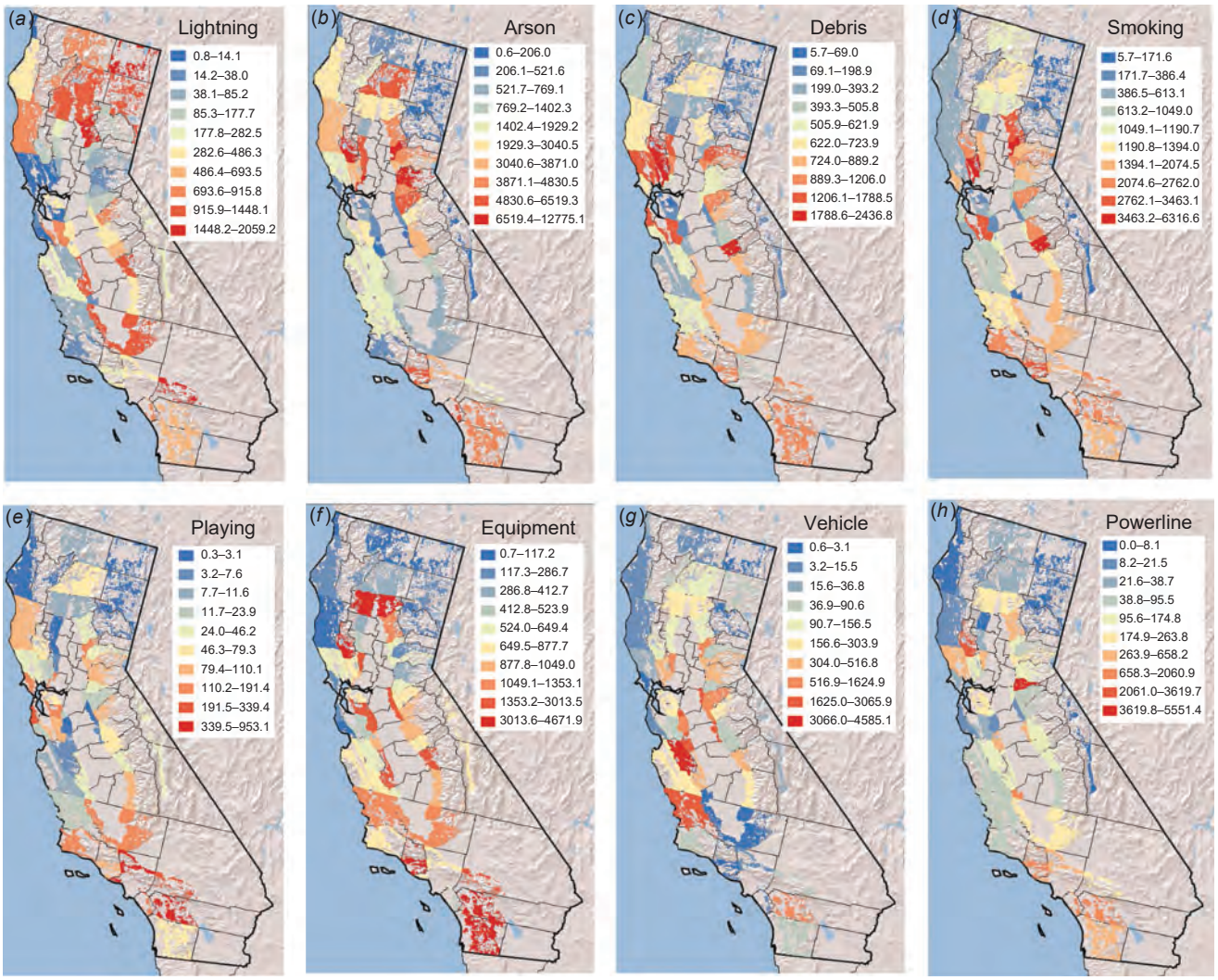

Fig. 3. Area burned by different ignition sources on Cal Fire protected lands in California for the years 1919–2016 (ha burned/year/10^6 ha); note change in scales for each source.

burning, children playing with fire, smoking, vehicles and powerlines (Tables S3–S6). Sources, such as railroads and lumber practices, did cause many fires in the early part of the record, but are of minor significance today (this change not shown).

These ignition sources exhibited marked geographical variation in their importance (Fig. 2–5). On lower elevation Cal Fire landscapes, arson was responsible for much of the area burned in the northern Sierra Nevada Mountains. (Fig. 3*b*), whereas debris burning was responsible for much of the area burned north and south of San Francisco (Fig. 3*c*), vehicles were the cause of much of the burning in the central coastal ranges (Fig. 3*g*) and equipment fires in southern California (Fig. 3*f*). Powerlines were responsible for significant number of fires in the north bay area of San Francisco and coastal communities from Santa Barbara south to the border (Fig. 3*h*).

In USFS forests, area burned in the South Coast was most heavily affected by arson and powerlines (Fig. 5*b*, *h*), but equipment and debris burning dominated in the Central Coast (Fig. 5*c*,*f*). Forests adjacent to high density metropolitan areas in Los Angeles and western San Bernardino counties had substantial burning due to smoking, children playing with fire, and powerlines (Fig. 5*d*, *e*, *h*).

Changing ignition patterns over time

The historical pattern of fire frequency on lower elevation Cal Fire-protected lands for 97 years and USFS lands for 107 years is illustrated in Fig. 6 for the five climate divisions. There was a common pattern across both Cal Fire and USFS lands and consistent within each of the five climate divisions – a highly significant increase in fire frequency from the beginning of records to 1979, and a switch to a highly significant decline in fires from 1980 to 2016 (Fig. 6), the single exception being the South Coast USFS lands (Fig. 6*r*). Despite a significant fit of these data to the linear regression models, there were some marked departures on Cal Fire lands during the early record. Plotting of linear regression residuals from 1919 to 1979 shows

Table 3. USFS forests total number of fires, percentage ignited by humans and regression coefficients for population density *v.* number of fires (per year per million ha) for years 1910–2016

Division	Forest	Total	Percentage human	<1980		≥1980	
				r	*P*	*r*	*P*
North Coast	Klamath	192	28	0.23	0.057	−0.33	0.045
	Mendocino	97	51	0.26	0.032	−0.36	0.030
	Six Rivers	137	65	0.46	0.007	0.11	0.528
North Interior	Lassen	271	38	0.66	0.000	−0.43	0.008
	Modoc	118	21	0.42	0.000	−0.06	0.730
	Plumas	280	46	0.36	0.002	−0.37	0.024
	Shast-Trinity	188	50	0.15	0.142	−0.41	0.012
	Tahoe	257	54	0.22	0.067	−0.44	0.007
Sierra Nevada	Eldorado	67	58	0.43	0.000	−0.25	0.129
	Inyo-Mono	237	40	0.85	0.000	−0.67	0.000
	Sequoia	79	39	0.75	0.000	−0.76	0.000
	Sierra	213	48	0.63	0.000	−0.68	0.000
	Stanislaus	201	49	0.50	0.000	−0.55	0.000
Central Coast	Los Padres	203	82	0.51	0.000	−0.50	0.002
South Coast	Angeles	367	87	0.58	0.000	0.49	0.002
	Cleveland	292	88	0.71	0.000	0.05	0.773
	Sbernardino	478	74	0.89	0.000	−0.50	0.002

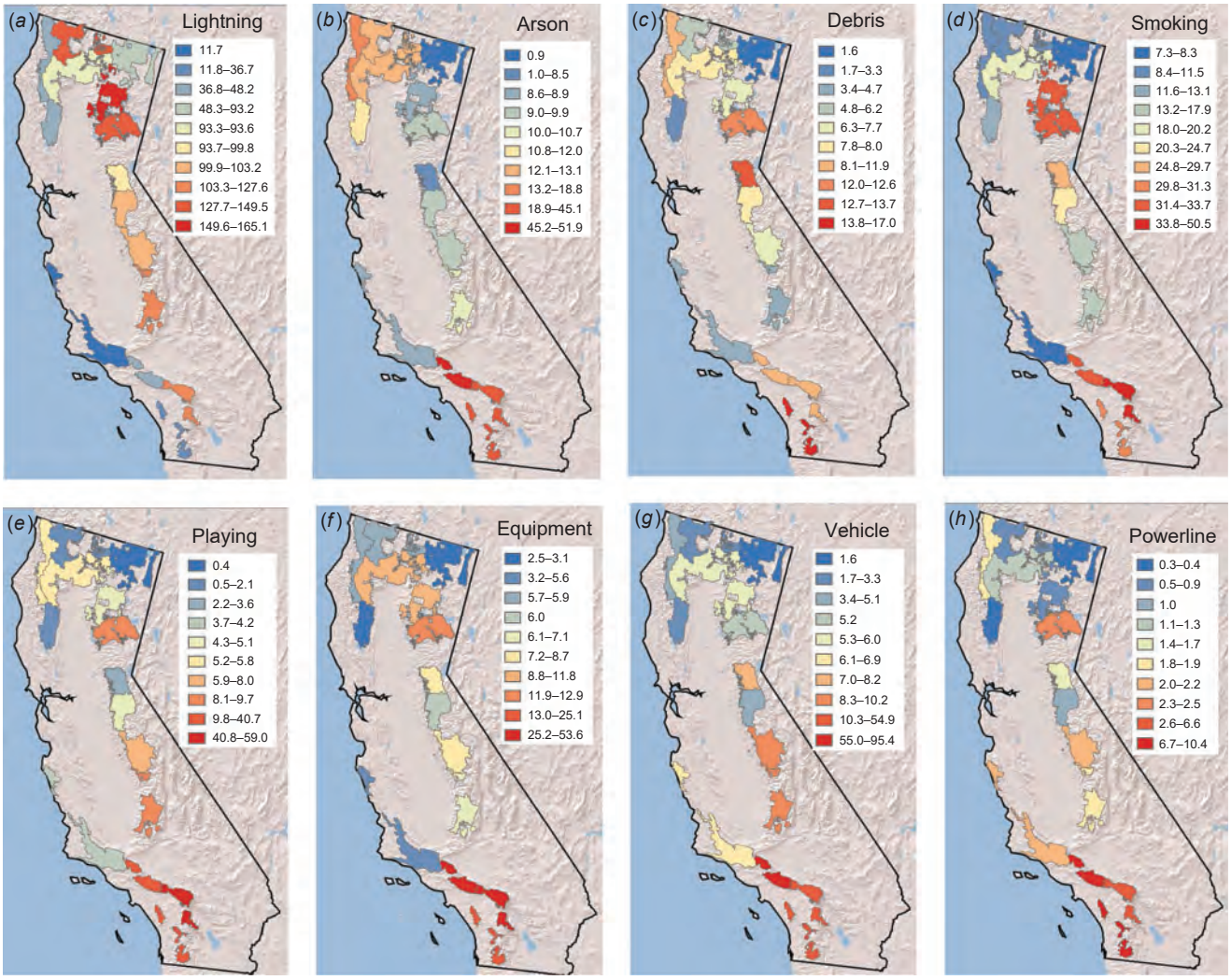

Fig. 4. Fire frequency for different ignition sources on USFS protected lands in California for the years 1910–2016 (n/year/10^6 ha); note change in scales for each source.

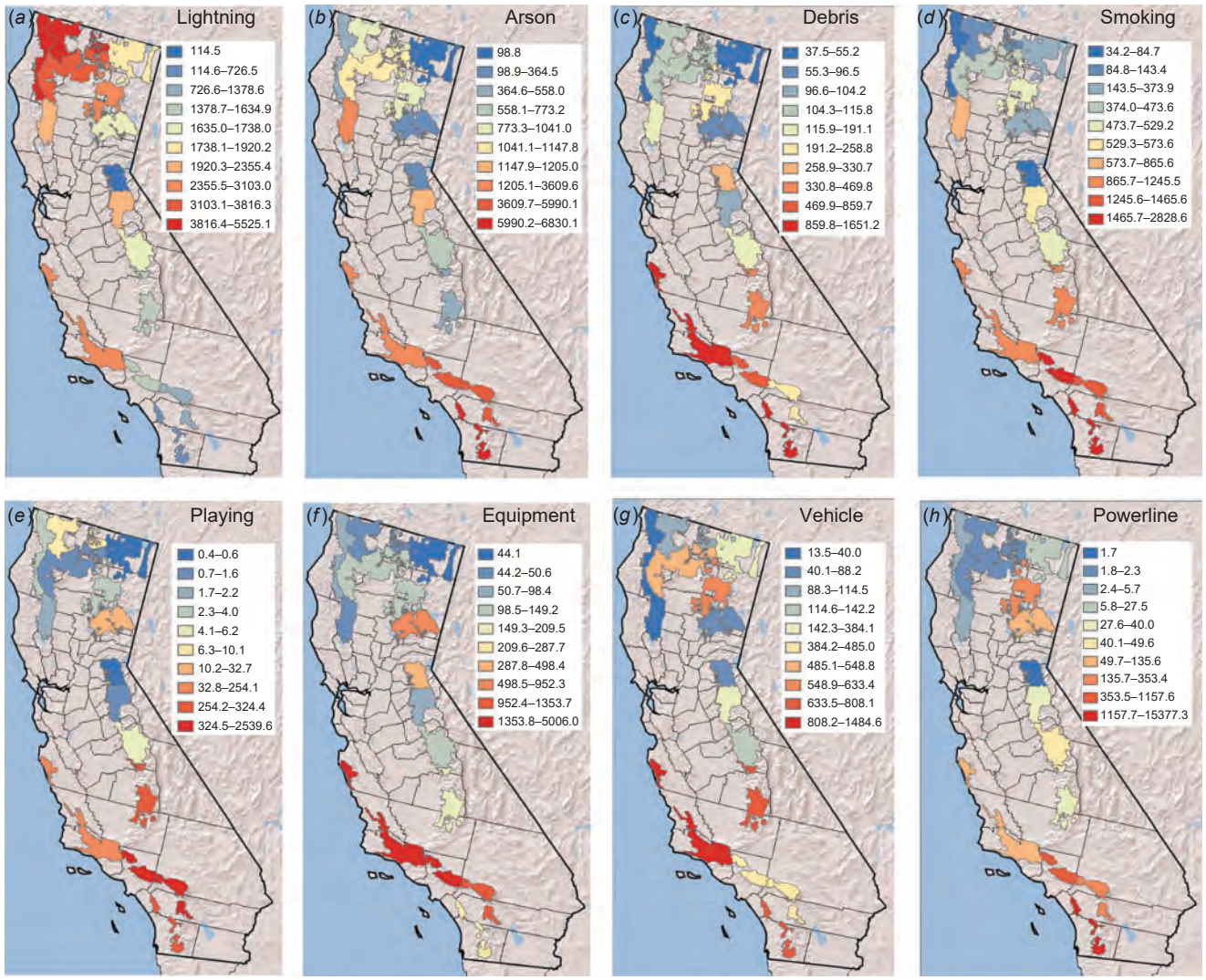

Fig. 5. Area burned by different ignition sources on USFS protected lands in California for the years 1910–2016 (ha burned/year/10^6 ha); note change in scales for each source.

marked and consistent diversions in most divisions (Fig. 7). Although the residuals early in the record are closely aligned with the regression line, during the 1920s and 1930s from the Sierra Nevada north there was a marked increase in ignitions. This pattern was less obvious in coastal central and southern California. In the 1950s and 1960s, there was a marked depression in ignitions in all climate divisions. It is worth noting that in the former period it was drier than the long-term average and in the latter period wetter (Fig. S3).

Changes in area burned did not closely follow changes in fire frequency (Fig. 6) – while fire frequency increased in the first three-quarters of the 20th century, area burned declined or stayed more or less constant. USFS forests in the northern part of the state showed a tendency for increased area burned in the last 4 decades (Fig. 6*d*, *l*) but in general there were no strong trends in area burned after 1980.

Of particular interest is how specific ignition sources have changed and, in order to simplify this presentation, we have consolidated climate divisions in the north (North Coast, North Interior and Sierra Nevada) and in the south (Central Coast and South Coast), which is justified by the marked similarities in ignition patterns within these two regions (see Fig. 2–5).

On Cal Fire-protected lands, it is noteworthy that changes in number of ignitions for lightning-ignited fires matched that of many human ignition sources, specifically increased ignitions during the first part of the record and decreased ignitions in recent decades (Fig. 8*a*, *e*). Numbers of lightning ignitions were more than double in the north than in the south, and substantially fewer than the leading anthropogenic causes. On USFS forests, lighting fire frequency (Fig. 9*a*, *e*) followed a temporal pattern similar to Cal Fire lands but were ~3 times more abundant than on Cal Fire landscapes and were one of the dominant ignition sources in forests. Despite changes in number of lightning-ignited fires, the area burned by this source did not exhibit consistent trends, although, in northern California forests, area burned by lightning-ignited fires has increased since 1980 (Fig. 8*i*, *m*, 9*i*, *m*).

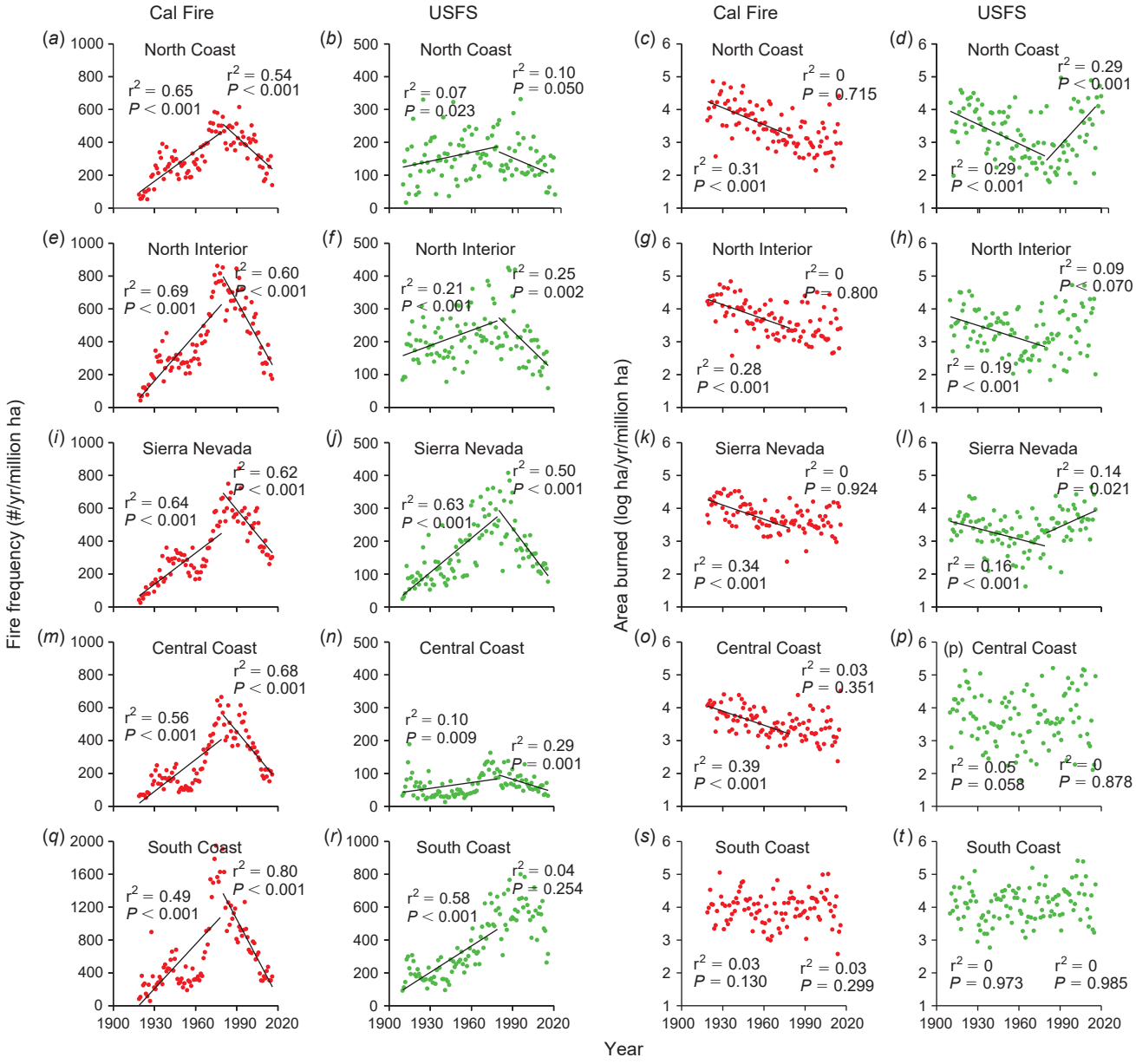

Fig. 6. Fire frequency for Cal Fire protected lands (*a*, *c*, *i*, *m*, *q*) and USFS lands (*b*, *f*, *j*, *n*, *r*) and area burned on Cal Fire (*c*, *g*, *k*, *o*, *s*) and USFS (*d*, *h*, *l*, *p*, *t*) lands. Note for frequency the change in scale between the South Coast and other divisions and between Cal Fire and USFS lands.

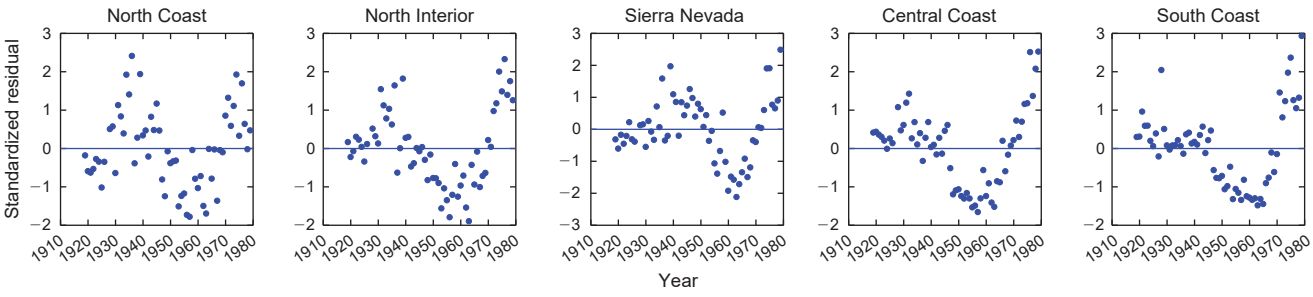

Fig. 7. Ignition sources recorded throughout the period 1919–2016 on Cal Fire protected lands by frequency (*a*–*h*) and area burned (*i*–*p*) in the north (climate divisions North Coast, North Interior, and Sierra Nevada) and the south (Central Coast and South Coast) with lines for significant regressions from 1919 to 1979 and from 1980 to 2016; note the change in scale between lightning and anthropogenic sources for fire frequency.

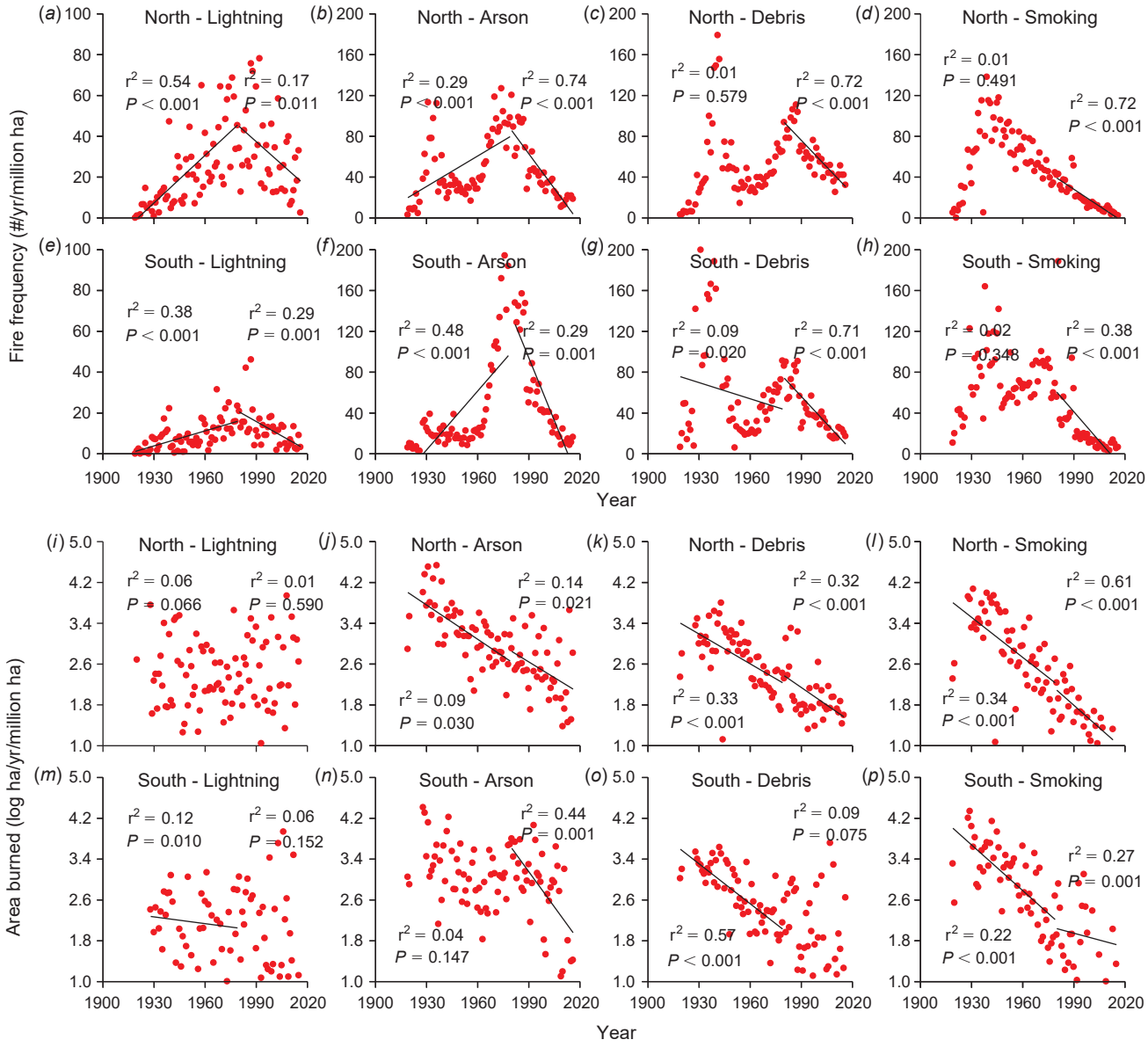

Fig. 8. Ignition sources not reported separately before 1960 on Cal Fire protected lands by frequency (*a–h*) and area burned (*i–p*) in the north (climate divisions North Coast, North Interior, and Sierra Nevada) and the south (Central Coast and South Coast) with lines for significant regressions before 1980 and 1980–2016; note the change in scale for fire frequency.

The main anthropogenic ignition sources on Cal Fire lands were arson, debris burning and smoking, and all showed a significant decrease in recent decades (Fig. 8*b–d*, *f–h*). Also, area burned by these ignition sources mostly showed a marked decrease in recent decades (Fig. 8*j–l*, *n–p*).

On USFS lands, arson and smoking were very important but camping was also a significant cause (Fig. 9). Arson fires exhibited remarkable similarity in the south of both jurisdictions with a marked decline in frequency and area burned since 1980 (Fig. 9*f*, *n*).

On both Cal Fire and USFS lands, some ignition sources, such as children playing with fire, equipment, vehicles and powerlines, were not specifically recorded during the early years (Fig. 10, 11). Children playing with fire declined significantly in both jurisdictions in the north and south (Fig. 10*a*, *b*, 11*b*, *f*) as did area burned by this source (Fig.10*i*, *m*, 11*j*, *n*). Equipment-ignited fires increased markedly between 1960 and 1979 on Cal Fire lands (Fig. 10*b*, *f*) but, during the same period, declined on USFS lands (Fig. 11*c*, *g*). Since 1980, this source of ignitions has declined sharply on Cal Fire lands in the north and south (Fig. 10*b*, *f*) but increased on USFS lands in the south (Fig. 11*g*). In contrast to all other ignition sources, powerline fires on Cal Fire and USFS lands in both the north and south have not declined in the last 4 decades (Fig. 10*d*, *h*, 11*d*, *h*) nor has area burned by this ignition source (Fig. 10*p*, 11*p*).

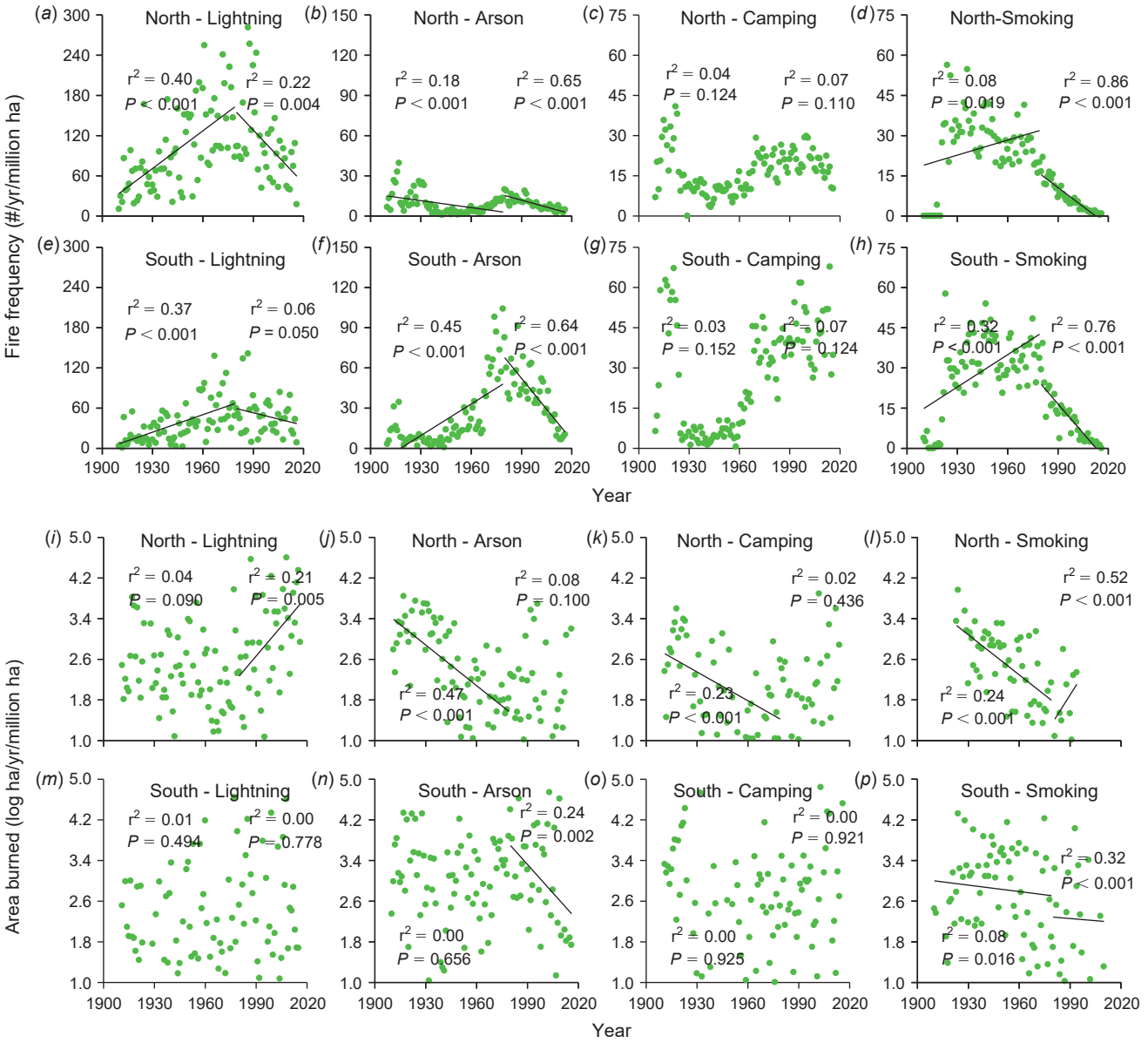

Fig. 9. Ignition sources recorded throughout the period 1910–2016 on USFS protected lands by frequency (*a–h*) and area burned (*i–p*) in the north (climate divisions North Coast, North Interior, and Sierra Nevada) and the south (Central Coast and South Coast) with lines for significant regressions from 1910 to 1979 and from 1980 to 2016; note the change in scale between lightning and anthropogenic sources for fire frequency.

Climate relationships to ignitions

Based on the sharp change in ignition patterns through the period of record, it is critical to understand to what extent climate variation may have played a role. Considering the marked changes in climate over the period of this study (illustrated as decadal anomalies in seasonal temperature and precipitation in Fig S3), it is reasonable to expect climate variation has some explanatory value in understanding changes in ignition sources.

Multi-variate models used mean temperature and total precipitation for winter, spring, summer and autumn plus the prior-year winter–spring precipitation. Presented in Table 4 are those ignition sources with a significant $P < 0.05$ model. Not all ignition sources exhibited a significant climate mode and the models determining fire frequency were not the same as those for area burned. We note that, before 1980, the biggest driver of debris and railroad fires was prior-year precipitation. Since 1980, there was a negative relationship with summer temperature for debris burning, playing with fire, smoking and railroad fires. In the south, where lightning-ignited fires were uncommon (Fig. 2*a*), before 1980, they were strongly associated with high summer temperatures and autumn precipitation.

Total area burned on Cal Fire lands in the north before 1980 was significantly tied to low winter precipitation and high spring temperatures. In the south, area burned by both arson and powerlines was significantly tied to climate variation.

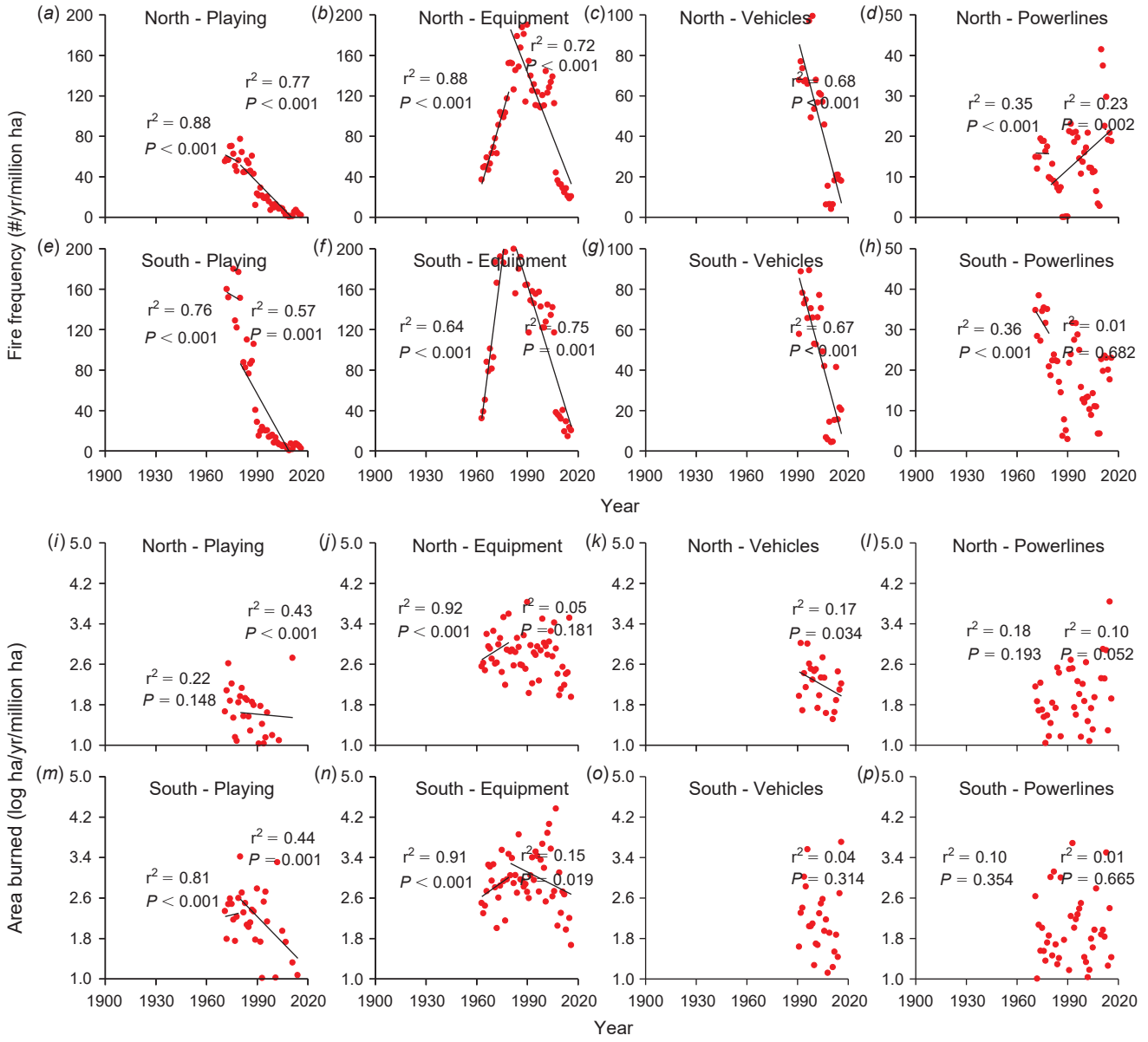

Fig. 10. Ignition sources variously recorded throughout the period 1910–2016 on USFS lands by frequency (*a–h*) and area burned (*i–p*) in the north (climate divisions North Coast, North Interior and Sierra Nevada) and the south (Central Coast and South Coast) with lines for significant regressions before 1980 and 1980–2016; note the change in scale for fire frequency.

On USFS lands, total number of fires and area burned in both the north and south exhibited many significant climate models (Table 5). However, the patterns are complicated and not easily summarised as the specific climate models varied both spatially and temporally, as well as being different for different ignition sources.

For example, lightning fire frequency and area burned in both the north and south and before and after 1980 were significantly associated with climate variation, but, before 1980 in the north, the frequency of lightning fires was positively associated with summer precipitation, but the area burned was negatively associated with summer precipitation. After 1980 in the north, the model switched and there was a very strong effect of prior-year precipitation and summer temperature.

Since 1980, one of the strongest climate variables affecting both frequency and area burned was a positive relationship with prior-year precipitation. Although higher summer temperatures were associated with increased frequency of arson fires, it was noteworthy that lower summer temperatures were associated with an increased incidence of smoking, camping and children playing with fire in the north. Frequency of powerline fires were associated with elevated autumn temperatures and higher prior-year precipitation.

Cal Fire area-burned data were also presented by vegetation type and showed that in the north, forest and shrubland area

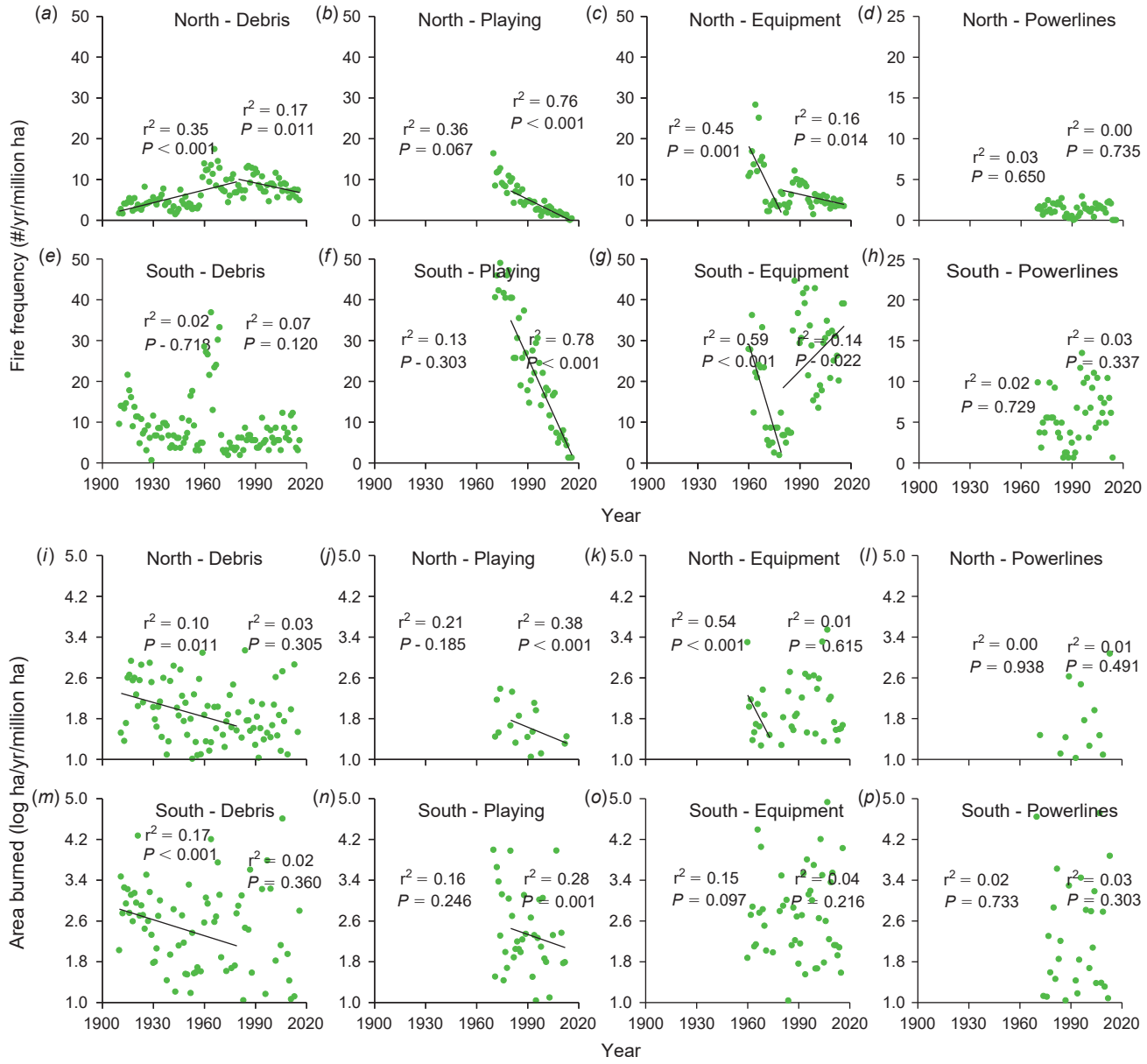

Fig. 11. Ignition sources variously recorded throughout the period 1910–2016 on USFS lands by frequency (*a–h*) and area burned (*i–p*) in the north (climate divisions North Coast, North Interior, and Sierra Nevada) and the south (Central Coast and South Coast) with lines for significant regressions prior to 1980 and 1980-2016; note the change in scale for fire frequency.

burned had significant relationships with climate variation before 1980 but not afterwards (Table 6). In the south, grasslands had a significant climate model after 1980.

Discussion

Particularly striking about California ignitions is the steady increase in number of fires since the early 1900s until a peak *c.* 1980, followed by a marked drop in fire frequency up to 2016. This happened on both lower-elevation Cal Fire-protected lands and higher-elevation USFS lands, and in most climate divisions (Fig. 6). Despite a significant increase in fires during the first three-quarters of the 20th century, there were marked departures from this linear model, with accelerated ignitions during the 1920s and 1930s and a marked drop in the 1950s and 1960s (Fig. 7). Climate may have had some role in these changes since the former decade was drier and the latter was wetter (Fig S3) and during this period total fires on USFS lands did have a significant climate model largely driven by high summer temperatures and low summer precipitation (Table 4). What is particularly striking is the disconnect between number of ignitions and area burned; during the first three-quarters of the 20th century, although ignitions were increasing, area burned was steadily decreasing through much of the state.

In contrast, since 1980, ignitions have steadily declined, yet area burned has either not changed or, in some northern parts of the state, has increased. In short, the number of ignitions does not directly explain area burned. However, as discussed below, this conclusion does not apply to individual ignition sources, and, in this respect, there may be particular sources worth targeting for fire management purposes.

Factors that may have played a role in these historical patterns of ignitions and area burned are changes in: population density, infrastructure development, fire-prevention success, fire-suppression effectiveness, vegetation-management practices, climate, and possibly record-keeping accuracy. The drivers behind changes in ignition patterns are quite possibly different for different sources, different parts of the state and at different times. First, we consider the patterns for natural lightning-ignited *v.* human-caused wildfires.

Lightning-ignited fires

In California, natural lightning-ignited fires decreased from north to south and from high (USFS) to low (Cal Fire) elevation (Fig. 2, 4). On USFS lands, Lassen and Plumas forests in the north-east averaged over 150 lightning-ignited fires per year per million hectares, whereas the coastal Los Padres Forest averaged one-tenth as many (Table S5). In northern California forests, such as the Klamath, Lassen, Modoc, Inyo-Mono and Sequoia, lightning accounted for the majority of fires, and on many others it is about equally important as human-ignited fires (Table 3). Notable exceptions are the coastal Los Padres and southern California Angeles, Cleveland and San Bernardino forests, where lightning accounted for less than one-quarter of all fires. In contrast, on lower-elevation Cal Fire-protected lands, lightning accounted for less than 10% of all fires in most counties, and in coastal areas from Sonoma County south, typically <1% of all ignitions (Table 2). These patterns closely follow the distribution of lightning strikes in the state (van Wagtendonk and Cayan 2008). In general, lightning-ignited fires in coastal California were substantially less than that observed over much of the USA (Prestemon *et al.* 2013). Thus, the report that extreme fire events driven by high winds are commonly due to human ignitions and not lightning (Abatzoglou *et al.* 2018) should not be too surprising in California because these extreme winds are largely restricted to coastal areas in southern California and the San Francisco Bay Area.

Area burned by lightning-ignited fires approximately paralleled these geographical patterns with a couple noteworthy exceptions. In the northern and central part of the state, more coastal USFS forests had low lightning-ignited fire frequency but these accounted for a substantial amount of area burned, although this was less evident on lower-elevation Cal Fire lands (Fig. 2–5). For interior forests where lightning is the dominant ignition source, fires have proven to be reasonably easy to extinguish, in large part because they typically occur in forests with a low-intensity surface-fire regime, and during lightning-storm weather conditions (van Wagtendonk and Cayan 2008), are conducive to rapid fire control. As a consequence, less than 1% of these forest lands burn each year and these landscapes have a fire-rotation interval of 100–200 years (Table 1), very different with what is believed to be the natural fire interval (Stephens 2005; Van de Water and Safford 2011; Safford and Van de Water 2014). In coastal central and southern California, lightning accounts for very little area burned, in large part because lightning strikes are very low, but also because human-ignited fires often occur under weather conditions more conducive to fire spread, contributing to a shorter fire-rotation interval, e.g. 40–50 years on southern California forest lands (Table 1).

Table 4. Significant climate models ($P < 0.05$) explaining frequency of ignitions and area burned for the period <1980 and ≥1980 for Cal Fire protected lands

Models tested mean temperature and total precipitation in winter, spring, summer and autumn, and prior year winter + spring precipitation (<1PptWinSpr)

Variable	Era	Adjusted R^2	P	Model
Frequency in North				
Debris	<1980	0.18	0.021	<1PptWinSpr
Debris	≥1980	0.24	0.050	- TempSum
Playing	≥1980	0.27	0.035	- TempSum + TempWin
Smoking	≥1980	0.32	0.016	- TempSum
Railroad	<1980	0.18	0.020	<1PptWinSpr + PptSpr
Railroad	≥1980	0.25	0.045	- TempSum + TempWin
Frequency in South				
Lightning	<1980	0.40	0.001	TempSum + PptAut
Debris	<1980	0.18	0.021	<1PptWinSpr – PptAut
Area in North:				
Total	<1980	0.23	0.007	- PptWin + TempSpr
Area in South:				
Arson	≥1980	0.25	0.045	- TempWin
Powerlines	<1980	0.99	0.046	- TempSum – PptSpr – PptAut
Powerlines	≥1980	0.24	0.050	- TempAut

Lightning fires have increased markedly over most of the 20th century on both Cal Fire and USFS lands, in the north and south (Fig. 8, 9). A possible explanation for this pattern is improvement in detection, as lightning-ignited fires often occur in remote areas and detection may have been less effective in the early part of the 20th century and improved in the latter part of the 20th century. However, there is there is reason to retain some level of scepticism that this pattern is an artefact of reporting (see the 'Methods' section), primarily because state and federal agencies have put in extraordinary effort at fire detection since the early 1900s (Clar 1969; Cermak 2005), including hundreds of thousands of kilometres of wilderness aircraft fire patrols beginning in 1919 (Cermak 1991).

Another reason for not simply dismissing historical patterns as an artefact of reporting is that there are physical factors that could account for such changes. For example, one potential factor for a 20th-century rise in lightning fires could be changes in forest fuel structure, which has been shown to affect lightning-ignited fire frequency on other landscapes (Krawchuk *et al.* 2006). In California, this would be expected based on the marked drop in area burned following the burning peak in the 1920s – for both Cal Fire and USFS lands, three times more area burned in that decade relative to the decadal average burned from 1950 to 1980 (Keeley and Syphard 2017). Thus, during the mid-20th century there was potentially an increase in fuels that

Table 5. Significant climate models ($P < 0.05$) explaining frequency of ignitions and area burned for the period <1980 and >1980 for USFS protected lands

Models tested mean temperature and total precipitation in winter, spring, summer and autumn, and prior year winter + spring precipitation (<1PptWinSpr)

Variable	Era	Adjusted R^2	P	Model
Frequency in North				
Total	<1980	0.27	0.001	TempSum – PptSum + PptAut
Lightning	<1980	0.21	0.005	TempSum + PptSum + PptAut
Arson	<1980	0.13	0.040	–PptAut – PptSpr
Arson	≥1980	0.28	0.030	TempSum
Smoking	≥1980	0.46	0.001	–TempSum – PptSum
Debris	≥1980	0.43	0.002	– PptWin – TempAut – PptSum
Camping	≥1980	0.26	0.039	–TempSum
Playing	≥1980	0.47	0.001	–TempSum – PptSum
Railroad	< 1980	0.28	0.007	PptAut
Railroad	≥1980	0.32	0.017	–PptWin + PptSpr
Equipment	≥1980	0.32	0.016	–TempSum – PptWin – PptSum
Powerlines	≥1980	0.35	0.010	<1PptWinSpr
Frequency in South				
Total	≥1980	0.29	0.026	Ppt–1WinSpr
Lightning	<1980	0.18	0.012	TempSum + PptAut
Powerlines	≥1980	0.28	0.029	TempAut + PptWin
Area in North:				
Total	<1980	0.35	<0.001	–PptWinSpr – PptSum
Total	≥1980	0.63	<0.001	<1PptWinSpr + TempSum – PptAut
Lighting	<1980	0.17	0.018	–PptSum
Lighting	≥1980	0.64	<0.001	<1PptWinSpr + TempSum
Arson	<1980	0.38	<0.001	–PptWin – PptAut – TempAut – TempWin
Debris	<1980	0.15	0.031	– PptWin –PptAut
Smoking	<1980	0.16	0.022	TempAut + TempSpr
Playing	≥1980	0.34	0.010	–TempSum –TempAut
Equipment	≥1980	0.28	0.030	<1PptWinSpr
Vehicles	≥1980	0.37	0.007	<1PptWinSpr
Powerlines	≥1980	0.47	0.001	–TempWin + <1PptWinSpr
Area in South				
Total	<1980	0.20	0.006	– PptAut – PptWin
Total	≥1980	0.24	0.048	TempSum – TempWin
Lighting	≥1980	0.25	0.043	–TempSpr – PptSpr

may have contributed to a greater chance of lightning strikes igniting fires.

Changes in reporting standards is also not likely to explain the pattern of decreased lightning-ignited fires from 1980 to 2016 (Fig. 8, 9). On Cal Fire and southern USFS lands, this did not produce any significant trend in area burned by this fire source, although northern California (including the Sierra Nevada) USFS lands showed an increase in area burned by this source, a pattern also seen in the northern Rocky Mountains (Stephens 2005). Climate is strongly implicated in this change (Table 5) as two-thirds of the annual variation in area burned by lightning-ignited fires is explained by a combination of prior-year precipitation and current-year summer temperature. Although the latter variable most likely affects fuel moisture at the time of fire, the former is thought to increase fires through its effect on herbaceous fuels in the following year (Littell *et al.* 2009; Crimmin and Comrie 2011; Keeley and Syphard 2016). A similar conclusion was drawn by Knapp (1995) for the climatic control of lightning-ignited fires in the Intermountain West.

The future projections are that lightning strikes will increase 50% over this century (Romps *et al.* 2014), but this is not easily translated into future lightning fire risks in California. Some landscapes, such as forests in the northeastern part of the state, may already be saturated with lightning ignitions and coastal landscapes have very few strikes and thus a 50% increase may not significantly change lightning-ignited fire risk. In addition, changes in lightning-strike frequency will have very different impacts dependent on which season those changes occur in as well the state of future fuel conditions.

Human-ignition sources

The fact that in all climate divisions, the number of ignitions is not a monotonic function of time over the past 100 years suggests a complex model of how ignition sources affect burning activity. Prestemon *et al.* (2013) presented a conceptual model of biophysical, social, prevention and management drivers in controlling human ignition sources. These factors are not static,

as illustrated by Guyette *et al.*'s (2002) dynamic anthropogenic fire regime model for the Ozark Mountains in Missouri. In their model, they found that the landscape changed over time from being ignition limited to fuel limited followed by stages dependent on fuel fragmentation and ultimately a culture-dependent stage. These temporal changes in drivers could explain a lot about the temporal changes observed in California ignitions.

It may be that the marked rise in ignitions during the first three-quarters of the 20th century in California is the result of increasing effectiveness of reporting, but this seems unlikely because the steepest rise in ignitions was in the latter part of the 20th century, i.e. 1960–1980 (Fig. 6). The 20th-century increase in ignitions was very strongly correlated with population growth (Tables 2, 3), but we believe that more is involved than just increasing population growth translates into more fires. This early–mid-20th-century growth spurt was correlated with road expansion throughout the state, which was bringing more people in contact with highly flammable fuels (Show 1945; Lockmann 1981; Keeley and Fotheringham 2003). In addition, because of migration patterns, growth included populations from less fire-prone parts of the US, and thus a population relatively naïve about the dangers of fire use in wildland areas (e.g. Zahn 1944; Show 1945). In addition, fire-prevention education was in its infancy and the population was slow to recognise their role in the fire problem. Included too is the widespread use of outdoor equipment that contributed to the sharpest rise in fires on Cal Fire landscapes between 1960 and 1980 (Fig. 10). On top of that, development of fire-response actions were far from perfect (Clar 1969). Also, during the period from 1940 to 1970 the State Resources Agency was actively involved in promoting burning of chaparral shrublands for the express purpose of type-converting native shrublands to exotic grasslands of greater economic value as rangelands (unpublished records in the State Archives). Indeed, the state was funding type conversion of private lands as this was perceived as a fire hazard reduction strategy, with an economic incentive of increasing rangeland.

Not directly related to changing demography is the significant decline in fires in the last several decades – while populations continued to grow after 1980, fire frequency was negatively related to population density (Tables 2, 3). This is consistent with the pattern of fire activity peaking under intermediate population density (Syphard *et al.* 2009). That is, the relationship between population density and ignition frequency is likely a function of finer-scale spatial processes regulating the degree of interspersion between development patterns and wildland vegetation. In other words, as both population and development expand into wildland areas, ignitions increase up to a point at which the area of development, or, impervious surface, far exceeds the area of wildland, and at that point, the relationship becomes negative. However, the timing of this switch varies with regions, e.g. south-east Australia continues to see a positive relationship in between population density and fire frequency (Collins *et al.* 2015).

Thus, these broad-scale patterns observed across the state may be reflecting macro-scale urbanisation trends over time. Massive areas of wildland vegetation have been developed and fragmented in California over the course of the 20th century (Hammer *et al.* 2007; Syphard *et al.* 2017), and the resulting extent and fragmentation of fuel surely has affected ignition trends and area burned. It may therefore be important to monitor areas that are becoming newly developed, as these may be the most fire-prone areas on the landscape, with sufficient people to start fires and wildland vegetation to carry fires (Radeloff *et al.* 2018).

Patterns such as these have been interpreted as indicating fires are not limited by human ignitions (Knorr *et al.* 2013; Moritz and Knowles 2016). This has prompted some to conclude that fire activity during the last several decades has been driven largely by climate change (Westerling *et al.* 2011). It is apparent that in mid–high-elevation forests in California seasonal climate variation has been an important factor in determining annual area burned (Table 5) and that global warming may exacerbate the fire situation on those landscapes (Keeley and Syphard 2016). However, in coastal California, climates are capable of generating large fire events most years (Keeley and Syphard 2017), with one exception being years with anomalous late spring rains (e.g. Dennison *et al.* 2008). In these coastal locations, big fire events occur during extreme wind events, however, these Santa Ana, Diablo or North Wind events occur predictably every year and yet big fires occur at unpredictable intervals, being determined by the coincidence of a human ignition with a wind event (Keeley and Zedler 2009).

During the first two-thirds of the 20th century more people translated into more fires, and greater fire activity. However, in recent decades the relationship between human population growth and fire activity has become more complex, nicely captured in Prestemon *et al.*'s (2013) model. In California in recent decades, increasing population density has increased the probability of ignitions under the worst weather conditions, either intentionally by arson for example or accidentally by powerline failures. This appears to be a widely seen situation throughout the USA where human-related ignitions are associated with conditions resulting in large wildfires (Nagy *et al.* 2018).

Decreasing ignitions over the last 4 decades is potentially reflective of increasing efficiency of fire prevention. However, it also likely reflects changes in human infrastructure; new roads in this era were tied to development projects that required demonstration of adequate fire response capabilities. In addition, an important factor behind declining ignitions is quite possibly the emergence of the California Fire Safe Council in the early 1990s (http://www.cafiresafecouncil.org/about-us/, accessed 11 August 2016), which made significant contributions to fire-safety education.

Arson has long been a major source of intentional human ignitions on both Cal Fire (Fig. 8) and USFS (Fig. 9) lands and on both jurisdictions arson ignitions increased during the first part of the 20th century and then dropped markedly in recent decades. Arson fires have always been one of the largest sources of area burned, although it was much higher in the early 20th century than in recent decades. This category comprises ignitions motivated for diverse reasons. Early in the 20th century, these were termed incendiary fires and were often motivated by goals of maintaining traditional burning practices (Coughlan 2016). As such practices became less socially (and legally) acceptable, the category was labelled arson fires. Arson fires exhibit interesting distribution patterns. On low-elevation Cal Fire lands they are a major ignition source in the northern Sierra Nevada (Fig. 2, 3) but on USFS lands they dominate in the

southern part of the state (Fig. 4, 5), suggesting a need for more concentrated anti-arson prevention measures in those regions. This clustering of arson fires has been observed in parts of the Mediterranean basin and has prompted an early alert system (Gonzalez-Olabarria *et al.* 2012).

One of the real success stories illustrated by these data is the marked decline since 1980 in frequency and area burned by arson fires on both Cal Fire and USFS lands (Fig. 8, 9). This reduction in arson fires is a pattern observed for other parts of the country (Prestemon *et al.* 2013). In California, this may be attributed to better neighbourhood-watch programs, which include patrols during red-flag warnings, but broadcasted fire prevention messaging may also be a factor. Another factor may be increased penalties for arson; e.g. the person found guilty of starting the 2003 Old Fire in southern California was sentenced to death, as was the arson convicted of the 2006 Esperanza Fire (Gabbert 2012).

Another source of burning on both Cal Fire and USFS lands has been smoking. This was a significant cause in the earliest records, recording even ignitions from cigarettes thrown from open cockpit planes. Throughout the first half of the 20th century, smoking was a major cause of wildfires and was the focus of one of the earliest fire prevention campaigns. In 1942, over 100 000 'fag bags' were distributed to persons entering the Angeles National Forest, bright red bags designed to carry smoking materials and with a prominent fire-safety reminder stamped on them (Show 1945). The late 20th-century decline in smoking caused such fires to decline at a much faster rate (Fig. 8, 9) than due to simple reduction in smoking (Prestemon *et al.* 2013). Reductions in smoking-caused fires are due to a combination of less smoking, more fire-resistant cigarettes, and improved fire prevention (Butry *et al.* 2014).

Children playing with fire has been an important ignition source and it has exhibited a marked decline in frequency in recent decades on both Cal Fire (Fig. 10) and USFS (Fig. 11) lands. Increased fire-prevention effectiveness through better messaging and development of childproof lighters are potential factors. Perhaps stricter ordinances in power-tool usage in wildlands under red-flag warnings may be a factor as well as requirements for more effective spark arrestors.

Vehicles present another accidental fire source that has declined sharply on Cal Fire protected lands. Catalytic converters, which were first required in 1975, are thought to have been a significant ignition factor (Bertagna 1999; http://www.cbs8.com/story/35871110/how-a-cars-catalytic-converter-can-spark-a-massive-fire, accessed 1 June 2017) when they overheated, igniting roadside vegetation. However, modern vehicles have warning lights when they overheat, which has the potential for reducing vehicle fires and could be a factor in the decline of such fires. Another factor potentially reducing vehicle fires is improved vegetation treatment along roadside verges.

Electrical powerlines have been reported ignition sources since 1905 (Show 1945). In the present study, this source of ignition stands out in that, unlike many other human ignition sources, powerline fires and area burned by this ignition source have not declined in recent decades (Fig. 10, 11). Although powerlines do not account for many fires, they often account for substantial area burned, and some of substantial size (Keeley *et al.* 2009; Syphard and Keeley 2015). One reason that powerline fires are so dangerous is that they commonly occur during high winds and there are three effects of these winds: tree contact, line arcing, and metal fatigue resulting in lines down (Mitchell 2009). These winds create extremely dangerous fires capable of rapid spread over long distances. This is a serious problem in other regions such as southern Australia where it was found that electricity-caused wildfires are over-represented when fire danger is high (Miller *et al.* 2017) and similar conclusions were drawn by Ganteaume and Guerra (2018). Powerline distribution tends to follow roads and this may be part of the reason burning patterns are closely correlated with road distribution in southern California (Faivre *et al.* 2014). Also, they burn larger areas than fires ignited by most other causes and are associated with more significant impacts on lives and property (Collins *et al.* 2016).

Because these powerline failures typically occur in known extreme-wind corridors, it has been proposed that wiring these corridors with underground power could minimise the problem (Keeley *et al.* 2009). However, utility companies have shown a reluctance to accept this solution. One company in southern California, San Diego Gas & Electric, has opted for an alternative plan whereby they monitor weather throughout the county and use these data to shut down portions of the power grid when that area experiences high winds (https://www.cnbc.com/2017/12/13/southern-california-utilities-shut-off-power-to-prevent-wildfires.html, accessed 1 June 2017). In initial attempts to deal with fire hazards there have been significant complaints about the process of shutting down the power grid as it creates many unanticipated problems (https://www.nbcsandiego.com/news/local/Supervisor-Demands-State-Investigation-of-Power-Shut-offs-During-Lilac-Fire-467782743.html, accessed 1 June 2017). Other approaches have been to replace wooden poles with metal poles, however, this seems to be a distraction since wooden poles have not been blamed for starting fires (https://www.voiceofsandiego.org/topics/science-environment/sdge-environmentalists-are-at-opposite-poles-on-one-fire-prevention-method/, accessed 1 June 2017).

Climate change impacts on anthropogenic ignitions is rather difficult to parse out because climate affects both fire behaviour and human behaviour. For example, in forests, fire activity is enhanced by higher spring and summer temperatures through effects on fuel moisture (Westerling *et al.* 2006; Littell *et al.* 2009; Keeley and Syphard 2017). However, in the present study, fires started by camping, children playing with fire, and smoking were negatively correlated with summer temperatures, suggesting the possibility that cooler temperatures may have encouraged greater outdoor activity.

In general, climate variation exhibited a closer relationship with fire activity in the higher-elevation USFS lands in the northern part of the state, consistent with the flammability limited fire regimes in these regions (Keeley and Syphard 2017). Of particular significance is the importance of prior-year rainfall as this is well known to be due to increased fuel production in grass dominated ecosystems (Crimmins and Comrie 2004; Keeley and Syphard 2016). We found that this climate variable was strongly tied to powerline fires, suggesting perhaps that fine flashy fuels may be a marked hazard in association with powerlines and may be an additional management target.

Conclusions

Throughout California, fire frequency has increased steadily until a peak *c.* 1980, followed by a marked drop to the present. There was not a tight link between frequency of ignition sources and area burned by those sources and the relationships changed over time. Natural lightning-ignited fires decreased from north to south and from high to low elevation. Throughout most of the state human-caused fires dominated the record and were positively correlated with population density for the first two-thirds of the record, but this relationship reversed in recent decades. Most ignition sources have declined markedly in recent decades with one notable exception, powerline ignitions. One important avenue for future fire hazard reduction will be consideration of solutions to reduce this source of dangerous fires.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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NEXUS BETWEEN WILDFIRE, CLIMATE CHANGE AND POPULATION GROWTH IN CALIFORNIA

Jon E. Keeley and Alexandra D. Syphard

Since the year 2000 California has experienced a remarkable upsurge in wildfires. Over five million hectares have burned in the last 20 years, which is double the area burned in the previous two decades. Much of this increase has been driven by large fires of more than 50,000 hectares that cause catastrophic losses of lives and property (Keeley and Syphard 2019). This increased fire activity has been correlated with an increase in average temperature over this same period, leading many observers to assert that global climate change must be playing a major role. Climate models forecast continued warming and thus some have suggested these catastrophic fires are the "new normal" or the "new *ab*normal," (Birnbaum 2018). In contrast, others have declared that these fires are the result of "forest mismanagement" (Cranley 2018) and this has stimulated renewed interest in fuel reduction (Office of Governor 2019). It's almost as though these opinions aren't even in reference to the same fires, and as described below, there is some validity to this assertion.

Above: Smoky sunset in Butte County. *[Jennifer Jewell]*

Sorting out the factors driving this rise in fire activity requires an appreciation for the diversity of landscapes and fire regimes in the state. After all, California has the largest latitudinal range of any western state, comparable to that from southern New Mexico to Wyoming, and the largest altitudinal range (containing both the lowest and highest points in the lower 48 states). California also is the most populous state in the union: One out of eight Americans live here. And most live within dense metropolitan areas juxtaposed with fire-prone wildlands, while a great many more live widely dispersed in rural settings.

A key to sorting out the factors behind increased fire activity is understanding that we are looking at two very different types of fires: fuel-dominated vs wind-dominated fires. And each of these is controlled by different environmental and historical factors (Table 1). Understanding the differences between these two types of wildfires is helpful for navigating the confusing array of opinions expressed in the media as well as determining the appropriate management responses to reduce future fire impacts.

FUEL-DOMINATED FIRES

Many of the forest fires of the past two of decades have grown out of control due to anomalous fuel loads resulting from 20th century management practices. In the early 1900s increasing state and federal interest in timber resources led to vigorous suppression of natural fires in forests that historically had burned at decadal frequency (McKelvey and Busse 1996) (Fig. 1). In the moderately productive mid-elevation conifer forests of the Sierra Nevada there is typically a vertical separation between dead branches and other litter on the ground and the living tree canopies above, and thus frequent lightning-ignited fires were commonly restricted to low intensity surface fires (Fig. 2). As a result such fires were relatively easy to extinguish and thus many forests in the western U.S. have experienced over a century of near total fire exclusion.

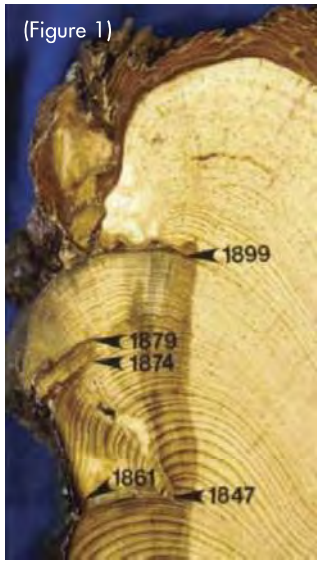


Figure 1. Cross section of ponderosa pine, upper edge is the outer bark, pith is towards the bottom. Dates indicate previous fires and none since active fire suppression in the early 1900s *(section from Bruce Kilgore, photo by Jon Keeley, USGS)*

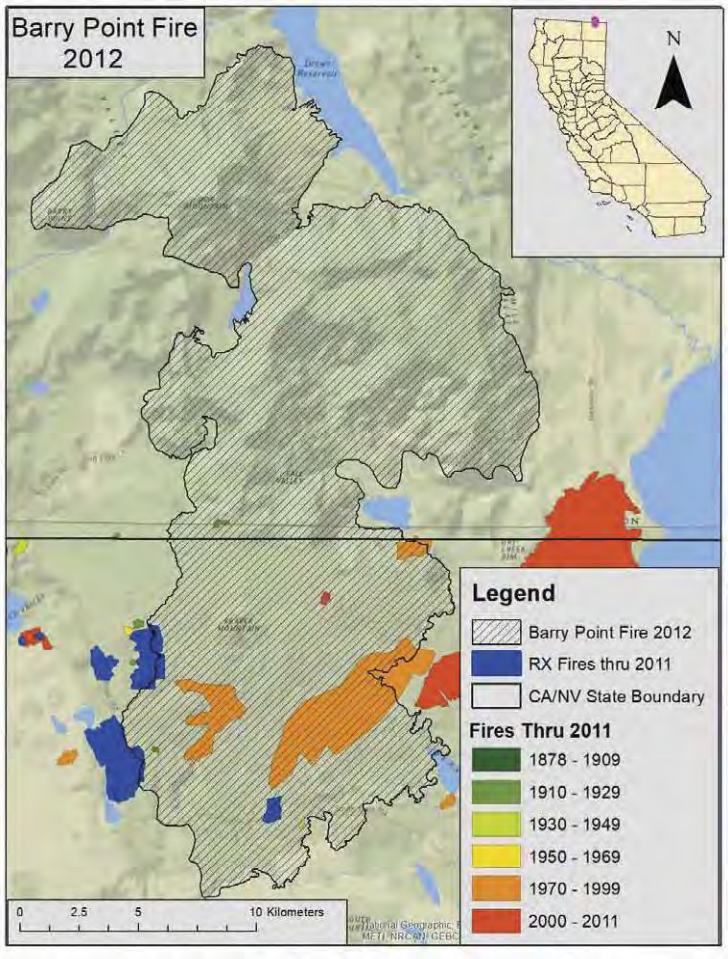
Figure 2. Low intensity surface fire typical of historical fires in many western forests *(Rim Fire burning in Yosemite National Park, photo by Jon Keeley, USGS)*

Figure 3. Fire perimeter for the 2012 Barry Point Fire, hatched area indicates no previous recorded fire from 1910 to 2012, roughly 90% of area burned in 2012, legend indicates other historical fire dates *(data from the State of California Fire and Resource Assessment Program, FRAP Fire History Database, https://frap.fire.ca.gov/mapping/gis-data/; accessed Jan 2020).*



One consequence is that some of these forests have accumulated understory surface fuels that represent fuel loads an order of magnitude greater than historical levels (Keifer et al. 2006), made even worse by the massive ingrowth of new saplings that not only further increase the fuel load but also act as ladder fuels carrying fire from the surface to the canopy. A century without fire has made these forests susceptible to high intensity crown fires, a fire pattern evident in many recent Sierra Nevada fires (Fig. 3). These types of fires are best described as fuel-dominated fires (Table 1).

To be sure, some fuel-dominated fires can produce their own extreme winds (e.g., the 2010 Station Fire in Los Angeles County or the 2018 Carr Fire in Shasta County), resulting from the high intensity burning of heavy fuel loads. The extreme heat produces pyrocumulonimbus clouds and are often described as plume-driven fires that can collapse, producing extreme wind events (Clements et al. 2018). However, such winds are internally generated, a phenomenon that could be altered by undertaking fuel treatments prior to fire events.



WIND-DOMINATED FIRES

On the other hand, wind-dominated fires are those controlled by external weather events. This is an important distinction, as we have no ability to alter such weather-driven wind events. Our most catastrophic fires of the past few decades have been just such wind-dominated fires. They typically occur in the western portions of California and burn over non-forested landscapes of shrubs, grasses, and woodlands. These fires grow rapidly due to extreme wind events and, as a result, pose severe challenges to fire suppression efforts. Readers will be familiar with several of these recent "firestorms," including the 2017 Napa-Sonoma "Wine Country" fires and the 2018 Camp Fire driven by North winds in northern California. (Historically this is the appropriate term; however, such winds are sometimes referred to as Diablo winds, a term spawned by a newspaper reporter who noted that the 1991 Oakland Hills Tunnel Fire was driven by winds coming from the direction of Mount Diablo, thus the term is less appropriate for wind-driven fires throughout the region.) Other such "firestorms" include the 2017 Thomas Fire and the 2018 Woolsey Fire driven by Santa Ana winds in southern California. While these winds may occur in both the spring and autumn (Fig.5a) they are most problematic in the autumn, following the three to six months of drought typical of our Mediterranean climate (Fig. 5b), leaving natural vegetation at its lowest moisture level. It is these autumn Santa Ana wind and North wind fires that account for the most catastrophic fires in the state (Table 1).





Figure 4. Offshore dispersion of smoke from a) North Wind driven fires in northern California, 2017, and b) Santa Ana Wind driven fires in southern California, 2003.

TABLE 1. Selected fires representing fuel-dominated and wind-dominated fires.

Year	Fire	County	Mon. (days)	Hectares	Cause	Lives	Structures
Fuel-Dominated Fires:							
2007	Marble C	Monterey	July -	71,980	Lightning	0	0
2012	Barry Point	Modoc	Aug -	37,630	Lightning	0	3
2012	Rush	Lassen	Aug -	110,080	Lightning	0	1
2013	Rim	Stanislaus	Aug -	104,220	Campfire	0	112
2014	King	El Dorado	Sept -	39,260	Arson	0	80
2015	Rough	Fresno	July -	61,360	Lightning	0	4
Wind-Dominated Fires:							
1889	Santiago	Orange	Sept (3)	125,000	Campfire	0	0
	Laguna	San Diego	Sept (3)	70,500	Powerline	5	382
2003	Cedar	San Diego	Oct (3)	109,500	Flares	15	2,820
2007	Witch	San Diego	Oct (2)	80,200	Powerline	2	1,265
2017	Tubbs	Sonoma	Oct (2)	14,900	Powerline	22	5,643
2017	Thomas	Ventura	Dec (10)	114,080	Powerline	2	1,063
2018	Camp	Butte	Nov (2)	62,060	Powerline	88	18,804
2019	Kincade	Sonoma	Nov (5)	31,470	Powerline	0	374

Table 1. Selected fires representing fuel-dominated and wind-dominated fires *(data from the State of California Fire and Resource Assessment Program, FRAP Fire History Database, https://frap.fire.ca.gov/mapping/gis-data/; accessed Jan 2020).*

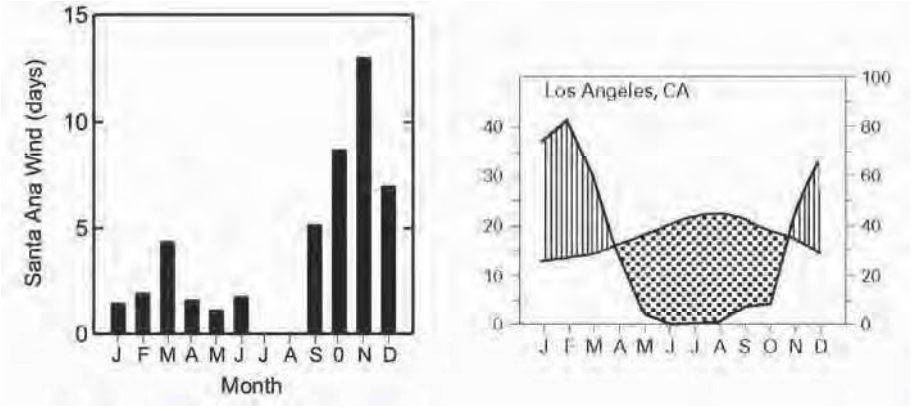


Figure 5. a) Days of Santa Ana winds and b) temperature and precipitation in Los Angeles illustrating typical Mediterranean climate of winter rains and summer droughts *(from Keeley et al. 2012).*

Historically these landscapes have not experienced the fire exclusion seen in many Sierra Nevada landscapes, despite being managed by the same fire suppression policy (Fig. 6). This is due to the fact that essentially all are caused by human ignitions, which are relatively common due to the high population density in the western portion of California (Keeley and Syphard 2018). As a consequence, there has not been any lack of fire and most large fire events burn across landscapes with an extensive fire history and no anomalous fuel accumulation. Indeed, some of these large fires—e.g., the Thomas Fire (Keeley and Syphard 2019)—have burned across areas where extensive prescription burning had occurred in recent years, pointing to the conclusion that prior fuel treatments are having limited effect on the spread of these fires. Even landscapes not experiencing high fire frequencies, such as the San Francisco Bay Area, are not outside their range of natural fire frequencies and so fuels have not accumulated due to fire suppression (Keeley 2005). To be sure, some communities in this region have dangerous fuels but these are often the result of urban plantings of *Acacia, Eucalyptus* and *Pinus* and not so much due to accumulation of wildland fuels from elimination of natural fires.

Every year there are many Santa Ana wind events but most years we don't see major wind-driven fires because they are entirely dependent on a human ignition happening during an extreme wind event. Indeed, only about five percent of the Santa Ana wind days are accompanied by a large fire event (Rolinski et al. 2019). Some have suggested that these Santa Ana winds are increasing in frequency, duration, and intensity, but records do not show a change in the character of these winds since the mid-1900s (Williams et al. 2019). Rolinksi et al. (2016) found that fires during extreme weather events are larger than ones in less extreme Santa Ana conditions, and some have interpreted this to mean that fires are becoming worse because Santa Ana winds are becoming more extreme. However, this study only considered Santa Ana winds after an ignition had occurred, thus ignition sources are critically important. It's important to recognize that Rolinksi's Santa Ana Wind Threat Index is not an indication of when an extreme fire will occur but only how bad the fire will be once ignited. What determines an extreme fire year is the untimely human ignition during an extreme wind event. This is illustrated by the fact that the frequency of these wind events is not correlated with area burned (Keeley and Syphard 2018) and our largest fire years occur in high as well as low Santa Ana wind intensity years

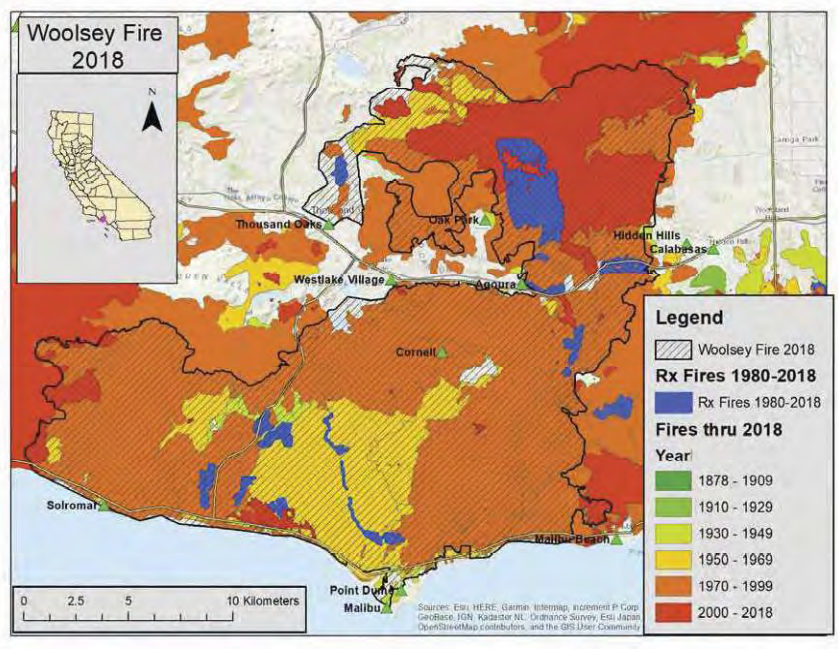


Figure 6. Fire history within the perimeter of the 2018 Woolsey Fire. Hatched area indicates less than 1% of the area unburned prior to 2018, legend indicates other fire dates *(data from the State of California Fire and Resource Assessment Program, FRAP Fire History Database, https://frap.fire.ca.gov/mapping/gis-data/; accessed Jan 2020).*

(Fig. 7). Ultimately it is all determined by an untimely human ignition event. Of course climate is peripherally related as it has been found that these fires are less likely to occur when relative humidity is high (Jin et al. 2014) and this most certainly is tied to decreased probability of such fires after early autumn precipitation (Keeley and Syphard 2017).

Indeed, Santa Ana wind events occur multiple times every year, yet during most such wind events there is no human ignition and thus no fire (Keeley and Syphard 2017). There is little evidence that the increase in the number of catastrophic fires is the result of increased intensity of Santa Ana wind events. For example Guzman-et al (2016) mapped the annual intensity of Santa Ana wind events (Fig. 7) yet when we overlaid extreme fire years of over 100,000 hectares burned in southern California (Fig. 7), we find that such extreme fire years are associated with low as well as high intensity Santa Ana wind years; e.g., the catastrophic 2003 Cedar Fire (Table 1) occurred during a year with low intensity Santa Ana winds.

CHANGING IGNITION SOURCES

Lightning is a common ignition source in forests of the Sierra Nevada and northeastern California and thus accounts for many fuel-dominated fires (Table 1). However, lightning is relatively uncommon in coastal regions (Keeley and Syphard 2018) and does not occur under the synoptic conditions that create extreme Santa Ana and North wind events. Thus, these wind-dominated fires are ~ 100% human-ignited fires (either from intentional causes, such as arson, or accidental causes, such as sparks from equipment).

In the last decade, the majority of these large fires—including some of the biggest fires in 2017, 2018, and 2019—have been ignited by powerline failures during extreme wind events. Indeed, since the year 2000 over half a million acres have burned due to powerline failures, which is five times more than in the prior two decades (Keeley unpublished data). The increased impact of powerline-ignited fires is not the result of increased frequency or intensity of extreme wind events. There are two likely explanations for this increase in powerline-ignited fires: 1) expansion of the electrical grid due to increased development, which provides more opportunities for powerline ignited fires, and/or 2) deteriorating powerline equipment resulting from age and inadequate maintenance (one California regulator contends that electrical grid equipment is being run to the point of failure (Penn et al. 2019)).

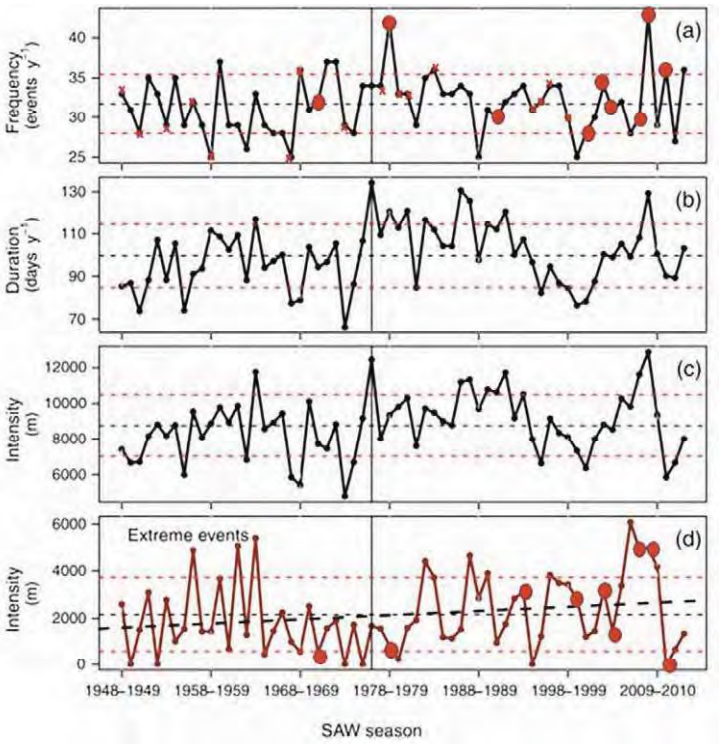


Figure 7. Pattern of Santa Ana wind (SAW) characteristics from Guzman-Morales et al. 2017 and with red dots indicating very high fire years exceeding a hundred thousand hectares burned *(from Keeley and Syphard 2017).* Correlation analysis between frequency of Santa Ana wind events or the intensity of extreme Santa Ana wind events with area burned there is no significant relationship in southern California.

GLOBAL CLIMATE CHANGE

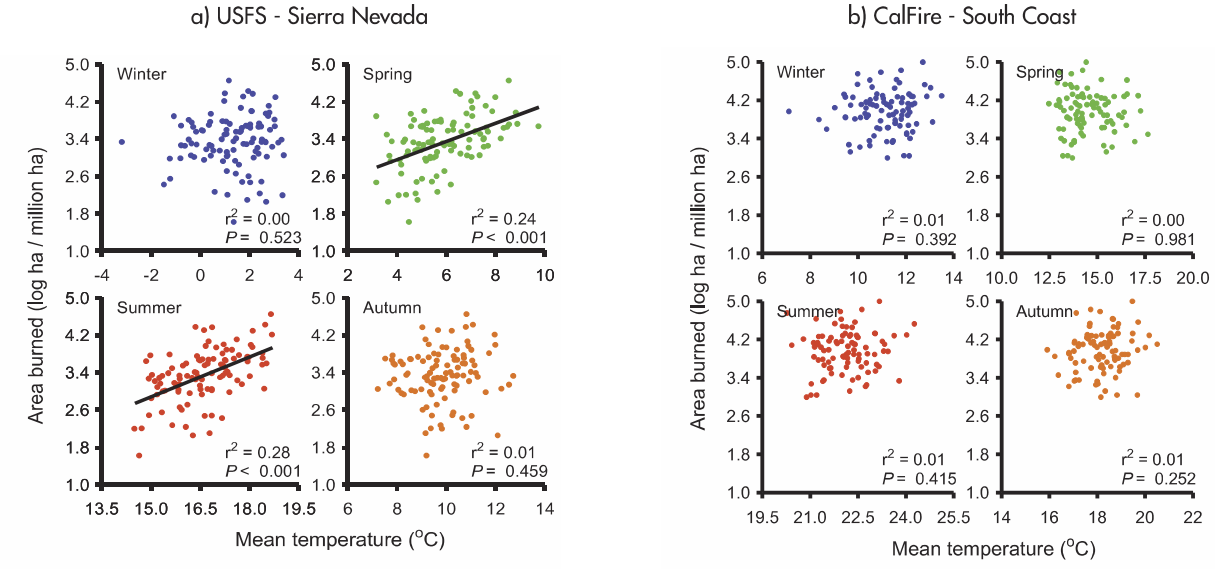
Some forecasts of future fire regimes based on different climate change simulations predict huge increases in California wildfires (Westerling 2018). These models need to be viewed in light of the fact that they are driven by untested assumptions, they don't adequately account for the complexity of fire driven changes in vegetation (Syphard et al. 2018b), and they don't consider changes in fire-climate relationships over time, as well as changes in human-ignition patterns.

An alternative approach to future modeling is retrospective studies. Confucius stated "If one wants to define the future, they must study the past" (Castro 2012). We recently conducted a study that took an empirical approach and asked how seasonal variation in temperature and precipitation has correlated with area burned, year to year, in the past. This investigation, which differs from those using algorithms of future fire-climate relationships, covered much of the last 100 years and separated out the effect of different seasonal temperatures (Keeley and Syphard 2017).

One interesting finding is that in no region of the state did winter temperature play a role in determining subsequent fire activity. This may be important since some climate models predict the greatest global warming to occur in the winter in the northern hemisphere. So perhaps this type of warming might not translate into changes in fire severity and frequency in California.

We can summarize our findings by contrasting U.S. Forest Service lands in the Sierra Nevada (Fig. 8a) with the lower elevation California Department of Forestry and Fire Protection responsibility lands in southern California (Fig. 8b). In Sierra Nevada forests there is a significant relationship between higher spring and summer temperatures and area burned; indeed, in the last 50 years, the combination of these two climate variables (spring and summer temperature) could explain over 50% of the year-to-year variation in area burned (Keeley and Syphard 2017). This is consistent with claims that global warming has played a role in increased burning in western forests in recent decades (Abatzoglou and Williams 2016).

In contrast, on non-forested landscapes in southern California we found little correlation between seasonal temperatures and area burned (Fig. 8b), a pattern consistent with other recent studies (Williams et al. 2019). We surmise that this is likely due to the fact that in southern California it is hot and dry enough every year to support large fires. (Note that maximum summer temperatures in the Sierra Nevada, when fires are most extensive, are similar to the lowest temperatures observed in southern California in the summer, Fig. 8a&b). The lack of a strong annual climate relationship with fires in southern California is due to climate being overridden by other factors, such as extreme wind events, increasing human ignitions during severe wind events, and long-term drought. Interestingly, while there has been an effect in the last 50 years of prior year precipitation on fires in southern California, this effect is well known in grasslands and savannas throughout the southwest and is tied to elevated grass fuel loads following high rainfall years (Keeley and Syphard 2017). We believe the reason this relationship showed up for southern California in the last half of the long-term record (Fig. 8b) is due to the well-documented increase in type conversion from shrublands to grasslands in the region (Syphard et al. 2018a).



Akaike IC regression models

Sierra Nevada (USFS)	r2	
1910 - 2013	0.39	Temp spr+Temp sum-Ppt spr
1910 – 1959	0.42	- Ppt spr - Ppt win
1960 - 2013	0.52	Temp spr + Temp sum

South Coast (CalFire)	r2	
1919 - 2013	0.00	
1919 - 1959	0.00	
1960 - 2013	0.25	Prior ppt-Ppt aut -Ppt sum

Figure 8. a) annual area burned from 1910 – 2013 for USFS lands in the Sierra Nevada plotted against winter, spring, summer, autumn temperatures and multiple regression models using all temperature and precipitation data for these four seasons, and b) annual area burned from 1919 – 2013 on CalFire lands in southern California and multiple regression analysis *(from Keeley and Syphard 2017).*

One climate factor not considered when investigating annual climates is the impact of long-term droughts; i.e., those that last for multiple years. Recently California experienced an intense drought that began in 2012 and lasted for three years in the Sierra Nevada and eight years in southern California (Jacobsen and Pratt 2018). It was accompanied by an immense dieback of trees in the Sierra Nevada (Stephens et al. 2018) and of shrublands in southern California (Keeley and Syphard 2019). This creation of massive dead fuel loads represents a legacy on the landscape that may persist through subsequent years of higher rainfall. If drought-induced dieback proves to have been a critical factor in making the 2017 and 2018 fire years so extreme it raises doubts as to whether these fire years represent a new normal for California, since although droughts are expected to be more severe under climate change, there is no evidence that such extreme droughts will be a normal feature going forward.

What can we conclude about how climate change may impact these coastal wind-driven fires? Global warming may reduce grass growth leading to reduced fire frequency in these grass-dominated landscapes. On the other hand, higher temperatures have the potential for increasing the intensity of plant stress during droughts, perhaps elevating dieback of woody plants that would exacerbate fire spread and intensity; a study by Williams et al. (2015) concluded that the last severe drought in the Sierra Nevada increased the stress by ~10-15 percent. A further impact of global warming is that it will likely alter postfire recovery of shrublands by changing the competitive balance to favor alien grasses, increasing type conversion to highly flammable herbaceous fuels, leading perhaps to increased fire frequency (Syphard et al. 2018a, 2019, Park et al. 2018).

In summary, there is good reason to conclude that global warming is affecting Sierra Nevada forest fires. In montane forests with fuel-dominated fires, summer temperatures—although fluctuating greatly from year to year—have been on an upward trajectory for many decades and it is reasonable to assume a causal relationship between increased fire activity and global warming. However, over this same period there has been a steady increase in understory fuels. This raises an interesting question: Would the strength of the observed climate impact (Fig. 8a) have been as strong in the absence of this anomalous fuel accumulation due to fire suppression? In contrast, in the coastal regions there is limited evidence that climate change is impacting wind-dominated fires (Fig. 8b). However, global warming has the potential for a number of indirect impacts on vegetation that may alter fire regimes.

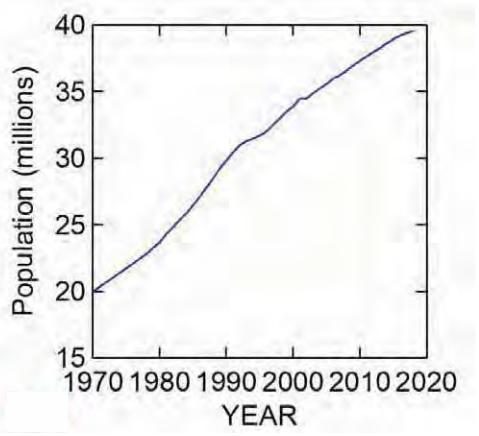


Figure 9. California population from Census Bureau *(https://www.census.gov/data; accessed June 2019)*

POPULATION GROWTH

Roger Kennedy, a former National Park Service director, was one of the first to bring attention to the role of population growth in raising the threat of wildfire (Kennedy 2006). It is true that since 2000 California has experienced a highly variable and subtle rise in temperature. However, less noticed is that there has also been a steep rise in population, adding about six million people (Fig. 9) over the last two decades. Since ~100% of the wind-dominated fires are ignited by humans or human infrastructure, there is likely a causal relationship between this population growth and the increased incidence of catastrophic wind-dominated wildfires.

Although local, state, and federal agencies have made significant progress in reducing the overall number of fires in the state over the last several decades (Keeley and Syphard 2018), there has been an increase in ignitions during extreme wind events. Thus, the real driver of wind-dominated fires is not the extreme wind events per se, but rather untimely human ignitions during such extreme wind events. And, of course, the addition of 300,000 more people every year in the state increases the probability of such an ignition event; moreover, urban sprawl into wildland areas increases the probability of losses of lives and property. An illustration of this is the 2017 Tubbs Fire that roared through sections of Santa Rosa, Sonoma County (Fig. 10b) causing the deaths of 22 people and destroying more than 5500 structures. Fifty years earlier the Hanly Fire had burned through

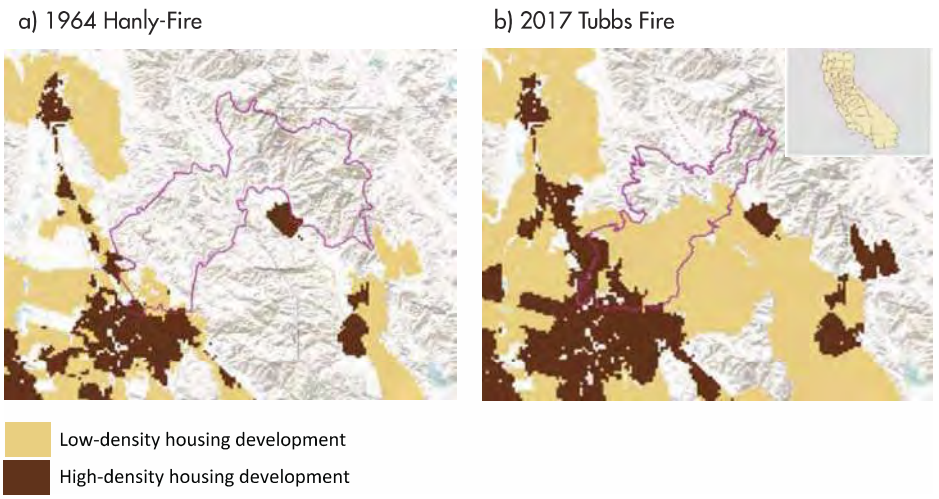


Figure 10. a) 1964 Hanly Fire perimeter in pink, and b) 2017 Tubbs Fire perimeter in pink, with changes in low density and high density housing *(from Keeley and Syphard 2019).*

much of the same landscape during a North wind event (Fig. 10a), yet no one died and only about 100 structures were lost. Some researchers have discounted this comparison because the Hanly Fire burned over a longer period of time and therefore it is assumed it was not driven by severe winds. However, that fire burned for a longer duration because it was was nearly three times the size of the Tubbs Fire and when it made its run towards Santa Rosa (overlapping with the perimeter of the much later Tubbs Fire) it was driven by extreme dry winds (*The Press Democrat*, September 26, 1964, front page), suggesting fire behavior similar to the 2017 Tubbs Fire. The difference in impact of these two fires is likely due to the fact that during this 50-year period Santa Rosa's population grew from 30,000 to 170,000 people and the urban footprint had expanded such that in 2017 development had expanded so that two thirds of the area burned by the Tubbs Fire was low density housing (Fig. 10b). This urban expansion was accompanied by expansion of the electric power grid, increasing the chances of a powerline failure during North wind events that drove both the Hanly and Tubbs fires.

MANAGEMENT CONSIDERATIONS

Fuel-dominated and wind-dominated fires exhibit important differences (Table 1) that inform how to manage these events. First, the fuel-dominated fires are largely forest fires in lightly populated regions such as the Sierra Nevada. In contrast, most wind-dominated fires occur in non-forested ecosystems in the western half of the state, though they may also occasionally occur in more interior sites, such as the 2018 Camp Fire that burned in Paradise. Wind-dominated fires occur in densely populated landscapes and these fires are responsible for the greatest loss of lives and property.

MANAGEMENT CONSIDERATIONS—FUEL-DOMINATED FIRES

Montane forests have an anomalous accumulation of fuels due to more than a century of fire suppression and logging and therefore require concerted efforts at reducing the present fuel load (North et al. 2012). In the late 1960s, staff at Sequoia National Park began prescription (Rx) burning and soon after the other national parks in the Sierra Nevada followed suit (Keeley and Syphard 2019). Over time these parks greatly exceeded the area burned by adjacent forests. In recent years the USFS lands have accelerated the amount of Rx burning. However, all Sierra Nevada lands are a long way from burning at a rate sufficient to restore natural historical fire frequencies. There are many limitations, including funding, air quality restrictions, diversion of personnel from Rx burns due to wildfires, among others.

MANAGEMENT CONSIDERATIONS—WIND-DOMINATED FIRES: THE 5 P'S

The distinction between fuel-dominated and wind-dominated fires is similar to the dichotomy between katabatic and non-katabatic wind-driven fires made by Kolden and Abatzoglou (2018). They point out that in southern California there are summer "fuel-dominated fires" and autumn "wind-dominated fires." While both types of fires occur in the region, it is the latter type that account for the vast amount of acreage burned, loss of lives and destruction of property. While management needs to be cognizant of both types of fire, it needs to be appreciated that summer fires are the least threatening fires and we should put our greatest effort toward autumn wind-dominated fires. Although all fires are a threat if fuels around homes have not been reduced,

there are five points to consider with respect to the catastrophic wind-dominated fires:

1) ***People:*** On these landscapes, fire is more of a people problem than a fuel problem. More people translates into a greater probability of an ignition during a severe wind event, and more development in highly fire prone landscapes inevitably results in greater losses of lives and homes.

2) ***Prevention:*** Rather than focusing on fuel treatments the scientific evidence clearly points to a need for a much greater emphasis on fire prevention. Although progress has been made in reducing the number of fires, the area burned has increased (Keeley and Syphard 2018). Powerline failures are a major cause of large fires and solutions to this increasing threat remain elusive. As widely reported in the media, three major utility companies in the state have implemented plans to monitor winds and shut down the power grid during extreme wind events. Such so-called Public Safety Power Shutdowns (PSPS) have the potential to decrease fire starts and limit damage (and, as a by-product, raise public awareness of fire threats). But there are many accompanying problems, as became evident during the recent Kincade Fire (Table 1) in October 2019, which was started by an electric failure, despite widespread power outages at the time. Such shutdowns impacted a multitude of vital services, including medical equipment, water pumps, traffic signals, communication equipment etc. One solution might be undergrounding the power lines in areas known to be corridors for extreme winds (Keeley et al. 2009). However, this would be much more expensive for the utilities to install and maintain. In addition, in areas where sensitive natural resources are present, overhead power lines may be less destructive. Nonetheless, San Diego Gas & Electric, which has led the way with responding to powerline-ignited wildfires, reports that 60% of its distribution lines are currently underground (Joe Vaccaro, Fire Mitigation & Climate Adaptation Manager, San Diego Gas & Electric Company, personal communication, 5 Dec 2019).

3) ***Planning:*** Community planning needs to devote similar attention and resources to fire as to other hazards. Since we have limited ability to control earthquakes and floods, some urban planners have utilized zoning restrictions to reduce impacts of these hazards. Yet, zoning restrictions are largely lacking when it comes to fire hazards, in large part because fires have been perceived as controllable. However it is increasingly obvious that this is not always the case and many communities are currently very vulnerable. Fire-zoning (Kennedy 2006) needs to be given more consideration as well as urban planning that insures adequate ingress for fire fighters and egress for residents during extreme fire events. Perhaps replacing community planning with a more regional approach might contribute to these efforts.

4) ***Protection:*** High intensity fires generally do not directly ignite homes when separated from vegetation by 30 meters (Cohen 2000). Home ignitions are usually the result of embers blown onto the structure and this is particularly true under extreme wind conditions. Ember cast firebrands often travel over a distance of half a mile or more. Embers ignite only under specific circumstances and this is most likely when they land on dead fuels (Zhou et al. 2019). Homeowners can diminish the probability of damage by addressing those factors that affect embers igniting their home, such as reducing plant litter on roofs and gutters, enclosing eves so that vent orientation is less susceptible to ember entry, closing open eves, placing fine mesh screens on vents, and installing double-pane windows and appropriate siding (Syphard and Keeley 2019). Well-watered trees with significant foliage can provide protection from ember cast onto a home (Keeley and Syphard 2019). In fact, watered trees with green foliage may not be susceptible to ignitions by embers, but rather could serve to extinguish them and deprive them of dry fuels. While the notion of trees as "ember catchers" is appealing it is a largely untested idea.

Roof top sprinklers may provide an added measure of protection and may be justified by the observation that trees adjacent to destroyed homes often survive because their foliage is moist, whereas combustible materials in homes represent dead fuels that are likely at equilibrium with ambient relative humidity of 10 percent or less. However, such sprinklers would need to address a number of issues. For example, metropolitan water lines and water supplies are sometimes compromised during fire events and thus there would need to be a stand-alone water tank. Also, shutting down the power grid is happening more often and thus solar or other alternative power would need to be available to pump water. In addition, there is the need for further research on how to engineer such a system in order to prevent the water spray from being dissipated to the atmosphere due to the high winds. Incorporating a system like this would likely be a significant expenditure that may not be possible for many home owners.

Fuel treatment around homes is critical but needs to be focused on the 'house out', i.e., putting the greatest effort into the area nearest the home and less as one moves further into the wildlands. Reducing fuels within 30 meters of the house is generally sufficient and further clearance beyond that is of doubtful value (Syphard et al. 2012).

5) ***Prediction:*** There is an urgent need for improved meteorological and fire behavior models that can provide real time prediction of wind patterns and fire spread during these extreme events, coupled with improvements in communication systems for providing that information to agencies and homeowners.

Acknowledgments

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Cougar space use and movements in the wildland–urban landscape of western Washington

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Abstract. The wildland–urban interface lies at the confluence of human-dominated and wild landscapes, creating a number of management and conservation challenges. Because wildlife ecology, behavior, and evolution at this interface are shaped by both natural and human phenomena, this requires greater understanding of how diverse factors affect ecosystem and population processes. We illustrate the challenge of understanding and managing a frequent and often undesired inhabitant of the wildland–urban landscape, the cougar (*Puma concolor*). In wildland and residential areas of western Washington State, USA, we captured and radiotracked 27 cougars to model space use and understand the role of landscape features in interactions (sightings, encounters, and depredations) between cougars and humans. Resource utilization functions (RUFs) identified cougar use of areas with features that were probably attractive to prey, influential on prey vulnerability, and associated with limited or no residential development. Early-successional forest (+), conifer forest (+), distance to road (–), residential density (–), and elevation (–) were significant positive and negative predictors of use for the population, whereas use of other landscape features was highly variable. Space use and movement rates in wildland and residential areas were similar because cougars used wildland-like forest patches, reserves, and corridors in residential portions of their home range. The population RUF was a good predictor of confirmed cougar interactions, with 72% of confirmed reports occurring in the 50% of the landscape predicted to be medium-high and high cougar use areas. We believe that there is a threshold residential density at which the level of development modifies the habitat but maintains enough wildland characteristics to encourage moderate levels of cougar use and maximize the probability of interaction. Wildlife managers trying to reduce interactions between cougars and people should incorporate information on spatial ecology and landscape characteristics to identify areas with the highest overlap of human and cougar use to focus management, education, and landscape planning. Resource utilization functions provide a proactive tool to guide these activities for improved coexistence with wildlife using both wildland and residential portions of the landscape.

Key words: cougar; interaction; Puma concolor; *resource utilization functions (RUF); space use; Washington State, USA; wildland–urban interface.*

Introduction

Human beings dominate the world's diverse ecosystems (Vitousek et al. 1997). Our alteration of landscapes, modification of fundamental ecosystem and evolutionary processes, and direct utilization and relocation of plants and animals requires rethinking the science of ecology (Alberti et al. 2003) and the conservation of biological diversity (Turner et al. 1991, McKinney 2002, Jenkins 2003). Foremost in this reconsideration is an understanding of the variation in human action and its spatially explicit role as a driver of other species' ecology and natural history (Marzluff and Ewing 2001, Sanderson et al. 2002).

In North America, residential development of natural landscapes is substantial and influential (Brown et al. 2005, Theobald 2005, Wade and Theobald 2010). Residential development threatens the long-term viability of many wildlife species (Ewing et al. 2005) because of direct loss of suitable habitat (McDonald et al. 2009, Wade and Theobald 2010), fragmentation of remaining habitat (Gonzalez-Abraham et al. 2007, Weng 2007), introduction and expansion of invasive species (Hansen et al. 2005, McDonald et al. 2009), and increased risk of

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mortality from a number of factors associated with increased human presence on the landscape (Taylor et al. 2002, Riley et al. 2004). The impacts of residential development are particularly acute at the wildland–urban interface, the confluence of human-dominated and wildland portions of the landscape (Radeloff et al. 2005, Theobald and Romme 2007). This confluence can be spatially complex, depending upon the number of residences present and how they are distributed (Radeloff et al. 2005, Theobald and Romme 2007). Wildlife communities in these wildland–urban landscapes are not fully understood, as both wildland and residential dynamics shape the ecology, behavior, and evolution of the species present. Impacts are likely to vary between species, but expanding residential development is particularly problematic for many large carnivores because of low population densities, large home ranges, and extensive prey biomass requirements (Linnell et al. 2001, Inskip and Zimmermann 2009). Competition and conflict between carnivores and humans has increased, and now poses a significant threat to the long-term viability of many species (Jackson and Nowell 1996, Novaro and Walker 2005, Inskip and Zimmerman 2009).

The cougar (*Puma concolor*) is a solitary, far-ranging felid that occupies a broad range of habitats in temperate and tropical environments throughout the western hemisphere (Sunquist and Sunquist 2002). Although primarily associated with wildlands (Gill 2009), cougars can, and do, use areas with an extensive human presence (Beier et al. 2010, Burdett et al. 2010). In western North America, cougar managers face many challenges in residential areas. Principal among these challenges is the need to understand the spatial ecology of cougars along a gradient of residential development and use this knowledge to decrease the occurrence of cougar–human interactions: sightings, encounters, depredations on livestock and pets, and attacks on people (Cougar Management Guidelines Working Group 2005). Understanding the resource requirements and spatial ecology of a species is fundamental for its successful management and conservation (Morrison et al. 2006), and this information may provide insights into the incompletely understood underlying causes of interactions between cougars and people (Sweanor et al. 2008).

Cougar habitat requirements have been studied extensively in a variety of North American wildland settings (Logan and Irwin 1985, Van Dyke et al. 1986, Laing 1988, Koehler and Hornocker 1991, Williams et al. 1995, Goh 2000). Cougars are considered habitat generalists because of the diversity of ecosystems they reside in throughout their range, but the presence of sufficient prey populations and stalking, resting, and security cover for the capture and consumption of prey and rearing of young are considered prerequisites for use (Seidensticker et al. 1973, Logan and Irwin 1985, Koehler and Hornocker 1991, Williams et al. 1995, Dickson and Beier 2002, Dickson et al. 2005). Cover is a combination of biotic and abiotic features that help to decrease visibility, conceal the predator, and increase the vulnerability of prey. Cover includes both the overstory and understory vegetation, physical structure and arrangement of the vegetation, and topography. Cougars are adaptable predators that consume a variety of prey (Murphy and Ruth 2009). Accordingly, cover requirements vary depending on the prey being hunted, and cover may be more abundant or advantageous within particular plant communities (e.g., riparian; Dickson and Beier 2002) or landscape configurations (e.g., edges; Altendorf et al. 2001, Holmes and Laundré 2006).

Our knowledge of cougar space use and movements in wildland–urban environments is limited (Beier et al. 2010). Previous investigations have indicated that cougars reduce their use of areas with increased human presence (Beier 1993, Burdett et al. 2010), but these studies did not directly compare spatial ecology in wildland and residential areas, nor did they directly evaluate the role of landscape features in interactions between cougars and humans. Western Washington State, USA, presents an opportunity to increase our understanding of cougar ecology in landscape settings juxtaposing wildland and residential development. Western Washington's substantial population growth (United States Census Bureau 2008), habitat alteration (Alberti et al. 2001, Robinson et al. 2005, Hepinstall et al. 2008), and reported levels of interaction between cougars and people (Washington Department of Fish and Wildlife 2008) are representative of conditions present in many portions of the western United States. Decreasing interactions while maintaining viable cougar populations is a management priority in Washington (Washington Department of Fish and Wildlife 2009), and understanding how landscape features correlate with cougar use may provide valuable information to meet these objectives.

We investigated cougar space use and movements in western Washington's wildland–urban environment to understand how residential development impacts the spatial ecology of a wide-ranging, large carnivore and its interactions with people. We developed individual- and population-level multivariate resource utilization functions (RUFs) to identify key landscape features and compare use of these features in wildland (0 residences/km^2) and residential (>0 residences/km^2) settings. To assess the effects of location and time on movement, we quantified and compared movement rates in wildland and residential areas during different periods of the day. We tested the null hypothesis that space use patterns and movement rates do not differ between wildland and residential portions of individual home ranges. We mapped predicted use throughout the study area and evaluated the utility of our population-level model to describe reported and confirmed interactions. We discuss how these findings may be used to design strategies that may reduce the probability of interactions between cougars and humans.



FIG. 1. Location of the 3500-km^2 cougar study area encompassing both wildland and residential portions of western Washington State, USA. The wildland–urban interface is depicted by the white line in the study area. Residential development occurred across the western one-third of the study area, with residential densities largely increasing from east to west.

STUDY AREA

We examined cougar space use and movement patterns in a 3500-km^2 study area in wildland and residential portions of King and Snohomish Counties, Washington State, USA (590 000 E, 5 260 000 N; Fig. 1). Land ownership was a composite of state, federal, municipal, and private holdings managed for timber production, municipal water resources, multiple-use, wilderness, commercial use, and private residences. Major landowners included the U.S. Forest Service, Washington Department of Natural Resources (WADNR), City of Seattle, King County, Hancock Resource Management Group, and Fruit Growers Supply, Inc. The western portion of the study area ($\sim$1000 km^2) consisted of fragmented forest patches and reserves within a matrix of suburban and urban development (Robinson et al. 2005). Remaining urban (>10 residences/ha) and suburban (205–210 residences/ha) development was concentrated along the Interstate 90, U.S. Highway 2, and Washington State Highway 203 corridors with exurban development extending into the foothills of the Cascade Mountains.

Wildland portions of the study area were characterized by dense, coniferous forest of varying seral stages arrayed along elevation and moisture gradients at the confluence of the recognized north and south divisions of the Cascade Mountains (Franklin and Dyrness 1973, Lasmanis 1991, Koehler and Pierce 2003). The study area was topographically complex, with large peaked and rounded mountains rising above U-shaped valleys formed by glaciation (Spencer et al. 2001). Elevations ranged from 10 to 2005 m with Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) forest associations dominant below 750 m and Pacific silver fir (*Abies amabilis*) and mountain hemlock (*Tsuga mertensiana*) forest associations dominant above 750 m (Franklin and Dyrness 1973). The climate was moderated by the proximity of a mild, maritime environment and temperature extremes were rare. Mean annual precipitation ranged from 142 cm in the west to 257

cm in the east and occurred primarily between 1 October and 1 July (Western Region Climate Center 2009).

Materials and Methods

Capture, collaring, and monitoring

We attempted to capture cougars present in the study area throughout the year from November 2003 to December 2008 using trained dogs and large, steel cage traps baited with cougar-killed or road-killed black-tailed deer (*Odocoileus heminous columbianus*) and elk (*Cervus elaphus*; Kertson 2010). Captured individuals were immobilized with a 10:1 mixture of ketamine hydrochloride and xylazine hydrochloride (Plum Creek Pharmaceuticals, Amarillo, Texas, USA) administered intramuscularly at a dosage of 8.8 mg/kg ketamine and 0.88 mg/kg xylazine via a 3.0-mL plastic dart fired from a CO_2-powered dart gun (Dan Inject North America, Fort Collins, Colorado, USA; Spencer et al. 2001). Immobilized cougars were given a physical examination, ear-tagged, and outfitted with a 600-g GPS radio collar (Model GPS Plus-2, Vectronics Aerospace, Berlin, Germany; Model GPS-Telus and GPS-Simplex, Televilt, Lindesberg, Sweden). During 2005–2006, six cougars were outfitted with standard VHF radio collars (Advanced Telemetry Solutions, Isanti, Minnesota, USA). All cougar captures and handling were performed in accordance with the University of Washington's Institutional Animal Care and Use Committee under Protocol No. 2185-36.

Global Positioning System radio collars were programmed to attempt a satellite fix for 180 s every 4 h at 2, 6, 10, 14, 18, and 22 h in an attempt to maximize both battery life and data acquisition (Cain et al. 2005, DeCesare et al. 2005, D'Eon and Delparte 2005, Lewis et al. 2007). We randomly located individuals weekly using ground-based radiotelemetry techniques (Mech 1983) and remotely downloaded GPS data sets every 14–21 days from Vectronics collars and every 4 weeks from Televilt collars.

Space use

We examined use as a continuous variable represented by a utilization distribution (UD) and related this use to landscape features using multivariate resource utilization functions (RUFs; Marzluff et al. 2004, Hepinstall et al. 2005, Millspaugh et al. 2006). The UD is a probability density function that quantifies an individual's relative use of space (van Winkle 1975). Relating resources to a probabilistic measure of space use correctly identifies the individual animal, not individual locations, as the experimental unit, measures use continuously instead of discretely, accounts for variable intensity of use, and avoids problems associated with estimating resource availability (Aebischer et al. 1993, Otis and White 1999, Manly et al. 2002, Marzluff et al. 2004, Millspaugh et al. 2006, Kertson and Marzluff 2010). We used the fixed-kernel density estimator in Hawth's Tools (Beyer 2004), available for ArcMap 9.3 (ESRI 2008) to estimate a home range (Worton 1989, Seaman and Powell 1996, Kernohan et al. 2001) for each cougar with more than 30 GPS or VHF relocations within a calendar year (January–December; Seaman et al. 1999). We used the hpi function within the KernSmooth package available in R (Wand 2006) to estimate the bivariate plug-in bandwidth values (h_{pi}; high-speed portable Internet) for each kernel (Wand and Jones 1995). We selected the bivariate h_{pi} to smooth kernels based on the configuration of cougar relocation data and recommendations provided by Gitzen et al. (2006), coupled with observations that h_{pi} minimizes over-smoothing in resulting kernels generated from GPS data (Kertson and Marzluff 2010). We defined the used area for cougars as the 99% fixed-kernel boundary, and we assigned each 30×30 m pixel within this area a value between 1 (lowest use) and 99 (highest use), based on the volume (height) of the UD (Marzluff et al. 2004, Kertson and Marzluff 2010). For cougars monitored >1 year, we considered each calendar year to be independent because individual space use patterns changed annually, most likely because of high levels of mortality in the population leading to home range shifts (Logan and Sweanor 2001), changes in social or reproductive status, and landscape alteration, primarily in the form of commercial logging and residential development (B. Kertson, *unpublished data*).

We used the Ruf.fit package available for R (see Marzluff et al. 2004) to estimate RUFs for all cougars to determine the influence of landscape features on use within the home range (Level III; Johnson 1980) and the potential for interactions with people, based on the distribution of these features. Important landscape characteristics for cougars in lowland Douglas-fir/western hemlock forests of the Pacific Northwest were unknown, so we selected landscape features that we hypothesized would be good predictors of use based on our observations of cougar predation ecology (i.e., the presence of prey and cover), their potential for characterizing anthropogenic land change, and/or their potential for characterizing patches of suitable cougar habitat within portions of the study area with residential development. Black-tailed deer, elk, and beaver (*Castor canadensis*) constituted 87% of documented prey items in western Washington ($n = 304$ kills; Kertson 2010), and cougars frequently hunted and captured prey in forest $<$ 30.0 years of age, in low-elevation areas, or close to water and edges. We did not have direct measurements of abundance or density for all potential prey across the study area, nor did we have direct measures of all types of potential stalking and security cover for cougars. Consequently, we focused on a variety of landscape features to serve as proxies for prey and cover. We selected six variables indicative of cougar predation ecology: percentage clearcut and regenerating forest (percent squared within 150 m^2), distance to water (streams, rivers, wetlands, and lakes; in meters), distance to patch edge (meters), patch shape as the corrected

ratio of patch perimeter length to patch area (corrected perimeter : area ratio, CPAR; Farina 2000), slope (degrees), and elevation (decimeters; Kertson 2010), and five additional variables indicative of anthropogenic disturbance and/or suitable cougar habitat in residential portions of the study area: percentage conifer forest (percent squared within 150 m^2), percentage forest (percent squared within 1.0 km^2), distance to road (meters), distance to residential lots (meters), and residential density (number of residential structures within 1.0 km^2; Kertson 2010). We derived the distance to water grid using high-resolution imagery from the National Hydrography Database (*available online*)[7] and the Spatial Analyst Euclidean distance tool in ArcMap 9.3. Distance to edge was estimated using a 14-class land cover grid developed by Hepinstall et al. (2008) for King, Snohomish, and Pierce counties, the "Extract Raster Edge" function in Hawth's Tools (Beyer 2004), and Spatial Analyst Euclidean distance. To estimate PAR, we converted the 14-class land cover raster to a polygon shapefile and used the "Add AREA/PERIMETER to table" function in Hawth's Tools (Beyer 2004) to measure the perimeter and area of each patch. We calculated CPAR using the field calculator and the equation provided by Farina (2000):

$$\text{CPAR} = \frac{0.282(\text{Perimeter})}{\sqrt{\text{Area}}}$$

and created a new raster grid of these values. We obtained elevation values from a mosaic United States Geological Survey 10-m digital elevation model (DEM) of UTM Zone 10 from the Washington State Geospatial Data Archive (WAGDA; *available online*).[8] Slope was derived using the "Slope Surface" function in Spatial Analyst and the USGS 10-m DEM for UTM Zone 10. Percentage clearcut and regenerating forest and percentage conifer forest were estimated for King, Snohomish, and Pierce counties using a 150-m moving window analysis with Fragstats 3.3 (*available online*).[9] Percentage forest was estimated using a 1.0-km moving window (Hepinstall et al. 2008). We calculated distance to roads from vector line coverage of all roads in King, Snohomish, and Pierce counties and Spatial Analyst Euclidean distance. We used 2008 tax parcel records for King, Snohomish, and Pierce counties and "Select by Attribute" in ArcMap 9.3 to identify all parcels containing a residential structure (e.g., single-family home, multi-family home, or apartment complex). We used "Generate Polygon Centroid Points" in Hawth's Tools (Beyer 2004) to create a point layer of residential structures and measured distance to these points using Spatial Analyst Euclidean distance. We used the residential point layer and Spatial Analyst point density to create a grid of residential density within 1.0 km^2. We output all landscape attributes on a 30×30 m grid to match the spatial resolution of cougar use estimates, and all percentage forest measures were arcsine-transformed. To assure that correlated ($|r| > 0.70$) covariates were not included in our model (Hosmer and Lemeshow 2000), we quantified the amount of multicollinearity between predictor variables using the Pearson's correlation matrix available in the STATS package of R (R Development Core Team 2006). Isolated occurrences of correlation existed within individual UDs, primarily between the forest metrics, but we included all covariates because none were consistently correlated for the population.

We used the Hawth's Tools extension (Beyer 2004) available for ArcMap 9.3 and Spatial Analyst Extraction to generate the spatially explicit data file required by Ruf.fit (Kertson and Marzluff 2010). We estimated unstandardized and standardized coefficients for landscape features using the complete data set of each cougar-year (Kertson and Marzluff 2010). To derive population-level inferences of covariate significance, we averaged the standardized coefficients and constructed 95% confidence intervals using a standard error estimate that included inter-animal variation (Marzluff et al. 2004). Confidence intervals that did not include zero were considered significant predictors of use for the population. We ranked the relative importance of significant landscape features using the absolute value of the mean standardized coefficient (Marzluff et al. 2004) and tested for statistical differences between coefficients ($\alpha = 0.05$) using multiple comparison techniques controlling for Type I error with Tukey's hsd (Oehlert 2000). We used each cougar-year's standardized coefficients and 95% confidence intervals to quantify the number of cougars with significant use positively and negatively correlated with each resource metric (Marzluff et al. 2004).

Wildland and residential space use comparison

Cougars using both wildland and residential areas within their home range allowed us to test for differences between space use patterns within locales with residential development and those without, while controlling for potential differences between individual cougars. We used the Year 2000 Rural I-3 classification of the SERGoM v1 landcover model (Theobald 2005) and the Raster Calculator in ArcMap 9.3 to create a residential land cover polygon to delineate the wildland–urban interface in King, Snohomish, and Pierce counties. We used 1.0-m resolution 2002 aerial photographs of the study area, 2008 tax parcel records for King, Snohomish, and Pierce counties, and ArcMap 9.3 to adjust the wildland–urban interface delineation misclassified by SERGoM v1 (Kertson 2010). We identified areas with residential development from the wildland–urban interface delineation and created a residential polygon in ArcMap 9.3 to overlay each cougar's UD to identify

[7] ⟨http://nhd.usgs.gov/⟩
[8] ⟨http://wagda.lib.washington.edu/⟩
[9] ⟨www.umass.edu/landeco/research/fragstats/fragstats.html⟩

individuals with $\geq$1.0% of their use within residential portions of the landscape (Kertson 2010). For these individuals, we estimated separate residential and wildland RUFs from portions of their spatially explicit use–landscape feature file that fell within and outside of the residential portion of the study area. We averaged residential and wildland standardized coefficients and tested for statistical differences ($\alpha = 0.05$) between use patterns using paired t tests (Marzluff et al. 2004). We hypothesized that use associated with landscape features within the residential environment would be less variable than the wildland environment stemming from reduced access to suitable habitat. To test this hypothesis, we constructed 95% confidence intervals for each cougar from standardized coefficients and associated standard errors to determine the proportion of individuals with use positively and negatively correlated with each resource (Marzluff et al. 2004).

Movement analysis

To further understand how use of the residential landscape may, or may not, differ from use of wildlands, we compared cougar movement rates during different diel periods in residential and wildland portions of the landscape. We used relocation data from 10 wildland–urban cougars with GPS collars having successful satellite fix rates $\geq$ 70.0%. We focused our analysis on these individuals in an attempt to minimize the effects of missed satellite fixes on movement rate calculations (Joly 2005). We classified the time (nocturnal, 02:00 and 20:00 hours; diurnal, 10:00 and 14:00; crepuscular, 06:00 and 18:00) and location (residential or wildland) of each GPS location. We calculated the straight-line distances (meters) and elapsed times (hours) between relocation points to estimate a movement rate (meters/hour) for each observation. We used an ANOVA fixed-effects model (Zar 1999) to examine the influence of location (wildland vs. residential), time, and the interaction of location and time on cougar movements. We tested for specific differences between combined location and time classes using multiple comparison techniques controlling for Type I error with Tukey's hsd (Oehlert 2000).

Cougar–human interaction

Interactions between cougars and people are a function of the probability of a human encountering a cougar. We evaluated the ability of the cougar RUF model to predict interactions within the study area based on cougar use. We mapped predictions of cougar use throughout the study area on a 30 $\times$ 30 m grid using averaged unstandardized resource coefficients from the population RUF (Marzluff et al. 2004). We classified predicted use into quartiles and labeled them: low (0–25%), medium-low (26–50%), medium-high (51–75%), and high (76–100%). We evaluated the ability of the population RUF to predict interactions using 175 reports received by the Washington Department of Fish in Wildlife (WDFW) within the study area from January 2006 to December 2008 and a subsample of 21 interaction reports confirmed by our on-site investigation because of the low degree of confirmation associated with the WDFW data set (Kertson 2010). To provide additional insights into the predictive ability of the population RUF, we used total reports, the bivariate plug in bandwidth estimator, and the fixed-kernel density estimator in Hawth's Tools to construct an interaction UD and we calculated the volume of intersection (V.I.; Kernohan et al. 2001) with the population RUF model. We restricted both evaluations to residential portions of the study area with rescaled UD values because 98% of reported interactions occurred within this setting (Kertson 2010).

Results

Space use

We estimated a population-based RUF from 27 cougars over 33 cougar-years with an average of 585 $\pm$ 563 relocations per individual (mean $\pm$ SD). These cougars spent an average of 16.86% $\pm$ 17.05% (mean $\pm$ SD) of their time in residential areas and generated 2323 observations (12.15% of relocations) $\leq$ 500 m from a residential structure. The population RUF revealed highest use of areas within home ranges with higher levels of early-successional forest, higher levels of conifer forest, lower levels of total forest cover, closer to water, closer to edge, closer to roads, farther from residential lots, lower residential densities, land cover patches with more edge (higher CPAR values), steeper slopes, and lower elevations (Table 1, Fig. 2). However, individual RUFs indicated that resource use was highly variable among the cats. Each of the 11 landscape features was significantly correlated with use for a majority of cougars (range 73–94%), but use was only consistent within the population for percentage conifer forest (71% positive), distance to road (73% negative), residential density (86% negative), slope (67% positive), and elevation (90% negative); see Table 2. The high degree of individuality was reflected in the population-based RUF, as >99.0% of total variation for each covariate was generated by inter-animal variation. Subsequent 95% confidence intervals for percentage forest, distance to water, distance to edge, distance to residential lots, CPAR, and slope included 0.0 (Table 2). Differences in home range size accounted for 3.6% $\pm$ 4.1% (mean $\pm$ SD) of observed variation in each resource coefficient and differences between sexes accounted for an average of 5.3% $\pm$ 5.5% (mean $\pm$ SD).

The relative importance of landscape features differed between all cougars and years, as no two cougars used the landscape in the same way. Ranking of significant landscape metrics from the population RUF indicated elevation as the most important predictor of cougar use, followed by residential density, clearcut and regenerating forest, conifer forest, and distance to road. Multiple comparisons of standardized coefficients revealed differences between elevation and percentage clearcut and

TABLE 1. Estimated resource utilization function (RUF) unstandardized coefficients for cougars ($n = 27$) in a wildland–urban environment in western Washington State, USA, 2003–2008.

Landscape metric	No. cougar-years	Unstandardized RUF coefficients	
		$\bar{\beta}$	SE
Intercept	33	30.392	2.092
Percentage clearcut and regenerating forest	33	5.383×10^{-2}	1.775×10^{-2}
Percentage conifer forest	33	3.505×10^{-2}	1.496×10^{-2}
Percentage forest	33	-3.401×10^{-2}	2.988×10^{-2}
Distance to water	33	-9.970×10^{-4}	2.313×10^{-3}
Distance to edge	33	-5.071×10^{-3}	4.338×10^{-3}
Distance to road	33	-3.236×10^{-3}	1.700×10^{-3}
Distance to residential development	33	-4.900×10^{-4}	7.730×10^{-4}
Residential density	31	-6.907×10^{-1}	2.866×10^{-2}
Perimeter : area ratio	33	1.033×10^{-2}	3.323×10^{-2}
Slope	33	1.600×10^{-2}	1.292×10^{-2}
Elevation	33	-2.060×10^{-3}	5.250×10^{-4}

Notes: Multiple years of monitoring for the same individual were considered independent (cougar-years). Conservative standard errors were estimated with measures of inter-animal variation included using Eq. 3 minus Eq. 2 from Marzluff et al. (2004).

regenerating forest (difference = 5.15, $P < 0.001$), elevation and conifer forest (difference = 5.12, $P < 0.001$), elevation and distance to road (difference = 2.96, $P < 0.01$), residential density and clearcut and regenerating forest (difference = −3.31, $P < 0.01$), and residential density and conifer forest (difference = −3.28, $P < 0.01$). Average ranking of landscape metrics characterizing the level of anthropogenic disturbance and metrics related to cougar predation ecology were not statistically different ($t = -0.35$, $P = 0.74$, df = 9).

Wildland and residential space use comparison

We estimated separate wildland and residential RUFs from 19 cougars (24 cougar-years) that had at least 1.0% of their UD occurring within residential areas (residential use 21.95% ± 14.65%; mean ± SD). Cougar use of both wildland and residential portions of the home range increased with increasing levels of clearcut and regenerating forest, increasing levels of conifer forest, decreasing distance to water, decreasing distance to edge, decreasing distance to road, and decreasing slope (Table 3). Increasing levels of forest cover within 1.0 km^2 increased cougar use in residential areas and decreased use in wildlands ($t = 1.69$, $P = 0.10$, df = 23); increasing distance to residential lots increased use in residential areas and decreased use in wildlands ($t = 1.73$, $P = 0.10$, df = 23); and use of land cover patches in urban areas decreased with increases in perimeter : area ratio, but increased use in wildland land cover patches ($t = -0.84$, $P = 0.41$, df = 23). Elevation was the greatest predictor of cougar use in both models (Table 4) and coefficients were significantly different in residential and wildland areas: higher use was correlated with lower elevations in wildlands but with higher elevations in residential portions of the home range ($t = 8.76$, $P < 0.001$, df = 23; Table 4).

Comparison of wildland and residential standardized coefficients did not support the hypothesis of greater variability between individual cougars in wildland landscapes; space use patterns were slightly more variable within residential portions of home ranges. Use correlated with distance to water, CPAR, and slope was variable in both residential and wildland areas, whereas use correlated with percentage forest and distance to residential lots was variable in residential portions of the home range (Table 4).

Movement analysis

Cougars ($n = 10$) were estimated to move an average of 289.5 ± 97.2 m/h (mean ± SE for all movement rates) in residential areas and 197.0 ± 18.1 m/h in wildlands. Nocturnal movement rates (267.0 ± 30.9 m/h) were higher than diurnal (136.5 ± 11.1 m/h) and crepuscular periods (187.2 ± 18.5 m/h) and similar during each time period in wildland and residential settings (Fig. 3). The effect of time on movement rate was significant ($F_{2,53} = 4.18$, $P = 0.02$), but the effects of location ($F_{1,53} = 1.14$, $P = 0.29$) and the interaction of location and time ($F_{2,53} = 0.50$, $P = 0.61$) were not. Multiple comparisons of movement rates from specific location and time classes were not significant, despite up to a 2.7-fold difference in average values (Fig. 3).

Cougar–human interaction

Despite significant variation in resource use among cats, the population-wide RUF accurately predicted interactions between cougars and humans. This model was a good predictor of confirmed interaction, with 28.6% of reports occurring in predicted high-use areas, 42.9% in medium-high, 19.0% in medium-low, and 9.5% in predicted low-use areas. All confirmed reports occurring in medium-low and low-use areas were <2.0 km from high-use areas (871.7 ± 702.4 m; mean ± SD, $n = 6$). The majority of unconfirmed interaction reports occurred in less used areas, with 46.8% of reports located in predicted low-use areas, 26.9% in medium-low, 20.0% in medium-high, and 6.3% in predicted high-use areas. Comparison of the interaction UD and the

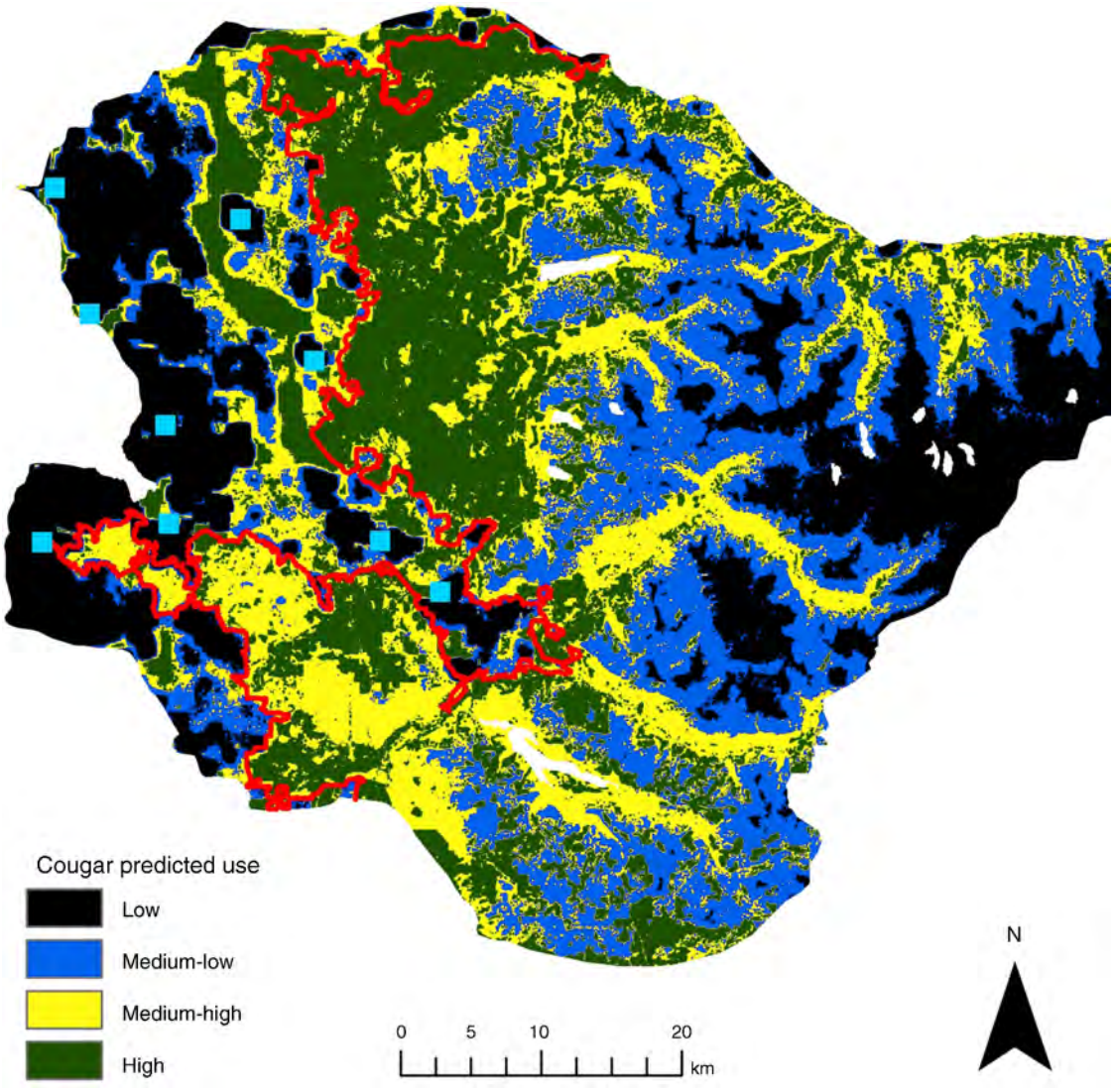

FIG. 2. Predicted relative probability of cougar use in the 3500-km^2 project study area located in portions of King and Snohomish counties, Washington (USA). Values were derived from resource utilization function (RUF) unstandardized coefficients averaged for a sample of 27 cougars over 33 cougar-years from 2003 to 2008. The red line represents the wildland–urban interface, and the light blue squares depict the geometric center of incorporated cities.

cougar RUF yielded a V.I. of 65.3%, indicating a moderate level of congruence between reported interaction and the population RUF's predicted cougar use.

DISCUSSION

Large carnivores in wildland–urban environments must capture prey, acquire mates, and engage in a full suite of natural behaviors just like their predominantly wildland counterparts. Although large carnivores may encounter direct persecution and unique risks as they navigate the heavily fragmented human landscape (Jackson and Nowell 1996, Novaro and Walker 2005, Inskip and Zimmermann 2009), our findings reveal similar space use and movement patterns in both wildland and built environments that allow individuals to exploit resources and minimize interactions with people. Quantifying the spatial ecology of a top-tier, far-ranging carnivore provides insights into the ecology of the wildland–urban environment with opportunities to develop broad management and conservation strategies (Beier 2009).

Space use

Cougars concentrated their use in suspected prey-rich areas with advantageous foraging characteristics and a limited anthropogenic presence. Maximizing predation opportunities and minimizing exposure to residential development appear equally important in the wildland–urban environment and may not be mutually exclusive. These findings are important because they reveal that

TABLE 2. Standardized RUF coefficients for 27 cougars over 31–33 years in a wildland–urban environment in western Washington, 2003–2008, and the number of individuals with significant positive (+) or negative (−) use ($P < 0.05$) associated with each landscape feature.

Landscape metric	No. cougar-years	Standardized $\bar{\beta}$	95% CL	$P(\bar{\beta} = 0)$	No. cougars with use significantly associated with attribute	
					+	−
Percentage clearcut and regenerating forest	33	1.257	0.112, 2.403	0.019	17	11
Percentage conifer forest	33	1.230	0.054, 2.405	0.024	20	9
Percentage forest	33	−1.210	−2.662, 0.242	0.056	11	18
Distance to water	33	0.132†	−0.756, 1.020	0.386	13	13
Distance to edge	33	−0.200	−0.612, 0.212	0.174	9	16
Distance to road	33	−0.926	−1.662, −0.190	0.010	7	21
Distance to residential	33	−0.062	−2.195, 2.320	0.479	17	14
Residential density	31	−2.048	−2.768, −1.328	<0.001	4	25
Perimeter : area ratio	33	0.230	−0.561, 1.021	0.286	13	12
Slope	33	0.501	−0.051, 1.053	0.042	16	8
Elevation	33	−3.891	−5.781, −2.001	<0.001	3	28

Notes: Conservative standard errors used to generate the confidence limits were estimated with measures of inter-animal variation included using Eq. 3 minus Eq. 2 from Marzluff et al. (2004). For the P values, df = 31 except for residential density, where df = 29.

† Differences in sign between standardized and unstandardized coefficients may occur for nonsignificant predictors, as each is estimated during separate, independent runs using an iterative process in Ruf.fit.

cougars in this setting use the landscape in ways that minimize the potential for interactions with people while remaining consistent with their role as an apex predator in Pacific Northwest ecosystems.

Our model results were consistent with our observations in the field of cougars killing prey in low-elevation, early-successional forests or areas close to rivers, creeks, or wetlands while utilizing areas with steep slopes, close to edge, or within landscape patches with higher amounts of edge. Cougars within the study area appear to employ a flexible hunting strategy that uses areas where the principal prey, black-tailed deer, and alternative prey, including beaver and elk, are abundant and/or vulnerable. Early-successional forests provide high amounts of forage and browse for both deer and elk in western Washington (Witmer et al. 1985), with dense vegetation and high stem densities providing stalking cover for cougars. Areas close to water can provide dense stalking cover and high-quality food for ungulates (Ripple and Beschta 2006), but also abundant beaver, raccoon, and mountain beaver populations (Baldwin et al. 2006, Arjo et al. 2007). Over 60% of all kills occurred within 100 m of water and the availability of beaver as alternative prey appears to be particularly important: this species constituted 22% of the total prey items documented (Kertson 2010). Predation risk for ungulates and smaller prey may be greater near edges and within smaller landscape patches (Altendorf et al. 2001, Holmes and Laundré 2006), and topography can be an effective form of cover (Williams et al. 1995). Elevations above 1000 m within the study area provide limited resources for ungulates (Hovey and Harestad 1992), with difficult travel conditions for much of the year because of deep snowpack (Western Region Climate Center 2009); and deer at lower elevations are more susceptible to predation (McNay and Voller 1995).

Previous studies of cougar space use have focused on population-level patterns and have largely ignored

TABLE 3. Mean unstandardized RUF coefficients for cougars ($n = 19$) over 24 cougar-years in wildland and residential portions of their home range in western Washington, 2003–2008.

Landscape metric	Wildland		Residential	
	$\bar{\beta}$	SE	$\bar{\beta}$	SE
Intercept	42.110	3.155	10.569	2.931
Percentage clearcut and regenerating forest	2.516×10^{-2}	1.907×10^{-2}	2.731×10^{-2}	2.262×10^{-2}
Percentage conifer forest	1.797×10^{-2}	1.849×10^{-2}	3.084×10^{-2}	1.509×10^{-2}
Percentage forest	-4.323×10^{-2}	3.294×10^{-2}	4.914×10^{-2}	4.950×10^{-2}
Distance to water	-2.350×10^{-4}	3.080×10^{-3}	-2.936×10^{-3}	3.270×10^{-3}
Distance to edge	-3.719×10^{-3}	3.890×10^{-3}	-5.263×10^{-3}	5.210×10^{-3}
Distance to road	-7.283×10^{-3}	2.110×10^{-3}	-6.005×10^{-3}	3.980×10^{-3}
Distance to residential	-1.720×10^{-3}	9.300×10^{-4}	1.086×10^{-3}	2.920×10^{-3}
Perimeter : area ratio	3.946×10^{-2}	4.298×10^{-2}	-3.491×10^{-2}	6.592×10^{-2}
Slope	2.130×10^{-1}	1.660×10^{-2}	-1.030×10^{-2}	1.655×10^{-2}
Elevation	2.484×10^{-3}	6.600×10^{-4}	3.846×10^{-3}	1.350×10^{-3}

Note: Conservative standard errors were estimated with measures of inter-animal variation included using Eq. 3 minus Eq. 2 from Marzluff et al. (2004).

individual variation; that approach may fail to capture important components of cougar behavior and ecology. Our observed differences in landscape use between individuals might be explained by differences in age, sex, and social characteristics (Kertson 2010) because cougars within these demographic classes employ different strategies to maximize their fitness (Spreadbury et al. 1996, Logan and Sweanor 2001) and these strategies may translate into different space use patterns. Home range size, including differences between males and females, failed to account for observed variation in landscape use, explaining <5% of model variation (Kertson 2010). Although the underlying sources of variability between individuals may not be fully understood, a large degree of variation in space use patterns may be a common characteristic of adaptable habitat generalists. The leopard (*Panthera pardus*) may have highly individualized space use patterns based on the distribution of prey biomass, species hunted, precipitation levels, and anthropogenic disturbance (Marker and Dickman 2005). The distribution of food resources throughout the landscape was also believed to be primary reason for individual variation in space use and movement patterns of Common Ravens (*Corvus corax*) in California (Roth et al. 2004). Marzluff et al. (2004) documented extensive variation in space use patterns of Steller's Jays (*Cyanocitta stelleri*), driven by timber harvest and the distribution of people and associated resources on the Olympic Peninsula of Washington. Transient coyotes (*Canis latrans*) employ different space use patterns in an attempt to minimize contact with resident family groups (Kamler and Gipson 2000). The cougar is a highly adaptable predator, having the largest geographic distribution of any terrestrial mammal in the western hemisphere. Observed variation in resource use may be a function of differences between resource abundance and distribution within home ranges, coupled with innate and/or learned behavioral adaptations allowing individuals to exploit local landscape characteristics and prey availability to their advantage. Alternatively, an ideal model of cougar space use consisting of direct measures of cover, prey availability, and the simultaneous spatial relationship of all cougars within the population would probably generate less variation among individuals. The large amount of variation observed for some covariates may simply demonstrate a landscape feature to be a poor surrogate for cover and prey availability within some home ranges.

Wildland and residential space use comparison

Cougars used wildland portions of the landscape and patches and corridors with wildland-like characteristics within the matrix of residential development (Kertson 2010). Urban and suburban settings provide fewer resources for cougars than wildland habitats and an increased risk of mortality (Beier et al. 2010, Burdett et al. 2010). High-speed roads can impede movements and can become a significant source of mortality (Dickson and Beier 2002, Taylor et al. 2002); increased cougar use closer to highways, arterials, and paved roads would be unexpected. However, home ranges consisted mostly of wildlands where unpaved, low-speed forest roads were commonplace and were frequently used by cats for both traveling and hunting.

Within residential developments, cougars used areas with abundant native land cover, greater use by black-tailed deer (Bender et al. 2004), and the least amount of anthropogenic disturbance (Fig. 4). Subsequently, the wildland–urban interface and associated portions of exurban and suburban habitats appear to function as modified, rather than unsuitable, habitat for cougars, which is consistent with observations of black bears (*Ursus americanus*; Lyons 2005) coyotes (Bounds and Shaw 1997, Atwood et al. 2004, Grubbs and Krausman 2009), and bobcats (*Lynx rufus*; Tigas et al. 2002, George and Crooks 2006) within the wildland–urban environment. Differences in signs associated with some coefficients, elevation in particular, reflect the effects of landscape features on cougar spatial ecology, because individuals may have attempted to minimize their exposure to people within residential areas and exploit the potential benefits (i.e., edge effects) associated with the wildland–urban interface in wildland portions of their home range. Higher elevations within many residential areas retained more native land cover, which attracted a diversity of prey. More variation in residential space use patterns suggests that individual cougars may have employed unique strategies to meet their life history requirements closer to people.

Similar movement rates in wildland and residential settings during different times of day provide further evidence that cougar spatial ecology at the wildland–urban interface and surrounding residential areas does not differ substantially from patterns in wildland habitats. Cougars were active throughout the day and we suspect that they used dense understory vegetation to conceal movements throughout the landscape. However, individuals were most active during nocturnal periods when ungulate prey are more active and darkness may act as an additional form of cover for cougars (Van Dyke et al. 1986, Beier et al. 1995). Similar movement rates during diurnal and crepuscular periods probably represent movements associated with resting, feeding, and localized hunting activity (Beier et al. 1995). We observed 119 movements > 1.0 km during daylight hours in wildland settings, but patch-to-patch and patch-to-wildland movements > 500 m within residential areas were limited to nocturnal periods (B. Kertson, *unpublished data*). The effects of residential development and human activity can alter movement rates and periods for a number of carnivore species. Black bears in suburban and exurban areas of California had higher movement rates and shifted activity to nocturnal periods to minimize interactions with people and maximize

TABLE 4. Standardized RUF coefficients, 95% CIs, significant use associated with each landscape feature, and wildland–residential beta comparisons for cougars ($n = 19$) over 24 cougar-years in wildland and residential portions of their home range in western Washington, 2003–2008.

	Wildland			
	Standardized coefficients		No. cougars with use significantly associated with attribute	
Landscape metric	$\tilde{\beta}$ (SE)	95% CL	+	−
Percentage clearcut and regenerating forest	1.066 (0.581)	−0.072, 2.205	15	7
Percentage conifer forest	0.730 (0.621)	−0.488, 1.947	12	6
Percentage forest	−0.609 (0.713)	−2.006, 0.789	6	11
Distance to water	−0.104 (0.502)	−1.088, 0.880	10	10
Distance to edge	−0.220 (0.302)	−0.811, 0.371	6	13
Distance to road	−1.549 (0.498)	−2.525, −0.573	5	16
Distance to residential	−2.286 (1.223)	−4.683, 0.110	8	15
Perimeter : area ratio	0.327 (0.516)	−0.685, 1.340	9	7
Slope	−0.625 (0.437)	−1.482, 0.232	8	11
Elevation	−4.834 (1.075)	−6.941, −2.726	3	21

Notes: Conservative standard errors were estimated with measures of inter-animal variation included using Eq. 3 minus Eq. 2 from Marzluff et al. (2004). For the P values, df = 23.

access to anthropogenic food resources (Lyons 2005). Similarly, coyotes and bobcats using residential portions of the southern California landscape moved shorter distances and were least active during daylight, suggesting some avoidance of human activities (Tigas et al. 2002). Movement rates for coyotes in Indiana were comparable during different time periods, but rural coyotes traveled greater distances at higher rates than their suburban counterparts (Atwood et al. 2004). Small sample sizes limit the statistical inferences of our movement analysis, yet higher movement rates by some individuals in residential areas at night were biologically meaningful. Traversing the residential matrix rapidly at night probably represents cougar attempts to limit interactions with people and potential risks associated with crossing one or more high-speed roads (Taylor et al. 2002) and areas with limited cover (Beier et al. 1995). High levels of variation associated with nocturnal movements in residential areas may also reflect individualized behavior patterns and different tolerances for anthropogenic disturbance in these environments.

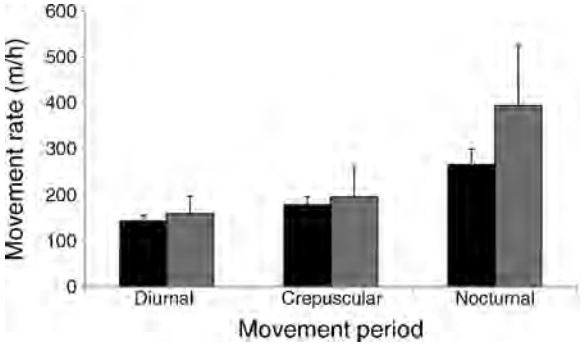

FIG. 3. Comparison of movement rates (mean + SE) quantified for cougars ($n = 10$) in wildland (black) and residential (gray) areas in western Washington during different periods of the day for the years 2003 to 2008.

Cougar–human interaction

The interaction of cougars and humans explicitly is a function of the spatial and temporal overlap of cougars and people. Our models of cougar space use patterns provided a valuable tool for understanding how landscape features affect this interaction. Most confirmed interactions between humans and cougars occurred in landscapes moderately used by cougars (Fig. 2; medium-high use). The residential landscapes most likely to spawn human interactions with cougars are those that retain the vegetative characteristics of wildland (coniferous forests) and maintain connectivity with higher quality, core cougar habitats (Kertson 2010). Low-density residential development (<25 homes/km^2) maintains enough wildland characteristics to encourage cougar use and probably maximizes the spatiotemporal overlap of cougars and people. With this understanding, it is not surprising that the highest use areas did not account for a greater number of confirmed interactions, as these areas are used more by cougars in large part because they have fewer people present. Confirmed interactions in low-use areas were likely the result of the proximity of these locations to areas frequented by cougars and possibly one or more unknown factors, such as behavioral characteristics or unique space use patterns of the individual involved in the interaction and/or the presence of additional landscape features that may increase use, but were not included in our model.

Management and conservation

The default management strategy to reduce cougar–human interactions is to lethally control cougars. However, this strategy is incomplete because it fails to account for cougar spatial ecology. Because the wildland–urban interface and adjacent residential areas function as modified, not unsuitable, habitat for cougars, an increased cougar harvest is unlikely to

TABLE 4. Extended.

Residential					
Standardized coefficients		No. cougars with use significantly associated with attribute			
$\bar{\beta}$ (SE)	95% CL	+	−	t	$P(\bar{\beta}_W = \bar{\beta}_R)$
1.102 (0.487)	0.148, 2.055	13	6	0.051	0.959
0.478 (0.340)	−0.188, 1.143	13	9	−0.376	0.710
1.272 (0.882)	−0.456, 3.000	14	8	1.691	0.104
−0.048 (0.838)	−1.619, 1.595	9	11	0.088	0.931
−0.317 (0.159)	−0.628, −0.006	4	9	−0.355	0.726
−0.768 (0.305)	−1.365, −0.171	3	12	1.666	0.109
0.218 (0.718)	−1.189, 1.626	9	13	1.735	0.096
−0.137 (0.299)	−0.722, 0.449	7	8	−0.845	0.407
−0.315 (0.345)	−0.990, 0.361	9	10	0.551	0.587
2.680 (0.996)	0.728, 4.632	16	8	8.761	<0.001

decrease human interaction with cougars that will continue to use residential portions of the landscape if adequate cover, prey, and connectivity with wildland source habitats remain. Consequently, removal of individual cougars in higher quality habitats could have the unintended consequence of increased cougar use because a home range vacancy increases the probability of use by multiple individuals until residency of a single individual is established (Logan and Sweanor 2001, Maletzke 2010).

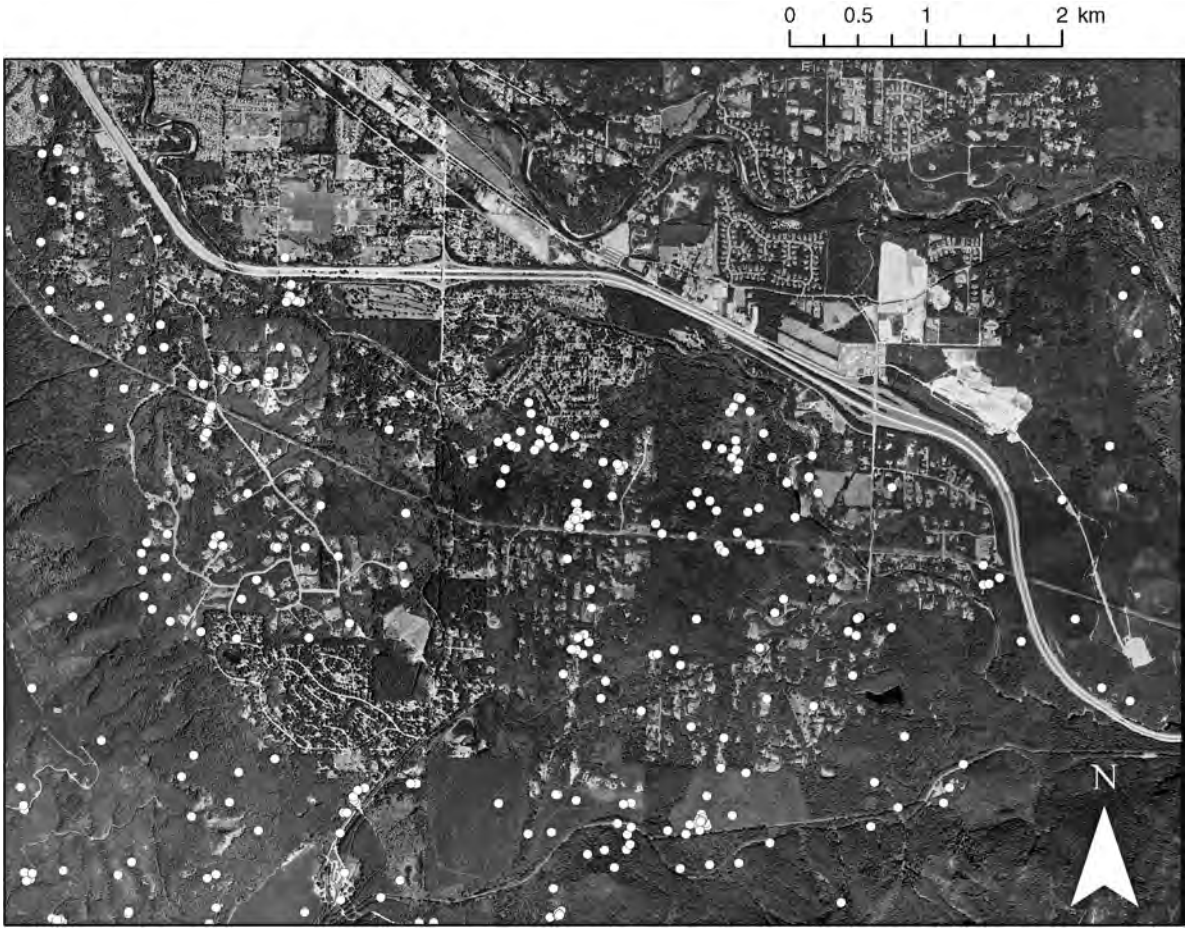

FIG. 4. Cougar ($n = 10$) Global Positioning System (GPS) locations (white dots) demonstrating use of suitable habitat within a residential portion of North Bend, Washington, 2003–2008.

Forest patches and corridors in residential areas provide ecological benefits to a multitude of wildlife species (Ferguson et al. 2001, Spencer et al. 2002, Markovchick-Nicholls et al. 2008). Altering the characteristics of these habitats (e.g., removing cover) could reduce use by cougars and the potential for interaction. However, ecological, economic, and social costs associated with the loss or alteration of these forests could be significant and likely exceed the risks associated with cougar use (Kertson 2010). A better strategy may be found in improved landscape planning. Cougar use has a significant inverse relationship with residential density, allowing for the design and implementation of residential development patterns and movement corridors that minimize interaction with limited detrimental impacts on cougars and other wildlife. Concentrating residential development and subdivisions in clusters with densities $>$ 10 homes/ha maximizes wildland area and minimizes wildland fragmentation (Marzluff and Ewing 2001, Gilham 2002) while probably decreasing the likelihood of cougar use of residential development. Corridors connecting wildland patches should be sufficiently large to facilitate cougar use (Beier 2009), with adjacent residential development at urban densities to increase movement rates and discourage increased proximity to homes. The highest levels of observed cougar use occurred in wildland portions of the landscape (Kertson 2010), and continued conservation of these areas is critical to minimizing interactions and maintaining the long-term viability of populations adjacent to residential centers.

Managers trying to reduce interactions between cougars and humans should develop alternative strategies designed to guide land practices and educate the public on how to coexist with cougars (Cougar Management Guidelines Working Group 2005, Kertson 2010). Our model of space use demonstrates that landscape characteristics accurately predict a large proportion of interactions and the population-wide model can be used as a proactive tool to guide managers dealing with vast landscapes. Cougar education and outreach, prey management, efforts to improve animal husbandry practices, potential adverse conditioning of cougars, and landscape planning should focus on areas of higher predicted use within, or close to, residential portions of the landscape, as this strategy is likely to provide the most efficient and cost-effective way to reduce interaction. For areas without space use data and predictive models, exurban habitats ($\leq$2.5 residences/ha; Marzluff 2001) and the wildland–urban interface have a higher probability of interaction because of relatively low residential densities coupled with moderate levels of cougar use. The occurrence of confirmed interactions in predicted low-use areas illustrates that a low probability of cougar use does not translate into a zero probability of interaction, and some level of education and outreach should be provided in these portions of the landscape as well.

Many places in the western United States contain substantial suitable cougar habitat despite high levels of residential development and urban sprawl. Wildlife managers and educators must inform citizens, without being alarmist, that some backyards, neighborhood greenbelts, and urban forests are used by cougars. Resource utilization functions provide an effective tool for characterizing space use, increasing our understanding of ecology and behavior, and developing better strategies for managing and conserving wildlife using wildland–urban environments.

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Conservation Biology

Review

Effects of Road Networks on Bird Populations

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Abstract: *One potential contributor to the worldwide decline of bird populations is the increasing prevalence of roads, which have several negative effects on birds and other vertebrates. We synthesized the results of studies and reviews that explore the effects of roads on birds with an emphasis on paved roads. The well-known direct effects of roads on birds include habitat loss and fragmentation, vehicle-caused mortality, pollution, and poisoning. Nevertheless, indirect effects may exert a greater influence on bird populations. These effects include noise, artificial light, barriers to movement, and edges associated with roads. Moreover, indirect and direct effects may act synergistically to cause decreases in population density and species richness. Of the many effects of roads, it appears that road mortality and traffic noise may have the most substantial effects on birds relative to other effects and taxonomic groups. Potential measures for mitigating the detrimental effects of roads include noise-reduction strategies and changes to roadway lighting and vegetation and traffic flow. Road networks and traffic volumes are projected to increase in many countries around the world. Increasing habitat loss and fragmentation and predicted species distribution shifts due to climate change are likely to compound the overall effects of roads on birds.*

Keywords: bird populations, roads, road mortality, roadway lighting, surface transportation, traffic noise

Efectos de las Redes de Caminos sobre Poblaciones de Aves

Resumen: *El incremento en la prevalencia de caminos, que han tenido varios efectos negativos sobre aves y otros vertebrados, es un potencial contribuyente a la declinación mundial de poblaciones de aves. Sintetizamos los resultados de estudios y revisiones que exploran los efectos de los caminos sobre las aves, con énfasis en caminos pavimentados. Los bien conocidos efectos directos de los caminos sobre las aves incluyen la pérdida y fragmentación de hábitat, mortalidad causada por vehículos y envenenamiento. Sin embargo, los efectos indirectos pueden ejercer una mayor influencia sobre poblaciones de aves. Estos efectos incluyen ruido, luz artificial, barreras al movimiento y bordes asociados con caminos. Más aun, los efectos indirectos y directos pueden actuar sinérgicamente para causar decrementos en la densidad poblacional y en la riqueza de especies. De los muchos efectos de los caminos, parece que la mortalidad y el ruido del tráfico tienen los efectos más significativos sobre las aves en relación con otros efectos y grupos taxonómicos. Las medidas potenciales para mitigar los efectos perjudiciales de los caminos incluyen estrategias de reducción de ruido y cambios en la iluminación y vegetación de los caminos y en el flujo de tráfico. Se proyecta que las redes de caminos y los volúmenes de tráfico incrementen en muchos países en el mundo. Es probable que el incremento en la pérdida y fragmentación de hábitat y los cambios pronosticados en la distribución de especies debidos al cambio climático compliquen los efectos de los caminos sobre las aves.*

Palabras Clave: caminos, iluminación en caminos, poblaciones de aves, mortalidad en caminos, ruido de tráfico, transportación terrestre

Introduction

Bird populations are declining around the world (BirdLife International 2008*a*). In North America the abundances of at least 20 species previously categorized as common have declined more than 50% in the last 40 years (Butcher & Niven 2007; BirdLife International 2008*b*). Additionally, abundances of over half the species of Neotropical

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migrants have declined substantially. The reasons for these declines are not fully understood (Butcher & Niven 2007; BirdLife International 2008*c*). One likely contributor is the expansion of paved roads, mostly in terms of widening (National Research Council 2005), and corresponding increases in the speed and volume of vehicles on those roads (Ritters & Wickham 2003). We synthesized these effects on birds to balance the much greater attention that has hitherto been paid to the effects of roads on mammals and to examine the potentially negative effects of roads on birds worldwide.

Reduced breeding success is correlated with proximity of birds to roads and road density for species ranging from passerines (Catchpole & Phillips 1992; Reijnen & Foppen 1994) to vultures (Donazar et al. 1993). In some cases, avian communities adjacent to roads differ from nearby avian communities (Glennon & Porter 2005), presumably because of some combination of the direct and indirect effects of roads on animals in general (Forman & Alexander 1998; Trombulak & Frissell 2000; Fahrig & Rytwinski 2009).

There is a little understanding of whether declines in persistence of birds are more affected by direct or indirect effects. If this could be determined in urban areas, it may be possible to increase bird abundance and species richness. It is also important to identify and mitigate any negative road effects in protected areas, which are assumed to buffer populations of wild animals from human activities.

Many of the negative effects of roads on other vertebrates (e.g., mortality, habitat fragmentation, and audiovisual disturbance, chemical pollution) also apply to birds (Forman et al. 2003; Jacobson 2005). There are a few ways roads can benefit birds. For example, roads retain heat that can reduce metabolic costs for birds that rest on road surfaces (Whitford 1985), associated road infrastructure (e.g., poles and bridges) can create nesting sites (Forman 2000), and verges increase availability of food sources (Lambertucci et al. 2009) and link patches of habitat (Meunier et al. 1999; Huijser & Clevenger 2006; Reijnen & Foppen 2006). We reviewed recent reports and peer-reviewed articles focused primarily on direct and indirect negative effects of roads on bird populations and identified some potential forms of mitigation. Much of the literature we reviewed concerns paved roads because they have been the subject of more study and because their ecological effects are assumed to be greater than gravel, dirt, or ice roads (Forman et al. 2003; National Research Council 2005).

Direct Threats Posed to Birds by Roads and Traffic

For bird populations the most visible direct negative effects of roads are habitat loss and mortality due to collisions with vehicles. Because the effects of habitat loss on birds have been comprehensively reviewed elsewhere (Andren 1994), we did not focus on this effect here. Nonetheless, roads have other effects that are related to habitat loss. For example, maintenance activities in the right-of-way can further reduce habitat quality and destroy nests, which may reduce population viability for rare species (e.g., Burrowing Owl [*Athene cunicularia*]) (Catlin & Rosenberg 2006). We focused on the negative effects associated with vehicular traffic.

Vehicle-Caused Mortality

For individual birds and other vertebrate groups, a direct threat of roads is death due to collisions with vehicles (Erritzoe et al. 2003). In the United States, vehicles are estimated to cause approximately 80 million bird fatalities each year (Erickson et al. 2005). Despite the high number of mortalities each year, vehicle-caused mortality has been assumed to have less of an effect on persistence than some indirect effects of roads (Forman & Alexander 1998; Reijnen & Foppen 2006). Only three bird species found in the United States appear to suffer population declines as a result of them: Florida Scrub-Jay (*Aphelocoma coerulescens*) (Mumme et al. 2000; IUCN 2008), Audubon's Crested Caracara (*Polyborus plancus audubonii*), and Hawaiian Goose (*Branta sandvicensis*) (Huijser et al. 2007; IUCN 2008). A greater understanding of what makes some species more susceptible to vehicle collision and population decline as a result of vehicle-caused mortality is needed, but some generalities emerge from the literature.

First, birds are more likely to collide with vehicles if they forage, roost, or nest near roads (Erritzoe et al. 2003; Huijser et al. 2007). Collision frequency can increase near watercourses (Erritzoe et al. 2003; Ascensao & Mira 2006) and houses (Ascensao & Mira 2006). Collisions are also more likely to occur at lower elevations (Clevenger et al. 2003) and in open areas than in forests (e.g., Clevenger et al. 2003; Ascensao & Mira 2006; Ramp et al. 2006).

Several other factors have less consistent effects on vehicle-induced bird mortality. For many species, vehicle-induced mortality increases during breeding and migration (Fulton et al. 2008; Gryz & Krause 2008), but for other species it increases during winter (Loos & Kerlinger 1993; Boves 2007). Collisions can increase (Jackson 2003) or decrease as roadside lighting increases (Hernandez 1988). Roadside trees, hedgerows, and other features that cause birds to fly higher across roads typically decrease collision frequency (Pons 2000; Bard et al. 2002; Clevenger et al. 2003; Erritzoe et al. 2003; Taylor & Goldingay 2004; Orlowski 2005), but they can also increase it (Ramp et al. 2006; Varga et al. 2006). Birds also vary in their responses to roads. Some individuals appear to learn to avoid vehicles (Mumme et al. 2000), whereas others do not (Loos & Kerlinger 1993; Jackson 2002).

It is difficult to measure the true extent of vehicle-induced mortality because estimates are typically far lower than the actual number of birds killed (Erickson et al. 2005). Estimation accuracy is reduced by variation in searcher efficiency, scavenger bias (Erickson et al. 2005; Boves 2007), and incorrect attribution of cause of death (Kerlinger & Lein 1988). Even long-term studies in which 100% of individuals are marked, researchers can fail to detect all instances of vehicle-caused mortality (Mumme et al. 2000). Vehicle collisions may also cause nonfatal injuries that increase the probability birds will die from other causes (Orlowski & Siembieda 2005). In addition, inaccurate estimates of vehicle-induced mortality can result if only carcasses are studied in the absence of data on species abundance (Hernandez 1988; Aebischer et al. 2005). Missing information about population size makes it difficult to compare rates of mortality in different areas, especially on different continents (Erritzoe et al. 2003).

Pollution and Poisoning

Deicing agents, petroleum-based organic compounds, nutrients, sediments, agricultural chemicals, and other substances regularly run off paved roads during construction, maintenance, and use (Buckler & Granato 1999). Road salt is a common deicing agent that attracts birds. Its ingestion can lead to death, which dispels the notion that road salt has a negative effect only because it attracts birds to the road surface, making them subject to collisions with vehicles (Mineau & Brownlee 2005). Dust on unpaved roads can change the composition of vegetation (Walker & Everett 1987), which can affect birds (Kalisz & Powell 2003). Gravel roads are frequently treated with dust suppressants, the environmental and toxicological effects of which are not well understood (Fay & Kociolek 2009). Despite the ubiquity of road contaminants from vehicles and maintenance activities, toxic effects of roads appear to be rare, even in areas with high traffic volumes (Buckler & Granato 1999), and pollution appears to have fewer effects on birds than other road-related effects (Reijnen & Foppen 2006).

Indirect Threats Posed to Birds by Roads and Traffic

Even in the absence of direct deleterious effects, many bird species appear to avoid roads purposely (e.g., Bollinger & Gavin 2004; Balbontin 2005; Gavashelishvili & McGrady 2006). Some species may be present near roads for a time, but they are more likely to abandon nests near roads (Gorog et al. 2005). For birds, road avoidance appears to be associated with the physical barrier to movement roads present, noise, artificial light, and edge effects.

Physical Barriers

Of the indirect threats of roads, the barriers to movement roads present may have the greatest effect on vertebrates (Forman & Alexander 1998). Several forest-dwelling bird species are unlikely to cross gaps in forest cover $\geq$50 m in areas dominated by agriculture (Desrochers & Hannon 1997), timber harvesting (Awade & Metzger 2008), and urban infrastructure (Tremblay & St. Clair 2009). Some species exhibit reluctance to cross dirt roads that are 10–30 m wide (Develey & Stouffer 2001). Nonetheless, the barriers caused by roads may be a simple function of the width of the gap they create in the surrounding habitat, unless the roads are also noisy (St. Clair 2003; Tremblay & St. Clair 2009) or are associated with tall features such as power lines (Pruett et al. 2009).

Noise

Traffic noise probably has the most widespread and greatest indirect effect on birds (Reijnen et al. 1995 (Table 1). Noise likely causes reductions in population densities that have been reported for several bird species that are present near roads (Reijnen & Foppen 2006; Patricelli & Blickley 2006). In grasslands the effects of noise appear to extend farther from roads than in forests (Forman et al. 2002), perhaps because grasslands have less vegetation to absorb sound. In addition to the effects of traffic volume and its associated noise, there may be synergistic effects of noise, habitat loss and fragmentation (Forman & Deblinger 2000), and edge effects (Habib et al. 2007).

Birds may be affected by anthropogenic noise because they rely extensively on acoustic communication (Table 1). Chronic industrial noise can reduce species richness, alter population age structure, and change avian predator–prey dynamics (Francis et al. 2009). Like industrial noise, chronic traffic noise appears to produce younger age structures and reduces population densities in several bird species (Reijnen & Foppen 2006). These effects may occur because anthropogenic noise masks the frequencies of calls used to attract mates (Rheindt 2003; Pohl et al. 2009), communicate with flock members (Lohr et al. 2003; Slabbekoorn & Ripmeester 2008) or offspring (Leonard & Horn 2005), defend territories (Habib et al. 2007; Mockford & Marshall 2009), and detect predators (Slabbekoorn & Ripmeester 2008; Francis et al. 2009) (Table 1). Effects of noise on both birds and anurans seem to depend on the frequencies and amplitudes of species-specific signals (Lengagne 2008; Slabbekoorn & Ripmeester 2008; Hu & Cardoso 2009). Some species seem unaffected by roads or traffic (Kaseloo 2005; Reijnen & Foppen 2006), and others may not come near roads when traffic volume is high (Bautista et al. 2004). Several urban-dwelling songbird species appear to counteract the masking effects of traffic noise (Table 1) by singing at a higher pitch (Slabbekoorn & Peet 2003), increasing song amplitude (Brumm 2004b), or singing

Table 1. The effects of anthropogenic noise on avian communities and communication.

Category	*Effect*	*References*
Community		
species richness	reduced as noise increases	Stone 2000
density & abundance (all species)	reduced as noise increases	Reijnen et al. 1995, 1996; Kuitunen et al. 1998; Bayne et al. 2008
	no overall reduction	Peris & Pescador 2004
densities & abundance (specific species)	reduced as noise increases	Reijnen & Foppen 1994; Reijnen et al. 1995, 1997
	dependent on species	Kuitunen et al. 1998; Peris & Pescador 2004
	higher abundance of birds with higher song pitch near roads	Rheindt 2003
age structure	younger at noisy sites	Reijnen & Foppen 1994; Habib et al. 2007
physiology	increased stress at higher noise levels	Campo et al. 2005
	no stress difference at higher noise levels	Byers et al., unpublished data
Breeding cycle		
pairing and mate retention	decreased time devoted to courtship behavior	Goudie & Jones 2004
	reduced pairing success	Habib et al. 2007
	reduced mate preference	Swaddle & Page 2007
territory and nest-site selection	farther from noise sources	Francis et al. 2009
nest success	increased as noise increases for some species	Francis et al. 2009
Foraging		
begging calls	reduced parental discrimination in noisy locations	Leonard & Horn 2005
prey location and probability of predation	predator reduction increases nest success in noisy locations	Francis et al. 2009
	potential alterations to interspecies interactions	Slabbekoorn & Halfwerk 2009
	increased vigilance as noise increases	Quinn et al. 2006
Communication		
temporal adjustment	sing more at night in noisy locations	Fuller et al. 2007
amplitude increase	sing louder as noise increases (Lombard effect)	Cynx et al. 1998; Brumm 2004a, 2004b; Brumm et al. 2009; Osmanski & Dooling 2009
	louder begging calls in noisy locations	Leonard & Horn 2005
pitch modification	increased pitch in noisy locations	Slabbekoorn & Peet 2003; Fernandez-Juricic et al. 2005; Slabbekoorn & den Boer-Visser 2006; Wood & Yezerinac 2006; Parris & Schneider 2009; Kirschel et al. 2009; Nemeth & Brumm 2009
redundancy	no correlation between pitch and road noise	Skiba 2000
detection of con- and heterospecific vocal signals	more repetition in noisy locations	Brumm & Slater 2006
	reduced detection probability of signals in noisy locations	Langemann et al. 1998; Lohr et al. 2003
response to signals	strongest response to played-back signals when ambient noise levels are similar to local environment	Mockford & Marshall 2009
reviews	effects of noise and implications	Patricelli & Blickley 2006; Slabbekoorn & Ripmeester 2008; Barber et al. 2010
Brain response		
gene activation	immediate early-gene ZENK expression in the neural pathway of the avian brain not modified by noise playback	Vignal et al. 2004

during periods of low traffic noise (Fuller et al. 2007). Other species may be unable to adapt their songs to accommodate chronic noise (Slabbekoorn & Ripmeester 2008; Barber et al. 2010), and pairing success of birds with relatively high amplitude songs is reduced when they are exposed to high levels of chronic noise (Habib et al. 2007).

Artificial Light

Light from roadways can have negative effects on many animals (Rich & Longcore 2006), including birds (Ogden 1996; Van De Laar 2007). Some lighting structures attract migrating bird species, which increases the probability they will be preyed on or collide with structures and often causes them to redirect flight paths and thus deplete energy stores (van de Laar 2007). Artificial lighting can also affect avian patterns of nestling development, singing, breeding, molting, and migration (De Molenaar et al. 2006). There is some evidence that roadway lighting may reduce habitat quality and change the timing of breeding for the Black-tailed Godwit (*Limosa limosa*), a species associated with grasslands in Africa, Europe, and Asia (De Molenaar et al. 2006). American Robins (*Turdus migratorius*) sing earlier in the morning in areas with more anthropogenic light (Miller 2006), but this response may be difficult to disentangle from the associated effect of road noise, which is more important than light for explaining nocturnal singing by European Robins (*Erithacus rubecula*; Fuller et al. 2007).

Edge Effects

Positive and negative effects of edges on breeding birds have been documented in many studies (Stephens et al. 2003). The edge effects of roads may be particularly acute when introduced species, such as rats (*Rattus rattus*), prey on ground-nesting birds (Delgado et al. 2001) or parasitic species, such as Brown-headed Cowbirds (*Molothrus ater*), target the nests of species of conservation concern (Chace et al. 2003). In some cases, these edge effects are contradictory (Bergin et al. 2000; Lariviere 2003).

Mitigation

Paved roads are a pervasive feature across much of North America, and existing roads are being widened, new roads are being built, and, and traffic volume is increasing (Forman et al. 2003; National Research Council 2005) throughout the world (Urban Land Institute 2007; Bhattacharya 2008). Efforts to mitigate road effects are most likely to increase probabilities of persistence of birds when applied across extensive areas (Stutchbury 2009).

New information about the ubiquity of the effects of noise on birds suggests reducing road noise may be cost-effective because it can benefit both birds and humans (Bluhm et al. 2007; Slabbekoorn & Ripmeester 2008; Barber et al. 2010). Promising measures to reduce road noise include temporal adjustments to traffic flow (Reijnen & Foppen 2006) and increased reliance on mass transit (Barber et al. 2010). The unvegetated area created by light-rail train tracks is more permeable to bird movement than roads of equivalent sizes, perhaps because they are quieter (Tremblay & St. Clair 2009). New tire designs (Carstens 2003) and noise-absorbing porous asphalt (Piepers 2001) can substantially reduce levels of highway noise (Elvik & Greibe 2003). Other noise-reducing strategies include the use of earth berms and vegetation that, unlike walls (Varga et al. 2006), do not create vertical barriers to animal movement, although this may depend on the animal. These features typically also increase quality of life and property values for human residents.

Changing roadway lighting may also benefit both birds and people through reductions in energy consumption and increases in safety (De Molenaar et al. 2006). Replacing red or white lights with green lights greatly reduces the negative effect of artificial lights on oil platforms on birds (van de Laar 2007). Such lighting could be used on highway (Poot et al. 2008).

Edge effects might be partially mitigated with vegetation management and restoration. Poisoning and nonpoint source pollution can be mitigated, in part, by policy aimed at encouraging use of nontoxic agents to maintain safe driving conditions. A practice that would reduce vehicle-induced bird mortality would be to refrain from planting along roadsides fruit-bearing vegetation that attracts birds.

Future Implications

In the United States road area is expected to increase by 27,900 km^2 by 2030, and lanes added to existing roadways to accommodate increased traffic volume is projected to increase road area by an additional 94,100 km^2 (Theobald 2010). Exponential increases in the road network and traffic volume are anticipated to occur in large, densely populated, countries such as China and India (Bhattacharya 2008). Among the factors studied to date, it appears that traffic noise has the greatest potential to reduce population abundance and species richness of birds (Reijnen & Foppen 2006; Barber et al. 2010). Although vehicle-caused mortality does not appear to affect persistence for most populations, it is a problem for some species (Huijser et al. 2007) and may exacerbate other anthropogenic threats to birds (Erickson et al. 2005). Given global traffic projections and in light of losses due to collisions, road-induced mortality of birds should be examined more systematically and comprehensively. Other road-related disturbances such as light and chemical

pollution appear to have minor effects at the population level, but their spatial extent may still generate a large collective effect on birds. Finally, increasing habitat loss and fragmentation, in addition to predicted species distribution shifts due to climate change, are likely to compound the overall effect of roads (Heller & Zavaleta 2009).

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Microbial spatial footprint as a driver of soil carbon stabilization

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Increasing the potential of soil to store carbon (C) is an acknowledged and emphasized strategy for capturing atmospheric CO_2. Well-recognized approaches for soil C accretion include reducing soil disturbance, increasing plant biomass inputs, and enhancing plant diversity. Yet experimental evidence often fails to support anticipated C gains, suggesting that our integrated understanding of soil C accretion remains insufficient. Here we use a unique combination of X-ray micro-tomography and micro-scale enzyme mapping to demonstrate for the first time that plant-stimulated soil pore formation appears to be a major, hitherto unrecognized, determinant of whether new C inputs are stored or lost to the atmosphere. Unlike monocultures, diverse plant communities favor the development of 30–150 μm pores. Such pores are the micro-environments associated with higher enzyme activities, and greater abundance of such pores translates into a greater spatial footprint that microorganisms make on the soil and consequently soil C storage capacity.

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Soil C is crucial for soil fertility, and the recovery of some portion of the 133 Pg C lost upon agricultural land-use conversion[1] is a prominent strategy for helping to keep global temperature rises below 1.5 °C[2,3]. Various land management practices are known to build soil C. These practices include reducing soil disturbance[4,5], increasing quantity of plant biomass added to soil[6], and increasing plant diversity[7,8], and perenniality[9,10]. All aim at the two key components necessary to achieve C gains: boosting new C addtions[11,12] and enhancing physical protection of the newly added C[11-13].

However, abundant unexplained examples of these practices working in some but not other circumstances signal that our understanding is incomplete[14]. For example, row crop systems with cover crops can accumulate C even in presence of aggressive tillage[15,16], and some perennial bioenergy systems such as switchgrass (*Panicum virgatum*) can be slow to increase soil C despite large below ground C inputs and the lack of soil disturbance[9,17]. Such discrepancies suggest a substantial knowledge gap with respect to the plant-soil-microbial interactions that drive soil C accretion. This deficiency is unfortunate, since strategies for effective soil C accrual can only be efficiently developed with a full understanding of the underlying controlling mechanisms.

Whether soil C will be gained or lost stems from the balance between microbial decomposition of new C inputs and protection of new C, either as plant-derived or microbially processed compounds[18], within the soil matrix. Majority of the fresh organic matter inputs comes from plants, i.e., above ground litter and especially roots[19,20], and is subsequently utilized by the microbial community to produce CO_2 and decomposition intermediates[21,22]. Intermediate products can escape further decomposition by forming organo-mineral associations with soil mineral surfaces, or by entrapment in small soil pores where they become inaccessible to microorganisms and their exoenzymes[23,24]. Such aspects of soil C balance as sizes and chemical composition of C inputs[19,20], their microbial processing[25], and strength of the physical protection due to soil textural[26,27] and structural[28,29] characteristics have been extensively studied and well understood. Yet, a crucial element kept escaping the research focus: the need for new C to be transported from the micro-sites of its entry and initial processing to the micro-sites where it can be protected from further decomposition. Most studies implicitly assume that C processing and protection are spatially collocated. We suggest that processing and protection take place in different micro-sites of the soil matrix. The need for the new C to be transported to the protective sites prior to protection to occur is the currently overlooked underlying cause for the mentioned above discrepancies in expected and realized C gains.

Transport in soil occurs via pores, which are conduits for gases, water, nutrients, and dissolved organic C, and are habitats for microorganisms[30,31]. Here we provide novel evidence that development of pores of certain sizes can have a controlling effect on C accrual. Pores in the 30–150 µm radius size range may be especially important[32] because they function as likely routes of O_2 influx[33,34] and localities of new C inputs from fine plant roots[35]. Their special role is evidenced by greater microbial activity[36–39], higher abundance of diverse taxa[40], and presence of dissolved organic matter enriched in lipids and depleted in lignin[41,42].

We hypothesize that the abundant presence of such pores, along with ample, fresh C inputs and able microbial communities, is necessary for prompt C accrual. We posit that high abundance of such pores contribute to C accrual in a multi-prong fashion. Specifically, they influence influx of fresh C inputs, affect activities of microbial decomposers by modifying their habitats, and optimize conditions for transport of microbial decomposition products into protective soil matrix. Non-invasive X-ray computed micro-tomography (µCT) scanning supplies detailed 3D information regarding the material density distribution within intact soil samples. Hence it is very well suited to outline the locations and geometry of soil pores, promoting, in turn, understanding of chemical and biological processes taking place within the soil pore space[43,44]. We studied soils from five replicated bioenergy cropping systems, established in 2008, to represent a gradient of plant biodiversity[45]. The five systems consist of two monocultures differing in perenniality, namely continuous corn (*Zea mays* L.) and switchgrass, a two-species system of continuous corn with a winter rye (*Secale cereale* L.) cover crop, and two systems with high plant diversity, i.e., poplars (*Populus* sp. hybrid) with an herbaceous understory and a native successional community abandoned from agriculture in 2008. We evaluated cropping system effects on the soil volume in the vicinity of ≥30 µm radii pores, which serves as an indicator of the size of the spatial influence generated by the microorganisms residing in such pores. Using the new approach of in situ zymography we assessed micro-scale spatial patterns in the distribution of six extracellular enzymes representing microbial activities related to C, nitrogen (N), and phosphorus (P) cycling. Then, combining information from 2D zymography and 3D µCT scanning, we localized associations between microbial substrate utilization, as reflected in enzyme activities, and the abundance of soil pores.

Our results suggest that pores with 30–150 µm radii contain the most active microorganisms capable of responding rapidly to fresh C inputs and thus, of producing the greatest amounts of microbially processed C products. These products are important contributors to soil organic matter accumulation[13,46]. Once they move into the adjacent soil matrix, they stabilize there via various physico-chemical mechanisms. The greater the presence of 30–150 µm pores and their spread throughout the soil, the greater the volume of the soil matrix receiving and protecting the products of microbial decomposition, and subsequently the higher soil C accrual. Greater plant diversity stimulates development of 30–150 µm pores and such stimulation is a previously unknown mechanism by which ecosystems with diverse plant communities enhance soil C accrual.

Results

Effects of cropping systems on soil C accrual and soil pores. We collected disturbed soil samples and undisturbed samples, referred to as intact cores, at a replicated field experiment in southwest Michigan, USA. The studied cropping systems were in-place for 9 years, an experimental duration regarded as typically sufficient for detecting soil C changes[47]. Intact soil cores were subjected to X-ray µCT scanning, followed by pore characterization from 3D images (Supplementary Fig. 1).

Consistent with previous reports from this site[9], of the five cropping systems only the two systems with high plant diversity, poplar and native succession, resulted in higher levels of total soil C (Fig. 1a). Lower C levels were observed in continuous corn with and without cover crops and in the switchgrass system. Short-term respiration, an indicator of labile C, followed the same pattern as the soil organic C and was lower in corn and switchgrass than in the native succession system (Supplementary Fig. 2). However, microbial biomass C in switchgrass system was significantly higher than that of continuous corn and not different from that of poplar and native succession systems (Fig. 1a). Belowground primary productivity of the two perennial herbaceous systems, switchgrass and native succession, was similar at the start of the experiment in 2009; however, 3–4 years later, monoculture switchgrass exceeded native succession by 10–20 fold (Fig. 1b).

We assessed the volume of the soil matrix that was in close proximity to ≥30 µm pores (Fig. 2a), that is, within <180 µm

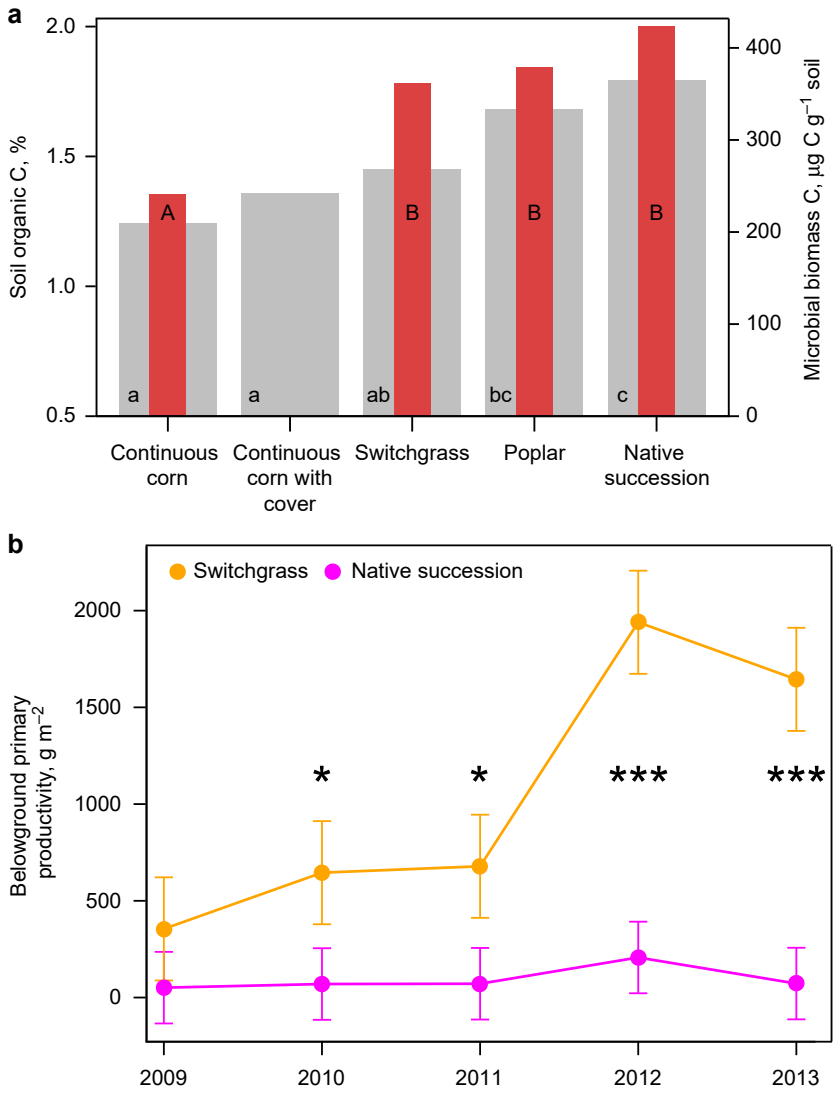

Fig. 1 Soil organic C, microbial biomass C, and belowground primary productivity in soil of the studied cropping systems 9 years after their implementation. **a** Average soil organic C (gray) and microbial biomass C (red) for five studied systems (5–10 cm soil depth). Lower and upper case letters represent statistically significant differences in terms of soil organic C and microbial biomass C, respectively ($p < 0.05$). Standard errors are equal to 0.1% and 28.5 µg C g^{-1} for soil organic C and microbial biomass C, respectively. Note that microbial biomass C could not be analyzed in the continuous corn with cover crop system. **b** Average belowground primary productivity for switchgrass and native succession vegetation systems from 2009 (the year of establishment) till 2013 (0–10 cm soil depth). Error bars represent s.e.m. Years when switchgrass belowground primary productivity exceeded that of native succession vegetation are marked with $*p < 0.1$ or $***p < 0.01$. Source data are provided as a Source Data file

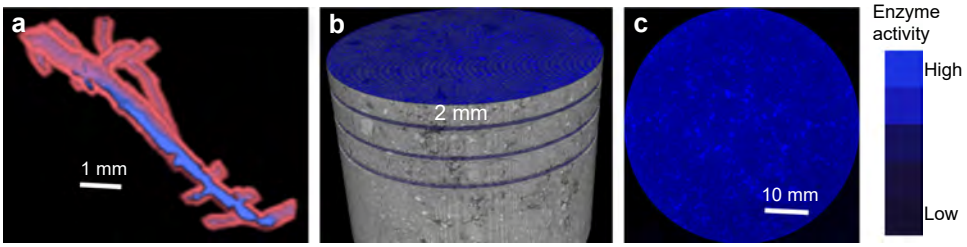

Fig. 2 Illustration of the steps involved in pore characterization and in combining 2D zymography and 3D X-ray µCT scanning. **a** The volume of the soil matrix (pink) within 180 µm distance from ≥30 µm pores (blue) was used as an approximate indicator of the size of the soil matrix that can be potentially affected by C processing taking place within pores. **b** After µCT scanning (at 30 µm resolution) each soil core was cut into slices, with 2 mm distance between the slices. Each core contained 8–16 slices, and, in most of the cores, zymograms of each enzyme were obtained on two slices per core. **c** A membrane saturated with an enzyme-specific substrate was placed on the surface of each slice and a zymogram was obtained

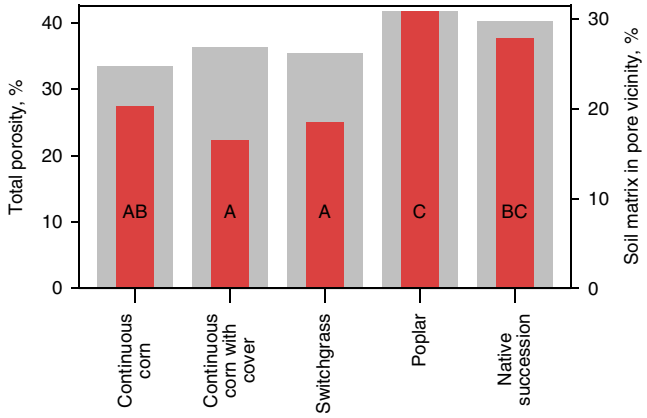

Fig. 3 Soil pore characteristics of the studied cropping systems 9 years after their implementation. Total porosity (gray bars, left *y*-axis) and percent of soil matrix located within <180 µm distance from the nearest ≥30 µm pore (red bars, right *y*-axis). Letters mark significant differences among the systems in terms of percent of soil matrix located within <180 µm distance from the nearest ≥30 µm pore ($p < 0.05$). Source data are provided as a Source Data file

distance from the pore boundaries. The 180 µm distance was used as an approximate indicator of a soil volume potentially affected by processes taking place within the pores and its value was selected as consistent with spatial patterns in microbial and C distributions observed in soil matrixes at similar experimental scales[30,48]. A much smaller portion of the soil matrix in continuous corn and switchgrass was in the vicinity of these pores as compared to poplar and successional soils (Fig. 3). More specifically, the proportion of the soil matrix located close to such pores in native succession and poplar systems exceeded that in switchgrass by 51% and 67%, respectively. Total porosity in the poplar and native succession systems differed considerably from the others (Fig. 3). Since prior to 2008 the experimental site belonged to an agricultural field with common land use and management history, the observed differences are solely a product of contrasting root activities during the last 9 years.

Associations between enzyme activities and soil pores. After µCT scanning, the intact soil cores were subjected to 2D zymography. Combining zymograms from >130 soil slices of intact soil cores with 3D X-ray µCT images provided a unique opportunity to associate enzyme activities with pores of different sizes (Fig. 2b, c).

Spatial associations of enzyme activities with soil pores substantially differed between the poplar and successional systems versus the continuous corn and switchgrass systems (Fig. 4a and Supplementary Table 1). Enzyme activities in soils of successional systems were the same in regions with prevalence of <30 µm and 30–150 µm pores, while in poplars the activities associated with prevalence of <30 µm exceeded those in the regions with prevalence of 30–150 µm pores. In contrast, in both corn systems and in switchgrass, the enzyme activities were much lower in the regions dominated by <30 µm pores than in the regions dominated by 30–150 µm pores. This effect was particularly strong in switchgrass soils, and was observed for all studied enzymes except cellobiohydrolase (Supplementary Fig. 3). In all systems the lowest activities were associated with very large (>180 µm) pores.

Notwithstanding differences in enzyme activities among pore sizes, soil enzyme activities from disturbed samples were not much different among the systems (Supplementary Fig. 4). The systems differed only in acid phosphatase activity, which was the highest in the native succession soil and the lowest in continuous corn.

Enzyme activities and soil pores after addition of fresh C. To address our expectation that 30–150 µm pores harbor active microbial communities capable of processing fresh C inputs, we also conducted zymography measurements after soil cores were incubated with fresh plant litter (Supplementary Fig. 1d). Zymography after incubation of soils with fresh plant litter showed more pronounced contrast in spatial associations between enzyme activities and soil pores compared to soil without fresh C (Fig. 4b). The enzyme activity increased in response to fresh C additions especially in the areas with 30–150 µm pores as compared to those with greater abundance of the smaller pores.

Discussion

Nine years of implementing cropping systems with different plant species diversities led to the formation of contrasting soil pore size distributions[49]. The more diverse systems, i.e., poplar and native succession, developed higher soil porosity (Fig. 3) and a greater presence of 60–150 µm pores[49] and had concomitantly higher soil C contents (Fig. 1a). The systems with low plant diversity, i.e., continuous corn with and without cover crops and switchgrass, had no pore increases and did not experience soil C gains. In the latter three systems greater enzyme activities were associated with 30–150 µm pores (Fig. 4a). Yet, soil under switchgrass acquired significantly higher microbial biomass than continuous corn, comparable to that of poplar and native succession systems (Fig. 1a).

The finding that greater presence of pores benefits C accrual does appear paradoxical. However, it actually reflects a previously unrecognized micro-scale spatial interaction between physical and microbiological contributors to soil C sequestration. We posit that in soils with fewer 30–150 µm pores, microbial communities have a smaller spatial footprint, which we define as the volume of the soil matrix that can be immediately influenced by microbial decomposition products. A smaller footprint implies a smaller soil volume for entombing microbial decomposition products[50].

We propose the following conceptual model integrating this mechanism in the existing concept of plant-soil-microbial interactions (Fig. 5): Plant roots are the key agents in formation of soil pore architecture. Pores in 30–150 µm size range are the preferential locations of new C inputs and active microbial communities, where active processing of C inputs takes place. The greater the volume of the soil matrix in contact with such pores, the greater is the potential for microbial decomposition products to be transported to and be protected within the soil matrix inaccessible to microbial decomposers. Plant systems that stimulate creation of such pores enhance opportunities for microbial decomposition products to reach inaccessible soil matrix and thus stimulate C gains. Below we provide the evidence from the current study and published literature in support of the proposed concept.

A significant body of research supports the notion that pores in the range of tens-of-µm play an outsized role in C processing. Pores of this size demonstrate faster organic matter decomposition, greater presence of labile organic compounds, and higher microbial abundances[36–42]. The special role of pores of this size range is driven by two factors. First, they are likely preferential locations of fine roots, typically ~30 µm. Fine roots are covered by root hairs contributing to rhizodeposition and have maximal exudation rates. Stable isotope analysis showed that these pores indeed receive and process large amounts of fresh C inputs[51]. Second, these pores possess optimal micro-environmental conditions in terms of water and oxygen supply to resident microbial

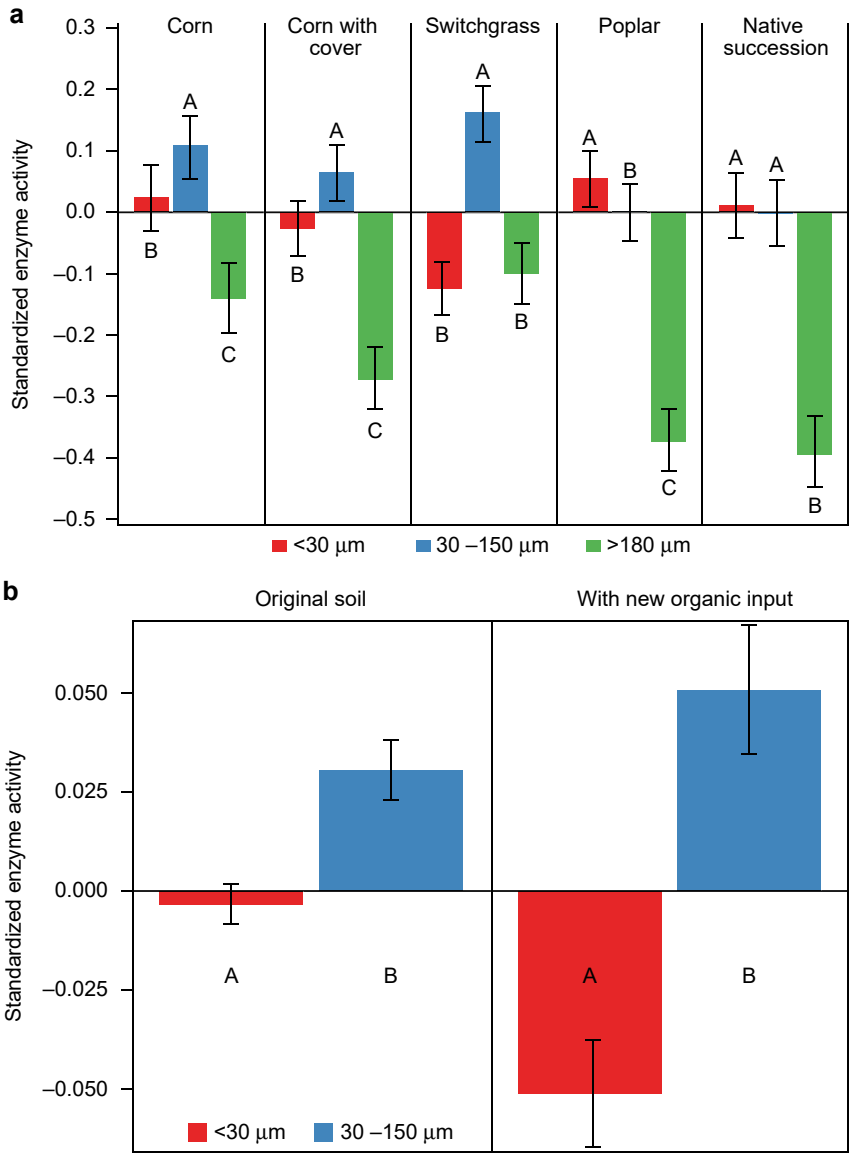

Fig. 4 Standardized enzyme activities in soil micro-sites with prevalence of pores of three size groups (<30 µm, 30–150 µm, and >180 µm). **a** Enzyme activities from soil slices not subjected to incubations with fresh C inputs. Shown are means across all studied enzymes. Error bars are s.e.m. (based on 139 zymography layers from 13 soil cores). Letters within each cropping system mark statistically significant differences among pore size classes ($p < 0.05$). **b** Enzyme activities from slices subjected and not subjected to incubations with fresh nutrient inputs; shown are means across all systems and enzymes. Error bars are s.e.m. (based on 88 and 14 zymography layers without and with new organic inputs, respectively, from 10 soil cores). Letters mark significant differences between enzyme activities in localities with <30 and 30–150 µm pores ($p < 0.05$). Summary data are provided as a Source Data file

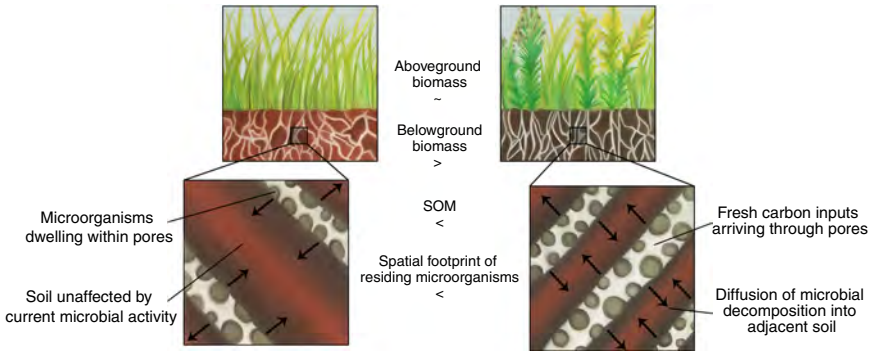

Fig. 5 Microbial footprint defines the soil volume available for C protection. Schematic representation of the effect that the abundance of 30–150 µm pores has on the size of the spatial footprint of microorganisms residing in such pores in perennial switchgrass monoculture and biodiverse native vegetation systems

communities. Smaller pores tend to have longer periods of anoxia[52] and larger pores tend to have longer periods of water shortage[53]. Higher enzyme activities associated with 30–150 µm pores (Fig. 4) confirm that these pores provide micro-environmental conditions optimal for microbial functioning and also harbor active microbial communities capable of a speedy response to new C inputs.

Our findings suggest that the ability of root systems to generate such pores can be a decisive factor in producing soil C gains. The roots of the two more diverse cropping systems, i.e., poplars and native succession, which quickly accumulated high levels of soil C, apparently stimulated the formation of ≥30 µm pores[49]. Once formation was initiated, these pores became, first, the locations of enhanced microbial activity and intensive processing of new C inputs; and second, the major source of microbially processed C that diffused into and became physico-chemically protected within the surrounding soil matrix by forming associations with mineral surfaces which protected them from further decomposition[11,13]. High abundance of such pores ensured a large proportion of the soil matrix in close proximity to active microbial communities as represented by the percent of soil matrix located within 180 µm of the nearest ≥30 µm pore (Fig. 3).

The switchgrass system with its low abundance of 30–150 µm pores[49], exceptionally high belowground biomass production (Fig. 1b), and a surprising lack of C gains (Fig. 1a; Supplementary Fig. 1) epitomizes the importance of this mechanism. The switchgrass system is very similar to poplar and native successional vegetation in terms of possessing all the components known to be necessary for rapid and extensive soil C accrual. As a perennial system, switchgrass management does not involve annual tillage; its belowground production is massive[54] and greatly exceeds that of the native succession vegetation (Fig. 1b). Switchgrass soils have highly diverse microbial communities, with microbial biomass (Fig. 1a) and bacterial diversity indices greatly exceeding those in the continuous corn system and similar to those in poplar and native succession[55]. Fungal biomass in the switchgrass soils likewise exceeds that of corn and is similar to poplar and native succession[56], and greater fungal abundance is typically associated with greater C accrual[13]. The production of fine roots in switchgrass is also comparable to that of the native succession system[57]. The switchgrass system was in place for nine years, a sufficient time for changes in soil C to take place[47]. Yet even labile soil C fractions, which typically indicate coming changes in total soil C did not increase under switchgrass (Supplementary Fig. 1 and ref. [9]). It should be noted that these results are not unique to the current study. While the conversion of annual cropland to switchgrass often leads to soil C gains[58,59], no or slow increases in soil C concentrations under switchgrass as well as high variability in observed C gains[60] have also been reported, including diverse experimental sites in North Dakota, South Dakota, and Nebraska[61], southeastern US[62], and northern Italy[17].

In soils under switchgrass, high root C inputs[63] stimulated microbial activity, but in the absence of a sufficient abundance of 30–150 µm pores, most of this C was apparently oxidized to CO_2 rather than entombed as organo-mineral associations in the nearby soil matrix. While the 30–150 µm pores in switchgrass soil were the sites of intensive enzyme activities and C processing (Fig. 4), the volume of the soil matrix adjacent to such pores was relatively small (Fig. 3). Thus, the pore-adjacent layer likely became quickly saturated with microbial C inputs, with limited diffusion farther from the pores. This is consistent with observations of Chenu et al.[36] who noted that once a new C source was applied to the surface of soil aggregates it was actively microbially consumed in situ with only small amounts diffusing into aggregate centers. A large volume of soil matrix, with high potential for C physico-chemical protection, therefore remained unutilized, not receiving C, and resulting in overall low soil C levels. Indeed, in switchgrass soil intensive microbial processing and C turnover have been demonstrated in a number of ^{13}C isotope based studies[64–67]. It can be surmised that the new C inputs were either fully decomposed and lost as CO_2 or lost as dissolved organic C during convective flow events.

Developed differences in soil pore characteristics between monoculture switchgrass and biodiverse poplar and native succession systems could be a result of several physical and biological factors. A potential physical factor is a difference in water usage by plant communities. Systems where soils experience greater drying in summer would be expected to have a greater presence of large pores (cracks) due to soil shrinkage. This phenomenon is commonly observed in soils with high clay contents (2:1), but still, though to a lesser extent, is present in sandy loam soils. Systems with greater soil moisture levels prior to soil freezing in winter would be expected to develop greater pore presence due to more extensive soil expansion during freezing/thawing cycles. However, experimental evidence suggests that in our systems these physical mechanisms could be only minor contributors to the observed pore differences, especially so since the studied soils do not contain significant amounts of shrink-swell clays. Over the years, soil water content under poplars, with its greater pore abundances, tended to differ from that in the other systems (Supplementary Fig. 5). However the observed tendency was actually disadvantageous to pore formation via wetting-drying and freezing-thawing mechanisms mentioned above, because poplar soil tended to be more moist in spring and summer, and drier in fall prior to soil freezing.

Biological factors are thus likely to dominate. Differences in root architecture, including root density, diameter, strength, fine root biomass and mycorrhization, are well known to affect soil porosity[68–70]; and amounts and compositions of root exudates are likewise affected by root characteristics[63]. Systems with greater plant diversity have a greater variety of root architectures with correspondingly different effects on porosity. Moreover, in the systems with no soil disturbance and low plant diversity the reuse of the old root channels by the new plant roots is more likely[71,72], further reducing possibilities for new pore formations.

Overall, our results point to a heretofore missing link in understanding plant-soil-microbial interactions. Plant community composition defines not only the composition of the soil microbial community, but, by affecting presence and characteristics of soil pores, it also defines spatial distribution patterns of regions where the microorganisms can most effectively reside and function as related to C turnover and sequestration. That pattern then defines the spatial footprint that microorganisms can make on the surrounding soil matrix. For soil C processing the size of this footprint translates into the size of the soil volume involved in the protection of microbially-processed C inputs.

Our finding was enabled by comparisons between a monoculture switchgrass and biodiverse native succession and poplar systems– the systems that possessed great similarities in all their features except for pore characteristics. Very high inputs of fresh C in the switchgrass system made the effects of pore presence on microbial functioning especially pronounced and their detection possible using 2D zymography and X-ray µCT tools. We surmise that similar considerations are applicable to the no-till continuous corn systems of this study, where small microbial footprint is probably one of the contributors to their low C levels.

Our work demonstrates how better understanding of micro-scale interactions between plants, microorganisms, and soil characteristics can have a direct impact on macro-scale (landscape) features of terrestrial ecosystems, i.e., accrual of soil C, and how it can lead to new strategies in sustainable agricultural

management. A potential strategy is the maximization of root diversity as a prerequisite of efficient C accrual, which can be achieved by planting more diverse switchgrass stands, promoting diverse understory in poplar plantations, and intensively using polyculture cover crops in row crop systems.

Methods

Field experiment. The Great Lakes Bioenergy Research Center (GLBRC) experiment had been established in 2008 at Kellogg Biological Station's Long-term Ecological Research Site, Michigan, USA on well-drained Alfisols[73]. Soil texture consists of 65% sand, 27% silt, and 8% clay. The field experiment is a randomized complete block design with five replications[45]. The five bioenergy land use and management system are: no-till continuous corn and no-till continuous corn with winter cover crop of cereal rye, a monoculture switchgrass, a hybrid poplar (*Populus nigra* × *P. maximowiczii* NM6) with herbaceous understory[9], and an early successional community abandoned from agriculture in 2008. The experimental site was plowed prior to establishment and no further plowing was conducted in either of the systems. All systems were managed using local best agronomic practices[45].

Two intact soil cores (5 cm Ø × 5 cm height) were collected from four replicated plots of each bioenergy system for a total of 40 cores in early spring 2017. The soil cores were taken using a soil core sampler (Soil Moisture Equipment Corp.) into an acrylic cylinder located within the sampler. The sampler had two rings, 5-cm height each, and soil from the first ring was discarded. Thus, the cores were collected precisely from 5–10 cm depth within the soil profile. A disturbed soil sample and an additional soil core for bulk density measurement were also collected from each sampling location. Bulk density was measured for each sampling location using the core method[74] and is reported in ref. [49]. Soil temperatures were around 5 °C at the time of sampling and soil water content levels were around field capacity. During the time period prior to the zymography measurements the cores were kept in a dark at 4 °C, except for times of shipping and during µCT scanning. To preserve the cores during shipping each core was tightly closed on both ends with ridged foil caps and wrapped in several layers of plastic using duct tape. The disturbed samples were stored air-dried.

X-ray computed µCT scanning and image analysis. Intact soil cores were subjected to X-ray scanning using a GE Phoenix v|tome|x m scanner at the Institute of Soil and Environment at the Swedish University of Agricultural Sciences in Uppsala, as described in ref. [49]. In brief, the X-ray scanner was equipped with a 240 kV tube, a tungsten target and a 16′′ flat panel detector with 2014 × 2014 detector crystals (GE DRX250RT). Each 3D X-ray µCT image was reconstructed from 2000 projections, with a tube voltage of 130 kV and an electron current of 200 µA. No optical filters were used. Soil cores were scanned inside their acrylic rings. Beam hardening artefacts were not observed. 3D µCT X-ray images were reconstructed using the filtered back-projection approach (GE software datos|x). The entire soil core, including the acrylic cylinder, was scanned. Each image had a voxel size of 29 µm in x, y and z direction.

Two examples of the scanned images are shown in Supplementary Fig. 1a, b. The image processing was conducted using ImageJ/Fiji software. The same image processing procedures were applied to soil samples from all studied systems. Preprocessing consisted of a 3D median filter with a radius of two voxels in all directions using Median 3D filter tool from ImageJ. After that we removed 0.5 cm border parts around each core to avoid artifacts associated with sample wall effects.

For segmenting the images into pores and non-pores we used the minimum error approach[75] on the respective image histograms. The grayscale histograms (8-bit) of all soil cores exhibited a two-distribution pattern, with one distribution corresponding to air + liquid and the other to solid portions of the images. Thus, following ref. [76], the two-Gaussian fits were applied to the histograms. The threshold was computed as a greyscale value that minimized the difference between the overlapping areas of the two distributions. This approach conserves the voxel balance between the two segmented phases (solid and air + liquid). The necessary computations were performed in the Regression Wizard tool of the SigmaPlot software (Systat Software, Inc). The segmentations were conducted separately for each soil core.

Then, visible pores (≥30 µm) were obtained using the Xlib plugin for ImageJ[77]. We used the continuous 3D pore-size distribution option of the software, which provides radii of the largest spheres, that fit into the 3D pore volume, as described in detail in ref. [77]. Therefore, the pore size at a specific location was defined as the radius of the maximally inscribable sphere at this location. Particulate organic matter, including plant roots, in the images was identified as described in ref. [49] and in further analyses particulate organic matter was separated from pore and solid fractions. Pore-size distribution data from the studied cores are reported in ref. [49].

As a measure of the soil matrix fraction that was potentially affected by C processing taking place within the visible pores (≥30 µm), we used the soil matrix volume located within 180 µm distance from these pores (Fig. 2a). The volume was determined via a series of 3D dilations using ImageJ until ~180 µm distance from the pore surface was reached. The value of 180 µm was selected as consistent with distances for spatial correlations in microbial colony distributions[30] and spatial patterns of soil C distributions[48] in previous micro-scale studies of soil matrix.

Soil measurements. The total porosity of each intact soil sample was calculated from its soil volume determined from the µCT image, gravimetric soil moisture content measured at the end of the study, and soil weight. A particle density of 2.6 g cm^{-3} was assumed for the total porosity calculations. Porosity <30 µm was determined as the difference between the total porosity and the image-based porosity, that is, the volume of pores with radii >30 µm, obtained from the images.

For total soil C measurements, disturbed samples were sieved and ground followed by combustion analysis on Carlo-Erba Elemental Analyzer (Costech Analytical Technologies, Valencia, CA). Short-term respiration was determined by incubating 10 g soil samples for 7 days at 20 °C in the dark[78]. Measurements of CO_2 emissions were conducted using infrared Photoacoustic Spectroscopy (PAS) (1412 Photoacoustic multi-gas monitors; INNOVA Air Tech Instruments, Ballerup, Denmark) in the gas circulation mode. Microbial biomass C was measured using chloroform fumigation incubation method[79]. After 24 h of fumigation with ethanol-free chloroform, 5 g fumigated and non-fumigated (control) soil samples, were subjected to 10 day incubations followed by CO_2 measurements as described above. Microbial biomass C was calculated based on the amounts of CO_2 emitted from fumigated and control samples[80].

Gravimetric soil water content monitoring was conducted on a bi-weekly basis from each replicated experimental plot at the GLBRC experimental site. Soil samples for gravimetric soil water content measurements were collected from 0–25 cm depth using a push probe (Ø 2 cm) during growing seasons of 2009–2015. Soil was dried for 48 h at 60 °C.

Root biomass at 0–10 cm depth was measured in soil cores (Ø 7.6 cm) collected in triplicates from each experimental plot. The cores were taken at three points along plant density gradients moving out from the center of a bunchgrass into the interstitial space. Cores were air-dried, sieved over a 2-mm sieve, and roots were washed, dried at 60 °C for 48 h, and weighed. Samples were collected in November from 2009–2013.

The following soil biological characteristics of the studied cropping systems were measured from the studied experimental plots 1–2 years prior to the current work and reported in peer-reviewed literature: microbial community composition and bacterial diversity indices[55], fungal biomass[56], fine root production[57], labile soil C fractions[9].

2D zymography of soil cores. Enzyme activities were mapped using soil zymography approach[81]. Zymography mapping consists of placing a membrane saturated with an enzyme-specific fluorogenic substrate on a surface of the soil sample. Once the substrate is enzymatically hydrolyzed, a fluorescent product is generated and the ensuing fluorescent patterns reflect the presence and activities of the enzymes. A photo of the membrane is taken in ultraviolet (UV) light, which then is used to produce a map of enzyme activities on the studied surface, referred to as a zymogram.

A schematic representation of the process of combining zymography with µCT information is shown on Supplementary Fig. 6, while a detailed description of the zymography procedures and soil processing for zymography analyses used in this study are provided in ref. [82]. In brief, the following specific settings were used: membrane—hydrophilic polyamide filters (100 µm thick, Tao Yuan, China)[81]; camera—Nikon D90 camera (Nikon Inc.) with a Sigma 18–250 mm f/3.5–6.3 DC Macro OS HSM lens (Sigma Corp. of America); source of UV light—a 22 W Blue Fluorescent Circline Lamp—FC8T9/BLB/RS (Damar Worldwide 4 LLC); extracellular enzymes—beta-glucosidase, cellobiohydrolase, xylanase, N acetyl-beta-glucosaminidase, leucine aminopeptidase, and acid phosphatase; respective enzyme-specific substrates: 4-Methylumbelliferyl-β-D-Glucoside, 4-Methylumbelliferyl-β-D-Cellobioside, 4-Methylumbelliferyl-β-D-Xylopyranoside, 4-Methylumbelliferyl-N-Acetyl- β-D-Glucosaminide, L-leucine-7-amido-4-methylcoumarin hydrochloride, and 4-methylumbelliferyl-phosphate[83].

Soil cores were cut into 2 mm slices (Fig. 2b) using a specially designed cutting table (Supplementary Fig. 1c), as described in detail in ref. [82]. A total of 13 soil cores were analyzed, with 10–16 zymograms taken per core, one map per each soil slice. Soil moisture levels were not manipulated prior to the measurements. Since good contact between a membrane and a soil surface is needed for obtaining reliable enzyme activity data[84], only portions of each membrane were usable. Such portions were identified via an MUF-staining approach[84] as described by ref. [82]. The areas with minimal contact were excluded from enzyme map analyses.

The zymogram was covered by a 1 mm^2 grid, and for each pixel of the grid we identified a corresponding 1 mm^3 voxel from the µCT image. The enzyme pixel was assumed to be located at the center of the µCT voxel (Supplementary Fig. 6). For each 1 mm^2 pixel of the zymogram we calculated the average grayscale value and standardized it based on the mean and standard deviation of the entire zymogram. For each 1 mm^3 voxel of the µCT image we also calculated averages for the studied characteristics, e.g., volumes of pores of different sizes and volume of the soil matrix in relative proximity to sizeable pores. The aggregation of the data to the 1 mm scale conducted here was required to address the uncertainties associated with soil cutting and matching of zymography and µCT images. Because it introduced smoothing into the resulting pore data, to ensure that the uncertainty in pore characteristics of individual voxels was minimized during the analyses of

the relationships between pores and enzyme activities, we only selected for such analyses the voxels where the pore values were above the 95th percentile value for the entire soil core (Supplementary Fig. 7). Specifically, for each core we constructed histograms for pores of all studied class sizes and calculated the 95th percentiles for abundances of each pore size class. Then each voxel of the core was examined and only the voxels with abundances exceeding the 95th percentiles were retained for further analyses. On very rare occasions when a voxel exceeded 95th percentile in more than one pore size class it was grouped in the larger of the size classes. While this approach reduced the number of data points available for the analyses, it ensured that the data used are highly representative in terms of their pore characteristics.

In order to evaluate how addition of new nutrient inputs influences relationships between soil pores and enzyme activities we conducted incubations with fresh plant inputs in 10 studied cores, with 1–2 soil slices per core for a total of 14 slices. Each slice was covered by a layer of nutrient source, either as an alder (*Alnus glutinosa* L.) leaf or as a layer of red clover (*Trifolium pratense* L.) leaves, as shown in Supplementary Fig. 1d. Prior to the experiment, the leaves were air-dried in a botanic press to ensure the maximum uniformity in their contact with the entire soil surface. After placing the dried leaves on the soil surface, 240 µl of water was evenly added with a pipette on top. The surface was covered with aluminum foil and a 100 g sandbag weight to maximize the contact with the soil, and incubated for 3–7 days. After the incubation, the leaves were carefully removed from the surface and an additional 0.2–0.3 mm of soil was cut off the surface to ensure that no leaf material remained on the soil surface subjected to zymography. Then, zymography measurements were conducted on the surface as described earlier.

Statistical analysis. Statistical analyses were conducted using PROC MIXED and PROC GLIMMIX procedures of SAS[85]. Implemented statistical models varied depending on the experimental units from which different response variables were collected. Specifically, comparisons among the bioenergy systems in terms of the response variables with a single observation per soil core, e.g., soil C or soil volume in pore vicinity, were conducted using the statistical model with a fixed effect of the bioenergy system and random effects of the experimental field block and experimental field plot (nested within the system). Statistical models for exploring standardized enzyme activities for different enzymes in different bioenergy systems and corresponding to areas with prevailing pores of different sizes included fixed effects of enzyme, system, and pore size class, as well as their interactions, and random effects of blocks, plots, cores (nested within the systems and plots), and also individual soil slices (nested within all of the above factors). Normality of the residuals and homogeneity of variances were checked for each studied variable. In case of marked deviations from normality the data were log-transformed, while in case of variance heterogeneity, unequal variance analysis was performed[86].

Data availability

Data collected for this study will be made publicly available on Dryad and will be preserved in the KBS LTER database available at http://lter.kbs.msu.edu/datatables. The source data underlying Figs. 1a–b, 2a–b, and Supplementary Figs. 2 and 5 as well as summary data underlying Fig. 4 and Supplementary Figs. 3 and 4 are provided as a Source Data file.

Code availability

Data and image analyses codes are available from the authors upon request.

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Author contributions

A.N.K. developed research concepts with inputs from A.K.G, B.S.R., G.P.R., and Y.K.; M.Y.Q. and A.K.G conducted the soil sampling; A.N.K., A.K.G., and B.S.R. conducted laboratory experiments and zymography analyses, with inputs from Y.K.; J.K. and M.Y.Q. conducted computed micro-tomography; A.N.K. and A.K.G. conducted data analyses; A.N.K., G.P.R. and Y.K. wrote the manuscript. All authors contributed to manuscript writing and reviewed the manuscript.

Additional information

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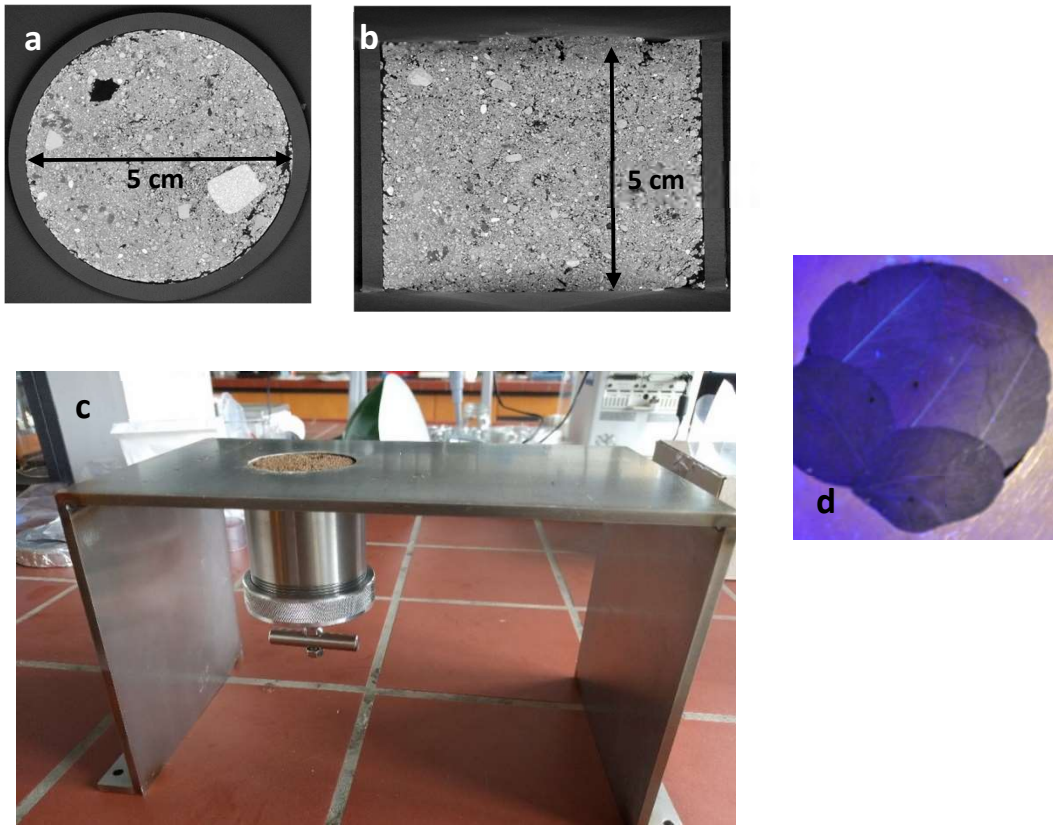
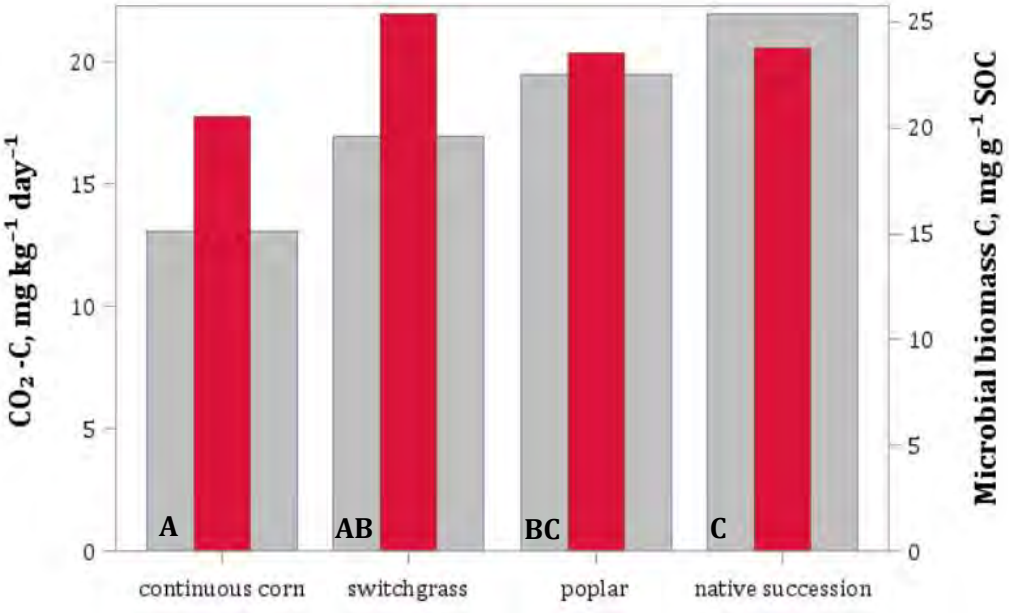
Microbial spatial footprint as a driver of soil carbon stabilization

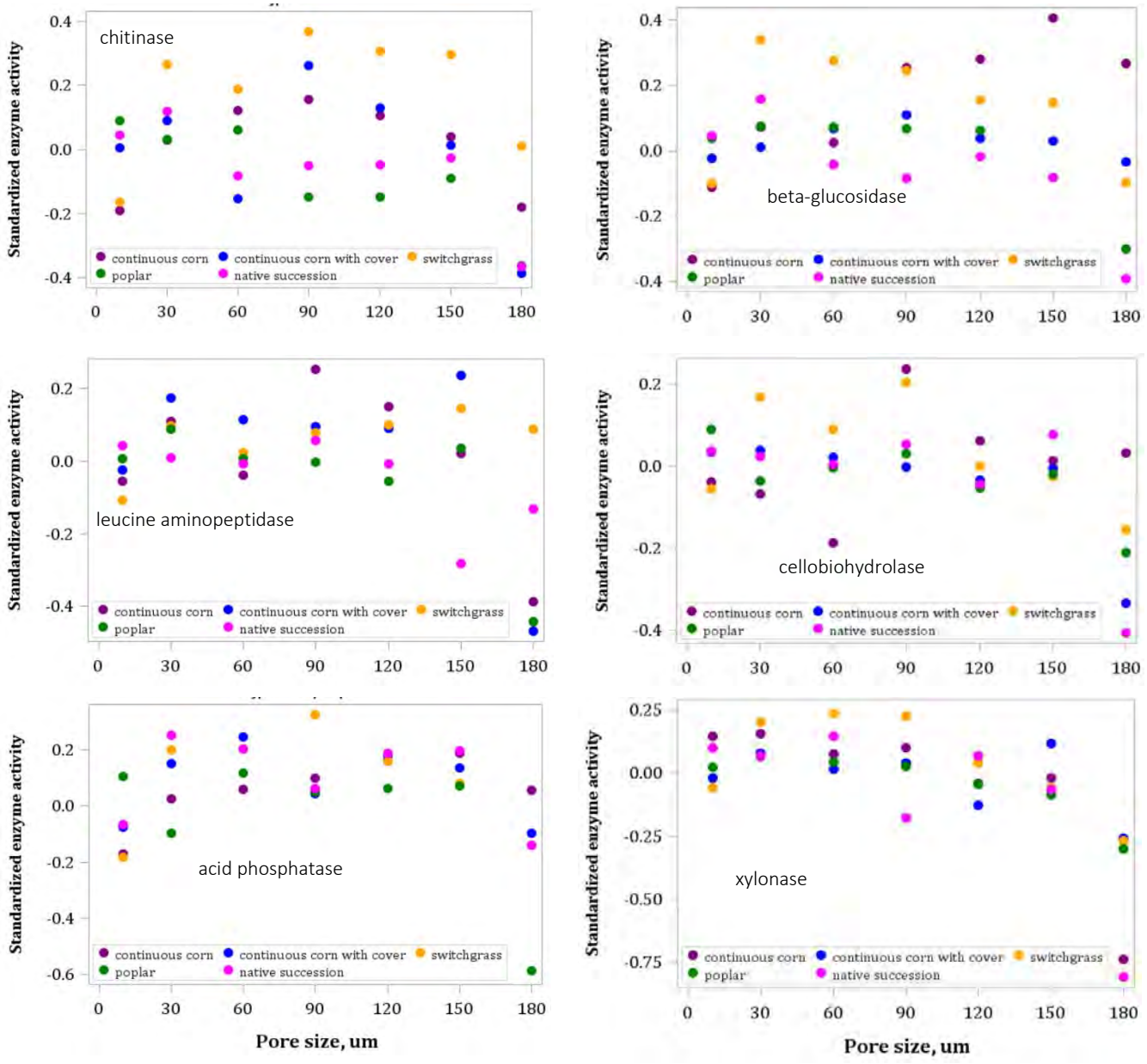
Kravchenko et al.



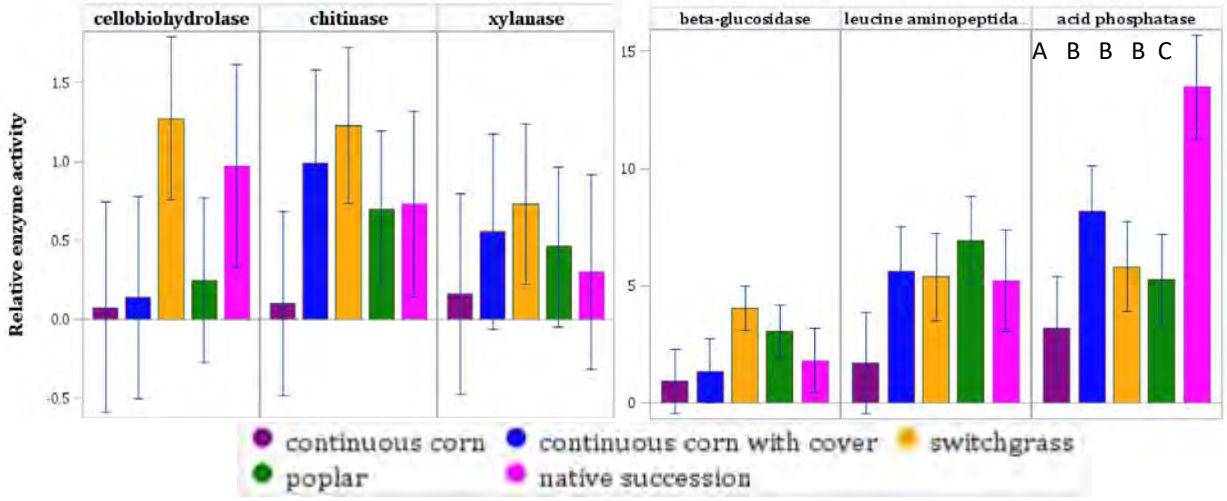
Supplementary Fig. 1. Illustration of the experimental set up. Example of **a** top and **b** front view of an X-ray µCT scanned soil core. **c** Experimental set up used to cut soil layers from X-ray µCT scanned soil cores. **d** Layer of clover leaves incubated on the surface of the soil sample.



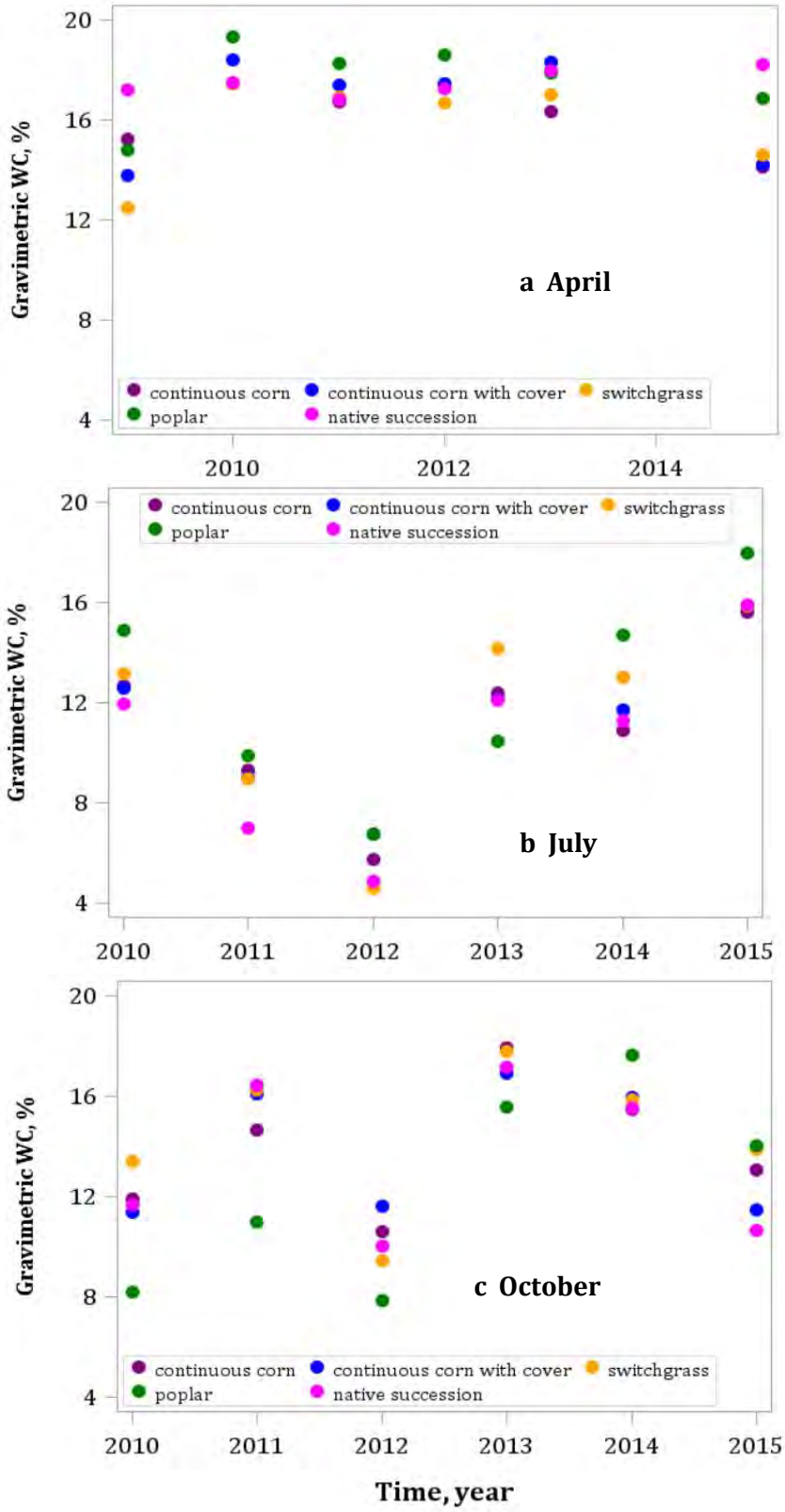
Supplementary Fig. 2. Short-term respiration and microbial biomass C. Cumulative amount of CO_2-C respired during short-term (7 day) incubation (gray) and microbial biomass C expressed per unit of soil organic C (red). Letters mark statistically significant differences among the cropping systems in terms of short-term respiration ($p<0.05$). Standard errors are equal to 2.0 mg kg^{-1} day^{-1} and 2.1 mg g^{-1} for CO_2-C and microbial biomass C, respectively. Source data are provided as a Source Data file.



Supplementary Fig. 3. Standardized activities of the studied enzymes. Standardized enzyme activities in soil localities with prevalence of pores of different sizes from soil slices not subjected to incubations with fresh C inputs. Shown are means for all studied enzymes. Summary data are provided as a Source Data file.



Supplementary Figure 4. Relative enzyme activities in the studied cropping systems. Letters mark statistically significant differences among the systems within specific enzymes ($p<0.05$). Errors bars represent s.e.m. Note that y-axis scales are different for cellobiohydrolase, chitinase, and xylanase, from that of the other three enzymes due to substantial differences in their activities and the need to visualize the differences among the systems on the graph. Summary data are provided as a Source Data file.



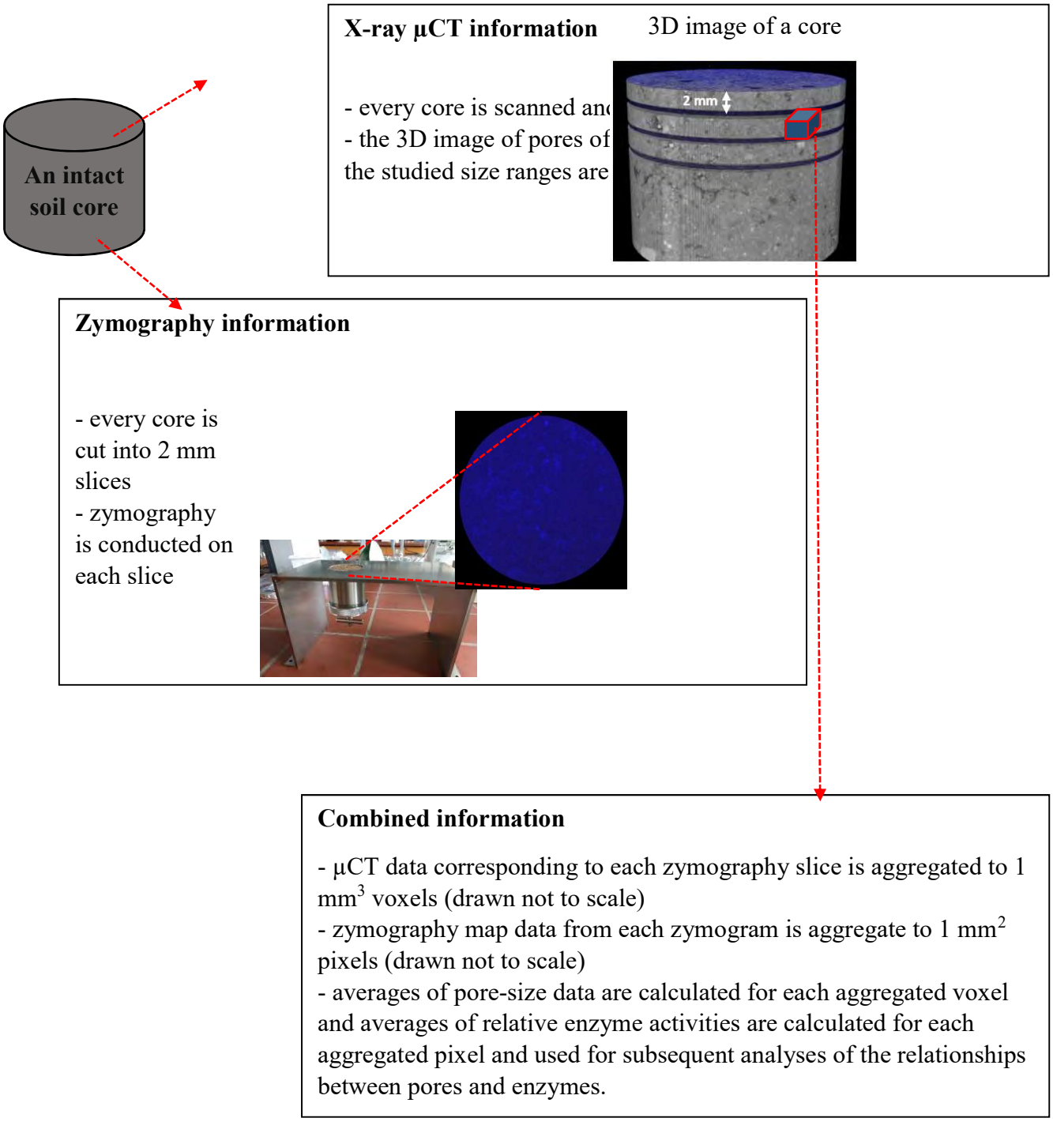
Supplementary Fig. 5. Soil moisture monitoring results. Monthly averages of soil gravimetric water content (WC) at 0-25 cm depth from 2009 to 2015 for (**a**) April, (**b**) July, and (**c**) October. Source data are provided as a Source Data file.

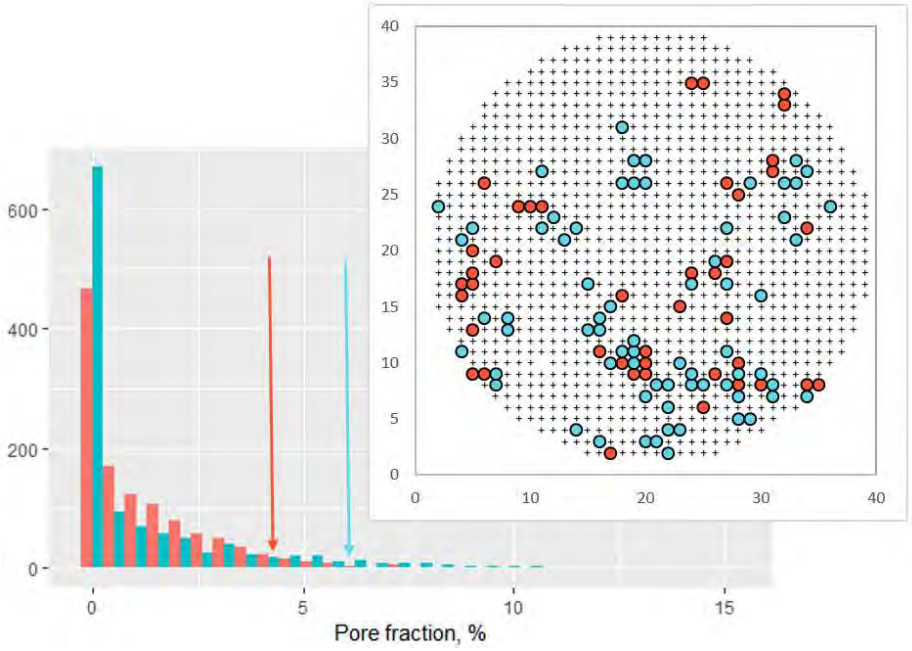
Supplementary Fig. 6. A set up for combining zymography with X-ray µCT information. The experimental set up used for zymography analyses of intact soil cores (**a**) and a schematic representation of the soil sample processing procedures for joint pore-size distribution and relative enzyme activity analyses (**b**).

a)



b)


An intact soil core
X-ray µCT information
3D image of a core
- every core is scanned an
- the 3D image of pores of
the studied size ranges are
2 mm
Zymography information
- every core is cut into 2 mm slices
- zymography is conducted on each slice
Combined information
- µCT data corresponding to each zymography slice is aggregated to 1 mm3 voxels (drawn not to scale)
- zymography map data from each zymogram is aggregate to 1 mm2 pixels (drawn not to scale)
- averages of pore-size data are calculated for each aggregated voxel and averages of relative enzyme activities are calculated for each aggregated pixel and used for subsequent analyses of the relationships between pores and enzymes.



Supplementary Fig. 7. **Illustration of pore data preparation**. Examples of histograms for abundances of pores in 60 µm (red) and 90 µm (blue) size range from one of the studied cores. Arrows mark locations of the respective 95th percentiles for these two pores sizes in the core. The insert shows the voxels where the abundances of these pores exceeded the respective 95th percentiles in one of the 2D zymography layers, and which were used in the subsequent analyses of the associations between pores and enzyme activities.

Supplementary Table 1. Standardized enzyme activities in soil localities with prevalence of pores of different sizes from soil slices not subjected to incubations with fresh C inputs. Shown are means, standard errors and letters marking significant differences among cropping systems in localities with prevalence of pores of different size classes ($p<0.05$) across all studied enzymes.

	Pore size class						
Cropping system	**<30 µm**	**30 µm**	**60 µm**	**90 µm**	**120 µm**	**150 µm**	**>180 µm**
continuous corn	-0.07/0.03ab	0.05/0.04a	0.01/0.04a	0.18/0.04cd	0.12/0.04bc	0.11/0.04b	-0.16/0.03c
continuous corn with cover	-0.02/0.02b	0.09/0.04a	0.05/0.04a	0.09/0.04bc	0.05/0.04abc	0.09/0.03b	-0.26/0.03b
switchgrass	-0.11/0.02a	0.21/0.03b	0.17/0.03b	0.24/0.04d	0.13/0.03c	0.10/0.03b	-0.09/0.03c
poplar	0.06/0.02c	0.02/0.03a	0.05/0.03a	0.00/0.03ab	-0.03/0.03a	-0.03/0.03a	-0.37/0.03a
native succession	0.03/0.02c	0.11/0.04a	0.04/0.04a	-0.02/0.04a	0.02/0.04ab	-0.03/0.04a	-0.37/0.03a

PLOS ONE

RESEARCH ARTICLE

Identifying riparian climate corridors to inform climate adaptation planning

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Abstract

Riparian habitats have been frequently identified as priority areas for conservation under climate change because they span climatic gradients and have cool, moist microclimates relative to surrounding areas. They are therefore expected to act as dispersal corridors for climate-induced species range shifts and to provide microclimatic refugia from warming. Despite recognition of these values, rigorous methods to identify which riparian areas are most likely to facilitate range shifts and provide refugia are currently lacking. We completed a novel analysis across the Pacific Northwest, USA, that identifies potential riparian corridors featuring characteristics expected to enhance their ability to facilitate range shifts and provide refugia. These features include large temperature gradients, high canopy cover, large relative width, low exposure to solar radiation, and low levels of human modification. These variables were used to calculate a riparian climate-corridor index using a multi-scale approach that incorporates results ranging in scale from local watersheds to the entire Pacific Northwest. Resulting index values for potential riparian corridors in the Pacific Northwest were highest within mountainous areas and lowest within relatively flat, lowland regions. We also calculated index values within ecoregions, to better identify high-value riparian climate corridors within the relatively flat, degraded areas where they may most contribute to climate adaptation. We found that high-value riparian climate-corridors are least protected in flat, lowland areas, suggesting that such corridors should be high priorities for future conservation effort. Our analysis provides critical information on valuable riparian climate-corridors to guide climate adaptation efforts (and riparian management and restoration efforts) in the Pacific Northwest, while offering a novel approach that may be applied to similar efforts in other geographies.

Introduction

As climate change progresses and concern grows over the ability of species and ecosystems to adapt [1–2], considerable effort has been devoted to identifying areas on the landscape expected to promote biological resilience to change [3–5]. Riparian areas have been frequently

design, data collection and analysis, decision to publish, or preparation of the manuscript.

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identified as important features to conserve for climate adaptation [6–9], because they span the climatic gradients species are likely to follow as they track shifting areas of climatic suitability [10–12] and contain microclimates that are significantly cooler and more humid than immediately surrounding areas [13]. For these reasons, they are expected to provide dispersal corridors for species undergoing climate-induced range shifts [7,9] and microclimatic refugia from warming for species with limited movement capacities [14,5–6]. Riparian areas may also offer especially effective conservation umbrellas under climate change, because they disproportionately contribute to regional species richness [15–16], provide habitat for many upland species as well as riparian specialists [15–16], and directly contribute to the climate resilience of adjacent freshwater aquatic habitats [17–18]. Despite this recognition, few methods have been proposed for identifying priority riparian areas for climate adaptation.

Riparian areas are frequently prioritized in conservation planning efforts (e.g., [19–20]), but there are few examples of approaches aimed at identifying those that are most likely to promote climate adaptation. Available approaches for identifying riparian corridors to promote climate-induced range shifts include a conservation planning analysis for South Africa that included riparian corridors constructed by applying a fixed buffer around rivers connecting coastal to inland habitats to promote elevational species range shifts [21]. Similarly, riparian areas associated with 2nd order streams linking the Pacific Ocean to high elevations were prioritized in a climate adaptation analysis for California, USA [22]. In another analysis, a land facet corridor analysis aimed at promoting species range shifts in Arizona, USA, connected large blocks of natural habitat using riparian corridors identified by applying a fixed buffer around expert-identified streams and riparian habitats [23]. Most of these analyses used rivers as coarse proxies for riparian habitat, and none rigorously accounted for variability in riparian area quality, which we argue strongly influences the degree to which riparian areas may facilitate range shifts and provide refugia.

To address the need for a rigorous approach to identify priority riparian areas for climate adaptation, we completed a novel analysis that identifies potential riparian corridors expected to promote the ability of biodiversity to respond to climate change. Specifically, we developed a riparian climate-corridor index to quantify the degree to which riparian areas may promote range shifts and provide refugia, identifying those riparian areas that: 1) span large temperature gradients, 2) have high levels of canopy cover, 3) are relatively wide, 4) have low solar insolation, and 5) exhibit low levels of human modification. These variables were derived from the theoretical and empirical literature on species' responses to observed and projected climatic change. For example, riparian corridors that span large climatic gradients may help promote climate-induced range shifts from warmer to cooler areas [11–12]; riparian areas are already used as movement corridors for both riparian and upland species [24–26], and those spanning climatic gradients may offer particularly effective conduits for range migration, particularly across flat, degraded landscapes [27]. The effectiveness of such corridors would be further enhanced by high levels of canopy cover and greater riparian area width, features that have been shown to increase wildlife use of riparian areas as movement corridors [25], and to help moderate temperatures within riparian areas and promote the resilience of neighboring aquatic systems [17, 28]. Riparian corridors with lower exposure to solar insolation may also feature cooler temperatures and greater moisture [13, 29], increasing their value as microclimatic refugia [30–32]. Finally, riparian corridors with lower levels of human modification are likely to be more permeable to wildlife movement [33], while also being less vulnerable to exotic species invasion and other stressors that may inhibit species movements and reduce refugia quality [34].

Because these characteristics are likely to vary by the scale of analysis, and because scales of climate-induced range shifts and microclimatic refugia are likely to vary among species and

over time [35,14], we developed a multi-scale approach to calculating riparian climate-corridor index values that incorporates results ranging in scale from local watersheds to the entire Pacific Northwest, USA. We also evaluated the protected status of riparian climate-corridors to help inform potential conservation action for maintaining riparian climate-corridor networks. Our analysis may thus provide critical information for guiding riparian management and climate adaptation efforts in the Pacific Northwest, while offering a novel approach that may be applied to similar efforts in other geographies.

Materials and methods

Study area

We completed our analysis for the Pacific Northwest, USA (USGS Water Resource Region 17; Fig 1). The Pacific Northwest includes a relatively cooler, moister region between the Pacific Coast and Cascade Range that is dominated by evergreen temperate forest; and a relatively drier region between the Cascade Range and Rocky Mountains that experiences more pronounced seasonality in temperature and features more diversity in vegetation types, from mixed forest at higher elevations to sagebrush-steppe in more arid lowlands.



Fig 1. Analysis extent. We completed our analysis for the Pacific Northwest hydrologic region (Water Resource Region 17, in dark gray).

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Analysis inputs

To identify high value riparian climate-corridors, we used a map of potential riparian areas identified by Theobald et al. [36], rather than a map of riparian vegetation. The potential riparian area map identifies the physical template where the dynamics of riparian vegetation are expected to occur, based on hydrological (stream discharge) and geomorphological (valley bottom shape) information rather than the (current) presence of riparian vegetation [36]. This 30 m data layer thus provides a comprehensive and consistent estimate of potential riparian area while avoiding many of the data gaps and inconsistencies [37] associated with existing maps of riparian vegetation derived from land cover (e.g., US LANDFIRE, US Fish & Wildlife Service National Wetland Inventory), which often have difficulty distinguishing riparian from non-riparian vegetation at 30 m resolution [37]. The potential riparian area dataset also provides key additional data layers (e.g., flow direction; see below) required by our analysis.

Our analysis aimed to identify the extent to which riparian corridors span large temperature gradients, have high levels of canopy cover, are relatively wide, have low exposure to solar radiation, and exhibit low levels of human modification. Our analysis thus included the following five variables (Table 1): mean annual temperature, canopy cover, riparian area width, potential relative radiation, and landscape condition.

We calculated mean annual temperature (T) as the 30-year mean of mean annual temperatures from 1961–1990, using a 90 m digital elevation model and the ClimateWNA tool [38], which extracts and downscales PRISM [39] monthly data and calculates climate variables for specific locations based on latitude, longitude, and elevation. For canopy cover (C), we used the percent tree canopy cover dataset for 2011 from the National Land Cover Dataset [40, 41]. We calculated potential riparian area (A), a measure of the width of potential riparian areas, directly from the 30 m potential riparian area data layer from Theobald et al. [36]. We used the 30 m National Elevation Dataset [42] to calculate potential relative radiation (R), a unitless measure of solar radiation that takes into account temporal changes in solar orientation as well as topographic shading from adjacent landforms [43]; such shading has been shown to contribute to lower temperatures in complex terrain [13–14]. We used the landscape condition (L) model [44] as a measure of the degree to which potential riparian areas have been affected by human activities. Although a more recent and higher-resolution dataset on human modification was available [45], we used L to be consistent with the Western Association of Fish and Wildlife Agencies Crucial Habitat Assessment Tool [46].

Table 1. Analysis variables and source data.

Analysis Variable	Base Layer	Base Layer Resolution	Year Represented by Base Layer	Base Layer Sources
Mean Annual Temperature (T)	PRISM Mean Annual Temperature (downscaled using Climate WNA)	90 m	1961–1990 (mean historical temperature)	Daly et al. [39] (http://prism.oregonstate.edu/), Wang et al. [38] (http://climatewna.com/)
Canopy Cover (C)	NLCD Percent Canopy Cover	30 m (resampled to 90 m using bilinear interpolation)	2011	National Land Cover Dataset [40]
Riparian Area (A)	Potential Riparian Area	90 m	2009 (digital elevation model)	Theobald et al. [36]
Potential Relative Radiation (R)	Potential Relative Radiation (calculated using digital elevation model)	30 m (resampled to 90 m using bilinear interpolation)	2009 (digital elevation model)	This study, following methods of Pierce et al. [43], and using a digital elevation model from the National Elevation Dataset (http://ned.usgs.gov/).
Landscape Condition (L)	Landscape Condition	270 m (resampled to 90 m using bilinear interpolation)	2010 (roads); 2006 (development); 2001 and 2006 (landcover)	Western Association of Fish and Wildlife Agencies Crucial Habitat Assessment Tool [46], based on the NatureServe Landscape Condition Model [44]

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Calculating a riparian climate-corridor index

We calculated an index of riparian climate-corridor quality for individual, ecologically-relevant spatial units that we call "potential riparian corridors," which we define as the potential riparian area that runs longitudinally along a stream/river from the stream outlet (or mouth) up through the hydrologic network of a watershed, ending at the stream initiation point (or headwater). For each potential riparian corridor, we calculated a riparian climate-corridor index using three main steps.

First, we accumulated the values of four variables (*C*, *A*, *R*, *L*) from locations (cells) within potential riparian areas laterally (i.e., orthogonal to the neighboring stream) to the nearest cell along the central flow path that follows the mid-line of streams/rivers (Fig 2a).

Second, we accumulated the values longitudinally along the central flow path within the stream/river, from its outlet to its headwater (Fig 2b). We accumulated values upstream rather than downstream to simulate the process of upward range movement along riparian corridors, from watershed outlets toward higher-elevation headwaters. Accumulating upstream also allowed us to calculate index values for individual riparian corridors adjacent to a stream/river reach running between its headwater and watershed outlet, because accumulating downstream would result in a single accumulated index value for an entire watershed. Third, we used these accumulated variable values to calculate an index of climate adaptation quality for the riparian climate-corridor from the outlet to headwater. Representing potential riparian corridors using a raster representation (rather than stream line vectors) allowed us to account for subtle gradients and variations within potential riparian areas—vital information lacking in previous

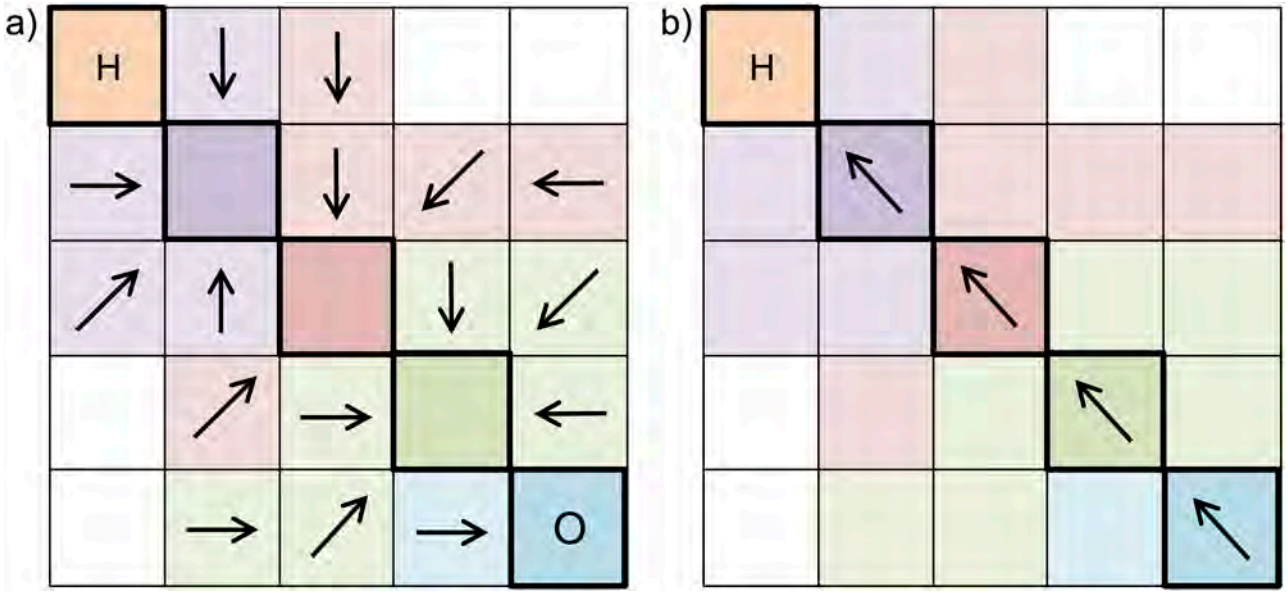

Fig 2. Using Flow Direction, Flow Accumulation, Flow Length tools to calculate the riparian climate-corridor index for a potential riparian corridor. a) For all potential riparian cells draining into a given cell in the streamline (outlined in bold, with it and all cells draining into it shown in the same color), we calculate, for each variable (*C*, *R*, *L*), the average value across the cells that contribute (accumulate) to the stream flow cell, and attribute this average value to the streamline cell (or the midline cell, for larger water bodies) using the Flow Direction and Flow Accumulation tools in ArcGIS. We calculate *A* as the number of potential riparian cells draining into the streamline cell. b) We then calculate, for each variable (*C*, *R*, *L*, *A*), the average value across all streamline cells from the outlet (O) to the headwater (H), and attribute this average value to the headwater using the Flow Length tool in ArcGIS. We also attribute a value for *T*, calculated as the absolute difference in temperature between the outlet and headwater cells. We then standardize (0–1) the average value for each variable (for equal weighting) and calculate the index, attributing this index value to the headwater cell. This is repeated for each downstream outlet until reaching the ocean, each time attributing the index value to the headwater cell. Each streamline cell is then given the average index value attributed to its upstream headwaters.

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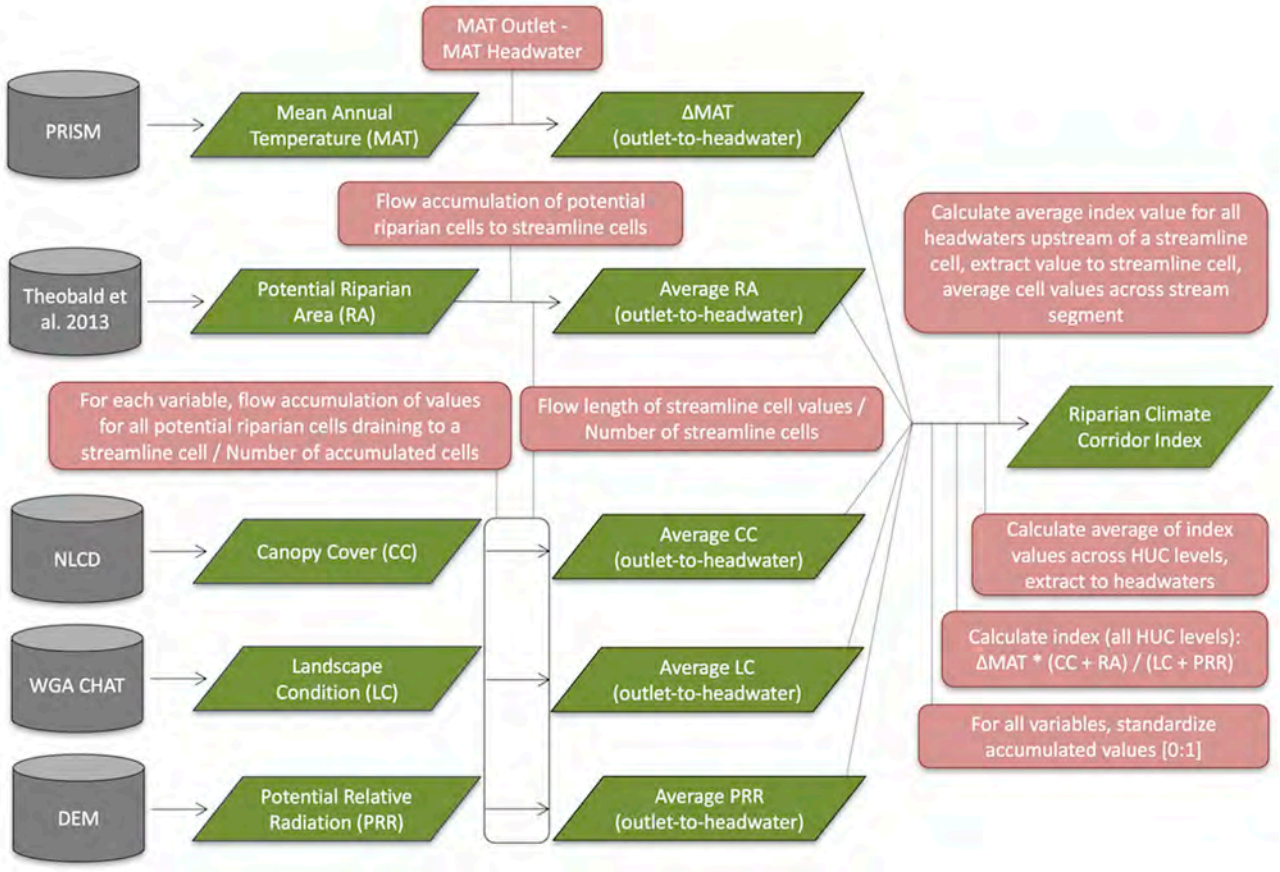

Fig 3. Summary of modeling approach, including key inputs, outputs, and analysis steps. Data sources are shown in gray, processing steps in pink, and inputs and outputs in green.

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studies. For rivers wider than 90 m, we excluded water cells when calculating variable values. Note that we represented spatial features, such as elevation and land cover, at 30 m resolution, but accumulated the up-scaled data at 90 m for computational purposes. A more detailed description of our analysis is provided below, and summarized in Fig 3.

1. Accumulate values within potential riparian corridors laterally to the stream line. We clipped the *C*, *R*, and *L* rasters to the extent of the potential riparian area. We then accumulated C, R, and L values along flow paths for all potential riparian cells draining into a given cell that represents the center of the stream line (i.e. the central flow path). That is, each cell located along the central flow path was attributed with the sum of the values for that variable for all the potential riparian cells that drain into it, using hydrologic tools in ArcGIS v10 software [47]. We then divided the accumulated value for each variable by the number of accumulated cells, so that, for each variable, each central flow path cell in the adjacent stream/river was ultimately attributed with the average variable value for its contributing potential riparian cells. The flow-accumulated area for the potential riparian area (*A*) was calculated in a similar manner, by accumulating the number of potential riparian cells draining into each central flow path cell in the adjacent stream/river. In cases where no potential riparian area cells drained into a central flow path cell, values for each variable were measured for only the central flow path cell itself, which was given an *A* value of 1.

2. Accumulate values for each variable longitudinally from stream/river outlet to headwater. We accumulated values along individual streamlines running from the watershed outlet to a stream's headwater, for each of the four variables (*C*, *A*, *R*, *L*). These accumulated values were then extracted to the central flow path cell at the stream/river's headwater, and divided by the number of contributing central flow path cells, to provide an average value for each variable for the associated potential riparian corridor. Mean annual temperature (*T*) was also extracted at each watershed outlet (or sink, in the case of closed basins) and for each headwater, and the difference between the two calculated and extracted to each stream/river's headwater. The average value for each variable was then divided by the largest value for that variable within the full study region, to standardize values to the range 0:1.

3. Calculate riparian climate-corridor index for each watershed-scale riparian corridor. We used the averaged, standardized values for each variable to calculate a Riparian Climate-Corridor Index for each watershed-scale riparian corridor, using the following formula:

$$Riparian\ \ Climate - Corridor\ \ Index = \Delta T \times [(C + A)/(R + L)]$$

Index values will thus be highest for those riparian corridors with the largest change in temperature (*T*) from outlet to headwater, highest percent canopy cover (*C*), greatest width (*A*), lowest exposure to solar radiation (*R*), and lowest level of human modification (*L*). Where ΔT was negative (indicating a higher temperature at the headwater than at the outlet), the index value was set to 0, to maintain higher index values for corridors leading from warmer to cooler areas across scales (see description of multi-scale approach, below). Our analysis is thus similar to other climate-gradient corridor approaches [11–12] in that it prioritizes corridors connecting warm areas to cool (in this case, headwater and outlets) using pathways that follow monotonic gradients (i.e., moving along gradients in only one direction, from warm to cool). All index values were extracted to the headwater associated with each potential riparian corridor.

4. Account for scale effects. We calculated a multi-scale, riparian climate-corridor index using the above procedure for riparian corridors within 6th, 5th, 4th, 3rd, 2nd, and 1st field HUCs (i.e., nested watersheds, from smallest to largest, respectively). HUCs are hierarchical hydrologic unit codes (HUC) assigned to all watersheds in the US [48]; the watershed cataloguing system nests watersheds into progressively larger units, similar to Pfafstetter codes that are also used globally. Our method should thus be applicable to any similar watershed cataloguing system in other countries. This procedure resulted in up to six index values being extracted to each headwater, corresponding to the index values of progressively longer downstream potential riparian corridors adjacent to each stream/river from its headwater to its outlet for progressively larger watersheds, eventually terminating at the ocean (or sink, in the case of closed basins). We scaled each of these nested index values to the range (0:1) and averaged them (equally-weighted), so that the final index value extracted to each headwater would reflect the climate adaptation value of all of its downstream riparian corridors. Finally, we calculated, for each individual central flow path cell within streams/rivers, the average of the index values attributed to all of its upstream headwaters. The final index values for each flow path cell within streams/rivers thus reflect the degree to which its adjacent potential riparian area cells are expected to help facilitate range shifts and provide refugia, from local to regional scales.

We also calculated a measure of riparian climate-corridor quality for entire watersheds by calculating the average of index values for all riparian climate-corridors within a given HUC. To account for differences in index values among ecoregions, and to more easily identify the highest quality riparian climate-corridors within each ecoregion, we binned all index values into 5 equal-area quintiles within each Level III ecoregion [49].

GAP analysis and sensitivity testing

We evaluated the degree to which high-value riparian climate-corridors identified by our analysis fall within currently designated protected areas by measuring the GAP status of riparian climate-corridors within 1) the top quintile of index scores, 2) the top two quintiles, and 3) all quintiles, for both the entire Pacific Northwest and within ecoregions. GAP status codes are provided by the US Geological Survey's Gap Analysis Program (GAP), and measure the degree to which lands in the US are managed for conservation [50]. Code 1 and 2 denote the highest degree of management for conservation (and meet the IUCN definition of protected), while Code 3 is given to lands that support multiple uses, including resource extraction. Code 4 lands are unprotected or have unknown management intent.

We also tested the sensitivity of the riparian climate-corridor index to the inclusion of individual input variables by removing individual variables one at a time, re-calculating the index, and measuring resulting differences across the study area. We also calculated correlation coefficients among these index values, as well as correlation coefficients among individual variables, to aid in interpretation of results.

Results

Riparian climate-corridor index values

We found that the climate adaptation potential of riparian corridors varies considerably, both across the Pacific Northwest (Fig 4) and within individual watersheds (Fig 5). Index values ranged from 0 to 0.83 (Fig 6), with the highest index values found in mountainous areas (e.g., the Cascade Range), and the lowest index values found in relatively flat, lowland regions such as the Columbia Plateau. Mountainous areas exhibited higher ΔT scores, on average, as well as higher canopy cover (C), solar insolation (R), and landscape condition (S1–S4 Figs). These effects were amplified by positive correlations among all input variables but riparian area (S5 Fig): relatively flat areas with low ΔT tended to also have lower canopy cover (C), were in poorer landscape condition (L), and had higher solar insolation (R). Indeed, removing ΔT from the index calculation resulted in a spatial pattern similar to that seen when the calculation included ΔT (Fig 7); including ΔT generally reinforced the pattern of lower values in areas with gentler topographic relief (often near outlets) and higher values in mountains (often near headwaters).

Most potential riparian corridors had relatively low index values (Fig 6). The relatively high number of potential riparian corridors with index values equal to 0 is due in large part to the relatively cool temperatures of the Pacific Northwest coast; many interior headwaters have warmer mean annual temperatures than their streams' coastal outlets. Because negative ΔT values were converted to zero and ΔT is multiplied by the rest of the index, such potential riparian corridors receive a zero value, though they may otherwise be of high quality (Fig 7). For example, the low index scores received by otherwise high-quality riparian areas in the western Olympic Peninsula were due to negative or relatively low ΔT between coastal stream outlets and headwaters (Fig 7, S1 Fig).

Areas with no headwaters (and thus no index scores) were seen in regions lacking surface water due to high aridity and/or high soil permeability (Fig 4).

GAP analysis and sensitivity testing

We found that riparian climate-corridors varied regionally in their level of protection (Fig 8). For riparian climate-corridors with the highest 20% of index scores, 35.5% were fully protected (GAP status 1–2) and 50.4% were partially protected (GAP status 3) across the Pacific

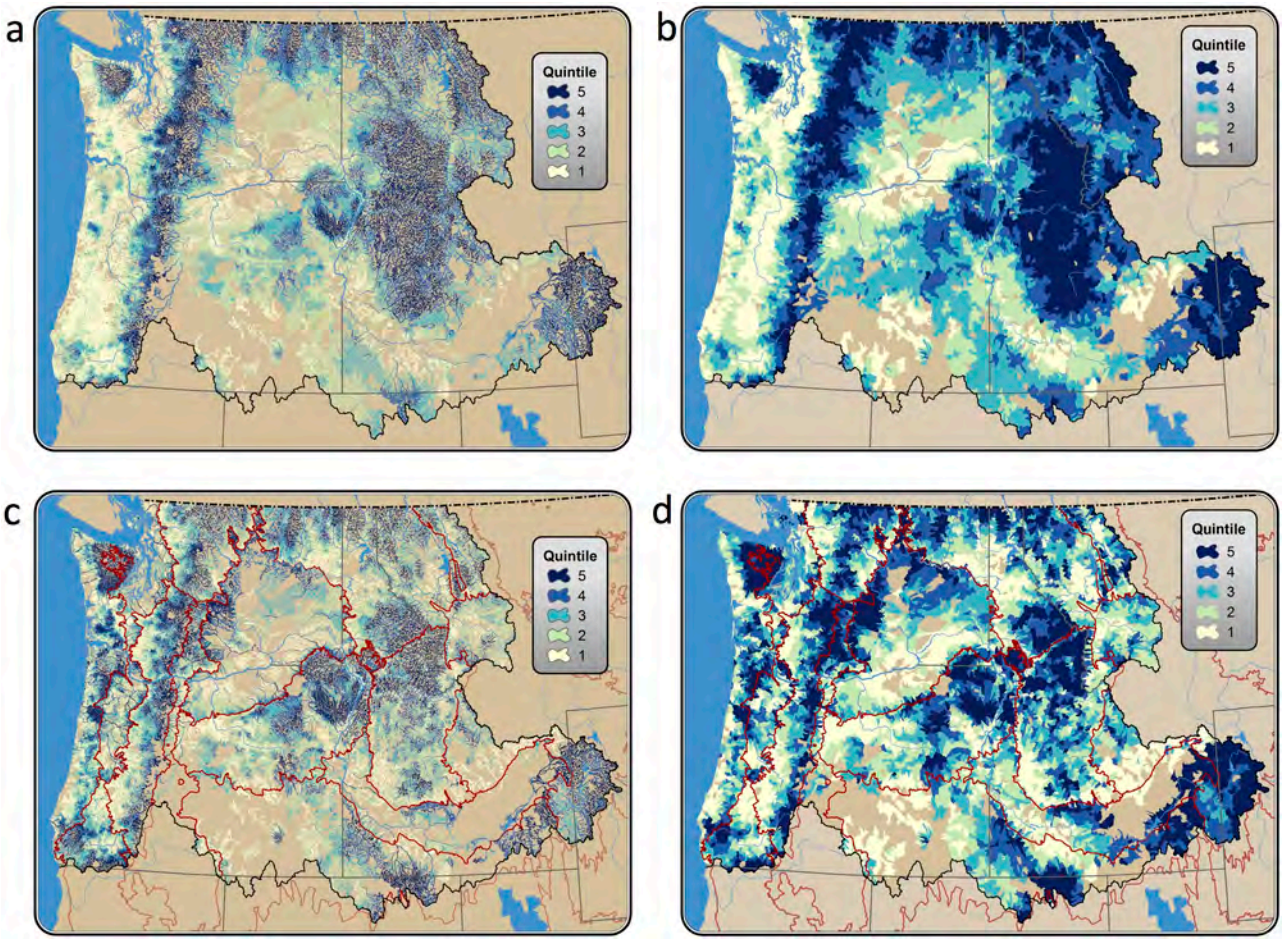

Fig 4. Riparian climate-corridor index values for the Pacific Northwest. Values are averaged across nested watershed scales (6th to 1st field HUCs), attributed to streamlines associated with potential riparian corridors. Values are shown by quintile for the Pacific Northwest, USA (panels a and b), and within ecoregions (panels c and d); and for both individual riparian corridors (panels a and c) and averaged across 6th field HUCs (panels b and d).

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Northwest. Within ecoregions, GAP status of riparian climate-corridors with the highest 20% of index scores varied from 83.8% fully protected and 14.6% partially protected in the North Cascades, to 1.3% fully protected and 18.8% partially protected in the Columbia Plateau.

We found that riparian climate-corridor index values were relatively insensitive to individual input variables (Fig 7). Removal of individual variables from the index calculation resulted in little change to index scores across the study area, resulting in an average change in index values of -0.0126 for removal of mean annual temperature (ΔT), +0.0051 for landscape condition (L), -0.0168 for canopy cover (C), -0.0607 for riparian area (A), and -0.1154 for potential relative radiation (R). Given the strong correlations among index variable values and elevation (i.e., that relatively flat areas with low ΔT also have lower canopy cover (C) and landscape condition (L), and higher solar insolation (R)), variable exclusion generally resulted in decreased values in mountainous areas and increased values in lower-elevation areas. Exclusion of R had a slightly stronger effect on index values in mountainous areas (lowering index values), and exclusion of T, C, and L had a slightly stronger effect on lower-elevation coastal areas (increasing values).

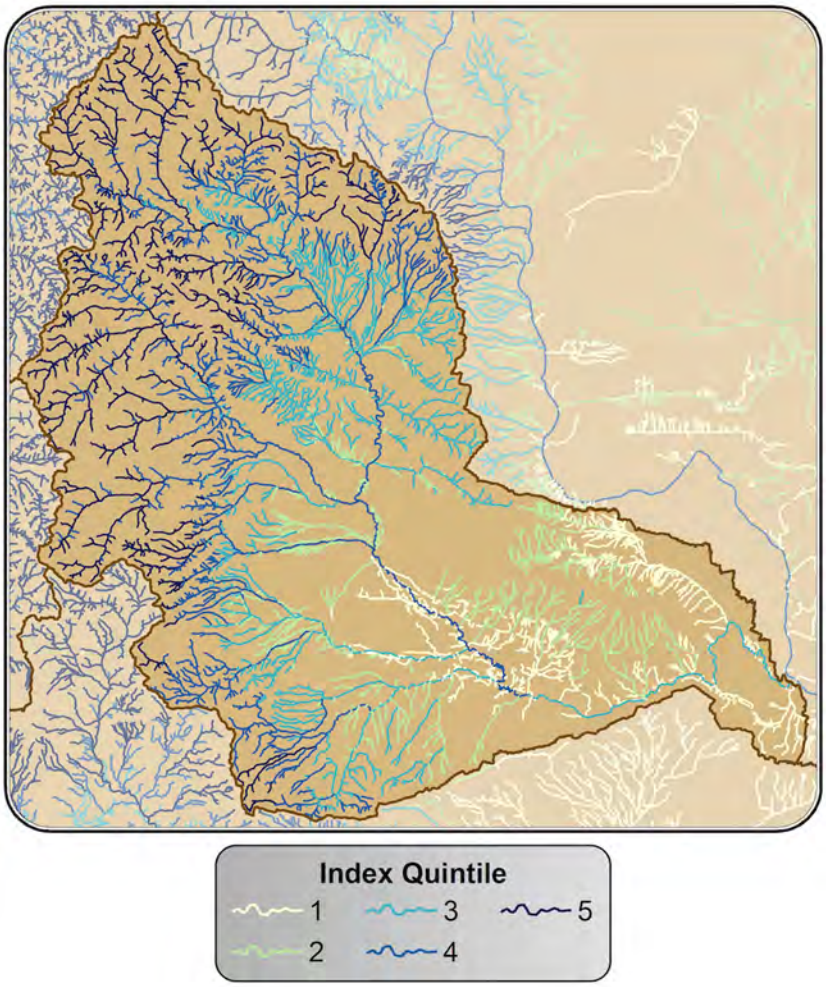

Fig 5. Riparian climate-corridor index values shown for an individual watershed. Values are shown by quintile and attributed to streamlines associated with potential riparian corridors.

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Discussion

Our analysis identified potential riparian corridors that span climatic gradients, have high canopy cover, low levels of solar exposure, low levels of human modification, and are relatively wide—characteristics expected to facilitate climate-induced range shifts and provide micro-climatic refugia. Not surprisingly, we found that potential riparian corridors in mountainous regions—which tend to be steep, forested, topographically shaded, and have low levels of human modification—had the highest riparian climate-corridor index values. We also found that potential riparian corridors in lowland areas—which tend to be flat and have low canopy cover, less topographic shading, and high levels of human modification—had the lowest values (Fig 4a and 4b). Because of the correlations of temperature with other variables, change in temperature—which we had expected to be a key variable for identifying riparian corridors with strong climatic gradients—in fact had a relatively modest impact on index scores (Fig 7), generally reinforcing the pattern of lower index values in areas with gentler topographic relief and higher values in mountains. The index is thus robust to our coarse approach to measuring temperature gradients along riparian corridors.

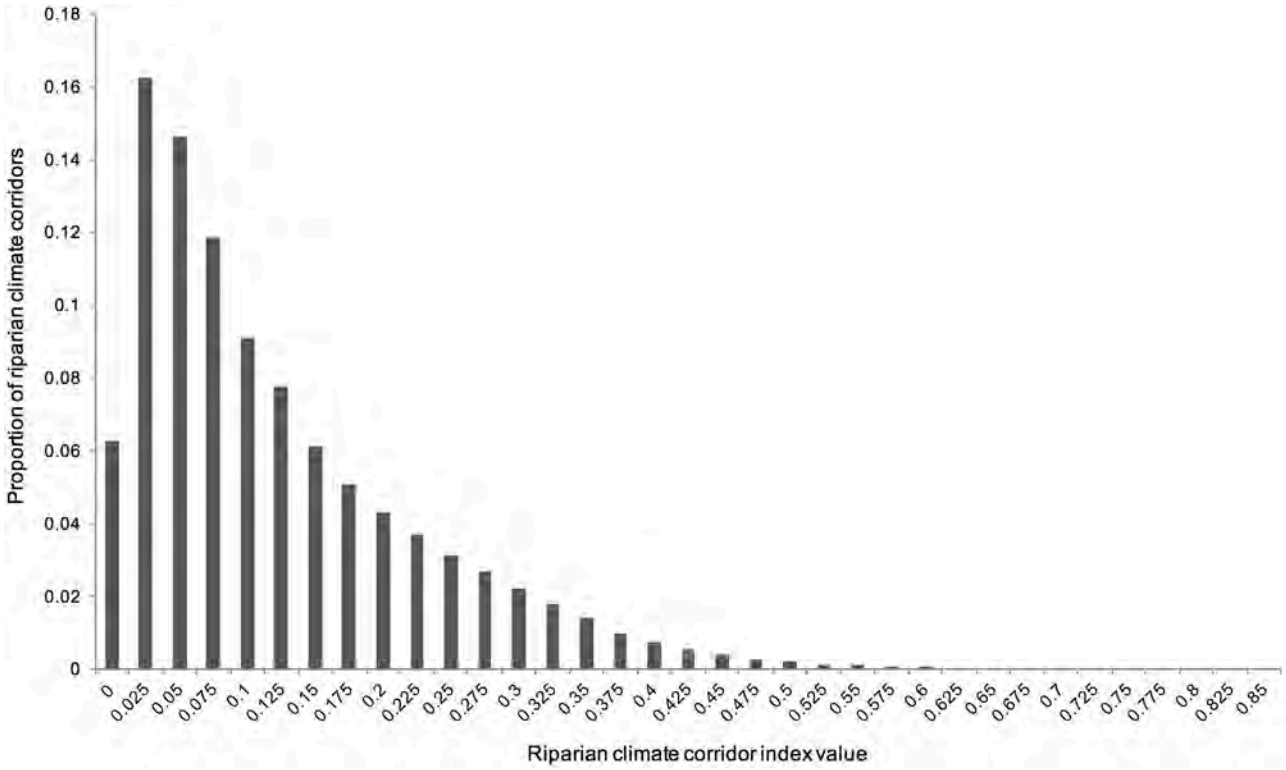

Fig 6. Distribution of riparian climate-corridor index values. Shown for all watershed-scale riparian corridors in the Pacific Northwest.

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We also found that relatively flat and highly modified ecoregions (e.g., the Columbia Plateau and Puget Lowlands ecoregions; Fig 4c and 4d) had the least protected high-scoring riparian climate-corridors among Pacific Northwest ecoregions (Fig 8). High-scoring riparian climate-corridors in these areas thus suggest immediate priorities for conservation action (e.g., protection or restoration), as they may provide some of the best adaptation opportunities in flat, highly modified landscapes that may limit species range movements and persistence in microclimatic refugia. We also found that a large number of otherwise high-quality potential riparian corridors along the coast received low index scores, because their interior headwaters have warmer mean annual temperatures than their streams' cooler, coastal outlets. These results emphasize that our index is designed to identify riparian climate-corridors expected to promote species range shifts from warmer to cooler areas, which may in some cases result in low scores for corridors that have high conservation value under static or current climates.

Index values for riparian climate-corridors along large rivers (e.g., the Columbia River) often had higher values than corridors within nearby lower-order streams (e.g., headwater streams). This is because higher-order streams frequently have tributaries at higher elevations; riparian climate-corridors associated with these higher-elevation tributaries tend to have relatively high index values, and the index values of riparian climate corridors along higher-order streams incorporate these upstream values. The high index values of riparian climate-corridors along higher order streams thus reflect their connectivity to high-scoring upstream corridors, and thus their capacity to promote range shifts and provide access to climatic refugia at a regional scale. Indeed, shorter riparian corridors, such as those that would be found along headwater streams, have been shown to be more effective at promoting species movements [51]. Thus, the trade-off of this multi-scale approach—designed to accommodate diverse

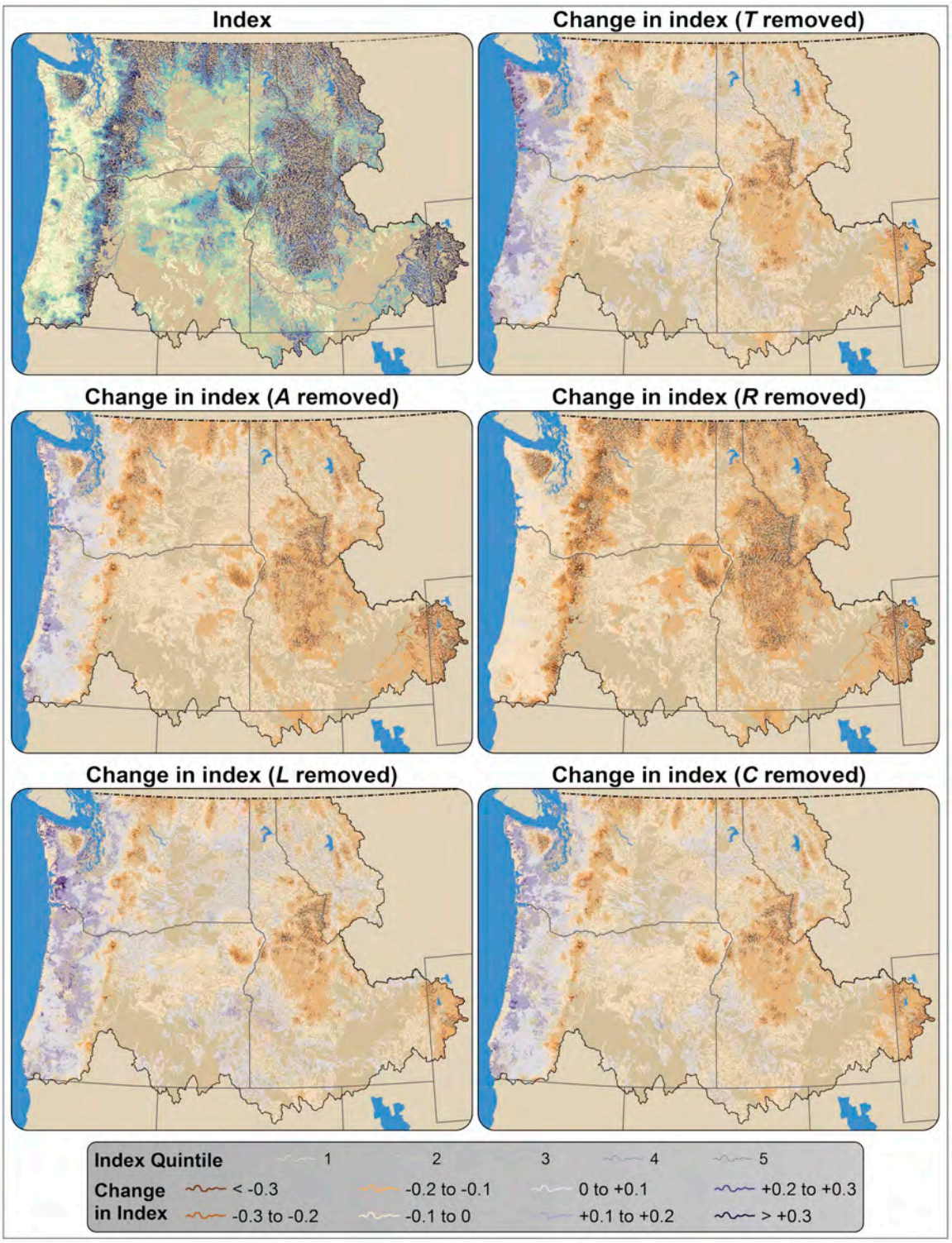

Fig 7. Sensitivity of riparian climate-corridor index values to individual analysis variables. Panels show the index with all variables included (top left), and the index with change in mean annual temperature (*T*) removed, with riparian area (*A*) removed, with potential relative radiation (*R*) removed, with landscape condition (*L*) removed, and with canopy cover (*C*) removed.

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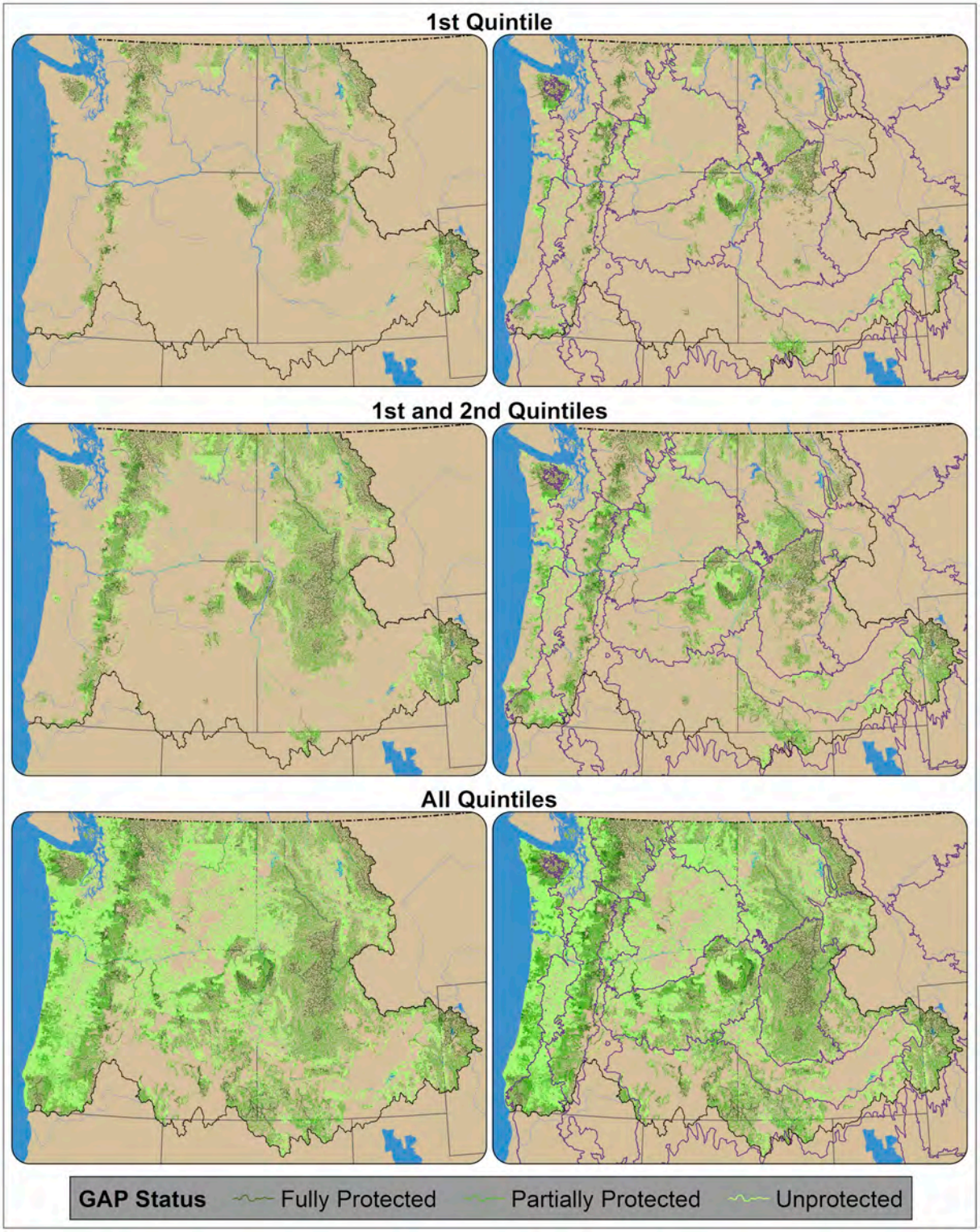

Fig 8. GAP status of riparian climate-corridors. GAP status is shown for riparian corridors within the top quintile of riparian climate-corridor index values (top row), top two quintiles (middle row), and all quintiles (bottom row); by both the entire Pacific Northwest (left column) and within ecoregions (right column). GAP status is shown for fully protected (GAP status 1 and 2; forest green), partially protected (GAP status 3; kelly green), and unprotected (GAP status 4; lime green) riparian climate-corridors.

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species with needs for movement and refugia at a range of scales—is its potential to overlook riparian climate-corridors that may be valuable at a more local scale, but do not meaningfully contribute to broader-scale, regional adaptation. Identifying riparian climate-corridors with high index values within ecoregions (Fig 4c and 4d) or local watersheds (S6–S10 Figs) may help address needs for more local-scale prioritization.

We recommend considering several caveats when applying the riparian climate-corridor index. First, this approach only indirectly accounts for connectivity along riparian corridors; while index values will decrease with increasing human modification along a corridor, the effect of local but severe movement barriers (e.g., towns, cliffs) on index values could be muted if human modification is low elsewhere along the corridor, particularly at broader scales. The analysis could thus be improved by incorporating explicit connectivity measures that sufficiently penalize high-resistance, local barriers that could sever connectivity; a range of connectivity modeling approaches could be adapted for this purpose (e.g., [52]). The analysis could also be improved by further validating analysis inputs and assumptions, such as empirically measuring canopy cover and solar insolation across riparian areas and testing their influence on temperature, and, ultimately, range shifts and refugia. Future comparison of our index to other indices of riparian quality (e.g., [53]) would also aid in interpretation of results. Thus, we recommend using this analysis as a means of identifying priority riparian areas for additional evaluation (e.g., field validation, comparison with other data sets, integration with other conservation values) before making decisions regarding conservation action.

We also recognize the scaling challenges in mapping riparian vegetation and modeling potential riparian areas. Our analysis provides estimates of potential riparian climate-corridors at (>90 m) due to data resolution and computation limitations. Future work can apply our approach using high resolution data that have (or will likely) become available. An additional caveat is the risk of unintended negative consequences (e.g., spread of invasive species or disease) by protecting or restoring riparian climate corridors to promote species movements. Our analysis reduces this risk by prioritizing those riparian areas that are in good condition, and therefore expected to be less vulnerable to invasion. Further, previous research has shown that the benefits of corridors outweigh potential negative effects [54], including potential risks related to climate-induced range shifts [55]. Indeed, the synergistic threats of habitat loss, fragmentation and climate change present an urgent need to restore landscape features such as riparian corridors that have historically provided natural conduits for species movement.

Although riparian areas are expected to provide critical movement corridors and refugia under climate change [6–7,9], they are also among the most threatened habitats in many regions [56]. Our analysis offers a first step toward identifying, for large regions, those riparian areas most likely to promote species' ability to respond to climate change, as well as those that may be most vulnerable to climate change and in need of restoration measures. Such information may offer valuable guidance for future investments in riparian protection and restoration as part of climate adaptation efforts.

Supporting information

S1 Fig. Mean annual temperature (*T*), based on the 30-year mean of mean annual temperatures from 1961–1990, using a 90 m digital elevation model and the ClimateWNA tool [34], which extracts and downscales PRISM [35] monthly data and calculates climate variables for specific locations based on latitude, longitude, and elevation.
(TIFF)

S2 Fig. Canopy cover (*C*), based on the percent tree canopy cover dataset from the National Land Cover Dataset [36].
(TIFF)

S3 Fig. Potential relative radiation (*R*), a unit-less measure of solar radiation that takes into account temporal changes in solar orientation as well as shading effects from neighboring topography [38], based on a 30 m digital elevation model from the National Elevation Dataset [36].
(TIFF)

S4 Fig. Landscape condition (*L*), provided by the Western Governors' Association's Crucial Habitat Assessment Tool (WGA 2013) as a measure of the degree to which potential riparian areas have been affected by human activities using the landscape condition model [39], where higher values correspond to lower landscape intactness.
(TIFF)

S5 Fig. Riparian area (*A*), based on the potential riparian area data layer from Theobald et al [32].
(TIFF)

S6 Fig. Riparian climate-corridor index values averaged across individual watersheds (6th field HUCs).
(TIFF)

S7 Fig. Riparian climate-corridor index values averaged across individual watersheds (5th field HUCs).
(TIFF)

S8 Fig. Riparian climate-corridor index values averaged across individual watersheds (4th field HUCs).
(TIFF)

S9 Fig. Riparian climate-corridor index values averaged across individual watersheds (3th field HUCs).
(TIFF)

S10 Fig. Riparian climate-corridor index values averaged across individual watersheds (2nd field HUCs).
(TIFF)

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Methodology: Meade Krosby, David M. Theobald, Robert Norheim, Brad H. McRae.

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Writing – original draft: Meade Krosby, David M. Theobald.

Writing – review & editing: Meade Krosby, David M. Theobald, Robert Norheim, Brad H. McRae.

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Gene flow and pathogen transmission among bobcats (*Lynx rufus*) in a fragmented urban landscape

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Abstract

Urbanization can result in the fragmentation of once contiguous natural landscapes into a patchy habitat interspersed within a growing urban matrix. Animals living in fragmented landscapes often have reduced movement among habitat patches because of avoidance of intervening human development, which potentially leads to both reduced gene flow and pathogen transmission between patches. Mammalian carnivores with large home ranges, such as bobcats (*Lynx rufus*), may be particularly sensitive to habitat fragmentation. We performed genetic analyses on bobcats and their directly transmitted viral pathogen, feline immunodeficiency virus (FIV), to investigate the effects of urbanization on bobcat movement. We predicted that urban development, including major freeways, would limit bobcat movement and result in genetically structured host and pathogen populations. We analysed molecular markers from 106 bobcats and 19 FIV isolates from seropositive animals in urban southern California. Our findings indicate that reduced gene flow between two primary habitat patches has resulted in genetically distinct bobcat subpopulations separated by urban development including a major highway. However, the distribution of genetic diversity among FIV isolates determined through phylogenetic analyses indicates that pathogen genotypes are less spatially structured—exhibiting a more even distribution between habitat fragments. We conclude that the types of movement and contact sufficient for disease transmission occur with enough frequency to preclude structuring among the viral population, but that the bobcat population is structured owing to low levels of effective bobcat migration resulting in gene flow. We illustrate the utility in using multiple molecular markers that differentially detect movement and gene flow between subpopulations when assessing connectivity.

Keywords: carnivores, disease ecology, gene flow, habitat fragmentation, microsatellites, viral phylogenetics

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Introduction

Habitat loss and degradation are the leading causes of species declines around the world (http://www.iucnredlist.org/). Urbanization, an extreme form of habitat degradation, results in immediate displacement of wildlife from developed areas, followed by the increasing isolation of groups of animals confined to shrinking natural areas (McKinney 2002; McDonald *et al.* 2008). A common effect of urbanization is the fragmentation of once contiguous landscapes into smaller patches of non-contiguous habitat.

Maintaining functional connectivity, the extent to which organisms and genetic material move between

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habitat patches, can be essential for population persistence in fragmented landscapes (Crooks & Sanjayan 2006). Reduced functional connectivity between habitat patches can result in physically and genetically isolated subpopulations prone to inbreeding and to the loss of genetic diversity through genetic drift (Frankham 2006). However, measuring functional connectivity can be difficult, especially for cryptic solitary species such as large carnivores (Crooks 2002). One commonly used method of evaluating functional connectivity involves characterizing patterns of gene flow using molecular markers to evaluate the distribution of genetic diversity within and among groups of individuals (Frankham 2006; Balkenhol & Waits 2009; Ruell *et al.* in press). Populations with high connectivity should exhibit homogenous distributions of genetic diversity. Populations with low connectivity will be genetically structured, exhibiting localized variations in genetic diversity as a consequence of reduced gene flow among isolated groups of individuals.

Microsatellites are neutral heritable molecular markers commonly used to evaluate genetic structure, and hence connectivity, among natural populations (Avise 2004; Hedrick 2005a). These polymorphic, codominant markers provide a powerful means for assessing gene flow. However, microsatellite markers only reflect individual movement within structured populations if a migrant is sampled or if a migrant successfully reproduces and at least one offspring is sampled. Transient movements between subpopulations, or migrants that do not reproduce, may not be detected by analysing microsatellites (Riley *et al.* 2006). Therefore, while powerful, host genetic markers may not accurately characterize connectivity when individual movements do not result in gene flow.

Because directly transmitted obligate pathogens are inextricably linked to their hosts, pathogens can serve as alternative or additional markers for studies of wildlife population dynamics (Nieberding & Olivieri 2007; Liu *et al.* 2008). Feline immunodeficiency virus (FIV), a retrovirus that naturally infects many felid species (Troyer *et al.* 2005; Vandewoude & Apetrei 2006), has many characteristics that render it potentially useful as a marker of population dynamics in wild cats. First, the mutation rate of FIV is significantly faster than that of host genetic markers (approximately $\mu = 1$–3% every 10 years in mountain lions) (Biek *et al.* 2003). Also, infection with FIV is life-long because an obligatory step in viral replication involves the permanent insertion of a copy of the viral genome into the host's chromosomal DNA. Therefore, FIV genotypes have the capacity to serve as life-long molecular markers for each infected individual. Furthermore, the virus cannot be transmitted by insect vectors, nor is it stable in the environment, and thus, transmission events are indicators of direct contact between individuals.

Finally, the strains of FIV, which infect domestic cats, are genetically distinct from the strains isolated from wild felids. The domestic cat strains have never been documented to infect nondomestic felids in the wild, and therefore, the genetic diversity of FIV among nondomestic felids is only influenced by the distribution, movement and contact rates among conspecifics across the landscape.

Indeed, previous studies have demonstrated that patterns of FIV relatedness closely reflect the geographical distribution of bobcats, mountain lions and African lions at various geographical scales (Biek *et al.* 2006; Franklin *et al.* 2007a; Antunes *et al.* 2008). Specifically, Franklin *et al.* (2007a) demonstrated that the FIV isolates infecting bobcats north and south of Los Angeles, CA are genetically distinct, having diverged since the isolation of the two host populations. Because of these characteristics, viral genetic analyses may provide novel and powerful techniques for assessing connectivity and population structure with improved resolution, supplementing that which is currently possible using host genetic markers.

Bobcats (*Lynx rufus*), with large home ranges and high resource requirements, are susceptible to the effects of habitat loss and fragmentation in urbanizing systems (Crooks 2002; Riley *et al.* 2003, 2006, 2010). We investigated patterns of genetic diversity among bobcats and FIV isolates from a fragmented landscape in southern California to evaluate how urbanization affects connectivity among bobcats in this region. We specifically evaluated the extent to which several large freeways, and the developed areas surrounding them, are barriers to gene flow and pathogen transmission between habitat patches. We predicted that decreases in connectivity would lead to significant genetic structure among both host and pathogen populations. We performed standard population genetics analyses using 16 unlinked microsatellite loci from 106 bobcats. We also constructed phylogenetic trees to assess patterns of relatedness among FIV isolates from 19 of these individuals infected by the virus.

Our findings, presented below, demonstrate that two spatially structured, genetically distinct bobcat subpopulations exist. However, the pathogen phylogeny revealed no association between FIV relatedness and bobcat population structure, suggesting movements, contacts and disease transmission between subpopulations continue despite very low levels of host gene flow. This finding was inconsistent with our hypothesis that decreased gene flow among bobcats would lead to similar genetic structure among the virus population. However, these results are consistent with other studies that have found major roads and urban development to

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be more permeable to transient bobcat movements than to effective migration, allowing for the potential movement of pathogens in the absence of gene flow (Riley *et al.* 2006; Ruell *et al.* in press). We illustrate the utility in using multiple molecular markers, each with different determinants of movement throughout populations, to assess complex questions of connectivity.

Methods

Location and field sampling

This study was located south and west of Los Angeles, CA and included four habitat patches divided by three large freeways—Interstate-5 (I-5), the Riverside Freeway (SR-91) and the San Joaquin Hills Transportation Corridor (SR-73) (Fig. 1). I-5 through this region was constructed from 1944 to 1958 and has an average annual daily traffic volume (AADT) of ~262 000 cars per day (California DOT 2009). SR-91 was originally completed in 1971 and underwent a major expansion in 1995. The AADT of this freeway is ~264 000 cars per day (California DOT 2009). SR-73 was constructed in 1996 and has an AADT of ~73 000 cars per day (California DOT 2009). Aside from these roads and adjacent urban development, the only potential natural barrier to bobcat movement is the Santa Ana River, which flows about 100 m to the north of SR-91. No other natural barriers to gene flow (i.e. major mountain ranges) exist between these habitat patches, which are primarily characterized by chaparral, coastal scrub and grassland vegetative communities.

A total of 106 bobcats were included in this study. The majority of bobcats ($n = 75$) were live-captured between December 2002 and March 2009 using wire cage traps baited with visual and odour attractants (Lyren *et al.* 2006, 2008a,b). Animals were anesthetized, and blood samples were collected. Animals were captured, sampled and released with permission of cooperating agencies after approval by all appropriate animal care and use committees. The remaining individuals ($n = 31$) were opportunistically sampled postmortem; when possible, heart blood clots, thoracic fluid, ear punch and hair samples were collected from these bobcats. Blood and tissues were stored at USGS facilities in Irvine, CA, and aliquots were sent to Colorado State University for analysis as described below.

Putative subpopulation assignments

Bobcats were assigned to one of four putative subpopulations based on the GPS coordinates of the capture or road kill location relative to freeways I-5, SR-91 and SR-73 (Fig. 1). These three freeways were the focus of our investigation because they completely traverse the study area (i.e. animals cannot move between habitat fragments without crossing one of these freeways), and these roads represent a gradient of permeability to bobcat movements based on previous studies [see discussion and also Lyren *et al.* (2008a,b)]. The San Joaquin Hills west subpopulation [SJH-west ($n = 29$)] was located between the coast and SR-73, which merges with I-405 to the north and I-5 to the south. The San Joaquin Hills east subpopulation [SJH-east ($n = 20$)] included individuals sampled between SR-73 and I-5. The North Irvine Ranch [NIR ($n = 44$)] subpopulation comprised individuals captured east of I-5 and south of SR-91, whereas the Chino Puente Hills [CPH ($n = 12$)] subpopulation consisted of individuals captured east of

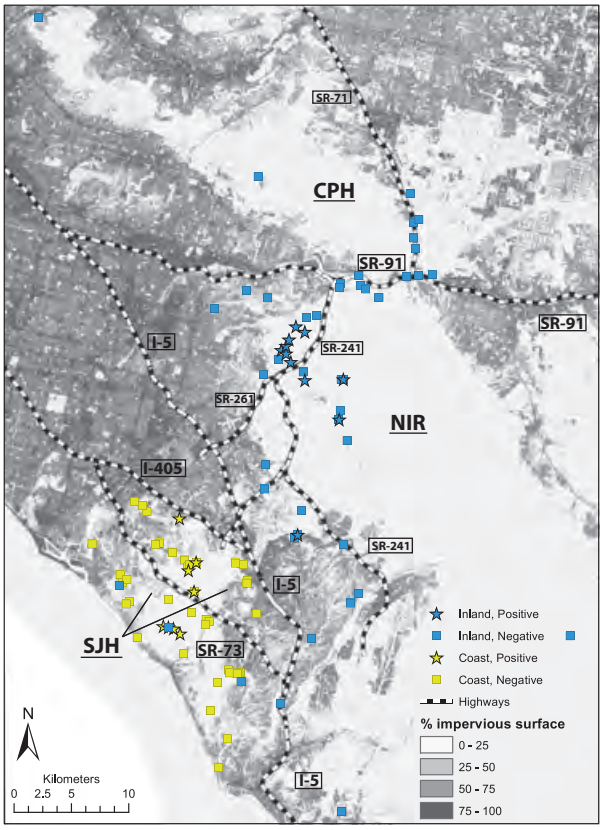

Fig. 1 Map of study locations southeast of Los Angeles, California. GPS capture locations of 105 bobcats indicated by squares [feline immunodeficiency virus (FIV) negative] or stars (FIV positive). Blue or yellow fill of each symbol represents the genetic assignment of an individual to an inland (east of I-5) or coastal (west of I-5) subpopulation, respectively (see Fig. 2). The a priori assignment of individuals to putative subpopulations (SJH-W: San Joaquin Hills West; SJH-E: San Joaquin Hills East; NIR: North Irvine Ranch; CPH: Chino Puente Hills) was based on the capture location of bobcats relative to the focal roads SR-73, I-5 and SR-91, which were investigated as potential barriers to gene flow. Degree of urban development (% impervious surface) is represented by grey shading.

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I-5 and north of SR-91. One individual did not have a recorded capture location, and thus, it was not included in analyses that required the above subpopulation assignments. The following population genetics analyses were, except where noted, performed using this a priori assignment of individuals to putative subpopulations and the multilocus microsatellite genotype data for each individual.

Genotyping microsatellites

Bobcat genomic DNA was extracted from whole blood, peripheral blood mononuclear cells (PBMCs) or tissue using QIAamp® DNeasy blood and tissue kit (Qiagen Inc., Valencia, CA, USA). Seventeen microsatellite loci (Table 1) were amplified using primer pairs for polymerase chain reaction (PCR) developed by Menotti-Raymond *et al.* (1999): FCA008, FCA023, FCA026, FCA031, FCA043, FCA045, FCA077, FCA090, FCA096, FCA132, FCA149, FCA559; Menotti-Raymond *et al.* (2005): FCA740, FCA742; and Faircloth *et al.* (2005): BCE5T, BCD8T, BCG8T. Primers BCE5T and BCG8T were modified to contain the M-13 sequence instead of the CAG sequence as published. We selected these primer pairs from the above publications based on the following criteria: longer repeat units, efficiency of amplification and maximal heterozygosity. The 5′ end of the forward primer of each primer pair was modified with a 16-bp tail comprising the M-13 sequence (5′–GTA AAA CGA CGG CCA G–3′). Reverse primers were not modified. All microsatellite PCR products were fluorescently labelled using a second forward primer consisting of the above M-13 sequence with 6-FAM on the 5′ end.

PCR methodologies were adapted from Boutin-Ganache *et al.* (2001) and Riley *et al.* (2006). PCR reaction conditions included 94 °C for 3 min followed by 22 cycles of (94 °C for 30 seconds; 59 °C for 30 seconds; and 72 °C for 45 seconds), followed by 10 cycles of (94 °C for 30 seconds; 53 °C for 30 seconds; and 72 °C for 45 seconds), and a final cycle of 72 °C for 10 min. Randomly selected PCR products as well as the negative control for each reaction were visualized under UV light using gel electrophoresis with ethidium bromide in 2% agarose gel to confirm the presence of amplicons of appropriate length. Precise PCR product fragment lengths were determined using an ABI 3730xl DNA Analyzer and Peak Scanner 1.0 software (Applied Biosystems, Foster City, CA, USA). PCR and genotyping were repeated in ten per cent of randomly chosen bobcat samples for each microsatellite locus to confirm genotypes and prevent scoring errors. All duplicated genotypes were consistent with the primary analysis, demonstrating a high degree of assay reproducibility and reducing the likelihood of genotyping errors owing to false alleles or allelic dropout.

Table 1 Characterization of 17 microsatellite loci in 106 bobcats

Locus	Size range	No. of alleles	Repeat	Chromosome	H_O	H_E	PIC	References
FCA008	140–156	8	di	A1	0.71	0.77	0.73	1
FCA023	144–158	6	di	B1	0.67	0.72	0.67	1
FCA026*	138–166	13	di	D3	0.79	0.83	0.81	1
FCA031	237–255	8	di	E3	0.78	0.80	0.77	1
FCA043†	131–139	5	di	C2	0.78	0.73	0.68	1
FCA045*	147–173	7	di	A1	0.63	0.83	0.81	1
FCA077†	130–140	6	di	C2	0.77	0.74	0.70	1
FCA090*	108–126	7	di	A1	0.41	0.52	0.48	1
FCA096	189–209	8	di	A2	0.80	0.77	0.75	1
FCA132*	182–194	7	di	D3	0.66	0.78	0.74	1
FCA149	133–149	9	di	B1	0.76	0.78	0.75	1
FCA559	115–135	6	tetra	B1	0.64	0.67	0.60	1
FCA740	333–353	6	tetra	C1	0.84	0.79	0.76	2
FCA742	104–134	7	tetra	D4	0.65	0.67	0.61	2
BCD8T	156–180	5	tetra	Unknown	0.21	0.21	0.20	3
BCE5T	256–280	7	tetra	Unknown	0.70	0.75	0.71	3
BCG8T	275–299	11	di	Unknown	0.73	0.78	0.74	3

H_O, observed heterozygosity; H_E, expected heterozygosity; PIC, polymorphic information content.
*Null alleles may exist in one subpopulation.
†FCA077 and FCA 043 were found to be in linkage disequilibrium; FCA043 was not used in population genetics analyses.
References: (1) Menotti-Raymond *et al.* (1999); (2) Menotti-Raymond *et al.* (2005); and (3) Faircloth *et al.* (2005).

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Validating and characterizing microsatellite data

Microsatellite data were screened for genotyping errors because of stuttering, null alleles and large allele dropout at all loci in MICROCHECKER 2.2.3 (Van Oosterhout *et al.* 2004). There was no evidence of errors because of stuttering or large allele dropout at any loci. The following three loci showed evidence of null alleles when testing across all individuals with no subpopulation information: FCA045, FCA090 and FCA132. The null alleles at these loci correspond to NIR (FCA045 and FCA090) and SJH-west (FCA132) when the same analysis was run with a priori subpopulation assignments.

Tests for linkage disequilibrium among loci were performed in GENEPOP 4.0 (Raymond & Rousset 1995; Rousset 2008). The results for linkage disequilibrium varied greatly between subpopulations with seven significant tests in SJH-west (120 total tests; $\alpha = 0.009313$), four significant tests in SJH-east (120 total tests; $\alpha = 0.009313$), two significant tests in NIR (136 total tests; $\alpha = 0.009102$) and one significant test in CPH (104 total tests; $\alpha = 0.009567$). Loci FCA077 and FCA043 were in linkage disequilibrium in all four putative subpopulations, and therefore, FCA043 was eliminated from further analyses.

Hardy–Weinberg equilibrium probabilities were calculated using GENEPOP 4.0 (Raymond & Rousset 1995; Rousset 2008). Three of four subpopulations significantly deviated from Hardy–Weinberg equilibrium at one unique locus: FCA023 in SJH-west (15 tests; $\alpha = 0.015068$), FCA045 in NIR (16 tests; $\alpha = 0.014790$) and BCE5T in CPH (16 tests; $\alpha = 0.014790$). The remaining loci in each subpopulation did not deviate from HW equilibrium, and therefore, all subpopulations were assumed to be in HW equilibrium. Observed and expected heterozygosity and the polymorphic information content (PIC) for each locus were determined using the program CERVUS 3.0 (Table 1) (Kalinowski *et al.* 2007).

Assessment of population structure

Population differentiation based on allele frequencies was calculated for each pair of putative subpopulations using GENEPOP 4.0 (96 tests; $\alpha = 0.0097$) (Raymond & Rousset 1995; Rousset 2008). Allelic richness, estimated using rarefaction to avoid bias caused by differences in sample size (Leberg 2002), was calculated for each putative subpopulation using FSTAT 2.9.3.2 (Goudet 1995). Allelic richness results were confirmed to be normally distributed using a Ryan Joiner Test in Minitab Student Version 14.11.1 (Ryan Joiner test; $P > 0.1$). Analysis of variance (ANOVA) was used to determine whether allelic richness differed significantly between subpopulations ($\alpha = 0.05$). Estimates of subpopulation differentiation (D_{est}) were calculated using the online program Software for Measurement of Genetic Diversity (Jost 2008; Crawford 2010). Fst values were calculated in FSTAT (Goudet 1995). The use of F_{ST} values as measures of population differentiation has recently been criticized (Hedrick 2005b; Jost 2008). Therefore, we include them here as supplemental information only to allow a general comparison among similar, previously published studies (Table S1, Supporting information).

Bayesian clustering in program STRUCTURE 2.3.3 was used to infer the number of genetically distinct subpopulations (K) and to assign each individual to the subpopulation with which they share the highest genetic similarity. Parameters were set to include 50 000 burn-in and 500 000 Markov Chain Monte Carlo iterations (Pritchard *et al.* 2000). Data were first analysed without a priori source population information for individuals. Independent allele frequencies among subpopulations and genetic admixture were included as parameters so as not to introduce an upward bias in the estimation of K (Pritchard *et al.* 2000). This analysis was repeated five times for each K to verify the consistency of likelihood values between runs. K was varied from $K = 1$ to 5, representing a range of greater than expected K values to ensure our analysis included all ecologically plausible values of K.

This was followed by additional analyses with the data set divided into two groups: coastal animals (SJH-west and SJH-east) and inland animals (NIR and CPH) to more closely evaluate possible substructure within each of these two groups (Pritchard *et al.* 2010). The parameters of this model were the same as above, with each analysis repeated five times for each K from $K = 1$ to 3 for each group. For all of the above analyses, posterior probability values were computed for each K according to Pritchard *et al.* (2010). Additionally, ΔK values, which have been shown to accurately reflect the actual number of genetic clusters, were calculated according to Evanno *et al.* (2005).

Structure was also used to identify individuals that were captured in one subpopulation but genetically assigned to another and thus represent migrants. The parameters for this analysis were the same as described above except subpopulation assignments were included in the analysis with the migration prior set to 0.05. Individuals with a probability of assignment to their source population ≤0.01 were considered migrants. Individuals with ambiguous assignment probabilities were considered hybrids.

An individual pairwise relatedness test was performed after correction for null alleles using the program Maximum-likelihood (ML)-Relate (Kalinowski *et al.* 2006; Wagner *et al.* 2006; Carlsson 2008). The

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average pairwise relatedness of each subpopulation was compared using a *t*-test.

Detection of FIV infection

All bobcats for which serum samples were available ($n = 91$) were screened for antibodies to FIV by Western blot as previously described (Franklin *et al.* 2007b). Of these, 24 (26.4%) were scored as 'weak positive' or 'positive' for FIV antibodies. PCR was used to confirm FIV infection in these samples (two to four PCR attempts per seropositive individual) using DNA extracted from whole blood or PBMCs. We used a set of degenerate nested primers, which was previously shown to amplify a region of the *RT-pol* gene from a diverse set of FIV isolates (Troyer *et al.* 2005). All bobcats that were not screened by Western blot ($n = 15$) were screened for FIV infection by the PCR method only. In total, 19 individual bobcat FIV isolates were amplified by PCR and included in the FIV genetic analyses.

FIV pol and env PCR amplification and sequencing

Two gene regions were analysed to evaluate viral phylogeny using both a highly conserved region (*RT-pol*, encoding the essential viral polymerase) and a region that is less evolutionarily constrained (*env*, encoding the surface envelope protein) (Pecon-Slattery *et al.* 2008). PCR amplification of a region of the *RT-pol* gene was performed using degenerate primers as previously described (Troyer *et al.* 2005). Primers to amplify a region of the *env* gene were designed by first performing an alignment of two previously published FIV sequences: PLV-14 [GeneBank (accession no. U03982)] isolated from a Florida panther (*Puma concolor coryi*) and PLV-1695 [GenBank (accession no. DQ192583)] isolated from a puma (*Puma concolor cougar*) in British Columbia. Degenerate nested primer pairs were designed from regions of homology including first-round primers mJLenvF1 (5′–GTG CAI GTC ATI AGA TGT AGA G–3′) and mPLVenvR7 (5′–GGG GTG TCA TTA TAA IIA GTA AAA TT–3′), amplifying a fragment of ~700 bp, and second-round primers mPLVenvF8 (5′–GGG TGC ATT IGT IAA AGA ICC ATT TTT AG–3′) and mPLVenvR6 (5′–GGT GCI TTG AAI GGA CAC ATT CC–3′), which amplified a 570-bp product. Underlined bases indicate 5′ tail sequences added to the primers to lengthen primers and increase strength of primer binding to the template DNA.

Fifty microlitre PCR reaction mixtures contained 25 μL iQSuperMix (Qiagen), 400 nM of each primer and 10 μL DNA. DNA concentrations varied among samples resulting in a range of ~100–500 ng template per reaction. PCR reaction conditions for both rounds included a hot start at 94 °C followed by 20 cycles of melting at 94 °C for 30 seconds, touchdown annealing temperatures ranging from 55 to 46 °C decreasing by 1 °C every 2 cycles for 30 seconds, extension at 72 °C for 30 seconds, followed by 25 cycles of melting at 94 °C for 30 seconds, annealing at 52 °C for 30 seconds and extension at 72 °C for 30 seconds with a final extension at 72 °C for 3 min. This protocol successfully amplified proviral *env* fragments from three FIV-positive bobcats.

The resulting sequences were aligned, and the regions of highest homology were used to develop the following nested primer pairs that successfully amplified *env* fragments from all remaining bobcats with amplified *pol* sequences ($n = 16$). First-round primers were envfw201 (5′–TTT CTC ATG TTC CTT GAA TGG TAC–3′) and envrv202 (5′–CAC ATT CCA CTT AAT TGG TAT TG–3′), resulting in approximately a 450-bp amplicon. Second-round primers were envfw202 (5′–TGG TAC ATT CTG GGT GTT TAA ATC–3′) and envrv201 (5′–CTA TTT TGG TCA CTC TCT GAT GC–3′), resulting in approximately a 400-bp product. PCR reagents and reaction conditions were the same as above with the exception that touchdown annealing temperatures ranged from 58 to 49 °C and the annealing temperature for the last 25 cycles was 54 °C. PCR products were visualized under UV light using gel electrophoresis with ethidium bromide in 2% agarose gel to confirm the presence of product bands.

PCR products were purified using the QIAquick PCR Purification Kit (Qiagen Inc.) prior to sequencing. Forward and reverse sequences were aligned using BLAST (National Center for Biotechnological Information, Bethesda, MD, USA), and a single consensus FIV sequence was produced for each infected bobcat. All sequences were verified manually. All sequences are available in the NCBI GenBank under accession numbers JN383436–JN383465.

Genetic alignments and phylogenetic analyses

Sequences were trimmed at the 5′ and 3′ ends resulting in all sequences having the same length (*pol* = 427 bp, *env* = 347 bp). Trimmed consensus sequences for each gene fragment ($n = 19$ *pol* & *env*) were converted to coding frame using an online DNA translator tool (Swiss Institute of Bioinformatics; http://www.isb-sib.ch/), prior to alignment in CLUSTAL X2 (Larkin *et al.* 2007). Alignments were input into JMODELTEST (Posada 2008) to estimate the best-fit model of nucleotide substitution, which was the TPM2uf model with among-site rate variation for both gene segments (Kimura 1981). The estimated model parameters used for *pol* were [Lset base = (0.4030 0.1312 0.1592) nst = 6 rmat = (7.3755

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50.7381 7.3755 1.0000 50.7381) rates = gamma shape = 0.2280 ncat = 4 pinvar = 0]. The model parameters for *env* included [Lset base = (0.3707 0.1869 0.1840) nst = 6 rmat = (4.2249 11.3706 4.2249 1.0000 11.3706) rates = gamma shape = 0.2250 ncat = 4 pinvar = 0].

Maximum-likelihood phylogenetic analyses were conducted in Phylogenetic Analysis Using Parsimony (PAUP) (Sinauer Associates, Sunderland, MA, USA) (Swofford 2003). The corresponding *pol* and *env* gene regions from an FIV isolate sequenced from a Florida panther in 1994 were included to provide a root for each tree (Langley *et al.* 1994). ML trees were constructed using an NJ starting tree, followed by a heuristic search using the tree-bisection-reconnection branch-swapping algorithm. The *pol* and *env* trees were found to be congruent, and therefore, a single *pol-env* concatenated sequence was used to construct the final phylogenetic tree for analysis. Bootstrap analyses were performed with 100 iterations for all trees. Viral isolates were divided into four 'FIV Groups' based on clusters of related isolates arising from a basal node supported with an ML bootstrap value of 70 or greater.

We estimated the number of FIV migration events between coastal and inland bobcat subpopulations by calculating the *s* statistic for the observed ML phylogenetic tree in Mesquite 2.75 (Maddison & Maddison 2011). The *s* statistic reflects the minimum number of parsimony steps that explain the discord between subpopulations as monophyletic groups on the tree (Slatkin & Maddison 1989).

To estimate the timeline of past virus transmissions within and between subpopulations, the concatenated viral sequence data were analysed in the coalescent framework as implemented by the program BEAST 1.6.2 (Drummond & Rambaut 2007). The SDR06 substitution model was used with a relaxed uncorrelated lognormal molecular clock (Drummond *et al.* 2006). The tree model included a piece-wise linear Bayesian Skyline prior with five groups and a randomly generated starting tree (Drummond *et al.* 2005). An initial run of 10 000 000 Markov chain Monte Carlo (MCMC) iterations, sampled every 1000 runs, was performed to estimate model parameter values. The first 10% of logged values were discarded as burn-in. From this analysis, the following model parameter priors were changed from default settings: (i) the relative rate parameters were set to vary from 0 to 10; (ii) the Bayesian Skyline population size was set to vary from 0 to 500; and (iii) the mean rate for the uncorrelated relaxed molecular clock was set to vary from 0 to 10.

The final analysis included the above settings with 50 000 000 MCMC iterations sampled every 1000 runs. The first ten per cent of logged values were again discarded as burn-in. The estimated values and associated effective sample size (ESS) for each model parameter were viewed in TRACER 1.5 (Rambaut & Drummond 2007). ESS values for all parameters were >500. The maximum clade credibility tree was produced in TREEANNOTATOR 1.6.2 (Rambaut & Drummond 2002). The resulting tree was viewed in FIGTREE 1.3.1 (Rambaut 2006), and the mean posterior probability heights with 95% highest posterior density (HPD) intervals were labelled on internal nodes.

Results

Bobcat population structure

Distribution of alleles. An analysis of population differentiation performed in GENEPOP indicated that the distribution of alleles among bobcats from the two coastal subpopulations, SJH-west and SJH-east, differed significantly ($P = 0.0064$) at only the FCA008 microsatellite locus. Therefore, the coastal bobcats, regardless of whether they were captured east or west of SR-73, had a similar distribution of alleles at 15 of the 16 microsatellite loci examined. Similarly, the two inland subpopulations, NIR and CPH, significantly differed in allelic distribution at only FCA026 ($P = 0.0025$) and FCA077 ($P = 0.0048$). This finding demonstrates that bobcats captured north and south of SR-91 had a similar distribution of alleles at 14 of the 16 microsatellite loci we analysed. However, the distribution of alleles differed greatly between the coastal and inland subpopulations. SJH-west bobcats significantly differed from NIR and CPH bobcats at 13 and 10 microsatellite loci, respectively, and SJH-east bobcats differed from both NIR and CPH bobcats at 13 loci ($P < 0.01$ all significant pairwise tests). These results indicate a high degree of genetic differentiation exists between bobcats separated by I-5 and its associated urban development.

Genetic diversity. No pairwise difference existed in allelic richness (Table S2, Supporting information) when comparing the two coastal subpopulations ($F_{1,29} = 2.59$, $P = 0.118$) or the two inland subpopulations ($P = 0.982$, $F_{1,30} = 0.00$). However, the coastal bobcats (combined SJH-W and SJH-E) had significantly lower allelic richness than the inland bobcats (combined NIR and CPH) ($P < 0.001$, $F_{1,62} = 12.62$). This further suggests that coastal and inland bobcats are genetically distinct and indicates that coastal bobcats have lower genetic diversity than inland bobcats. Interestingly, the BCD8T locus appears to have drifted to fixation in coastal bobcats as only one allele was sampled at this locus from all 49 coastal bobcats. Although the frequency of this allele was also high in NIR (0.82) and CPH (0.67), four and

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five alleles, respectively, were present at this locus in these subpopulations.

Departures from random mating. The overall estimate of genetic differentiation among the four putative subpopulations, D_{est} = 0.11, indicates a moderate amount of genetic structure exists within this population. Pairwise D_{est} values were lowest when comparing the two coastal subpopulations (D_{est} = 0.008, SJH-west:SJH-east) or the two inland subpopulations (D_{est} = 0.014, NIR:CPH) and highest between the coastal and inland subpopulations (D_{est} = 0.11, SJH-west:NIR; D_{est} = 0.13, SJH-west:CPH; D_{est} = 0.14, SJH-east:NIR; D_{est} = 0.19, SJH-east:CPH). The estimated differentiation between the coastal bobcats (combined SJH-W and SJH-E) and the inland bobcats (combined NIR and CPH) was D_{est} = 0.14. Locus-specific D_{est} values are reported in Table S2 (Supporting information).

We found no evidence of inbreeding within the overall population (F_{IS} = 0.013; 95% CI: −0.29–0.065), nor in any of the putative subpopulations [F_{IS} = (0.011, SJH-W; −0.045, SJH-E; 0.029, NIR; 0.034, CPH)].

Individual assignment tests. Bayesian clustering indicated the assumption of two genetically distinct subpopulations (K = 2) best explained the variation in our microsatellite data (Fig. S1, Supporting information). This result was the same regardless of whether or not source population information was used as a prior in the analysis. All bobcats caught east of I-5 (NIR and CPH bobcats n = 56) were assigned to one 'inland' subpopulation, while 46 of 49 bobcats caught west of I-5 (SJH-west and SJH-east bobcats) were assigned to a 'coastal' subpopulation (Fig. 2). Three individuals captured west of I-5 were genetically assigned to the inland subpopulation and thus represent possible migrants. However, no bobcats captured east of I-5 were genetically assigned to the coastal subpopulation. If any additional human development and/or freeways in this region (i.e. SR-91, SR-73, SR-241, SR-261) were causing genetic structure, a population model with K > 2 should have had the highest support. Therefore, the I-5 corridor is the only human development in this region implicated as a cause of genetic structure among bobcats during our period of sample collection.

Three individuals were identified as first-generation migrants as they were captured in the coastal area but had assignment probabilities of 1.00 to the inland population when capture locations were included in the Structure analysis (denoted by * in Fig. 2b). Three other bobcats captured in the coastal area had the genetic profile of hybrids with partial assignment to both subpopulations (denoted by # in Fig. 2b). No individuals sampled from the inland area were identified as migrants or hybrids from the coastal area.

Relatedness of individuals. The average relatedness of bobcats in the coastal population (R = 0.096; SE = 0.0037)

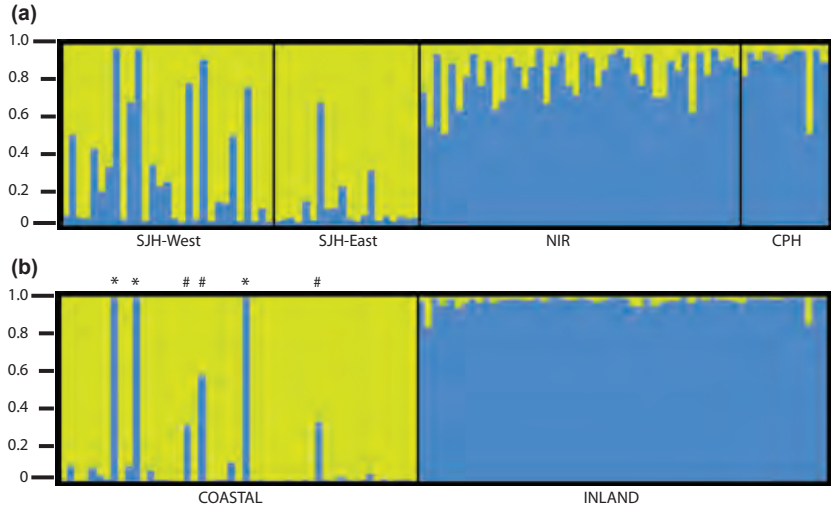

Fig. 2 Individual bobcat genetic assignments to each of two distinct subpopulations. Each vertical bar represents one individual. Values on the y-axis are the probability of assignment of each individual to one of the two genetic groups identified (Fig. S1). The shading of each bar corresponds to the probability of genetic assignment to either the coastal group (yellow) or the inland group (blue) of bobcats. (a) Results for simulation of K = 2 without including a priori capture locations. The majority of individuals captured west of I-5 had strong assignment to one subpopulation (coastal—yellow), while all of the individuals captured east of I-5 had a high probability of assignment to a second subpopulation (inland—blue). (b) Three migrants (*) and three hybrids (#) were identified in Structure using a priori assignments to coast or inland subpopulations based on capture locations. All gene flow was detected from the inland to the coastal subpopulation.

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was significantly higher (t_{5634} = 7.23; P < 0.001) than in the inland population (R = 0.064; SE = 0.0026).

FIV phylogenetic analyses

We amplified a 427-bp region of *pol* and 347-bp region of *env* by PCR from 19 bobcats (four in SJH-west, four in SJH-east and 11 in NIR) bobcats. These included 17 of the 24 (70.8%) bobcats putatively seropositive by Western blot, one bobcat that was negative by Western blot and one bobcat that was screened by PCR only. The inability to amplify FIV sequences from a subset of putatively seropositive bobcats is similar to the findings of previous studies (Troyer *et al.* 2005; Franklin *et al.* 2007b). This is probably the result of a difference in the sensitivity and specificity of these two assays and/or a relatively low FIV proviral load present in a subset of infected animals.

The demographic information for 18 of the 19 FIV-positive bobcats was known: 13 were adult males, one was a yearling male, two were adult females and two were yearling females. The age-specific prevalence of FIV was 14.2% (3/21) for yearlings and 23.8% (15/63) among adults.

The ML phylogenetic tree built from *pol-env* concatenated gene sequences (Fig. 3) shows no evidence of association between capture location (coastal vs. inland) and FIV relatedness (see also Fig. 4). The basal nodes have low bootstrap support, suggesting little overall genetic structuring within the virus population. The number of parsimony steps (*s* statistic) that best explains the discord of FIV relatedness between subpopulations indicates a minimum of three FIV transmission events have occurred between the coastal and inland subpopulations (Slatkin & Maddison 1989).

We estimated the past timeline of virus movement within and between bobcat subpopulations using a coalescent Bayesian model (Drummond *et al.* 2005; Drummond & Rambaut 2007). Figure 5 illustrates the maximum clade credibility tree with labels representing the estimated year of coalescence (mean posterior node ages) for each internal node. The age of the basal nodes is difficult to interpret because of large 95% HPD intervals (analogous to 95% confidence intervals). Therefore, it is impossible to reconstruct a precise timeline of ancestral divergence into the observed FIV groups. However, the more terminal nodes are insightful as they depict the estimated year of recent FIV coalescent events. FIV Group 4, the largest supported group of isolates, comprises six isolates from inland bobcats (x23, x24, x27, x31, x37 and x55) and two isolates from coastal bobcats (x240 and x46). The two coastal isolates in this group share a common ancestor with two of the

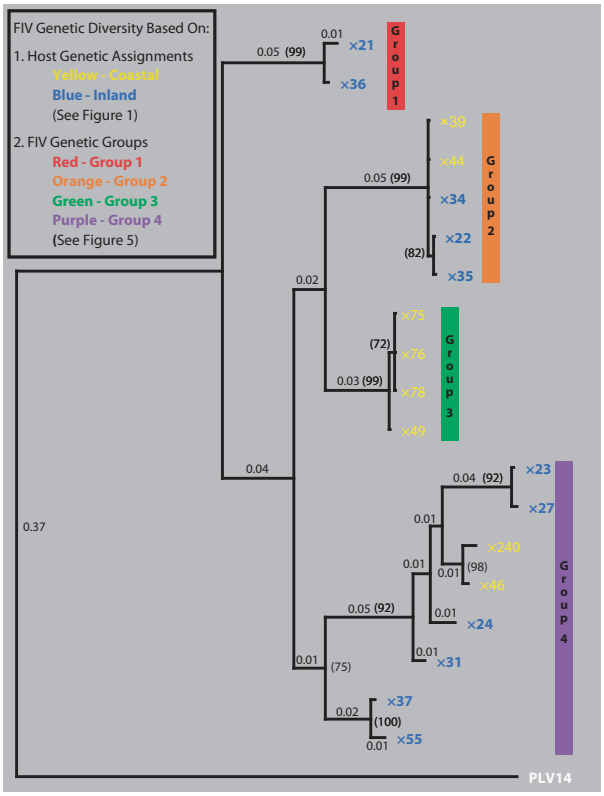

Fig. 3 Maximum-likelihood phylogenetic tree of feline immunodeficiency virus (FIV) concatenated *pol-env* sequences from 19 infected bobcats. The tree was constructed using a single 774-bp sequence (427 bp from *pol*, 347 bp from *env*) of proviral DNA from each individual. All sequences are in coding frame. Bootstrap values >70 are indicated in parentheses. Branch lengths ≥0.01 are also indicated. Individuals have been coloured to represent their genetic assignment based on the results of the *Structure* analysis (see Figs 1 and 2). Because no migrants were infected with FIV, the colour of an individual also represents whether an individual was captured west (yellow) or east (blue) of I-5. FIV isolates were assigned to groups based on the four most basal supported nodes to illustrate the distribution of FIV genetic diversity across the landscape (See Fig. 4). The tree is rooted with PLV-14, a viral sequence from the same FIV clade, which was sequenced from a Florida panther in 1994.

inland isolates (x23 and x27) in *c.* 1990 (Fig. 5; 95% HPD: 1967–2003). Similarly, FIV Group 2, with 99% bootstrap support, contains nearly identical sequences from three inland bobcats (x22, x34 and x35) and two coastal bobcats (x39 and x44), which share a common ancestor in approximately the year 2000 (Fig. 5; 95% HPD: 1995–2003).

Feline immunodeficiency virus Group 3 contains four closely related viral isolates (Fig. 3; x75, x76, x78 and x49) from related coastal bobcats (r > 0.25). To our knowledge, this is the first evidence of FIV familial transmission among bobcats. Familial transmission of

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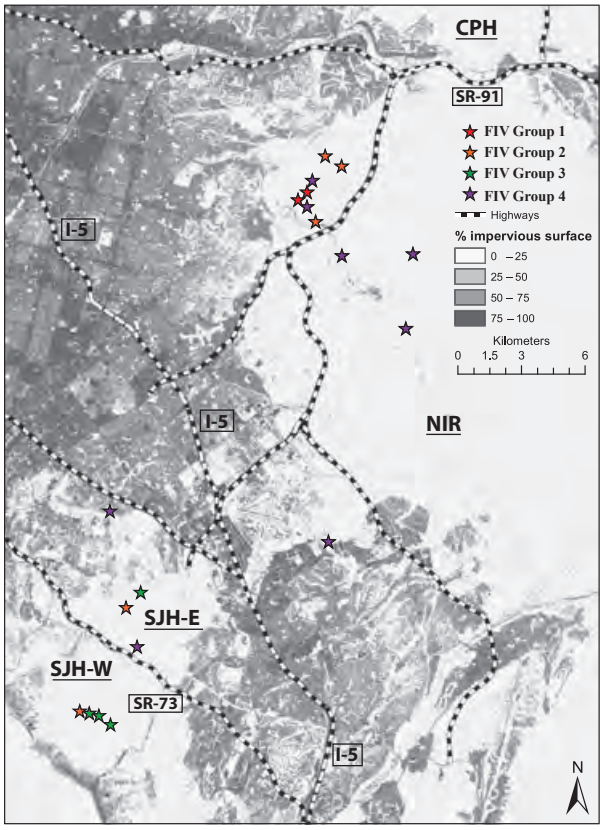

Fig. 4 Geographical distribution of feline immunodeficiency virus (FIV) genetic diversity among inland and coastal bobcats. Each star indicates the capture location of one FIV-positive bobcat. The stars are coloured corresponding to which of the four groups of related FIV isolates was sampled from each bobcat (See Fig. 3). FIV Groups 1 (red) and 3 (green) contain isolates sampled only from inland or coastal bobcats, respectively. FIV Groups 2 (orange) and 4 (purple), containing both inland and coastal bobcats, resulted from the movement of FIV across Interstate-5. Degree of urban development (% impervious surface) is represented by grey shading.

FIV has been previously documented in mountain lions (Poss *et al.* 2008).

Discussion

Bobcat population structure

Understanding the degree of connectivity among populations in heterogeneous landscapes is an important goal of ecology, population genetics and conservation biology (Taylor *et al.* 1993; Crooks & Sanjayan 2006; Fischer & Lindenmayer 2007). We evaluated host and pathogen genetic markers to investigate connectivity among bobcats throughout a fragmented urban landscape in southern California. Our results indicate that two genetically distinct groups of bobcats existed in our study area, defined as coastal and inland subpopulations, separated by urban development including Interstate-5 (Figs 1 and 3). This finding is in agreement with other analyses performed previously with a small subset of these bobcats and four of the 16 microsatellite loci utilized in this report (Ruell *et al.* in press).

Our results indicate that the coastal and inland bobcat subpopulations had a different distribution of alleles at most of the microsatellite loci examined and a low, unidirectional pattern of migration from the inland to the coastal area. We also observed reduced genetic diversity and increased relatedness among individuals in the coastal population. These findings suggest the observed genetic differentiation is because of decreased migration through the urban matrix between the inland and coastal habitat patches. We therefore conclude that urban development, including I-5, has been a physical barrier that has reduced bobcat movement and gene flow between isolated groups of individuals.

We did not detect substructure among bobcats separated by the two other freeways that we specifically evaluated, SR-91 and SR-73 and nor did we find evidence of genetic structure because of any other freeways (i.e. SR-241, SR-261) or human development in the region. The maintenance of gene flow across SR-91 and SR-73 is probably explained by the fact that these roadways are perforated by more functional wildlife underpasses and are bordered by more natural habitat than I-5. Therefore, the distance between habitat patches is shorter across SR-91 and SR-73 than across I-5, a factor that has been shown to be an important determinant in carnivore movement among habitat fragments in this region (Crooks 2002). It is possible that because SR-91 and SR-73 are newer roads, any isolation these may be causing has not yet resulted in detectable genetic structure.

Our findings, revealed by analyses of empirical genetic data, are supported by observations from remotely triggered cameras placed near underpasses of all three focal roadways. Cameras placed near the only potential wildlife corridor under I-5 that directly links SJH-E to NIR did not document any movement of bobcats between these habitat patches during 204 consecutive days of observation (Lyren *et al.* 2008a). Cameras, however, did not monitor another potential path across I-5 connecting NIR to SJH-W to the south; road kill carcasses and models of connectivity both suggest this path may be utilized by bobcats (Lyren *et al.* 2008a). In contrast to the lack of remote camera observations of bobcat movement across I-5, a similar duration of camera monitoring of potential wildlife corridors under SR-91 documented many successful movements between NIR and CPH (E. E. Boydston, unpublished data). Likewise, multiple bobcat movements between

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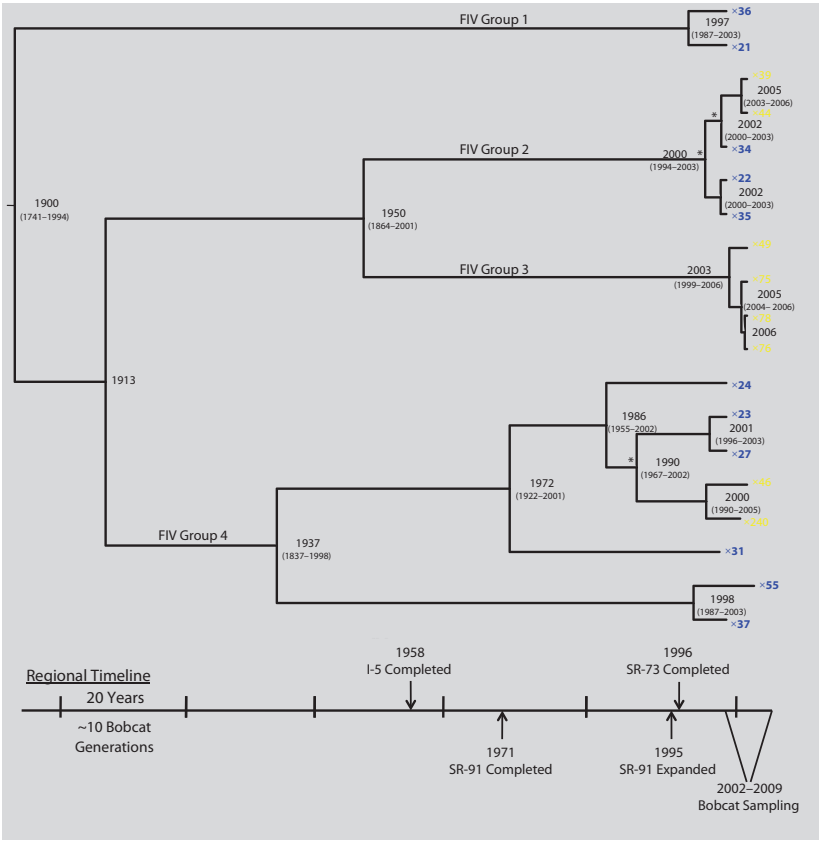

Fig. 5 The estimated timeline of viral coalescent events. Maximum clade credibility Bayesian phylogenetic tree of *pol-env* concatenated sequences constructed using dated tips. Internal node labels correspond to the highest mean posterior probability estimate [with 95% highest posterior density (HPD) interval] for the year of coalescence. The estimated dates on basal nodes lack precision; therefore, it is impossible to accurately reconstruct the timeline of ancestral diversification into the current four-group structure of feline immunodeficiency virus (FIV). Estimates of recent coalescent events are more precise and depict contemporary FIV transmission within and between bobcat subpopulations. *Indicates common ancestor to contemporary isolates sequenced from both inland and coastal bobcat isolates. Viral movement across I-5 has probably occurred since the estimated date of these coalescent events, resulting in the presence of related viral strains sampled in both subpopulations (See Fig. 4).

SJH-W and SJH-E were also recorded during 358 days of camera observations near SR-73 (Lyren *et al.* 2008b).

Interstate-5 and the surrounding urban matrix have greatly increased in size over time since the original construction was completed in 1958. While it is difficult to know when I-5 became a 'barrier' to bobcat movement, Crooks (2002) estimated that the coastal San Joaquin Hills might have become effectively isolated from inland natural areas around 1980. Given the generation time of bobcats (*c.* 2 years) (Knick *et al.* 1985), between 12 (*c.* 1980) and 25 (*c.* 1958) generations have passed because the inland and coastal bobcat subpopulations became physically isolated.

FIV phylogenetic analyses

Directly transmitted pathogens are inextricably linked to their hosts, and therefore, the geographical distribution of pathogens reflects the movement and contacts of their hosts throughout the landscape. We analysed two gene sequences from FIV, a retroviral pathogen of bobcats, to evaluate whether the gene flow (transmission) of the virus revealed information about bobcat movement not discernable from traditional host genetic analyses. We hypothesized that urban development, which limits bobcat gene flow, would also limit viral transmission between bobcat subpopulations. Given that only one in five bobcats are infected with FIV, the expected virus migration rate is five times lower than the host migration rate. Thus, we expected each of the two bobcat subpopulations would be infected with a genetically distinct viral strain, divergent from one another owing to years of isolation, low viral migration rates and the high mutation rate of FIV.

This prediction is consistent with previous literature demonstrating that geographical or social barriers,

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which prevent mixing between neighbouring host subpopulations, result in genetically structured retrovirus populations (Franklin *et al.* 2007a; Liu *et al.* 2008; see also Fig. S2, Supporting information—demonstrating clear divergence between FIVs isolated from bobcats north or south of Los Angeles). However, the phylogenetic trees constructed in this study from FIV gene segments demonstrated a pattern that differs from these previously published findings. The relatedness of FIV isolates is mixed among coastal and inland bobcat subpopulations, indicating that there is no association between FIV relatedness and the geographical/genetic structure of its host (Figs 3 and 4). While this finding differs from our prediction based on the ecology of FIV, it is consistent with previous studies of urban bobcats in southern California, which have found that individual movements (and thus opportunities for disease transmission) between fragmented habitat patches occur more frequently than predicted by observed levels of gene flow (Riley *et al.* 2006; Ruell *et al.* in press).

The topology of the ML phylogenetic tree (Fig. 3) illustrates that neither the coastal nor the inland bobcats are infected with a monophyletic cluster of viruses. Instead, we identified four groups of related FIV isolates but found no evidence to suggest these groups developed because of the population structure of bobcats. While two of the four groups contained only coastal or inland isolates (FIV Groups 1 and 3), these were the smallest groups sampled and the other two FIV groups did not follow this pattern. Instead, FIV Groups 2 and 4 contained closely related viruses arising from both bobcat subpopulations. The coastal isolates within each of these two groups shared recent common ancestry with inland viruses (Fig. 5), and thus, we conclude that FIV-infected bobcat migration events across I-5 are responsible for the observed mixing of isolates. Half of the viruses infecting coastal individuals (4/8) recently originated from, or were transmitted to, inland bobcats. The former is likely to have occurred in FIV Group 2 as suggested by the presence of multiple inland isolates basal to the two coastal isolates and evidence of a long Group 2 residence time within the inland subpopulation.

Utilizing host and pathogen genetics

The presence of related FIV strains on both sides of I-5 suggests that the intervening urban development is somewhat permeable to bobcat movement and disease transmission, despite the presence of distinct genetic structure among the host population. There may be several explanations for the discrepancy between the population structure of FIV and its host. One hypothesis is that a recent increase in bobcat migration across I-5 has led to the observed mixing of viral genotypes, but not enough time has passed for this recent increase in migration to counteract previously established genetic structure among the bobcats. While possible, we consider this unlikely as human development along the I-5 corridor has increased over time, and no notable changes have been made in the area (e.g. underpasses, culverts) that would account for a recent increase in connectivity between the two subpopulations.

An alternative hypothesis is that FIV exchange between the two subpopulations is not necessarily linked to bobcat gene flow. Transient movements of individuals across a semi-permeable barrier such as I-5 may not result in the exchange of genetic material, but may involve sufficient contact between individuals to allow for disease transmission. Under this hypothesis, the contrasting patterns of population structure may reflect differences in the underlying ecology of the two molecular markers.

Microsatellite markers are useful for detecting host gene flow, the specific process involving animal movement which results in the exchange of genetic material from one group of individuals to another (Endler 1977). According to this definition, gene flow is dependent upon successful mating after migration. FIV transmission, however, can occur both vertically *and* horizontally, allowing FIV isolates to move between individuals and subpopulations in the absence of gene flow. For example, Biek *et al.* (2003) reported that for one population of mountain lions, horizontal transmission among adults resulted in the majority of new FIV infections and accounted for the observed increasing prevalence of FIV with age. Vertical transmission, resulting in a cohort of young individuals infected prior to adolescence, was equally important in explaining the dynamics of FIV in the population.

Given that bobcats and mountain lions share many life history characteristics, it is probably that similar FIV transmission dynamics occur in bobcats. Indeed, the relative prevalence of FIV in yearlings (14%) vs. adults (24%) in this study is similar to the age–prevalence relationship described in Biek *et al.* (2003). Young infected individuals may therefore play an important role in the maintenance and spread of FIV in this population. At adolescence, juvenile (usually male) bobcats often make transient movements during dispersal from their natal range while attempting to establish a new home range (Kitchings & Story 1984; Knick 1990; Hansen 2007). Young bobcats infected prior to dispersal therefore represent a potentially important mode of virus movement within and between subpopulations.

In fragmented landscapes such as southern California, where urban development and freeways act as boundaries limiting animal movement, bobcat home

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ranges may shrink, and the amount of overlap between neighbouring home ranges may increase (Riley 2006; Riley *et al.* 2006). This pattern of 'home-range pile-up' has been described in other bobcat populations in California (Riley *et al.* 2006). This phenomenon decreases the probability that juveniles dispersing to a neighbouring subpopulation will successfully mate. Under these conditions, the actual rate of bobcat movements, contacts and opportunities for disease transmission between subpopulations would be higher than expected based on migration rates estimated from gene flow.

The low level of gene flow we detected across I-5 occurred in a unidirectional pattern from the inland area towards the coast. The coastal population, while reduced in overall genetic diversity, contains both migrants and hybrids from the inland population. This suggests that, while rare, inland bobcats can successfully migrate to and breed in the coastal population, while the reverse was not seen. However, inland FIV isolates do not form a monophyletic group; two of the three FIV groups infecting coastal bobcats also infect inland bobcats. There are two possible explanations to this pattern. One is that movement of FIV has occurred repeatedly one-way from the inland subpopulation to the coast, causing the diversity among coastal isolates to closely mirror that observed inland. This hypothesis is consistent with the one-way pattern of bobcat movement we detected from the microsatellite analysis.

The other possibility is that a coastal virus population diverged from inland viruses after the two groups were isolated by urban development and has since been transmitted back into the inland subpopulation multiple times via transient movements and contacts resulting in disease transmission but not gene flow. Tracking the movements of individual bobcats, evaluating FIV diversity in other neighbouring bobcat populations and utilizing spatially explicit phylogeographic analyses may help to distinguish between these alternatives.

In conclusion, our findings indicate that bobcats inhabiting this fragmented landscape in southern California are physically isolated and genetically structured. This pattern is consistent with decreased connectivity across urban development, resulting in low levels of migration and/or a low probability that migrants establish a home range and successfully mate. However, movements are apparently made, allowing for disease transmission between these habitat fragments. This conclusion carries with it conservation implications as populations with these characteristics are susceptible to decline as a result of a continued loss of genetic diversity from genetic drift and decreased individual fitness because of inbreeding depression (Frankham 2006). In addition, both subpopulations should be managed as a unit when considering treatment and prevention interventions during future disease outbreaks. Habitat conservation and restoration as well as connectivity enhancements such as functional underpasses to better facilitate movement of bobcats under roadways may help safeguard their persistence in the face of substantial ongoing threats posed by humans in this region.

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The authors are interested in research involving ecology, conservation, and/or infectious diseases of carnivores. They share particular interest for topics relating to the effects of human activities on carnivores.

Data accessibility

DNA sequences—GenBank accession numbers JN383436–JN383465. Microsatellite data—DRYAD entry doi:10.5061/dryad.mm317th7.

Supporting information

Additional supporting information may be found in the online version of this article.

Table S1 F_{ST} values calculated from 16 bobcat microsatellite loci.

Table S2 Measures of genetic structure among bobcats calculated from 16 microsatellite loci.

Fig. S1 Estimating the number of genetic subpopulations (*K*) of bobcats.

Fig. S2 Maximum-likelihood phylogenetic tree built from *pol* sequences using the same model parameters as those described to produce the Maximum-likelihood tree in Fig. 4 (see Methods).

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Review

Estimation of Bird-Vehicle Collision Mortality on U.S. Roads

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ABSTRACT Roads have numerous direct and indirect ecological impacts on wildlife. Vehicle collisions are a top impact of roads on birds, with tens of millions of birds thought to be killed each year in the United States. However, currently available mortality estimates are extrapolated from a single study. We reviewed the literature and used 20 mortality rates extracted from 13 studies to systematically quantify data-driven estimates of annual U.S. mortality from bird-vehicle collisions. We generated 4 separate estimates along with uncertainty using different subsets of data deemed to be rigorous enough to contribute relatively little bias to estimates. All of our estimates of vehicle mortality are higher than previous U.S. figures. When averaging across model iterations, we estimated that between 89 and 340 million birds die annually from vehicle collisions on U.S. roads. Sensitivity analyses indicated that uncertainty about survey-related biases (scavenger removal and searcher detection of carcasses) contributes the greatest amount of uncertainty to our mortality estimates. Future studies should account for these biases to provide more accurate local estimates of mortality rates and to inform more precise national mortality estimates. We found relatively little information available to quantify regional, seasonal, and taxonomic patterns of vehicle collision risk, and substantial uncertainty remains about whether collisions contribute to large-scale impacts on bird populations. Nonetheless, the large magnitude of bird mortality caused by vehicle collisions combined with evidence that collisions can contribute to local population declines for some species highlights the need for implementation of conservation and management actions to reduce this mortality. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS anthropogenic mortality, automobiles, birds, detection probability, roadkill, roads, scavenger removal, systematic review, United States, vehicles.

The global proliferation of road networks has led to a multitude of ecological impacts that affect biological diversity. In the United States, the greater than 6.5 million kilometers of roads (U.S. Department of Transportation 2012) ecologically affect at least 22% of the nation's land area (Forman 2000), causing loss and fragmentation of habitat; pollution with chemicals, light, and noise; alteration of animal movement and behavior; and direct mortality of wildlife from vehicle collisions (Forman and Alexander 1998, Trombulak and Frissell 2000, Forman et al. 2003, Coffin 2007). For birds, vehicle collisions are one of the greatest threats posed by roads (Kociolek et al. 2011), with as many as 80 million birds thought to be killed annually in the United States (Erickson et al. 2005) and roughly 13 million birds estimated to be killed annually in Canada (Bishop and Brogan 2013). Moreover, roadkills have the potential to constitute the vast majority of total mortality for some bird species—most notably, barn owls (*Tyto alba*) (Moore and Mangel 1996, Newton et al. 1997). Roadkill mortality can also result in the creation of population sinks (Mumme et al. 2000, Boves and Belthoff 2012, Grilo et al. 2012) and may be an additive source of mortality that contributes to population declines (Bujoczek et al. 2011).

A large body of literature has identified numerous factors that influence bird-vehicle collision rates. Mortality rates have been found to increase with increasing traffic speed and volume (Case 1978) and rates are generally highest during spring and summer. Mortality rates are also greater for juvenile birds, in areas with favorable bird habitat in close proximity to the road, and where bird populations are abundant (Loos and Kerlinger 1993, reviewed by Erritzoe et al. 2003, Gunson et al. 2010, Boves and Belthoff 2012). In some cases, mortality rates have been found to increase with increasing width of the road corridor (Oxley et al. 1974) or to be greater along road segments that are elevated above the surrounding land (Baudvin 1997, Lodé 2000). Often, 2 or

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more of the above factors are strongly correlated—i.e., wider roads usually have a higher traffic volume than narrow roads—making it difficult to dis-entangle the relative impact of each factor. Furthermore, exceptions to the above relationships occur and are illustrative of how mortality rate correlates are often region-, taxa-, and habitat-specific. For example, several studies have found no link between traffic volume and mortality rates (Massemin et al. 1998, Lodé 2000, Coelho et al. 2008, Kambourova-Ivanova et al. 2012).

Current estimates of annual U.S. bird mortality from vehicle collisions—ranging from 60 to 80 million—are highly speculative, based on extrapolation of mortality rates from a single British study (Hodson and Snow 1965) to the entire U.S. road network (Banks 1979, Erickson et al. 2005). Comprehensive meta-analyses of studies that quantify bird populations have concluded that roads are consistently associated with reductions in bird abundance (Fahrig and Rytwinski 2009, Benitez-Lopez et al. 2010), but no clear evidence exists that vehicle collision mortality is a significant driver of these road-related declines. In addition, no such comprehensive analyses have been completed to assess bird-vehicle collision mortality in the United States. When compared to speculative or extrapolative estimates based on small samples of data, such systematic and quantitative reviews provide a more rigorous approach to estimating mortality, an improved understanding of the sources of uncertainty associated with estimates (Loss et al. 2012, 2013*a*, 2014; Machtans et al. 2013), and a more valid evidence base on which to prioritize policy and management strategies and to identify major research needs (Calvert et al. 2013, Machtans and Thogmartin 2014).

We reviewed the North American and European bird-vehicle collision literature and defined inclusion criteria to screen and remove studies likely to bias our estimates substantially. Based on data extracted from the remaining studies, we 1) systematically quantified the magnitude of bird mortality (along with uncertainty) caused by collisions with vehicles on U.S. roads by combining probability distributions of mortality rates, the length of U.S. roads, and biases associated with surveys for dead birds; 2) used sensitivity analyses to quantitatively investigate factors contributing to estimate uncertainty and to identify major research needs; and 3) summarized the available species-specific data on bird-vehicle collisions in the United States.

METHODS

Literature Search and Inclusion Criteria

We used Google Scholar and the Web of Science database to search for publications about bird-vehicle collisions on roads. The search terms we used were "bird-vehicle collision," "bird-vehicle roadkill," the previous terms with "bird" replaced by "avian" and "vehicle" replaced by "automobile," "car," and "truck." We checked reference lists to locate additional sources, and we also referenced an annotated bibliography that included approximately 670 sources covering the impacts of roads on wildlife (Nietvelt 2002). For 5 North American studies (Nero and Copland 1981, Decker 1987, Smith et al. 1994, Sutton 1996, Potvin and Bishop 2010), we were unable to access full-text articles and instead extracted the data as summarized in a review of bird-vehicle collisions in Canada (Bishop and Brogan 2013). Because of the large quantity of international studies—many that are published in languages other than English or inaccessible online or through North American libraries—we could not exhaustively review this literature. However, our review of the North American literature was comprehensive, and we likely located all studies that included a systematic sampling component. We may have overlooked some North American publications containing descriptions of incidentally found roadkill victims; however, these studies would have been excluded from analyses based on our inclusion criteria described below.

We defined several criteria for studies to be included in our estimation models. We designed inclusion criteria to remove studies that were not useful for generating mortality rate estimates or that were likely to substantially bias estimates. We excluded studies prior to in-depth review if they included no original data; were conducted in a region other than the United States, Canada, or Europe; or were published in a language other than English. In addition, because we sought to generate mortality estimates that were relevant to relatively modern road types and traffic patterns, we arbitrarily selected 1970 as the earliest date for which publications could be included in analyses (see also Bishop and Brogan 2013). Following in-depth review of the remaining 53 studies, we also excluded studies that 1) were retrospective, based on assessment of opportunistically collected data sets or recoveries of banded or radio-tagged birds, 2) focused on particular bird species or groups without sampling or presenting data for all species and groups, 3) included an experimental component without presenting control and treatment data separately, 4) were prospective but also included incidentally collected data without presenting it separately, 5) did not provide information about the proportion of the year covered by sampling, 6) did not present the length of road corridor sampled or a per kilometer mortality rate, 7) were based on a single survey or a series of surveys that covered less than 1 month, and 8) did not separately report fatalities from vehicle collisions and other collision sources (e.g., roadside fences). After implementing the above inclusion criteria, 16 of the 53 reviewed studies remained (9 U.S. and 7 European studies; Table 1; see Table S1 for excluded studies).

For the summary of species representation of mortality, we included data from U.S. studies meeting criteria 1–4 and 7–8 above. We considered criteria 5 and 6 unnecessary for producing unbiased species summaries. We used 7 of the 9 U.S. studies meeting inclusion criteria for the mortality estimate for the species analysis. The 2 excluded studies did not provide data at the species level (Oxley et al. 1974, Gerow et al. 2010).

Data Extraction

From most studies meeting the above inclusion criteria, we extracted a single mortality rate. However, for studies that

Table 1. Meta-data and mortality rates for studies meeting inclusion criteria for 1) estimation of annual bird-vehicle collision mortality on U.S. roads and/or 2) species mortality summary.

Location	Sampling coverage	Used?		Road type	Mortality per km[c]	Study
		Total[a]	Species[b]			
United States						
Southern Idaho	Yr-round	Yes	Yes	4-lane paved	2.01	Boves and Belthoff (2012)
Bow River Valley, AB	Apr–Nov	Yes	Yes	2-lane paved	0.38	Clevenger et al. (2003)—Bow Valley Parkway
Bow River Valley, AB	Apr–Nov	Yes	Yes	4-lane paved	0.37	Clevenger et al. (2003)—Trans-Canada Highway
Tippecanoe County, IN	Yr-round	Yes	Yes	2-lane paved	6.54	Glista et al. (2008)—South River Road
Tippecanoe County, IN	Yr-round	Yes	Yes	2-lane paved	5.69	Glista et al. (2008)—State Road 26
Tippecanoe County, IN	Yr-round	Yes	Yes	2-lane paved	4.85	Glista et al. (2008)—U.S. Highway 231
Central California	25 May–26 Nov	Yes	Yes	4-lane paved	1.20	Moore and Mangel (1996)
Athens County, Ohio	Yr-round	Yes	Yes	4-lane paved	6.56	Seibert and Conover (1991)
Southern Ontario/Quebec	31 May–23 Sep	Yes	No	Unpaved	0.23	Oxley et al. (1974)—Gravel unpaved road 1
Southern Ontario/Quebec	31 May–23 Sep	Yes	No	Unpaved	2.11	Oxley et al. (1974)—Gravel unpaved road 2
Southern Ontario/Quebec	31 May–23 Sep	Yes	No	2-lane paved	2.96	Oxley et al. (1974)—2-lane paved highway
Southern Ontario/Quebec	31 May–23 Sep	Yes	No	4-lane paved	3.22	Oxley et al. (1974)—4-lane paved highway
Long Point, ON	Apr–Oct	No[d]	Yes	2-lane paved	91.43	Ashley and Robinson (1996)
Tippecanoe County, IN	Yr-round	No[d]	Yes	2-lane paved	24.44	Glista et al. (2008)—Lindberg Road
Alachua County, FL	Yr-round	No[d]	Yes	4-lane paved	43.44	Smith and Dodd (2003)
Saguaro Nat. Park, AZ	Yr-round	No[e]	No	?	NA	Gerow et al. (2010)—Rincon Mountain
Saguaro Nat. Park, AZ	Yr-round	No[e]	No	?	NA	Gerow et al. (2010)—Tucson Mountain
Europe						
Northeast France	Yr-round	Yes	No	2-lane paved	1.54	Baudvin (1996)
Northeast Poland	Yr-round	Yes	No	2-lane paved	11.55	Gryz and Krauze (2008)
Galanta, Slovakia	Yr-round	Yes	No	?	17.09	Hell et al. (2005)
Belovo, Bulgaria	Mar–Oct	Yes	No	?	3.00	Kambourova-Ivanova et al. (2012)—1st-class road
Belovo, Bulgaria	Mar–Oct	Yes	No	?	8.09	Kambourova-Ivanova et al. (2012)—Trakia highway
Western France	Apr–Nov	Yes	No	?	8.80	Lodé (2000)
Wroclaw, Poland	Mid-Mar–Oct	Yes	No	?	5.89	Orlowski (2005)
Spain and France	Yr-round	Yes	No	?	0.65	Pons (2000)

[a] Whether we used the mortality rate to estimate bird-vehicle collision mortality on U.S. roads.

[b] Whether we used the source to calculate average proportional representation for individual species (excluded U.S. studies focused on particular bird group(s) without including all species; we excluded all international studies).

[c] We calculated mortality rates using raw data (i.e., we did not directly extract reported rates from studies because calculation approaches varied among studies and were not always calculated transparently). We first divided the total number of fatalities reported for a road segment by the length of road corridor covered by that segment. For rates representing >1 year of sampling, we then divided by the number of years sampled; we applied a partial-year sampling correction in the mortality estimation model (see Methods section in main text for details).

[d] Study meets inclusion criteria but was removed from calculation of mortality rate probability distribution because mortality rate is a statistical outlier among studies meeting criteria.

[e] Study meets inclusion criteria but was removed from calculation of mortality rate probability distribution because mortality rate is adjusted for biases associated with carcass surveys (detection probability and scavenger removal); these biases were separately accounted for in our mortality estimation model.

sampled along more than 1 road type (e.g., paved and unpaved roads and/or roads with different numbers of lanes) or used different sampling methods (e.g., different sampling intervals or survey types) for different portions of the study area, we extracted separate mortality rates. This resulted in extraction of 25 mortality rates (17 U.S. and 8 European rates; Table 1) from the 16 included studies. We calculated all rates as the number of dead birds found per kilometer of road corridor sampled. This approach is different than that of some studies that calculate mortality rates using the total length of lanes sampled (e.g., for a 2-lane road, lane-length is twice the length of the road corridor). Some studies did not provide enough information to clarify how they calculated mortality rates. Therefore, rather than directly extracting the reported rates, we recalculated rates based on the number of fatalities reported for a road segment divided by the length of road corridor covered by that segment. Because we recalculated rates using this raw data, the mortality rate we

calculated was sometimes different than that presented in the original study.

We then used one of several approaches to convert multi-year mortality rates to annual rates. For multi-year studies that sampled across the entire calendar year in every year of the study, we divided mortality rates by the number of years to generate the annual rate (Table 1). We also took this approach for multi-year studies that only sampled a portion of each year; we accounted for partial-year sampling coverage separately (see following subsection). For 4 studies that sampled at least 1 entire calendar year as well as an additional partial year (Seibert and Conover 1991, Baudvin 1997, Hell et al. 2005, Glista et al. 2008), we treated the partial year as a full year when calculating the annual rate. This approach led to conservative rate estimates because mortality was spread across a longer time period than it actually occurred in.

We excluded 3 mortality rates from the above data set for being statistical outliers and 2 for being adjusted for various sampling biases that we accounted for separately in the mortality estimation model (see Supplementary Methods, available online at www.onlinelibrary.wiley.com). The final data set used for estimation of mortality therefore included 20 mortality rates (12 U.S. and 8 international rates) extracted from 13 studies (6 U.S. and 7 European studies; Table 1).

Quantification of Annual Bird Mortality

To increase the comparability of mortality estimates from different studies, mortality rates should ideally be standardized to account for varying proportions of the year being covered by sampling (Loss et al. 2012). Potential standardization approaches include 1) using mortality rates from year-round studies to proportionally correct partial-year studies (Longcore et al. 2012, Loss et al. 2013*a*), 2) including a correction factor in the mortality estimation model that accounts for partial-year sampling (Loss et al. 2014), or 3) using only full-year mortality rates to generate mortality estimates. We were unable to implement the first approach because year-round vehicle collision studies either do not present data separately for different portions of the year or only provide seasonal data for single bird species or taxa other than birds. Because the second and third approaches were both possible, we repeated mortality estimation using each approach. We expected the estimate generated using approach 2 would represent a maximum value because this approach assumed that mortality rates observed during the sampled portion of the year—typically the peak periods of vehicle collision mortality in spring, summer, and/or autumn —also applied to the un-sampled portion of the year (see Supplementary Methods).

Our approach for estimating mortality was to combine a mortality rate probability distribution with a probability distribution for the length of U.S. roads susceptible to that range of mortality rates. We defined the maximum susceptible road length to be the entire U.S. road network and the minimum susceptible length to be only the length of roads in rural areas (see Supplementary Methods). This approach assumes that mortality rates in urban areas are likely lower than in rural areas, but does not entirely discount mortality in urban areas. We also incorporated correction factors to account for sampling coverage of less than the entire calendar year (for estimates that included partial-year morality rates) and for biases associated with carcass surveys (all estimates), including removal of carcasses by scavengers and imperfect detection of carcasses by surveyors (Loss et al. 2013*a*, 2014). Because a preliminary analysis found little support for differences in mortality rates between 2-lane, 4-lane, and gravel roads, and because the sample of mortality rates was too small to generate separate probability distributions for different road types, we applied the same range of mortality rates across all U.S. road types. This simplified approach contributes uncertainty to our mortality estimate; however, we did not have enough available data to allow separate mortality estimates for different road types. In addition to repeating mortality estimation with and without inclusion of partial-year studies, we also estimated mortality with and without inclusion of European mortality rates. Thus, we generated 4 separate estimates of annual mortality using different subsets of data: U.S. year-round mortality rates, U.S. year-round and partial-year rates, U.S. and Europe year-round rates, and U.S. and Europe year-round and partial-year rates.

For the estimates based only on year-round mortality rates, we used the model:

$$\text{Mortality}_{\text{year-round studies}} = R \times K_{\text{year-round studies}} \times B \qquad (1)$$

where R is the length of U.S. roads susceptible to the range of mortality rates in the mortality rate probability distribution (K), K is the is the range of collision mortality rates per km of road corridor, and B is a bias correction factor to account for removal of carcasses by scavengers prior to surveys and imperfect detection of carcasses remaining at the time of surveys.

For the estimates based on year-round and partial-year rates, we used the model:

$$\begin{aligned}&\text{Mortality}_{\text{year-round and partial-year}}\\ &\quad = R \times K_{\text{year-round and partial-year}} \times Y \times B\end{aligned} \qquad (2)$$

where Y is a correction factor that accounts for the average proportion of the calendar year not covered by sampling in the studies used to develop the mortality rate distribution (Loss et al. 2014). The partial-year sampling correction factor was a fixed value; however, we defined all other parameters as uniform probability distributions (specific distributions shown in Table 2; rationale for distributions in Supplementary Methods). For all estimates, we used the runif function in Program R (R Version 3.0.1., <http://www.r-project.org/>. Accessed 14 Apr 2014) to draw random values from each probability distribution, and we calculated mortality using the above formulas. We repeated this calculation 10,000 times for each of the 4 estimation approaches to generate ranges of uncertainty for mortality estimates.

Sensitivity Analyses

We used sensitivity analyses to quantitatively investigate the factors contributing to uncertainty in our mortality estimates.

Table 2. Probability distributions used for estimation of annual bird-vehicle collision mortality on U.S. roads.

Parameter	Distribution type	Distribution parameters	Source
Total length of road corridors in the United States[a]	Uniform	Min. = 3.76 M; max. = 4.33 M	U.S. Department of Transportation (2012)
Morality rates (per km)			
U.S. studies (yr-round)[b]	Uniform	Min. = 3.48; max. = 6.78	95% CI across 5 rates meeting inclusion criteria
U.S. studies (all)[c]	Uniform	Min. = 2.78; max. = 6.73	95% CI across 12 rates meeting inclusion criteria
U.S. + Europe studies (yr-round)[b]	Uniform	Min. = 2.85; max. = 9.70	95% CI across 9 rates meeting inclusion criteria
U.S. + Europe studies (all)[c]	Uniform	Min. = 4.24, max. = 8.58	95% CI across 20 rates meeting inclusion criteria
Partial-yr sampling correction			
U.S. studies (all)[c]	NA[d]	Estimate = 1.49	1/average proportion of yr covered by mortality rates
U.S. + Europe studies (all)[c]	NA[d]	Estimate = 1.37	1/average proportion of yr covered by mortality rates
Bias correction factor	Uniform	Min. = 3.26; max. = 11.46	Bruun-Schmidt (1994), Gerow et al. (2010), Santos et al. (2011), Boves and Belthoff (2012), Texeira et al. (2013)

[a] Includes length in millions (M) of kilometers of all public roads in all states excluding Alaska and Hawaii.
[b] Estimate is based only on mortality rates from studies with year-round sampling coverage.
[c] Estimate is based on mortality rates from all studies meeting inclusion criteria.
[d] Parameter is a point estimate, not a probability distribution.

We defined univariate regression models with the 10,000 replicated mortality estimates as the dependent variable and randomly drawn values of model parameters as the independent variable. We repeated this analysis 4 times, once for each of the 4 mortality estimate models. We used the adjusted R^2 values for each independent variable (averaged across the 4 sensitivity analysis iterations) to interpret the percentage of estimate uncertainty attributable to each model parameter (Blancher 2013, Loss et al. 2013*a*).

Vehicle Collision Mortality by Species

In addition to estimating total annual mortality for all U.S. birds, we also calculated the average proportional representation of each bird species (Longcore et al. 2013, Loss et al. 2013*a*). We used this calculation rather than estimating species-specific mortality because the data from studies meeting inclusion criteria only represented 100 bird species. This value is likely much lower than the actual number of species killed along U.S. roadways each year. Estimates of species-specific mortality would therefore be biased high for observed species and biased low for species killed but not reported in the literature. Therefore, we would be unable to draw unbiased conclusions about species-specific collision risk. Nonetheless, to provide a rough summary of the findings to date, we estimated average proportional representation of species by 1) calculating the proportion of each study's total count represented by each species (i.e., multiple proportions calculated for each species, 1 from each study), and 2) averaging each species' individual-study proportions across all studies. For averaging, we only included zero-values of proportions (i.e., species was not found in study) when a species could have been found, as determined by overlap of breeding, migration, and/or wintering ranges with study sites (Sibley 2000).

RESULTS

We found considerable variation (41.8%) among median mortality estimates produced using the 4 models (Table 3). The model using only year-round mortality rates from the United States produced the lowest annual estimate (median = 145.7 million; 95% CI = 61.9–274.6 million), and the model including both year-round and partial-year mortality rates and rates from both the United States and Europe produced the highest estimate and the estimate with the greatest range of uncertainty (median = 250.5 million; 95% CI = 103.8–476.8 million). Averaging across all 4 models (i.e., averaging the 4 estimates produced in each model iteration and then averaging these values across 10,000 iterations) resulted in a median annual mortality estimate of 199.6 million birds (95% CI = 88.7–339.8 million). Regardless of the model used, sensitivity analyses indicated that the bias correction factor for scavenger removal and searcher detection contributed the greatest uncertainty to estimates (average variance explained = 63.2%), followed by the mortality rate (32.5%) and the road corridor length over which the mortality rate applies (1.3%).

Among the species documented in studies meeting inclusion criteria, the barn owl had the highest average proportional representation across studies, averaging 32.4% of total counts (all species proportions in Table S2). Four other species, including 3 in the Corvidae family, had average proportional representation of at least 5%: common raven (*Corvus corax*; 6.3%), gray jay (*Perisoreus canadensis*; 6.0%), black-billed magpie (*Pica hudsonia*; 5.0%), and European starling (*Sturnus vulgarus*; 5.0%). Several species were found in 3 or fewer studies, and these species' proportions were more likely to be biased by abnormally high or low counts documented in single studies. Given the small sample of

Table 3. Estimates of annual bird-vehicle collision mortality on U.S. roads.

	Total mortality (millions)		Mortality per km	
Mortality data used	**Median**	**95% CI**	**Median**	**95% CI**
United States	145.7[a]	61.9–274.6[a]	36.0[a]	15.3–68.0[a]
	197.1[b]	78.2–397.9[b]	48.8[b]	19.4–98.5[b]
United States + Europe	171.0[a]	59.6–381.5[a]	42.3[a]	14.8–94.4[a]
	250.5[b]	103.8–476.8[b]	62.0[b]	25.7–118.0[b]
Average across models	199.6	88.7–339.8	49.4	22.0–84.1

[a] Estimate based only on mortality data from studies with year-round sampling coverage.
[b] Estimate based on data from all studies meeting inclusion criteria.

studies included in the species summaries (7 studies including 3,246 total fatality records), caution should be used when interpreting these results.

DISCUSSION

Annual Bird-Vehicle Collision Mortality on U.S. Roads

All of our estimates of annual bird-vehicle collision mortality exceed the previous estimates of between 60 and 80 million birds, which were produced by extrapolating the results of 1 British study (Hodson and Snow 1965) across the entire U.S. road network (Banks 1979, Erickson et al. 2005). We improved upon these earlier estimates by systematically incorporating 20 mortality rates from 13 studies that used a prospective sampling design and reported results for all potentially killed bird species. Even when considering the lowest estimate range (between 62 and 275 million birds), our results suggest that bird-vehicle collisions outrank many other sources of direct anthropogenic mortality. Among threats with estimates that are data-driven and systematically derived, only predation by free-ranging domestic cats (Loss et al. 2013*a*) and collisions with buildings and their windows (Loss et al. 2014) are estimated to cause greater annual bird mortality in the United States. Estimates of total numbers of birds killed by anthropogenic threats are useful for prioritizing conservation and management efforts. However, increased attention should also be given to documenting which species and regions are most vulnerable to vehicle collisions and other mortality sources (Longcore et al. 2013; Loss et al. 2013*b*, 2014).

As expected, estimates that incorporated both year-round and partial-year mortality rates were higher than those that used only year-round rates. This likely occurred because the partial-year correction factor was calculated under the assumption that mortality rates were constant across all seasons. Among the studies we used, sampling periods typically covered spring, summer, and/or autumn, seasons characterized by relatively high mortality rates for most species (Loos and Kerlinger 1993, Smith and Dodd 2003, Orlowski 2005, Gryz and Krauze 2008). Extrapolating mortality rates from these peak seasons to un-sampled seasons that are generally characterized by lower mortality rates may have inflated our estimates. Estimates from models including partial-year rates should therefore be viewed as maximum values. Additional year-round studies that present results separately by month and/or season are needed to clarify intra-annual variation in vehicle collision mortality rates.

Estimates that included European mortality rates were higher than those that used only U.S. rates. This may have occurred due to the inclusion of 2 European rates that were not statistical outliers but were higher than all U.S. rates meeting inclusion criteria (11.6 and 17.0 birds/km/yr; Hell et al. 2005, Gryz and Krauze 2008). Although exceptionally high annual mortality rates of up to 91 birds/km (Ashley and Robinson 1996) have been documented locally in the United States, such rates likely do not apply across most roads. Roadkill fatalities are often clustered in hotspots (e.g., Gunson et al. 2010), and these areas are often the focus of mortality studies. This tendency to focus on areas already known to experience bird mortality may have contributed positive bias to individual estimates of mortality rates and to our national mortality estimates. Nonetheless, we sought to minimize this source of bias by removing mortality rates that were identified as statistical outliers.

We were unable to assess regional variation in bird-vehicle collision mortality rates and to produce regional mortality estimates. Only 6 U.S. studies met our inclusion criteria; this sample was insufficient to allow for quantification of regional variation. Filling this data gap will require rigorous and prospective studies across a broad cross-section of the United States within numerous ecosystems, states, and regions. Individual studies that randomly sample roadkill mortality across a large spatial scale (e.g., entire states or regions) will also provide increased understanding of regional variation.

Research Needs and Estimate Limitations

The relatively small sample of data meeting inclusion criteria resulted in substantial uncertainty in our mortality estimates. When assessing specific uncertainty contributions of individual model components, sensitivity analyses indicate that the model parameter contributing the greatest uncertainty to our estimates is the bias correction factor, which accounts for both scavenger removal and imperfect detection of carcasses. Further research on these biases may decrease the uncertainty associated with this correction factor and allow for increased precision of future mortality estimates. However, the magnitude of these biases depends on a suite of factors, including the local scavenger community, habitat type, traffic volume, and weather conditions (Santos et al. 2011, Boves and Belthoff 2012, Guinard et al. 2012, Texeira et al. 2013). Development of a

narrow distribution of bias correction factors that apply across a national scale may therefore not be possible. An alternative approach is for future studies to estimate scavenger removal and searcher detection rates to calculate adjusted mortality rate estimates. A large sample of locally adjusted mortality rates would obviate the need for post hoc correction factors (Loss et al. 2013*b*). Recent studies outline considerations for scavenger removal and detection trials (Santos et al. 2011, Texeira et al. 2013). Of particular promise are approaches that allow for estimation of both biases using a single experimental trial incorporated into standard fatality monitoring (Smallwood 2013) or using only the dead birds found during fatality monitoring, thus removing the need for separate experimental trials (Etterson 2013).

Mortality rate probability distributions also contributed substantial uncertainty to our estimates. The relatively small sample of studies meeting inclusion criteria along with the inherently variable nature of collision rates likely contributed to this uncertainty. To increase the number of mortality rates that can be used to estimate national mortality, future studies should seek to meet the level of rigor captured by our inclusion criteria. In particular, more studies are needed that sample and present data for all bird species. When summarizing average proportional representation of collision mortality, we found that a few species (particularly barn owls and several corvids) comprise a relatively large percentage of all fatalities that have been identified to species. However, sample sizes of usable studies and available data were small, and results of the species summary were likely biased by high detection probabilities for large species and by geographical biases in sampling. Taking a more species-inclusive approach to studying bird-vehicle collisions will improve understanding of species- and taxa-specific vulnerabilities to vehicle collisions. Because of the above limitations, species proportions should not be used to draw conclusions about national-scale vulnerabilities of bird species to vehicle collisions. Nonetheless, they provide a descriptive summary of the bird species that have been documented as roadkill victims along U.S. roads.

In addition to estimate bias caused by scavenger removal and imperfect detection of carcasses, an unknown number of birds that collide with vehicles fly out of detection range (i.e., crippling bias; Slater 2002, Texeira et al. 2013) or are destroyed or carried away by vehicles (Stewart 1973, Mumme et al. 2000). Because these biases have never been formally quantified in the context of vehicle collisions, substantial uncertainty remains about to what degree they contribute to under-estimation of roadkill mortality rates. Future research of these bias sources is necessary for fully understanding the magnitude of bird mortality caused by vehicle collisions.

Numerous biotic and abiotic factors influence bird collision mortality rates along roads. These correlates collectively result in bird fatalities being clustered along particular road segments (Clevenger et al. 2003, Smith and Dodd 2003, Glista et al. 2008, Gunson et al. 2010). Further research is needed to clarify the combination of factors that lead to carcass clustering (e.g., habitat, characteristics of the road and its cleared corridor, and community composition and population abundance of birds) and to assess how these correlates vary seasonally and regionally. When possible, studies should employ sampling designs that allow for separation of often-confounded mortality correlates (e.g., road width, traffic volume, and traffic speed).

The negative bias contributed to mortality rate estimates by scavenger removal is amplified with increasing time intervals between surveys. This occurs because—with all other factors held constant—more collisions occur between surveys, and a greater proportion of carcasses are removed by scavengers. Because carcass removal adjustment factors are less accurate across long search intervals (Smallwood 2013) and because carcass removal rates appear to be especially high along roadways (Bruun-Schmidt 1994, Antworth et al. 2005, Santos et al. 2011, Texeira et al. 2013), optimal search intervals for documenting roadkill mortality are very short (e.g., sampling on alternate days for large birds and daily for small birds; Santos et al. 2011). Because the search intervals in the studies we used were between 2 and 15 days, mortality rates in individual studies could have been substantially under-estimated. This under-estimation could have contributed negative bias to our mortality estimates.

In addition to using long search intervals for carcass surveys, the studies we used conducted surveys using various transportation methods, including foot, bicycle, and automobile. Because of the relatively high speed at which sampling is conducted, automobile surveys usually detect only a small fraction of carcasses (Slater 2002, Gerow et al. 2010, Guinard et al. 2012, Texeira et al. 2013). In the sample of mortality rates extracted from studies meeting our inclusion criteria, the majority of rates (15 of 20) were based on automobile surveys, and estimated mortality rates for automobile surveys averaged 2.3 times lower than for other survey types. Therefore, the use of automobile surveys may have contributed additional under-estimation bias to our mortality estimates. The use of automobile surveys may have also influenced our species summary, with surveys likely over-representing large-bodied species (e.g., raptors and corvids) that are relatively easy to detect from a fast-moving automobile.

MANAGEMENT IMPLICATIONS

The large magnitude of mortality caused by vehicle collisions combined with the potential for impacts at the population level highlights the need for conservation and management attention to mitigate this threat. Mitigation efforts may be most relevant at areas known to experience exceptionally high rates of collision mortality (e.g., clear examples include the studies that were identified as statistical outliers for our mortality estimate). Following identification of mortality hotspots, potential options to reduce bird collision mortality along roads include (see also Boves and Belthoff 2012, Bishop and Brogan 2013) placing flight deflectors along roadsides to force birds to fly above vehicle height (Bard et al. 2001, Ramsden 2003, Gomes et al. 2009), locally reducing speed limits and erecting signage to alert drivers, reducing or removing the amount of favorable bird habitat

along roadsides, and using visual or auditory deterrents. All of these approaches have rarely been implemented and remain largely untested. Research is therefore needed to determine which combinations of the above approaches are most effective at reducing mortality and to clarify how responses vary by bird species, region, habitat, season, and road type. Identification and implementation of effective conservation measures is especially crucial given the increasing length of U.S. roadways, increasing traffic volume, and an increasing number of direct and indirect anthropogenic threats to bird populations.

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Mature semiarid chaparral ecosystems can be a significant sink for atmospheric carbon dioxide

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Abstract

Carbon flux in arid and semiarid area shrublands, especially in old-growth shrub ecosystems, has been rarely studied using eddy covariance techniques. In this study, eddy covariance measurements over a 100-year old-growth chamise-dominated chaparral shrub ecosystem were conducted for 7 years from 1996 to 2003. A carbon sink, from −96 to $-155\,g\,C\,m^{-2}\,yr^{-1}$, was determined under normal weather conditions, while a weak sink of $-18\,g\,C\,m^{-2}\,yr^{-1}$ and a strong source of $207\,g\,C\,m^{-2}\,yr^{-1}$ were observed as a consequence of a severe drought. The annual sink strength of carbon in the 7-year measurement period was $-52\,g\,C\,m^{-2}\,yr^{-1}$. The results from our study indicate that, in contrast to previous thought, the old-growth chaparral shrub ecosystem can be a significant sink of carbon under normal weather conditions and, therefore, be an important component of the global carbon budget.

Keywords: arid and semiarid area, carbon balance, chaparral ecosystem, eddy covariance, evapotranspiration (ET), net ecosystem exchange (NEE), old-growth, shrub, southern California

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Introduction

Human activity has increased global atmospheric CO_2 by about 30%, from 280 ppm to over 360 ppm, since the beginning of the Industrial Revolution (Amthor, 1995; Houghton *et al*., 2001), and this increase will continue if action is not taken. The average annual anthropogenic CO_2 emissions of approximately $8\,Gt\,C\,yr^{-1}$ ($6.3\,Gt\,C\,yr^{-1}$ from combustion of fossil fuels and $1.6\,Gt\,C\,yr^{-1}$ from changes in land use) is greater than the sum of atmospheric accumulation ($3.2\,Gt\,C\,yr^{-1}$), ocean uptake ($1.7\,Gt\,C\,yr^{-1}$) and land–atmosphere flux ($1.4\,Gt\,C\,yr^{-1}$). An additional sink of approximate 2–$4\,Gt\,C\,yr^{-1}$ is required to balance the global carbon budget (Schimel *et al*., 2001). Terrestrial ecosystems are thought to be the biggest reservoirs for this 'missing carbon' and could mitigate the rising levels of CO_2 in the atmosphere. Knowledge of the dynamics of carbon in terrestrial ecosystems is essential for understanding global carbon balance and for future management. In recent years, there has been a concerted effort to determine the magnitude, patterns and controls of terrestrial carbon flux using eddy covariance techniques (Valentini *et al*., 1996; Baldocchi *et al*., 2001; Yu *et al*., 2005). To this end, regional networks of eddy covariance towers have been established. These include Ameriflux and Fluxnet-Canada in North America, Large Scale Biosphere–Atmosphere Experiment in Amazonia (LBA) in South America, CarboEuroFlux in Europe, OzFlux in Australasia, China Flux and Asia Flux in Asia, and AfriFlux in Africa (Fluxnet http://daac.ornl.gov/FLUXNET/). Because of the large uncertainty of terrestrial fluxes (Tans *et al*., 1990), and the desire, by some, to emphasize large terrestrial carbon sinks, there has been a bias toward flux measurements in systems anticipated to represent large current or future CO_2 flux or carbon sequestration potential (Running *et al*., 1999). This has resulted in a preponderance of forest and agricultural studies (53% and 21%, respectively, of all Fluxnet eddy towers), and a relative paucity of studies in nonforest and nonagricultural ecosystems (a total of 26% of all Fluxnet towers), especially those expected to be of low current and future net carbon uptake (Fluxnet http://daac.ornl.gov/FLUXNET/). As a result, many stressed ecosystems (Buchmann & Schulze, 1999; Running *et al*., 1999; Reichstein *et al*., 2002; Hastings *et al*., 2005), as well as old-growth ecosystems (Jarvis, 1989; Melillo *et al*., 1996; Carey *et al*., 2001), have been little studied even though they may be significant in their contribution to current carbon balance and may be important in carbon sequestration or release in the future (Oechel *et al*., 1993, 2000).

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Among ecosystems poorly understood and underrepresented in the eddy covariance studies of CO_2 flux are arid and semiarid ecosystems, especially shrublands. Arid and semiarid woody shrublands make up approximately 35% of the global terrestrial surface area and 24% of the global soil organic carbon, and 16% of the global aboveground biomass (Atjay *et al*., 1979; Shmida, 1985), yet represent only 6% of the currently installed eddy covariance towers in Ameriflux and 17% in Fluxnet (based on the eddy tower information on Fluxnet http://daac.ornl.gov/FLUXNET/). We lack sufficient data and understanding of arid and semiarid ecosystems to properly parameterize and validate models of current and future global terrestrial carbon balance. Shrublands are a major component of arid and semiarid ecosystems worldwide and little effort has been made to adequately understand them. Given their large area and potentially large carbon sink or source, woody shrubs deserve serious study.

Despite the vigorous growth of global carbon research, the role of old-growth stands in the carbon balance remains a controversy. Carbon exchanges between old stands and the atmosphere were predominantly assumed to be in a state of dynamic equilibrium (Odum, 1969; Salati & Vose, 1984) and an insignificant carbon sink (Jarvis, 1989; Melillo *et al*., 1996). However, in recent years, observations (Malhi *et al*., 1998; Carey *et al*., 2001; Paw *et al*., 2004), ecosystem models (Chambers *et al*., 2001) and biomass inventories (Phillips *et al*., 1998) have suggested that old-growth forests can be significant carbon sinks. The underestimate of carbon sequestration by old-growth terrestrial stands could be as high as 4.3–7.6% of the missing sink (Carey *et al*., 2001). Therefore, old-growth stands may have been seriously underestimated in their capability of carbon uptake globally. This may be due, in part, to applying mono-specific, even age-growth models to natural stands, as well as to assuming that the ratio of respiring biomass to photosynthetic canopy increases as age increases (Carey *et al*., 2001). As a result of concerns for the climatic effects of increasing atmospheric CO_2, the identification of the source sink relationships of natural ecosystems (including old and undisturbed ecosystems) has recently drawn considerable attention (Keeling *et al*., 1996; Malhi *et al*., 1998; Carey *et al*., 2001). The paradigm regarding the insignificant carbon sequestration of old-growth forests has been revaluated (Malhi *et al*., 1998; Carey *et al*., 2001; Knohl *et al*., 2003; Paw *et al*., 2004). However, the assessment of carbon uptake for the old-growth shrubland has remained largely unexplored.

In this study, we report on the net ecosystem exchange (NEE) of CO_2 for 7 years in a 100-year-old mature Mediterranean-type chamise (*Adenostoma fasciculatum*)-dominant chaparral ecosystem in southern California using eddy covariance techniques. This semiarid Mediterranean type chaparral ecosystem occurs in the southwest United States and northern central Mexico. Our study site lies at a location only 20 km from the desert floor to the east and in the position of the climatic gradient between desert and semiarid (Scheid & Zedler, 1983). It was selected to provide insights into the carbon dynamics of mature arid and semiarid shrub ecosystems. Average historical fire frequency for this chaparral-type ecosystem is about 35 years (Zammit & Zedler, 1994). Stands older than 60 years have been considered 'decadent' (Hanes, 1971) as their physiological functions (Rundel & Parsons, 1980), biomass, leaf area, and cover may be decreased (Oechel & Reid, 1984; Reid, 1985) and tissue respiration increased (Oechel & Reid, 1984). Thus, chaparral with an age of 100 years was considered 'mature' or 'old-growth,' even 'over-mature' or 'senescent.'

Based on previous studies, we asked: (1) is this 100-year-old chaparral stand senescent at the level of ecosystem metabolism, specifically in carbon exchange with the atmosphere (i.e. little or no net CO_2 uptake)? (2) What is the status and strength of any sink or source? and (3) what is the relationship between NEE and interannual variability in rainfall, the major limiting factor in most arid and semiarid ecosystems? To answer these questions, we quantified the magnitude of NEE, addressed the seasonality and interannual variability of NEE for this semiarid open shrubland ecosystem and monitored climatic and other environmental parameters.

Materials and methods

Site description

This study was conducted at the Sky Oaks Field Station (33°23′N, 116°37′W), operated by San Diego State University and located in southern California, at about 1420 m elevation and 75 km east of Pacific Ocean. This region lies at the climatic gradient between desert and semiarid area and is characterized by a Mediterranean climate with cold, wet winters and hot, dry summers. Most precipitation falls between the months of November and April (Poole & Miller, 1975) with an average annual precipitation of 349 mm. Light snow occurs several days during the winter, and occasionally hot, dry Santa Ana winds blow from northeast over the desert in the late summer and fall. This stand was a chamise (*A. fasciculatum*)-dominated chaparral ecosystem, which is the typical chaparral type in California occupying most of the hills and lower mountain slopes (Hanes, 1971, 1977). In addition, Red Shank (*Adenostoma sparsifolium*) was a major component of this ecosystem.

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Chamise is a drought tolerant scherophyllous evergreen shrub with a belowground lignotuber. While chaparral typically burns on average about every 35 years, the last fire at this site was in 1901 (Zammit & Zedler, 1994). Soil types include Sheephead (Ultic Haploxeroll) and Tollhouse (Entic Haploxeroll), both of which are considered loamy, mixed, mesic and shallow. The terrain is rough broken land over substrates of granite or micaceous schist. Soil fertility is quite low (Greenwood, 1983).

Environmental measurements

The following micrometeorological variables were measured every 10 s and stored as 30 min means using a data logger (CR23X, Campbell Scientific Inc., Logan, UT, USA): wind vector (RM Young Wind Sentry, R. M. Young Company, Traverse, MI, USA) at 6 m above the ground, relative humidity (RH) and air temperature (HMP45C, Vaisala Inc., Helsinki, Finland) at both 5.8 and 2.5 m, incident solar radiation between 400 and 1100 nm (LI-200S pyranometer, Li-COR Inc., Lincoln, NE, USA) and photosynthetically active radiation (PAR; LI-190SB, Li-COR Inc.) at 2.3 m, net radiation (Q*7.1, Radiation Energy Balance Systems (REBS) Inc., Seattle, WA, USA) at 2.5 m above ground, precipitation (TR525, Texas Electronics Inc., Dallas, TX, USA) at 2.3 m, soil temperature (type-T thermocouples, Omega Engineering, Stamford, CT, USA) at 2, 5, 10, 20, 30, and 40 cm depths, soil moisture (Hydra, Vitel Inc., Chantilly, VA, USA before August 30, 2002 and CS615, Campbell Scientific Inc. Logan, UT, USA after August 30, 2002) at 5, 10, 20, 30, and 40 cm depths, and atmospheric pressure (PTB101B, Vaisala Inc.), and four soil heat flux plates (HFT3, REBS Inc.) at 2 cm depth below the ground surface to measure ground heat flux.

Eddy covariance measurements

NEE was measured using the eddy covariance techniques (Baldocchi *et al.*, 1988). Eddy covariance measurements were made from March 17, 1997 to July 16, 2003 when the stand and equipment were consumed and measurements were interrupted by a natural fire thereafter. Fluctuations in vertical, streamwise and lateral wind speed, wind direction, and temperature were measured at 10 Hz using a three-dimensional sonic anemometer–thermometer (before October 25, 2001, Model SWS-211/3K, Applied Technologies Inc, Boulder, CO, USA, then switched to a Windmaster Pro, Gill Instruments Ltd., Lymington, Hampshire, UK). CO_2 and H_2O vapor fluctuations were measured using a fast response, 10 Hz, closed-path infra-red gas analyzer (IRGA) with a pressure transducer (LI-6262, Li-COR Inc.) on dates before October 25, 2001. After this date, CO_2 and H_2O vapor fluctuations were measured using a 10 Hz open path analyzer (LI-7500, Li-COR Inc.). The sonic anemometer and open-path IRGA were 4.5 m above the ground surface and 2.5 m above the mean height of the vegetation. Calibration was carried out every 2–4 weeks using a gas standard for CO_2 and a dew point generator (LI-610, Li-COR Inc.) for water vapor.

Raw CO_2 and H_2O vapor fluctuations were recorded as mean voltages and converted to densities by multiplying by the requisite calibration constant (Vourlitis & Oechel, 1997). Mass (CO_2 and H_2O vapor), energy and momentum fluxes were computed following a coordinate rotation of the vertical and lateral wind vectors, and stored on a laptop computer as 30 min averages using a 400 s running mean and digital recursive filtering technique (McMillen, 1988). Carbon and water flux estimates were corrected for the simultaneous flux of heat and H_2O vapor for the measurements from the open-path IRGA and only H_2O vapor correction for the measurements from the closed-path IRGA (Webb *et al.*, 1980; Suyker & Verma, 1993).

Eddy covariance data reduction and gap filling

The percentage of eddy covariance data collected during the measurement period varied from 60% to 99% among 7 years. Data gaps were primary caused by power, computer, or sensor failures, instrument calibration, and data rejection following quality assessment during data postprocessing. The rejection criteria used to screen data in the postprocessing included: rain and snow events, incomplete 30 min data collections, out-of-range signals from either the sonic anemometer or IRGA, spikes with the standard deviation of CO_2, H_2O and/or temperature variance greater than 2 from the mean.

A critical friction velocity (u^*) threshold is often used to exclude eddy flux data and avoid the underestimation of carbon source strength under calm wind conditions (Goulden, 1996; Reichstein *et al.*, 2002). At our study site, the u^* threshold was determined to be $0.275\,m\,s^{-1}$ (Fig. 1). At this point, increasing u^* yielded little increase in apparent CO_2 efflux. The night-time NEE data showed a linear increase with u^* when $u^* < 0.275\,m\,s^{-1}$, and an asymptotic NEE of approximately 0.042 ($mg\,CO_2\,m^{-2}\,s^{-1}$) after $u^* \geq 0.275\,m\,s^{-1}$ (Fig. 1). Carbon flux in the range where $u^* < 0.275\,m\,s^{-1}$ were corrected based on the relationship between u^* and night-time carbon flux with $u^* \geq 0.275\,m\,s^{-1}$.

For half-hourly data, short gaps of 1/2 h during the daytime and 1/2 to 3 h during the night-time with relatively uniform conditions or rates of environmental change were filled by linear interpolation (Falge *et al.*, 2001). The mean diurnal variation with a 10-day window was used to fill larger gaps (Falge *et al.*,

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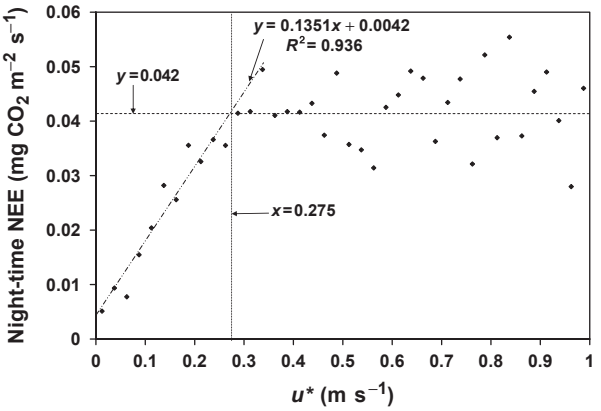

Fig. 1 Night-time net ecosystem exchange (NEE) as a function of friction velocity (u^*). Data measured during 1996 to 2003 were sorted by u^* with intervals of $0.025\,m\,s^{-1}$ and the average values are presented. The threshold of u^* was determined to be $0.275\,m\,s^{-1}$. The night-time NEE data showed a linear increase with u^* when $u^* < 0.275\,m\,s^{-1}$, and an asymptotic NEE of approximately 0.042 ($mg\,CO_2\,m^{-2}\,s^{-1}$) after $u^* \geq 0.275\,m\,s^{-1}$.

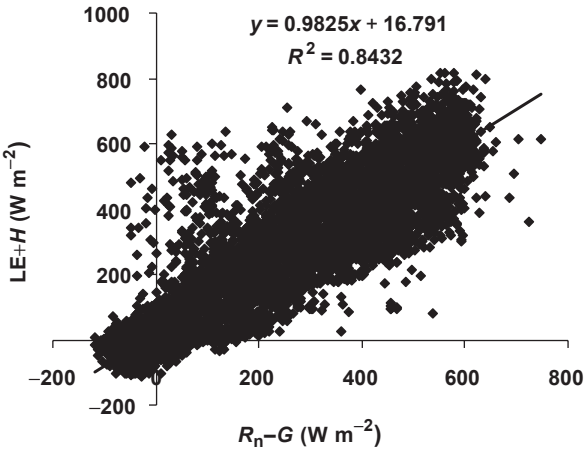

Fig. 2 Energy enclosure at 1999 to show an example of the relationship between $H + LE$ measured by eddy covariance and $R_n - G$ measured by meteorological sensors.

2001). And the half-hourly data were integrated into daily data. The remaining gaps in daily NEE were filled using BIOMAP modeling (BIOMAP http://www.fs.fed.us/pnw/corvallis/mdr/mapss/biomap.htm) and water vapor evapotranspiration (ET) were filled by BiomeBGC modeling (Thornton *et al*., 2002). For annual sums of NEE and ET, a large gap was not filled from August 5, 1998 to April 4, 1999, which was too large to estimate with confidence. However, NEE and ET during this period were estimated for long-term cumulative fluxes from precipitation.

Data in the measurement period were processed and analyzed based on the hydrological year, which started on July 1st and ended on June 30th of the following year. Each hydrological year was divided into three seasons: the dry season (July 1st to October 31st, generally hot temperatures and low water availability), the winter season (November 1st to February 28th, generally adequate water but low radiation and temperatures) and the growing season (March 1st to June 30th, generally favorable warm and moist conditions and plants were typically growing fastest).

Results

System performance

Energy balance closure was used to assess the performance of the eddy covariance system (McMillen, 1988; Vourlitis *et al*., 2001). The 30 min values of sensible heat flux (H) plus latent heat flux (LE) were compared against the net radiation (R_n) minus ground heat flux (G) for each hydrological year (see Fig. 2 for an example at 1999). The least-square regression curves were fitted to the graphs. The goodness of fit was quantified with an average r^2 of 0.84 ± 0.05, average slope of regression was 0.93 ± 0.06 and the average intercept was $22 \pm 14\,W\,m^{-2}$ during measuring period. These results indicated that our eddy covariance system had generally good performance, but slightly underestimated $H + LE$ compared with $R_n - G$. This energy closure deficit might be explained by the difference among the sampling frequencies and measuring footprints of various sensors. In addition, the energy stored under plant canopy and in the soil layer between the soil surface and the soil heat flux plates was not considered.

Environmental conditions

Over the measurement period of 1996–2003, the overall annual mean of R_n, PAR, RH, air temperature and surface soil temperature at the depth of 0–30 cm were $127\,W\,m^{-2}$, $460\,\mu mol\,m^{-2}\,s^{-1}$, 43%, 14 and 15 °C, respectively. The interannual patterns of the radiation, air temperature and RH were similar from year to year, while the magnitude and temporal distribution of precipitation at the study site varied significantly. The annual total precipitation during the measurement period ranged from 175.3 mm (2001–2002) to 804.7 mm (1997–1998) with a mean of 374.7 mm during the study period.

The environmental variables showed strong seasonality at the study site. According to the calculated overall seasonal means in 1996–2003, the winter season had lower radiation (R_n $60\,W\,m^{-2}$ and PAR $260\,\mu mol\,m^{-2}\,s^{-1}$) than the dry season ($152\,W\,m^{-2}$ and $547\,\mu mol\,m^{-2}\,s^{-1}$) and the growing season ($160\,W\,m^{-2}$

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Table 1 Seasonal and annual means of micrometeorological variables during the measurement period of 1996–2003

Season	Net radiation ($W\,m^{-2}$)	PAR ($\mu mol\,m^{-2}\,s^{-1}$)	Air temperature (°C)	RH (%)	Soil surface temperature at 2 cm depth (°C)	Precipitation (mm)	Soil moisture between 0 and 30 cm (%)
Dry	152	547	21.0	31	22.5	64.4	9
Winter	60	260	8.3	48	6.2	209.5	13
Growing	160	550	13.1	48	15.6	100.7	17
Overall annual average	124	452	14.1	42	14.8	374.7*	13

The dry season started from July 1st and ended on October 31st, the winter season was from November 1st to February 28th in the following year, and the growing season was from March 1st to June 30th.
*Annual total precipitation.
PAR, photosynthetically active radiation; RH, relative humidity.

and 550 $\mu mol\,m^{-2}\,s^{-1}$; Table 1). However, there was no significant radiation difference between the growing season and the dry season. Both air and soil temperature at the surface were highest in the dry season (21.0 and 22.5 °C, respectively), with lower values duirng the growing season (13.1 and 15.6 °C, respectively) and the winter season (8.3 and 6.2 °C, respectively). RH was similar in the winter season and the growing season (48% and 48%), but lower in the dry season (31%). The winter season commonly had the greatest rainfall, followed by the growing season, while the dry season had the least, approximately 209, 100.7 and 64.4 mm, respectively, on average. Soil moisture was highest in the growing season (17% volumetric content) followed by the winter season (13%), and the dry season had lowest soil moisture (9%).

Net ecosystem exchange of carbon and water vapor

The overall averaged seasonal NEE in 1996–2003 was calculated to be a large sink of $-103.9\,g\,C\,m^{-2}\,season^{-1}$ during the growing season (Table 2), which was associated with a high leaf area index (LAI), mild temperature and sufficient water supply. The average NEE of the dry season and the winter season were 27.3 and $26.3\,g\,C\,m^{-2}\,season^{-1}$, respectively. Both seasons were weak sources, which resulted from NEE being limited by low radiation and temperature in the winter season and by low water availability in dry season (Krause, 1975). The highest seasonal ET occurred during the growing season with 192.8 $mm\,season^{-1}$ (Table 2). In that period, ET was almost double the amount of precipitation (100.7 $mm\,season^{-1}$). The large ET in this season was related to greater soil water availability, warm temperatures, high radiation and vigorous plant transpiration. During the dry season, ET

Table 2 Average seasonal net ecosystem exchange (NEE), evapotranspiration (ET) and precipitation in the measurement period of 1996–2003

Season	NEE ($g\,C\,m^{-2}$)	ET (mm)	Precipitation (mm)
Dry	27.3	107.5	64.4
Winter	26.3	80.4	209.5
Growing	−103.9	192.8	100.7

Negative values of NEE denoted for ecosystem carbon sink from atmosphere, and positive values of NEE denoted for ecosystem carbon source to atmosphere.

(107.5 $mm\,season^{-1}$) was higher than the seasonal precipitation (64.4 $mm\,season^{-1}$). This suggested that chaparral plants in this mature stand were able to access the water reserves stored at depth of weathered bedrock to supply their water needs when the incoming precipitation did not meet their demands (Sternberg *et al.*, 1996). ET and precipitation were calculated to be 80.4 and 209.5 $mm\,season^{-1}$, respectively, in the winter season, in which ET was lower than precipitation due to limited radiation levels and temperatures.

Annual total NEE varied greatly from year to year. Listed according to the sink strength from strong to weak, then to source, the hydrological year of 2000–2001 presented a strongest carbon sink of $-155\,g\,C\,m^{-2}$ (Fig. 3), followed by a carbon sink of $-100\,g\,C\,m^{-2}$ in 1999–2000, and a carbon sink in 1997–1998 was $-96\,g\,C\,m^{-2}$. The annual carbon budget for the period of 2001–2002 was close to being in balance with a weak carbon sink of $-18\,g\,C\,m^{-2}$. In contrast, the period of 2002–2003 showed a strong carbon source of $207\,g\,C\,m^{-2}$. Data gaps limited the ability to estimate annual NEE and ET in the hydrological years of 1996–1997 and 1998–1999.

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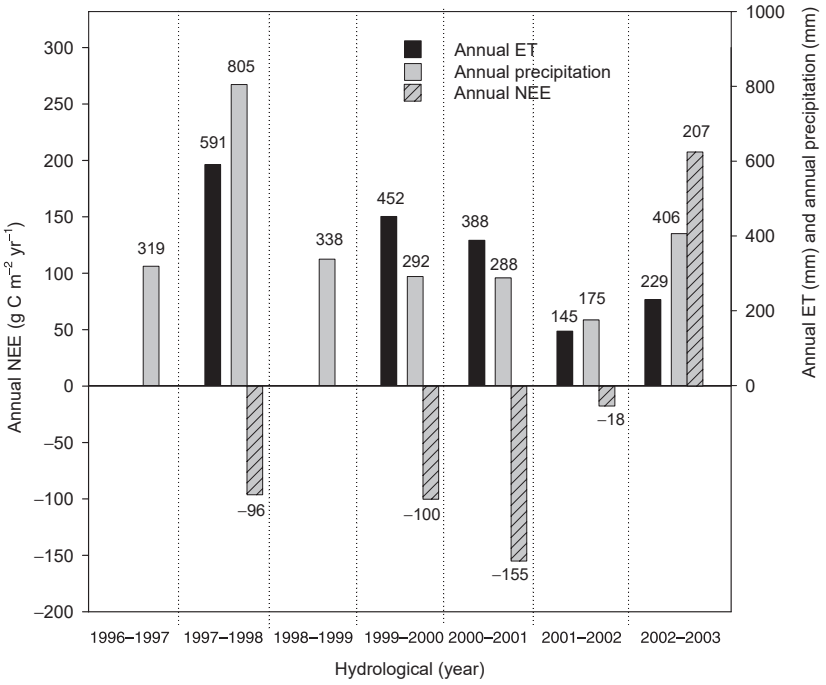

Fig. 3 Total annual net ecosystem exchange (NEE), evapotranspiration (ET) and precipitation over the measurement period of 1996–2003. Data availability limited the calculation of NEE and ET in 1996–1997 and 1998–1999.

The 60-year average annual precipitation was 349 mm at our study site (from 1949 to 2002), which was extrapolated from the nearby weather station at Palomar Mountain Observatory using MTCLIM method (Kimball *et al*., 1997; Thornton & Running, 1999). This value is close to the annual mean precipitation of 374.7 mm during the measurement period of 1996–2003. If the normal range was defined as precipitation variation within ±100 mm from the 60-year mean (349 mm), then the hydrological year of 1997–1998 (805 mm) can be considered a wet year, 1996–1997 (319 mm), 1998–1999 (338 mm), 1999–2000 (292 mm), 2000–2001 (288 mm) and 2002–2003 (406 mm) can be consider normal years, and 2001–2002 (175 mm) should be considered a severe drought year (Fig. 3).

The largest ET (591 mm) was recorded in 1997–1998, which coincided with the period of heaviest rain (805 mm) resulting from El Niño effects in the region (Fig. 3). The lowest ET (145 mm) occurred in 2001–2002, which also coincided with the lowest precipitation recorded (175 mm). This very low ET may have been the result of low soil water availability, plant stomatal closure, leaf and branch shedding and/or plant death from the severe drought (Dallman, 1998). The water budget between incoming rain and outgoing water vapor in 2001–2002 were similar with ET only 30 mm lower than the precipitation. The annual ET in 1997–1998 and 2002–2003 was 591 and 229 mm, respectively, which were much lower than precipitation for the same periods, 804 and 406 mm, respectively (Fig. 3). This might be a consequence of water loss as drainage or runoff in intensive rain events. In contrast to this, the annual ET in 1999–2000 and 2000–2001 (451 and 388 mm, respectively) exceeded the corresponding precipitation (291 and 288 mm, respectively; Fig. 3), which indicates that chamise has deep tap roots that can reach water at considerable depths to supply their biological demands (Krause, 1975; Poole & Miller, 1975; Jones & Graham, 1993). This survival strategy reflects the long-term adaptation of chaparral shrubs to the tough environmental conditions with low water availability.

To estimate NEE and ET during the full 7-year period, including the large gap, we plotted averaged daily NEE/ET against annual precipitation for each available season in each hydrological year. The least-square regression lines were fitted to find a regression equation for the dry, winter and growing season, respectively. Then the remaining gaps of cumulative NEE and ET were filled using these equations accordingly. This allowed us to generate cumulative estimates of NEE ($-361.3\,g\,C\,m^{-2}$) and ET (2839 mm) in the full 7-year period from 1996 to 2003 (Fig. 4). The observed precipitation in the same period was 2623 mm, which was 216 mm less than estimated ET. These calculations indicate that this ecosystem sequestered carbon at an approximate rate of $-52\,g\,C\,m^{-2}\,yr^{-1}$ and a ET rate of

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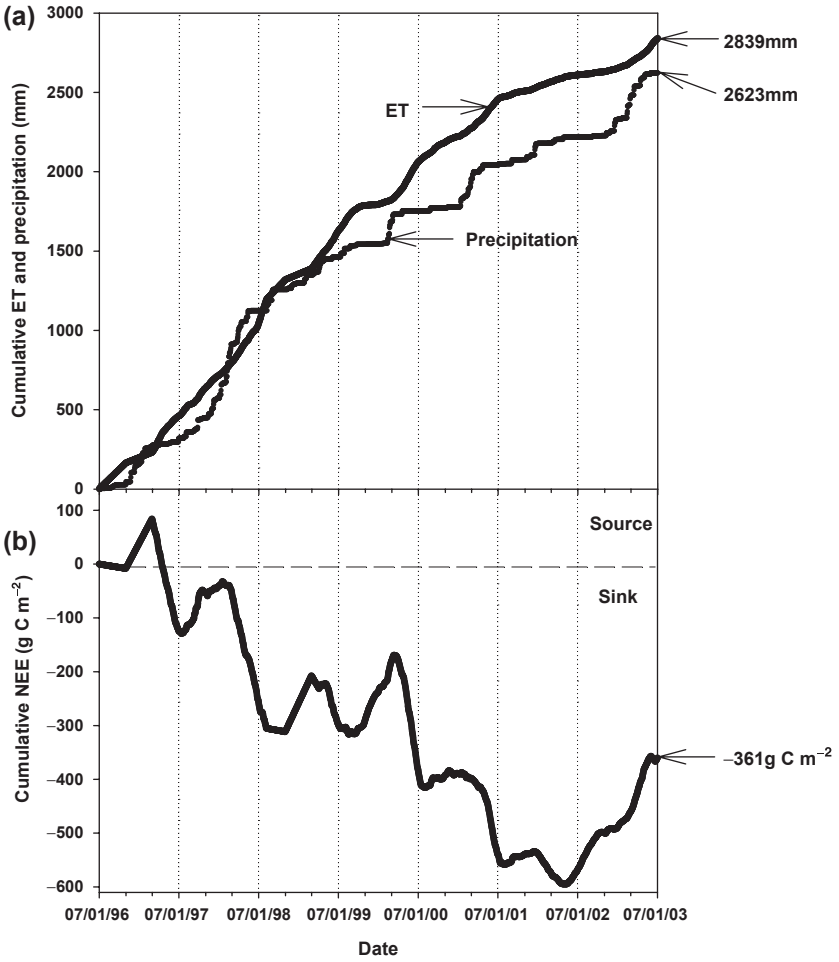

Fig. 4 (a) Cumulative evapotranspiration (ET) and precipitation and (b) cumulative net ecosystem exchange (NEE) during the 7-year measurement period of 1996–2003. The large gaps in 1996–1997 and 1998–1999 were filled according to the regression relationship between daily NEE/ET and annual precipitation.

406 mm yr^{-1} on average over the measurement period. Precipitation was about 30 mm yr^{-1} less than the estimated ET. The extra water supply for ET likely came from ground water draining from up slope during the rainy season and reserved at depth in the soil.

Discussion

Carbon sink in old-growth chaparral ecosystems

The annual NEE observed in this 100-year-old mature chaparral shrub ecosystem was −96, −100 and 155 g C m^{-2} yr^{-1} in 1997–1998, 1999–2000 and 2000–2001, respectively, under normal or humid weather conditions. These results are consistent with findings from many old-growth forest sites in the Fluxnet program (Malhi *et al.*, 1998; Carey *et al.*, 2001; Knohl *et al.*, 2003; Paw *et al.*, 2004) suggesting that old-growth stands of various types can be significant sinks of carbon. The observation of a carbon sink in this study is in opposition to Hanes' statement that chaparral stands, especially chamise-chaparral, older than 60 years are decadent with the respect to carbon sequestration (Hanes, 1971). Why this and other 'old-growth' stands are a sink of carbon is a source of continuing speculation. It has been suggested that the possible causes for the old-growth stands to actively sequester carbon since the late 20th century (Phillips *et al.*, 2002) include increase of CO_2 fertilization of plant growth from the fast rise of atmospheric CO_2 (West *et al.*, 1993; Oechel *et al.*, 1994; Grace *et al.*, 1995), and nutrient fertilization from nitrogen deposition (Rasse, 2002). Alternatively, so-called 'old-growth' chaparral shrub ecosystems may not senesce, and may maintain a productive ratio of gross primary production (GPP) to plant and soil respiration.

Global changes, extreme events and disturbances can markedly influence NEE, and even change the sign of fluxes. Tundra changed from a long term net carbon sink to a source as a result of global warming

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and drying of the soil (Oechel *et al.*, 1993). Fire changed a tallgrass prairie from net carbon sink to net carbon source (Suyker & Verma, 2001), and severe water stress reversed a rangeland from an average sink of $-120\,g\,C\,m^{-2}\,yr^{-1}$ to a net carbon source of $155\,g\,C\,m^{-2}\,yr^{-1}$ (Meyers, 2001). When this mature chaparral site experienced a severe drought in year 2001–2002 with precipitation of 175.3 mm (60-year mean was 349 mm), ecosystem exchange of carbon shifted from a strong net sink of $-155\,g\,C\,m^{-2}\,yr^{-1}$ in the previous year to a weak sink of $-18\,g\,C\,m^{-2}\,yr^{-1}$ in 2001–2002. This was due to the weakened physiological functions and self pruning of leaves and branches, which resulted in reduced active photosynthetic area. The negative effects of severe drought on carbon sequestration extended into the following year. When the rainy season brought adequate rainfall (406 mm) in the subsequent winter and spring, a large carbon loss ($207\,g\,C\,m^{-2}\,yr^{-1}$) was observed from the ecosystem in 2002–2003. This large loss could be explained in several ways. Firstly, soil decomposition and microbial activity accelerated due to increased water availability coupled with improved accessibility to organic substrates from previously undecomposed organic matter and new litters following leaf and branch shedding. Secondly, over the short term, high concentrations of CO_2 likely accumulated in the soil pores during drought. During rain events, rain water may have filled soil pores displacing CO_2 from soil (Huxman *et al.*, 2004). Thus, the microbial respiration and the physical efflux from the soil appeared to have outweighed the photosynthetic assimilation rates given reduced plant vitality and leaf area resulting in a large net carbon loss from the ecosystem in 2002–2003.

However, as an ecosystem that is adapted to hot and dry weather conditions, chaparral ecosystems have the ability to recover rapidly from the severe drought effects if the length of drought is not excessive. The time period for this chaparral ecosystem to recover from a drought can be as short as 1 year. This recovery was indicated in an adjacent area of the same mature chaparral stand that did not burn in 2003, and showed a moderate carbon sink of $-77\,g\,C\,m^{-2}\,yr^{-1}$ in 2004–2005 with an adequate rain fall of 511 mm.

Comparison with other studies

The number of eddy covariance measurement in old-growth stands is increasing and provides us better insights about carbon exchange in old-growth ecosystems. While some results support the conventional ecological assumption that old-growth stands are in dynamic equilibrium (DeBell & Franklin, 1987; Franklin, 2000; Saleska *et al.*, 2003), many old-growth forest studies present moderate to strong carbon sequestration. The old-growth forest of mixed whitebark pine (*Pinus albicaulis, Engelmann*) and a subalpine species (*Abies lasiocarpa, Nuttal*) in the Rocky Mountains showed a significant carbon sink (Carey *et al.*, 2001). A 500-year-old old-growth mixed forest of Douglas-fir and western hemlock in southwestern Washington exhibited a significant net annual carbon uptake of -150 to $-190\,g\,C\,m^{-2}\,yr^{-1}$ (Field & Kaduk, 2004; Paw *et al.*, 2004). Three boreal forests of old aspen, old black spruce and old jack pine were observed to have carbon uptake values of -122, -35 and $-78\,g\,C\,m^{-2}\,yr^{-1}$, respectively (Griffis *et al.*, 2003). Inventory studies indicated that the biomass of an undisturbed old-growth tropical forest increased in recent years (Phillips *et al.*, 2002). The carbon sink in this old-growth tropical forest was confirmed by eddy covariance measurements and other methods, which was estimated to be somewhere between a moderate sink of $-40\,g\,C\,m^{-2}\,yr^{-1}$ and a strong sink of $-590\,g\,C\,m^{-2}\,yr^{-1}$ (Malhi *et al.*, 1998; Tian *et al.*, 2000; Chambers *et al.*, 2001). The old-growth chaparral in this study sequestered carbon between -96 and $-155\,g\,C\,m^{-2}\,yr^{-1}$ in the measurement period under normal weather conditions, which was comparable with many published results from the old-growth forests worldwide. These findings demonstrate that old-growth stands of various types can be significant with respect to carbon sequestration, and the paradigm that old-growth ecosystems are in carbon equilibrium is not necessary true.

To accurately quantify landscape level carbon fluxes, various forms of disturbance should be considered. But current eddy covariance studies in shrub ecosystems are highly limited, thus constraining the comparison of our results to other shrub ecosystems. However, by comparison with those arid and semiarid ecosystems for which we do have data, a climax mature desert shrub site exhibited a net carbon sink of -39 and $-52\,g\,C\,m^{-2}\,yr^{-1}$ over 2 years (Hastings *et al.*, 2005). Carbon sink was about $-12\,g\,C\,m^{-2}\,yr^{-1}$ for a broad-leafed semiarid savanna in Southern Africa (Veenendaal *et al.*, 2004). The annual NEE observed over Mediterranean annual grassland in California was a sink of $-132\,g\,C\,m^{-2}\,yr^{-1}$ in 2000–2001 season and a source of $29\,g\,C\,m^{-2}\,yr^{-1}$ in 2001–2002 season (Xu & Baldocchi, 2004). Carbon gain over a *Picea abies* conifer forest ecosystem was $-450\,g\,C\,m^{-2}\,yr^{-1}$ (Valentini *et al.*, 2000) in Italy. Therefore, NEE of this mature chaparral shrub ecosystem ranging from -96 to $-155\,g\,C\,m^{-2}\,yr^{-1}$ fell between the desert ecosystem, the grassland, and forests in the arid and semiarid area.

The sink strength of this mature chaparral was even comparable with ecosystems in other biomes. This chaparral ecosystem gained more carbon than nonforest

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ecosystems, such as tundra (40 g C m^{-2} yr^{-1}, Oechel *et al.*, 2000), tall-grass prairie (0 g C m^{-2} yr^{-1}, Suyker & Verma, 2001), grazed grassland (41 g C m^{-2} yr^{-1}, Meyers, 2001), and even more than some evergreen forests, such as *Pinus sylvevestris* (−5 to 90 g C m^{-2} yr^{-1}, Lindroth *et al.*, 1998) and cypress (−37 to −84 g C m^{-2} yr^{-1}, Clark *et al.*, 1999). Although shrublands are commonly believed to sequester less carbon than that of forests, the chaparral stand studied sequestered carbon at a rate comparable with many other forest ecosystems, such as a beech ecosystem in Denmark (−124 to −169 g C m^{-2} yr^{-1}, Pilegaard *et al.*, 2001), an aspen ecosystem in Canada (−80 to −290 g C m^{-2} yr^{-1}, Black *et al.*, 1996), a broadleaf deciduous forest in Japan (−70 to −150 g C m^{-2} yr^{-1}, Yamamoto *et al.*, 1999) and even some tropical forests in the Amazon (−102 g C m^{-2} yr^{-1}, Malhi *et al.*, 1998). Contrasted to the well-accepted view that the old-growth stands are unimportant with respect to carbon uptake (Odum, 1969; Jarvis, 1989; Melillo *et al.*, 1996), the significant sequestration in this mature shrub ecosystem demonstrated that semiarid ecosystems can be as important as many more mesic ecosystems of the world. Many ecosystems with high GPP may also have high ecosystem respiration, and therefore, be not as productive with respect to carbon sequestration as at first expected.

Semiarid shrubs should be considered significant ecosystems in the global carbon budget. Despite the variation in weather and disturbance over the measurement period, the average carbon uptake still reached −52 g C m^{-2} yr^{-1}. As a result of anthropogenic CO_2 emission of 6.3 Gt C yr^{-1}, there is a net terrestrial uptake of carbon approximately 2 Gt C yr^{-1} (SRLUCF, 2000, for 1989–1998; Schimel *et al.*, 2001). This is actually only about −16 g C m^{-2} yr^{-1} in net carbon uptake for the entire terrestrial surface. Therefore, to understand current terrestrial carbon budgets, the accuracy in measuring NEE worldwide must be better than −16 g C m^{-2} yr^{-1} and very few vegetated ecosystems can, therefore, be ignored. Similarly, total uptake of all the anthropogenic CO_2 of 6.3 Gt C yr^{-1} (Schimel *et al.*, 2001) into terrestrial surface would require fluxes, on average, of only less than −50 g C m^{-2} yr^{-1}. The shrub ecosystem we studied with an average carbon sink of −52 g C m^{-2} yr^{-1} took up an amount of carbon larger than the terrestrial average needed worldwide to offset all anthropogenic release (on an annual basis) even though it is considered, by many, to be a 'low productivity ecosystem.' In general, other terrestrial ecosystems show a greater annual net uptake of CO_2. This implies that we are missing sufficient measurements across a sufficient range of biomes, ecosystems, land use categories and situations. Controls and management impacts on carbon flux in arid, semiarid regions, in shrub ecosystems and in old-growth ecosystems are all important as part of a complete plan for carbon management. Given its large land area (Atjay *et al.*, 1979) and its large potential to expand its area under heavy impacts from human activities and climate change (Goodale & Davidson, 2002; Jackson *et al.*, 2002), the arid and semiarid regions, including the shrub ecosystem phases, deserve more attentions from scientists and researchers. The existing old-growth shrubs, an important carbon pool of flux in arid and semiarid regions, should be evaluated as part of any management plan for optimal carbon fixation and maintenance of biodiversity and sustainability.

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Recent ecological responses to climate change support predictions of high extinction risk

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Predicted effects of climate change include high extinction risk for many species, but confidence in these predictions is undermined by a perceived lack of empirical support. Many studies have now documented ecological responses to recent climate change, providing the opportunity to test whether the magnitude and nature of recent responses match predictions. Here, we perform a global and multitaxon metaanalysis to show that empirical evidence for the realized effects of climate change supports predictions of future extinction risk. We use International Union for Conservation of Nature (IUCN) Red List criteria as a common scale to estimate extinction risks from a wide range of climate impacts, ecological responses, and methods of analysis, and we compare predictions with observations. Mean extinction probability across studies making predictions of the future effects of climate change was 7% by 2100 compared with 15% based on observed responses. After taking account of possible bias in the type of climate change impact analyzed and the parts of the world and taxa studied, there was less discrepancy between the two approaches: predictions suggested a mean extinction probability of 10% across taxa and regions, whereas empirical evidence gave a mean probability of 14%. As well as mean overall extinction probability, observations also supported predictions in terms of variability in extinction risk and the relative risk associated with broad taxonomic groups and geographic regions. These results suggest that predictions are robust to methodological assumptions and provide strong empirical support for the assertion that anthropogenic climate change is now a major threat to global biodiversity.

anthropogenic warming | elevated temperature | extinction crisis | climate warming

Many scientists argue that we are entering the sixth great mass extinction and that anthropogenic climate change is one of the major threats to global biodiversity (1–3). Comprehensive, multitaxon reviews suggest that 10–70% of plant and animal species assessed so far could be at increased risk of extinction from climate change (4) or that by 2050, climate-induced changes in habitat will commit 15–37% of species to extinction (1). Both these estimates are based on approaches that can be sensitive to ecological and methodological assumptions (5–8), and the latter study considers only geographical range shifts resulting from changes in temperature and rainfall (1). Many species are also expected to be adversely affected by changes in sea-level and ocean chemistry (9), and the impacts of climate change may include breakdowns in biological interactions as species respond individualistically to climate change (10), loss of habitat because of sea-level rise (11), and higher mortality because of increased ocean acidity (12). The spectrum of approaches used to predict ecological responses to climate change has also broadened in recent years, enabling more robust estimates of future changes to be made (13). Here, we use International Union for Conservation of Nature (IUCN) Red List Criteria (14) to derive estimates of extinction risk from a wide range of climate impacts, ecological responses, and methods of analysis. Importantly, the broad evidence base that now exists for realized ecological responses to recent climate change allows us to validate future predictions by comparison with responses that have already been observed.

We identified 130 observed and 188 predicted ecological responses to climate change using a robust review of 10 leading scientific journals from 2005 to 2009 (*Methods*). The responses included documented changes to extinction risk, population size, and geographic range size for 305 taxa from all major groups of organisms, covering a high proportion of the global terrestrial and marine surface (Table S1). All 318 climate change responses were expressed in terms of extinction risk using IUCN Red List criteria, which is possible, because the threshold values used to assign IUCN categories on the basis of population decline are linearly related to the logit transform of threshold extinction risk values (Fig. S1). Estimates of the mean extinction risk for taxa and the proportion subject to varying degrees of extinction risk were derived with an intercept-only generalized linear model with an inflated β-error distribution and logit link function (*Methods*).

A range of factors relating to the selection of study systems (climate impact type, taxon, and region) and the publication of results could influence whether the sampled climate change responses gave unbiased estimates of mean extinction risk. To determine whether there was publication bias, we investigated whether extinction risk was related to the journal in which the study was published and also, created a funnel plot of extinction risk against sample size (Fig. S2). The presence of asymmetry in a funnel plot signifies bias to the publication of significant results (15). To account for biases in the type of impact studied, we incorporated impact type as a factor into models and compared the results of averaging across impact types with those results obtained by averaging across studies. To account for possible phylogenetic nonindependence of extinction risk, we constructed a phylogenetic tree and added the residual of each tip relative to its branch to the mean across all tips in instances where branches were significant. Research carried out in regions where taxa are disproportionately threatened by climate change could also bias overall estimates of threat, and therefore, we controlled for spatial patterns in extinction risk by spatially averaging our results (*Methods*).

To examine whether there were consistent ecoregional and taxonomic patterns across studies making predictions and studies reporting empirical data, we subdivided our data into three major taxonomic groups (plants, invertebrates, and vertebrates) and four major ecoregions: (*i*) polar and boreal, (*ii*) temperate, (*iii*) tropical and subtropical, and (*iv*) marine; we compared observations with predictions.

Results and Discussion

Across all studies, the mean extinction risk over 90 y (i.e., to 2100) was 11.2%. Separating projections of extinction risk based on predicted and observed responses yielded a mean extinction

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risk of 6.7% based on predictions but 14.7% based on observations (Table 1).

The proportion of taxa qualifying as threatened by 2100 using IUCN criteria would be 7.6% based on predictions and 31.7% based on observations. The proportion of taxa more likely to go extinct than not was 1.9% based on predictions but 12.0% based on observations (Table 1). The degree of variability in extinction risk across observations and predictions is similar (Fig. 1), with the majority of taxa (>80%) at low risk (<5%) of extinction; this finding suggests that predictions are not invalidated by methodological assumptions. The symmetry of the funnel plots of extinction risk against sample size (Fig. S2) suggests very little evidence of publication bias. However, extinction risk for both observations and predictions was affected by climate impact type. More studies reported threats from changes in temperature and rainfall, but the few studies on the effects of reductions in sea ice and changes in ocean circulation patterns showed higher predicted extinction risk (Table S2). More studies on effects such as changes in oceanic circulation patterns and acidity on marine organisms would improve estimates of extinction risk. Nevertheless, models that controlled for climate impact type did not lead to marked changes in mean extinction risk, either for empirical observations or predictions (Fig. 1 and Table 1).

There was evidence of phylogenetic nonindependence of extinction risk, with both observations and predictions suggesting high levels of threat to vertebrates and lower levels of threat to plants and invertebrates. This finding was also supported by comparisons of extinction risk within each of these three major taxonomic groups (Fig. 2). There was a high degree of consistency between observations and predictions, with most taxa observed to be at high risk also predicted to be highly threatened in the future. After accounting for phylogeny, estimated extinction risks from observations decreased to 14%, whereas those risks from predictions did not change (Table 1). Thus, observed responses may be slightly exaggerated by work on more threatened taxa. Spatial averaging of results did not alter estimates of

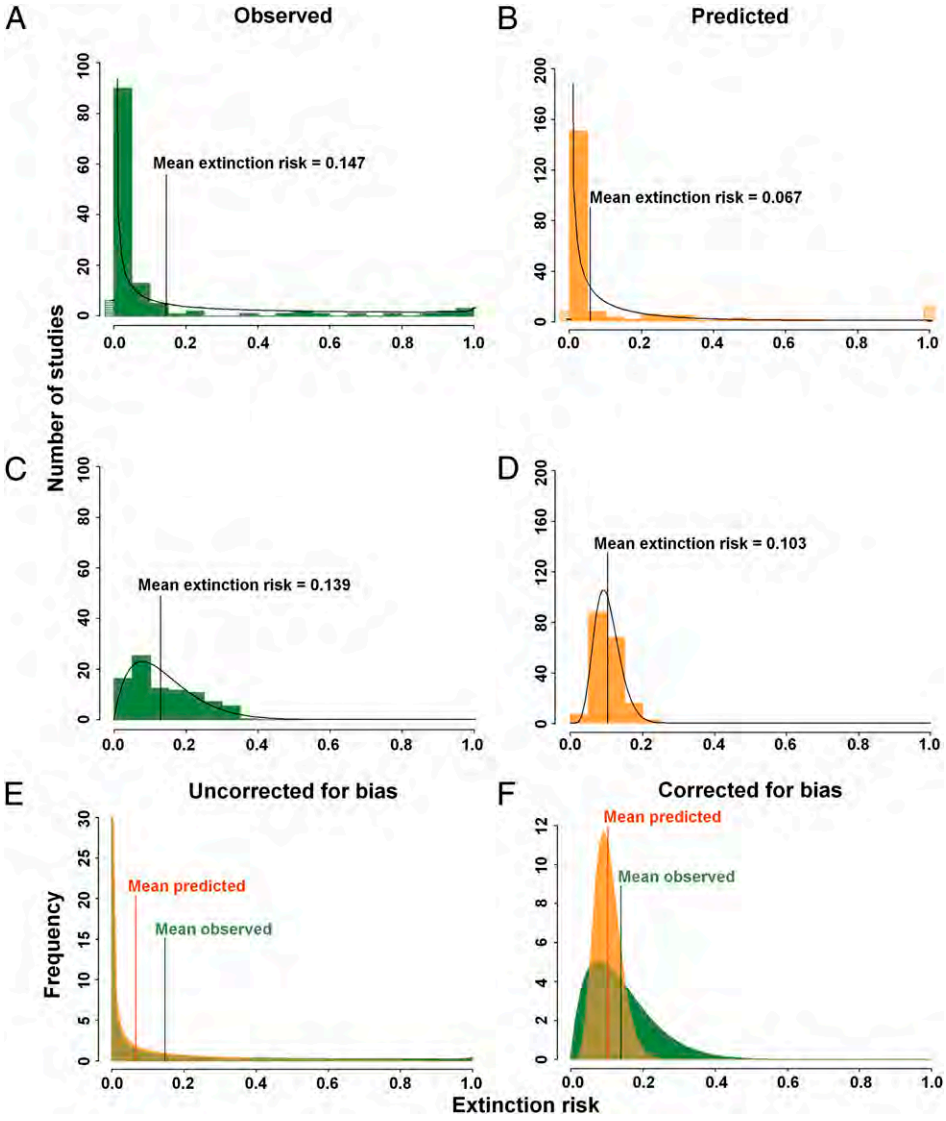

Fig. 1. Proportion of taxa subject to varying degrees of extinction risk by 2100. Actual proportion derived from studies (histogram bars) together with a fitted β-probability function (black curve). The horizontal hatched bars (actual) and horizontal black lines (modeled) represent the number of studies with an extinction risk of zero or one. (*A* and *B*) Uncorrected estimates derived from observed (*A*) and predicted (*B*) data. (*C* and *D*) Estimates accounting for biases (*Methods*) derived from observed (*C*) and predicted (*D*) data. (*E* and *F*) Modeled probability density functions (green, observed; orange, predicted) overlaid to show that, when uncorrected (*E*), the variance in extinction risk derived from observed and predicted data is similar, and when corrected (*F*), the means are similar.

Table 1. Projected extinction risk by 2100 based on observations and predictions

Method	Expected extinction risk			>50% probability of extinction			Threatened with extinction		
	All	Observed	Predicted	All	Observed	Predicted	All	Observed	Predicted
Estimate derived from values given in each study	0.112	0.147	0.067	0.069	0.120	0.019	0.291	0.318	0.076
Estimate obtained by averaging across impact types	0.116	0.158	0.061	0.073	0.132	0.035	0.298	0.333	0.204
Estimate obtained by averaging across taxa	0.104	0.140	0.061	0.051	0.104	0.049	0.296	0.329	0.375
Estimate obtained by spatially averaging across the globe	0.118	0.139	0.103	0.000	0.002	0.000	0.620	0.648	0.600

Expected extinction risk is based on the β-distribution of observed or predicted extinction risks ($n_{predicted}$ = 188; $n_{observed}$ = 130). Taxa categorized as threatened were those taxa exceeding a modeled extinction risk by 2100 of 0.09. IUCN categories: CR, critically endangered; EN, endangered; VU, vulnerable.

observed extinction risk (13.9%), whereas predicted risk increased (10.3%), implying that models of future effects of climate change may, to some extent, have neglected regions subject to higher levels of threat (Table 1). Comparisons of extinction risk in broad ecoregions suggest that marine taxa are particularly threatened and that taxa in the terrestrial tropics and subtropics are less threatened than those taxa in terrestrial temperate and high latitude areas, and the relative threat predicted for different regions was quite well-supported by empirical observations (Fig. 3). However, for both observations and predictions, there were few studies from the terrestrial tropics: the larger number of predictions from the subtropical and tropical category is mostly of tree responses in Mexico (16). In the marine environment, there is a bias to research on corals, which may be disproportionately affected by climate change. More research from tropical areas, where most species occur and are expected to have climates for which no current analog exists (17) and on a greater variety of marine taxa, would improve estimates of the realized threat to biodiversity from climate change.

Our approach, using IUCN criteria to translate between population or range changes and extinction risk, has allowed us to include more examples than simply population viability studies, which estimate extinction risk directly. We, thus, reduce possible bias in threat levels that could result, because particular methodologies might focus on endangered species. However, we make the assumption that the threshold values for criteria relating to decline and extinction risk are comparable (*SI Methods*). Although the rules used to assign taxa to IUCN categories represent inter-

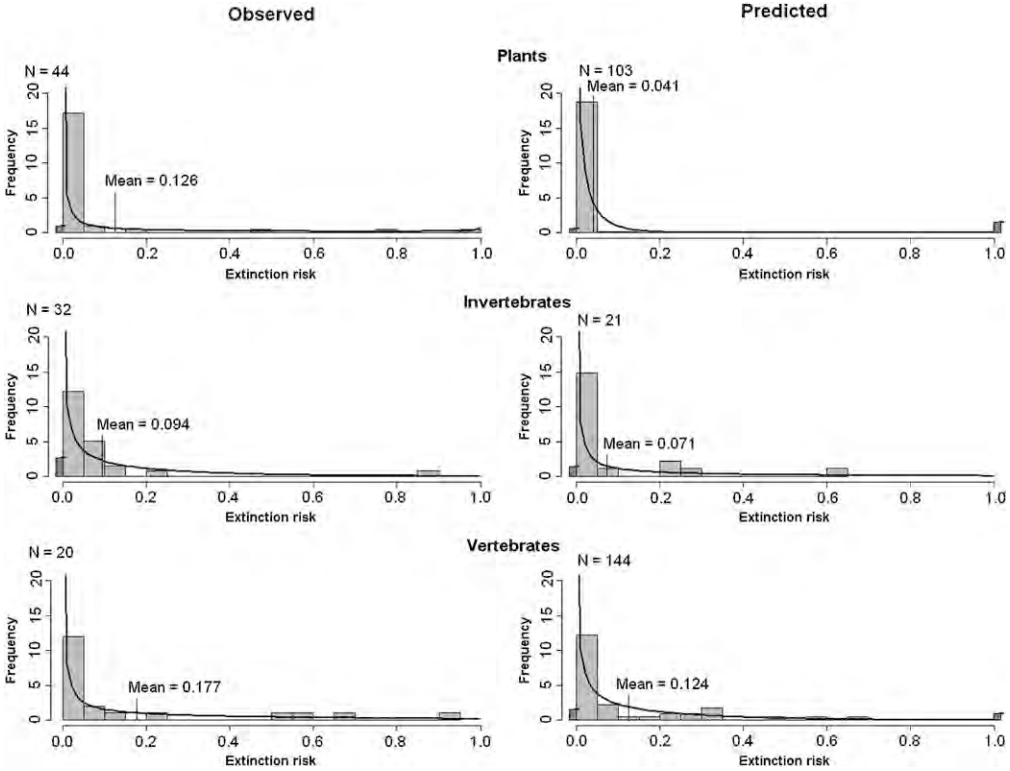

Fig. 2. Frequency distribution of extinction risk by 2100 in (*Left*) observed and (*Right*) predicted studies of taxa: (*Top Left* and *Top Right*) plants, (*Middle Left* and *Middle Right*) invertebrates, and (*Bottom Left* and *Bottom Right*) vertebrates. Actual proportion derived from studies (histogram bars) together with a fitted β-probability function (black curve). The dark bars (actual) and horizontal black lines (modeled) represent the frequency of studies with an extinction risk of zero or one. Data are scaled such that the total area of histogram bars and under the modeled extinction risk line is equal to one. *N* is the number of samples in each category.

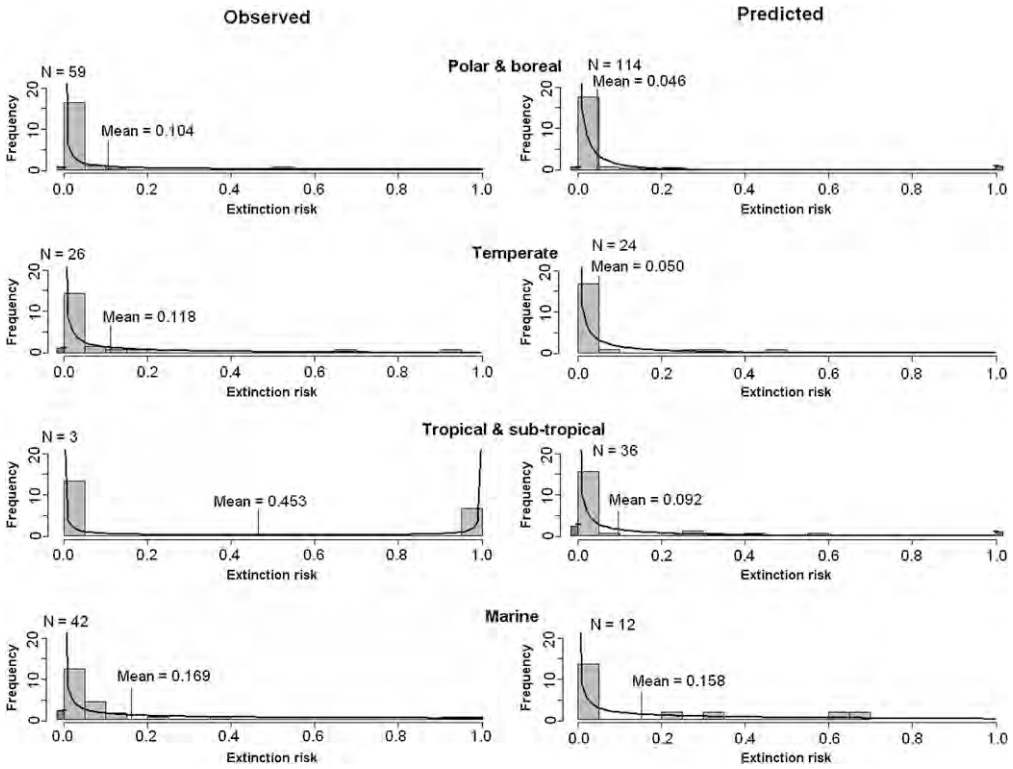

Fig. 3. Frequency distribution of extinction risk by 2100 in (*Left*) observed and (*Right*) predicted studies of ecoregions: (row 1) polar and boreal, (row 2) temperate, (row 3) tropical and subtropical, and (row 4) marine. Actual proportion derived from studies (histogram bars) together with a fitted β-probability function (black curve). The dark bars (actual) and horizontal black lines (modeled) represent the frequency of studies with an extinction risk of zero or one. Data are scaled such that the total area of histogram bars and under the modeled extinction risk line is equal to one. *N* is the number of samples in each category.

nationally accepted decision tools in conservation biology (14, 18) and broad consistency between criteria was sought during their development (19), variation among species makes it difficult to validate the equivalence of thresholds for different criteria (20). Moreover, phylogenetic nonindependence of extinction risk could also reflect difficulties in assessments for poorly known taxa, with generally fewer experts and less data available (14). For example, the apparent low threat to invertebrates may partly reflect the lack of detailed understanding of climate threats facing most insects, with the majority of studies being on Lepidoptera (21). Direct predictions of extinction, as determined, for example, by population viability analyses, yielded higher estimates of extinction risk than estimates provided by changes in population and range size (Fig. S3). However, we suspect that this finding is primarily caused by these studies focusing on particularly endangered species. Our results were not unduly sensitive to the assumed relationship between range change, population change, and extinction risk (Table S3), suggesting that our overall estimates of extinction risk are relatively robust to any lack of equivalency among IUCN criteria. Furthermore, interactions between taxonomic group and method did not significantly affect estimates of extinction risk, suggesting that variation in the degree of difficulty in estimating extinction risk across categories is unlikely to invalidate our cross-taxonomic findings.

Estimated extinction risk was not related to the journal of publication or the time period over which observations were carried out or predictions were made. The sample size in each study could still influence the reliability of results, but we did not use formal metaregression techniques for two reasons. First, it was our intention to report means and variances in extinction risk across taxa rather than provide a single measure. Each estimate is derived from different taxa and could stem from any one of a number of different responses. Consequently, the effect being measured is not common across studies, and there is no reason to attribute a higher weighting to studies with larger sample sizes. Second, many studies do not report complete or comparable measures of uncertainty. Therefore, the use of metaregression to calculate the uncertainty in extinction risk across all studies would not be valid. Consequently, we attached the same weighting to all studies, irrespective of sample size. This weighting is unlikely to cause major bias in estimates of extinction risk, because there was no evidence of a consistent relationship of reported extinction risks with either sample size or the number of species studied (*SI Methods* and Fig. S3).

There are many unknowns when projecting declines in biodiversity, and the values here should be interpreted with caution. Nevertheless, our results were robust to publication, taxonomic, geographical, and impact-type biases, and assumed theoretical relationships between extinction risk, population decline, and range change. Furthermore, the degree of variance is also similar across observations and predictions, suggesting that predictions are not invalidated by methodological assumptions. Given that climate change is expected to accelerate and hence, exacerbate impacts, empirical evidence suggests that many predictions of extinction risk may be somewhat conservative. However, in terms of consistent phylogenetic and ecoregional patterns, the results suggest that realized ecological responses to climate change support predictions of future change. Our estimates of extinction risk are lower than previous estimates of the proportion of species committed to extinction by 2050 (1), but they are within the same order of magnitude. Moreover, commitment to extinction is not the same as extinction risk, because decades may elapse between habitat loss or climate change and the resultant species-level extinctions (22). Consequently, one would expect estimated extinction risk over a specified period to be lower.

Our results lend support to the contention, based on entirely different data and methods (1), that anthropogenic climate

warming at least ranks alongside other recognized threats to global biodiversity. Based on published results, we endeavor to distinguish between responses to climate and other drivers of change, although in many cases, the mechanisms behind species responses to climate change are not known. Several studies suggest that changes to biotic interactions have led to increased extinction risk for at least one interacting species (10, 23). Habitat degradation (24), invasive species (25), and overexploitation (26) play additional roles, and interactions among these threats and climate change will increasingly threaten populations of species. In addition, rapid climate change has the potential to overwhelm the capacity for adaptation in many populations, reducing the ability to resist and recover from other environmental stressors (27). Our metaanalysis showing high predicted levels of extinction, backed up by consistent data for changes that have already occurred, shows the need to give climate change high priority in conservation planning and to communicate its potentially wide-ranging consequences to policy makers and the wider public.

Methods

Details of the studies and methods are provided in *SI Methods* and Table S1.

Selection of Studies. We reviewed 1,120 papers published from 2005 on in 10 leading journals focused on general science, ecology, or conservation. We searched all papers with climate change in the title, abstract, or keywords in *Biological Conservation*, *Conservation Biology*, *Ecological Applications*, *Ecology Letters*, *Journal of Applied Ecology*, *Nature*, *Proceedings of the Royal Society of London Series B Biological Sciences*, and *Science*, and all papers with climate change and biodiversity in *Global Change Biology* and PNAS. Those papers in which extinction probabilities, IUCN Red List categories, or a change in population size or range were reported were shortlisted for metaanalysis. We extracted data only from those articles in which changes could primarily be attributed to climate change or where climate was distinguished from other effects. From each paper, we recorded the taxon and number of species, the start and end of the study period, the type of climate change impact (changes in temperature and/or rainfall, ocean circulation patterns, ocean acidity, or sea ice, or responses to habitat change such as loss of habitat because of sea-level rise), and the number of spatial and temporal replicates. We also specified whether the response was observed or predicted. In all, we extracted data from 74 studies (32 observations and 42 predictions), providing 318 (130 observations and 188 predictions) taxon-specific climate change response estimates (*SI Methods* and Table S1).

Estimating Extinction Risk. We used IUCN Red List criteria to derive estimates of extinction risk from changes in population or range size, with a change in range size measured as the change in the area occupied. We assumed that a change in range is directly equivalent to a change in population size, an approach that is likely to give conservative estimates of population decline (28). Extinction risks can be standardized over any given period using multiple event probability theories (Eq. **1**):

$$E_s = 1 - (1 - E_t)^{\frac{s}{t}}, \quad [1]$$

where E_s is the extinction probability of the desired time period s and E_t is the extinction probability over time period t. When extinction probabilities associated with each of the three IUCN Red List categories are standardized to 55.628 y and logit transforms are applied to ensure a continuous range of values, there is a perfectly linear relationship with the equivalent population size reductions over 10 y in each of the categories (Fig. S1). It is, thus, possible to infer extinction risk for any given change in population size, including increases. We also included studies where species had been assigned to IUCN Red List categories by assuming conservatively that their extinction risk corresponded to the threshold value for the category in which they had been placed. We assessed extinction risk over a 90-y period to give estimates for 2100. Full details of the method used to infer extinction risk from each study are given in Table S1. Because extinction estimates are constrained to values between zero and one and were zero- and one-inflated, estimates of the mean extinction risk for taxa and the proportion subject to varying degrees of extinction risk were derived by fitting a zero- and one-inflated β-error distribution to the data with a logit link function using the R (29) package GAMLSS (30).

To test for publication bias to studies that reported a high extinction risk, we examined the relationship between extinction risk and sample size. To test for researcher bias to species particularly threatened by climate change, we applied the same method using the number of species studied instead of sample size. There was no evidence of either researcher or publication bias (*SI Methods* and Fig. S2).

The potential effects of mean time of study, journal, and impact type on extinction estimates were assessed using a generalized linear model in R (29). All combinations of variables, including the null model, were tried, and the final model was selected using Akaike's Information Criterion (31). For both observed and predicted data, models in which impact type was included yielded the lowest Akaike's Information Criterion. We, thus, averaged across impact types to give a revised estimate.

To examine whether there were consistent taxonomic patterns across studies making predictions and empirical data, we subdivided our data into three major taxonomic groups: plants, invertebrates, and vertebrates. Bacteria, fungi, and taxa such as algae that were resolved to insufficient taxonomic detail were excluded from these analyses. To examine whether there were consistent ecoregional patterns across studies, we subdivided our data into four major ecoregions: (*i*) polar and boreal (ice sheets, tundra, and taiga), including studies of high altitude taxa at mid-latitudes, (*ii*) temperate (forest and steppe), (*iii*) tropical and subtropical, including xeric and Mediterranean habitats, and (*iv*) marine (all latitudes). Freshwater wetland taxa were assigned to the ecoregion in which the wetland was located. Studies spanning more than one ecoregion were excluded from these analyses.

Phylogenetic Relationships. A composite phylogeny of all study taxa was constructed using information contained in ref. 32, with branch lengths scaled to be approximately equal to time since divergence. Often, extinction estimates were for groups of species only, and in such instances, a dummy species was created that branched from the node encompassing all species within the group. Using the standardized normal residuals from the Generalized Linear Model (GLM) modeling, the mean residual value across all descendant terminal taxa was then calculated for each branch using the analysis of traits function in Phylocom 4.1 (33). The significances of branch values relative to the mean value across all terminal taxa were calculated by randomizing values for each taxon across all tips. To control for the extent to which particular taxa differed in terms of their extinction risk when calculating global estimates, the residual of the tip relative to the branch was added to the mean across all tips in instances where branches were significant. To test the robustness of our results to uncertainties associated with divergence time estimation, we also ran our analyses on the same tree but with branch lengths set to one. This change did not affect observed estimates of extinction risk, but predicted estimates increased from 6.1% to 6.5%.

Spatial Relationships. The geographical boundaries of all study sites from which extinction estimates were derived were mapped as polygons in ArcGIS 9.2 using a Cylindrical Equal Area projection (ESRI). The centroids of all study areas were then calculated, and spatial kriging with a spherical semivariogram model was performed using the Spatial Analyst tool in ArcGIS. Because it is not possible to define a projection that preserves true distances between all points on the globe, a North Pole Azimuthal Equidistant projection was used to perform spatial kriging in the northern hemisphere, and a South Pole Azimuthal Equidistant projection was used to perform spatial kriging in the southern hemisphere. The two hemispheres were then joined and converted back to a cylindrical equal area projection with a 1-km^2 resolution. The individual pixel values were then exported as an ASCII file, and a zero- and one-inflated β-error distribution with a logit link function was fitted to these data to estimate the mean extinction risk and the proportion of taxa subject to varying degrees of extinction risk.

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Using Circuit Theory to Model Connectivity in Ecology, Evolution, and Conservation
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CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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USING CIRCUIT THEORY TO MODEL CONNECTIVITY IN ECOLOGY, EVOLUTION, AND CONSERVATION

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Abstract. Connectivity among populations and habitats is important for a wide range of ecological processes. Understanding, preserving, and restoring connectivity in complex landscapes requires connectivity models and metrics that are reliable, efficient, and process based. We introduce a new class of ecological connectivity models based in electrical circuit theory. Although they have been applied in other disciplines, circuit-theoretic connectivity models are new to ecology. They offer distinct advantages over common analytic connectivity models, including a theoretical basis in random walk theory and an ability to evaluate contributions of multiple dispersal pathways. Resistance, current, and voltage calculated across graphs or raster grids can be related to ecological processes (such as individual movement and gene flow) that occur across large population networks or landscapes. Efficient algorithms can quickly solve networks with millions of nodes, or landscapes with millions of raster cells. Here we review basic circuit theory, discuss relationships between circuit and random walk theories, and describe applications in ecology, evolution, and conservation. We provide examples of how circuit models can be used to predict movement patterns and fates of random walkers in complex landscapes and to identify important habitat patches and movement corridors for conservation planning.

Key words: circuit theory; dispersal; effective distance; gene flow; graph theory; habitat fragmentation; isolation; landscape connectivity; metapopulation theory; reserve design.

INTRODUCTION

Connectivity among habitats and populations is considered a critical factor determining a wide range of ecological phenomena, including gene flow, metapopulation dynamics, demographic rescue, seed dispersal, infectious disease spread, range expansion, exotic invasion, population persistence, and maintenance of biodiversity (Kareiva and Wennergren 1995, Ricketts 2001, Moilanen and Nieminen 2002, Calabrese and Fagan 2004, Moilanen et al. 2005, Crooks and Sanjayan 2006, Damschen et al. 2006, Fagan and Calabrese 2006). Preserving and restoring connectivity has become a major conservation priority, and conservation organizations are investing considerable resources to achieve these goals (Beier et al. 2006, Kareiva 2006).

Understanding broad-scale ecological processes that depend on connectivity, and making effective conservation planning decisions to conserve them, requires quantifying how connectivity is affected by landscape features. Thus, there is a need for efficient and reliable tools that relate landscape composition and pattern to connectivity for ecological processes. Many ways of predicting connectivity using landscape data have been developed (reviewed by Tischendorf and Fahrig 2000*a*, *b*, Moilanen and Nieminen 2002, Calabrese and Fagan 2004, Fagan and Calabrese 2006). Common approaches include the derivation of landscape pattern indices (e.g., Schumaker 1996), individual-based movement simulations (e.g., Schumaker 1998, Hargrove et al. 2005), and analytic measures of network connectivity, such as graph theory and least-cost path models (Keitt et al. 1997, Urban and Keitt 2001, Adriaensen et al. 2003, Minor and Urban 2007). The latter have gained increasing attention in recent years and are widely

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applied in connectivity modeling and in conservation planning.

We propose that connectivity models from electrical circuit theory can make a useful addition to the approaches available to ecologists and conservation planners. Circuit theory has been applied to connectivity analyses in chemical, neural, economic, and social networks, and has recently been used to model gene flow in heterogeneous landscapes (McRae 2006, McRae and Beier 2007). The same properties that make circuit theory useful in these fields hold promise for ecology and conservation as well. Because connectivity increases with multiple pathways in circuit networks, distance metrics based on electrical connectivity are applicable to processes that respond positively to increasing connections and redundancy. Additionally, previous work has shown that current, voltage, and resistance in electrical circuits all have precise relationships with random walks (Doyle and Snell 1984, Chandra et al. 1997). These relationships mean that circuit theory can be related to movement ecology via random-walk theory, providing concrete ecological interpretations of circuit-theoretic parameters and predictions. Finally, because algorithms to implement circuit models are well developed, they can be applied to large networks and raster grids.

Here we present several ways in which circuit theory can be used to model connectivity in ecology and conservation. We describe ecological applications of previously developed theory relating resistance, current, and voltage in electronic circuits to random walks on analogous graphs (Doyle and Snell 1984, Klein and Randic 1993, Chandra et al. 1997). This theory can be applied to predict movement patterns and probabilities of successful dispersal or mortality of random walkers moving across complex landscapes, to generate measures of connectivity or isolation of habitat patches, populations, or protected areas, and to identify important connective elements (e.g., corridors) for conservation planning. Our approach does not require new ways of representing landscape data; rather, it takes advantage of graph-theoretic data structures, which are already familiar to many ecologists, and can be applied in traditional graph-theoretic or raster GIS frameworks. Coupled with applications of circuit theory to predict equilibrium patterns of gene flow (McRae 2006, McRae and Beier 2007), these new applications comprise a modeling framework that integrates spatial aspects of ecology, evolution, and conservation.

Basic Concepts

Graph data structures and terminology

Connectivity models from circuit theory are applied to *graphs* (Harary 1969), so we will use the terminology of graph theory here (see Urban and Keitt 2001 for a review). Briefly, graphs are networks comprised of sets of *nodes* (connection points which represent, e.g., habitat patches, populations, or cells in a raster landscape) connected by *edges* (Fig. 1). Edges reflect functional connections, such as dispersal, between nodes. The *weight* of each edge typically corresponds to the strength of the connection (e.g., the ease of movement or number of dispersers exchanged) between the nodes it connects.

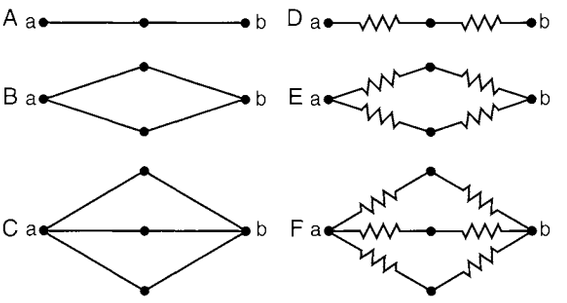

FIG. 1. Three graphs at left (A, B, C), with edge weights of 1. Traditional shortest path or geodesic distance, d, between nodes a and b is identical ($d = 2$) all three cases. At right (D, E, F), edges have been replaced with unit resistors to create analogous circuits. Effective resistance, $\hat{R}$, measured between nodes a and b decreases from top to bottom ($\hat{R} = 2$, 1, and 2/3, respectively), reflecting additional contributions from multiple pathways (figure modified from Klein and Randic [1993]).

Circuit theory

In this paper, circuits are defined as networks of nodes connected by *resistors* (electrical components that conduct current) and are used to represent and analyze graphs (Fig. 1). The basic concepts of resistance, conductance, current, and voltage all apply, and their definitions and ecological interpretations are summarized in Table 1. Recall Ohm's law, which states that when a voltage V is applied across a resistor, the amount of current I that flows through the resistor depends on (1) the voltage applied and (2) the resistance R, such that $I = V/R$. The lower the resistance (or the higher the conductance, G, which is simply the reciprocal of resistance), the greater the current flow per unit voltage. Similarly, when a voltage is applied across two nodes in a resistive circuit (e.g., between nodes a and b in the circuits shown in Fig. 1), the total amount of current that flows across the circuit is determined by (1) the voltage applied and (2) the configuration and the resistances of the resistors the circuit contains. The *effective resistance* ($\hat{R}$) between the nodes is the resistance of a single resistor that would conduct the same amount of current per unit voltage applied between the nodes as would the circuit itself, i.e., $\hat{R} = V/I$.

In simple circuits, such as those shown in Fig. 1, effective resistance can be calculated using some basic rules. First, two resistors connected in series may be replaced by a single resistor with a resistance is that the sum of the two resistances. Thus, the effective resistance in the top circuit in Fig. 1D would be $\hat{R} = R_1 + R_2 = 2$ ohms. Conversely, connecting resistors in parallel decreases their effective resistance, such that they may be replaced by a single resistor whose conductance is

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TABLE 1. Electrical terms and their ecological interpretations.

Electrical term (symbol, unit)	Ecological interpretation
Resistance (R, ohm), the opposition that a resistor offers to the flow of electrical current.	Opposition of a habitat type to movement of organisms, similar to ecological concepts of landscape resistance or friction. Graph edges or grid cells allowing less movement are assigned higher resistance.
Conductance (G, siemens), inverse of resistance and a measure of a resistor's ability to carry electrical current.	Analogous to habitat permeability. In random-walk applications, it is directly related to the likelihood of a walker choosing to move through a cell or along a graph edge relative to others available to it. In population genetic applications (see McRae 2006), it is a measure of migrants exchanged between neighboring populations.
Effective resistance ($\hat{R}$, ohm), the resistance to current flow between two nodes separated by a network of resistors.	Also known as the *resistance distance*, a measure of isolation between pairs of nodes on a graph or cells on a raster grid. Similar to ecological concept of effective distance, but it incorporates multiple pathways (Fig. 1D–F). It scales linearly with equilibrium genetic differentiation in population genetic applications.
Effective conductance ($\hat{G}$, siemens), inverse of effective resistance, a measure of a network's ability to carry current between two nodes.	A measure of connectivity between pairs of nodes on a graph or cells on a raster grid. It increases with additional available pathways and scales linearly with effective migration in population genetic applications.
Current (I, ampere), flow of charge through a node or resistor in a circuit.	Current through nodes or resistors can be used to predict expected net movement probabilities for random walkers moving through corresponding graph nodes or edges (Fig. 2).
Voltage (V, volt), the potential difference in electrical charge between two nodes in an electrical circuit. Related to current and resistance by $V = IR$.	Voltages can be used to predict the probability that random walkers leaving any point on a graph will reach a given destination (representing, e.g., successful dispersal) before another (representing, e.g., mortality; Fig. 3).

given by the sum of the conductances of the two resistors, that is, $\hat{G} = G_1 + G_2$. (In terms of resistance, these quantities are given by: $\hat{R} = R_1R_2/[R_1 + R_2]$.) Applying these equations to the circuits shown in Fig. 1, the effective resistance declines from the top to the bottom circuit.

Applying circuit theory to graphs involves preserving the same graph structure with interconnected nodes, but replacing graph edges with resistors, as in Fig. 1. The conductance of each resistor is typically a function of the corresponding edge weight or probability of movement between the pair of nodes it connects. The resistance of a resistor is the reciprocal of its conductance and can be thought of as representing isolation or movement cost between nodes.

INTERPRETATION OF RESISTANCE, CURRENT, AND VOLTAGE

Resistance and conductance

The simplest connectivity measure from circuit theory is the *resistance distance* (Klein and Randic 1993), a distance metric defined as the effective resistance between a pair of nodes when all graph edges are replaced by analogous resistors (as in Fig. 1D–F). A convenient property of the resistance distance is that it incorporates multiple pathways connecting nodes, with resistance distances measured between node pairs decreasing as more connections are added. Hence, the resistance distance does not reflect the distance traveled or movement cost accrued by a single individual. Rather, it incorporates both the minimum movement distance or cost and the availability of alternative pathways. As additional links are added, individuals do not necessarily travel shorter paths, but have more pathways available to them. For example, in the three graphs in Fig. 1A–C, the minimum distance required to travel from node a to b (called geodesic distance in graph theory) is the same. However, the resistance distance decreases as more connections are added, reflecting increased flow capacities and levels of redundancy. In short, the resistance distance is small when two nodes are connected by many paths with low resistance (high conductance) edges and large when there are few paths with high resistance. Resistance distances can be calculated across irregular networks or with continuous landscape data, which are typically represented as discretized lattices or grids. On continuous surfaces, the resistance distance increases linearly with Euclidean distance in homogeneous one-dimensional habitats and with its log transformation in two-dimensional habitats, a property important for modeling gene flow (McRae 2006).

Resistance distances can also be related to random-walk times between nodes. For the theory and examples that follow, we assume that conductances are chosen so that the probability of moving from a node along any given edge is equal to the conductance assigned to the edge divided by the sum of the conductances of all edges connected to the node. For an organism moving through a habitat network (the main focus of this paper), this would correspond to a scenario where the individual chooses to move along an edge in proportion to the edge's conductance, a surrogate for habitat quality or (inverse) perceived risk, relative to the quality of all other choices of direction; this choice is then repeated at each subsequent step. For genes moving across a network of populations over many generations, this would correspond to a scenario where edge conductances correspond to per-generation migration rates (McRae 2006).

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Chandra et al. (1997) showed that, when resistors are parameterized in this way, the resistance distance between a pair of nodes is precisely related to the *commute time* between the nodes, i.e., the expected time for a random walker to move from one node to the other and back again. The commute time between any pair of nodes u and v can be calculated using the following formula:

$$\text{Commute time} = \hat{R}_{uv} \sum_{x=1}^{n} \sum_{y=1}^{n} (1/R_{xy}) \qquad (1)$$

where R_{xy} is the resistance of the resistor connecting nodes x and y and n is the number of nodes in the network. Note that Eq. 1 accommodates resistors connecting a node to itself, which would reflect a nonzero probability of staying at the node for any time step. Chandra et al. (1997) also provided formulas to calculate a commute *cost*, if there is a cost imposed for each step that is independent of the resistance (and thus independent of the behavior of a random walker). An interesting result of Eq. 1 is that if the goal is to minimize commute times between a pair of nodes, there is a penalty for adding connections which is offset by the degree to which the new connections help to lower effective resistance between the two nodes. Within a fixed network, commute times between different pairs of nodes will be directly proportional to the effective resistances measured between them. Another potentially useful way to apply resistance calculations across graphs is to compute upper and lower bounds for the *cover time*, or the expected number of steps of a random walk visiting all nodes in the graph (Chandra et al. 1997).

"Functional" or "effective" distance.—Used as an ecological distance metric, the resistance distance provides a conceptual complement to commonly used least-cost distances in two important ways. First, it integrates all possible pathways into distance calculations, whereas least-cost distances are measured along a single optimal pathway. Second, it offers a measure of isolation assuming a random walk, whereas least-cost distances presumably reflect the route of choice if a disperser has complete knowledge of the landscape it is traversing.

The resistance distance also provides a quantitative complement to least-cost distances. If only a single pathway between two nodes is available (e.g., in Fig. 1A or in any graph that is a tree), the resistance distance will equal the least-cost distance. On the other hand, when two identical and independent pathways connect a pair of nodes in parallel, the resistance distance will be half the least-cost distance. This suggests an interpretation of the resistance distance as an indicator of redundancy in connections relative to the least-cost distance:

$$\text{Redundancy} = (\text{least-cost distance})/(\hat{R}).$$

Thus, the two measures can be compared directly, their ratio providing a rough measure of parallel pathways available to dispersers.

The relationship between resistance distances and commute times is one way to link circuit and ecological theories and is the basis of using resistance distances to predict patterns of gene flow and genetic structuring in heterogeneous landscapes (McRae 2006). Calculating commute times directly may provide valuable additional information because commute times take into account how efficiently a given landscape configuration will channel dispersal between source and destination nodes. Additional pathways that primarily result in increased wandering behavior rather than directed movement may reduce resistance distances but will increase commute times. Low commute times and low resistance distances between pairs of nodes indicate that dispersers will be efficiently directed between them.

Current

Currents in circuits can also be interpreted in terms of random walks on corresponding graphs. Consider again a graph in which the probability that a random walker will move from a node along any graph edge is proportional to its conductance. Doyle and Snell (1984) showed that when 1 A (ampere) of current is injected into one node (node a in Fig. 2A) and a second node (node e) is tied to ground, the current i_{xy} flowing through the resistor connecting any pair of nodes x and y is equivalent to the expected net number of times that a random walker, starting at a and walking until it reaches e, will move along that branch. Because we are tallying net passages through the branch, movements from x to y are counted as positive, whereas movements from y back to x are counted as negative.

Corridor identification and dispersal predictions.—By predicting net movement probabilities along branches or through nodes, current density can be used to identify landscape corridors or "pinch points," i.e., features through which dispersers have a high likelihood (or necessity) of passing. High current through a node or branch indicates that removing or converting it will have a high impact on connectivity. In Fig. 2, all the current passes through node b; removing that node (or the link between nodes a and b) would completely disconnect nodes a and e, whereas removing node c, through which only half the current passes, would reduce redundancy but would still leave nodes a and e connected via the lower branch. In graph terminology, node b is a *cutnode*, and the resistor connected nodes a and b is a *cutlink*.

Voltage

Doyle and Snell (1984) also showed that voltage can be related to random walk probabilities. Consider a graph in which a voltage source set to 1 V is connected to one node (or to a set of nodes), and another node (or set of nodes) is connected to ground (Fig. 3). The voltage measured at any remaining node on the graph will equal the probability that a random walker, starting at that

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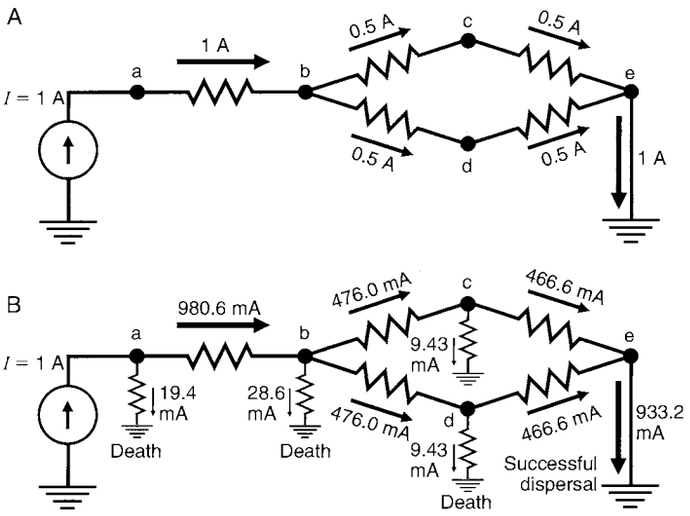

FIG. 2. (A) A simple circuit, with a 1-A (ampere) current source (I) placed at node a, and with node e tied to ground. Branch currents that would be observed with unit resistors are shown and reflect the net number of times that a random walker, starting at node a, is expected to pass along each branch before reaching node e. All random walkers must pass across the first branch, but half would be expected to take the upper pathway, and half the lower. Resistances connecting nodes were set to 1 ohm for this simple example; the methods we describe here can accommodate heterogeneous resistances with values from 0 to infinity. (B) The same circuit as in (A), but with ground resistors added to reflect a 1% probability of mortality as the random walker passes through each node. To achieve this, resistances to ground for nodes a–d were set to 99, 33, 49.5, and 49.5 ohms, respectively. Currents show the expected number of net movements along each branch, as well as the expected number of deaths at each node. For example, the proportion of dispersers leaving node a expected to successfully reach node e is 0.9332 (933.2 mA equivalent). Deaths at each node exceed 1% because nodes are visited multiple times by random walkers, with the highest numbers of deaths observed in nodes with the highest numbers of visits. Only one possible dispersal destination was included here, but the method can accommodate as many dispersal destinations as desired. Although we tied the destination node directly to ground, resistors could be added between destination nodes and ground, with their conductances set to reflect a finite probability that a walker would settle rather than continue walking once reaching a node.

node, will reach any of the nodes set to 1 V before reaching any node connected to ground. The most obvious application of this property is to predict the probability of successful dispersal via a random walk from any node on a graph. Suitable destination patches for dispersal can be set to 1 V, whereas mortality can be represented by resistors connected to ground, with their conductances reflecting probabilities of mortality (Fig. 3).

APPLYING CIRCUIT ANALYSES TO RASTER GRIDS

Predicting connectivity using circuit theory requires translating spatial data sets into a graph structure, but that doesn't mean that primary landscape data must be in a patch-based or network-style format. In fact, we envision most landscape applications operating on raster data, with a graph extracted from these data as is done for least-cost path analyses (Adriaensen et al. 2003). Since well-developed computer algorithms allow millions of cells to be processed, large raster landscapes can be accommodated.

Analyzing a raster grid involves first assigning resistances to different habitat types in the grid. Fig. 4 shows a simple example with three different habitat types: assigned unit, infinite, and zero resistance. The last is useful when practitioners wish to measure connectivity or identify important connective elements between areas (representing, for example, habitat patches or reserves), rather than points on a landscape. To represent a grid as a circuit, cells with finite resistances are converted to nodes (gray), whereas cells with infinite resistance (i.e., those representing complete barriers, black) are dropped. Adjacent nodes are connected by resistors, with resistances reflecting a function (typically the mean) of the resistances of the cells they connect. Adjacent cells with zero resistance (open) are consolidated into a single node that is then connected by resistors to all nodes adjacent to the zero-resistance patch. Following this procedure, the 16-cell

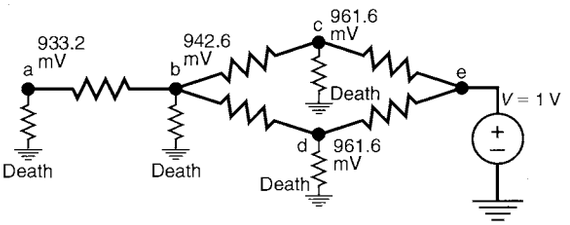

FIG. 3. The same circuit shown in Fig. 2B, but with a voltage source (V) of one volt at node e instead of a current source at node a. Node voltages reflect the probability that a random walker, starting at each node, will successfully reach node e. Consistent with the result from Fig. 2B, the probability of successful dispersal from node a to node e is 0.9332.

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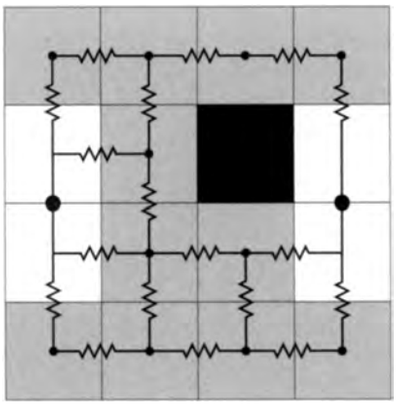

FIG. 4. A simple landscape represented as both a grid and a circuit. The landscape contains two contiguous patches of 0-resistance cells (open), dispersal habitat of finite resistance (gray), and one "barrier" cell with infinite resistance (black). Cells with finite resistance are replaced with nodes (small dots), and adjacent nodes are connected by resistors. Patches of cells with 0 resistance are each consolidated into a single node (large dots). Connections between diagonal neighbors and nonadjacent cells can also be incorporated, the latter representing "hops" over intervening cells. Current sources, voltage sources, and ground connections can be added as in Figs. 2 and 3.

grid in Fig. 4 is now represented as a circuit with 13 nodes and 18 resistors.

COMPUTATION

Although simple circuits can be solved by hand, *nodal analysis* is typically used to analyze larger circuits, such as those derived from raster grids (McRae 2006). Given a circuit with current or voltage sources, nodal analysis uses Kirchoff's and Ohm's laws in matrix form to solve for a vector, specifying voltages at each node; once these are known, Ohm's law can be used to calculate currents passing through individual resistors or nodes. Effective resistance between a pair of nodes is given by the voltage between them when one is connected to a 1-A current source and the other is connected to ground (e.g., Fig. 2A). The method is described in standard circuit theory textbooks (e.g., Dorf and Svoboda 2003); an example of its use to calculate effective resistances is provided by McRae (2006).

Computer languages used for scientific computing such as Java, C, MATLAB, and Python include linear solver routines that can solve for effective resistances on graphs. Fast graph operations can be used to define connected components in a landscape and discard from a graph any components that are completely isolated. Very large graphs can be processed relatively easily and efficiently; we have solved for effective resistances, voltages, and current on landscapes containing over 1 million cells using Java (Sun Microsystems, Mountain View, California, USA), and up to 48 million cells using a parallel version of MATLAB (MathWorks, Natick, Massachusetts, USA) implemented using Star-P (Interactive Supercomputing, Waltham, Massachusetts, USA). Solving 1 million cells on a notebook computer with a 2-GHz processor and 2 GB of RAM took us 16 minutes using Java and only 20 seconds using MATLAB. This calculation must be repeated for each configuration of current sources and grounds, but typical connectivity applications will require a small number of calculations (e.g., for each pair of populations or reserves between which connectivity is to be modeled). Calculations between multiple pairs can be sped up considerably using matrix preconditioning and/or parallel processing. Software implementing many of the algorithms in this manuscript is available (B. H. McRae, *unpublished data*).

EXAMPLE APPLICATIONS TO HETEROGENEOUS LANDSCAPES

Here we provide examples of the applications described above to predict connectivity and movement of random walkers across large raster grids. For the example analyses described next, we solved for effective resistances and node currents using code written in MATLAB R2007b. The example landscapes (i.e., resistance surfaces) were all created using ArcView GIS 3.2 (ESRI, Redlands, California, USA) and exported as ASCII raster grids, with cell values corresponding to resistances ranging from 0 to infinity (Fig. 5). For circuit analyses, cells with finite resistances were converted to nodes, whereas those with infinite resistances were dropped. Cells were connected to their eight neighbors such that the resistance between a pair of first-order neighbors was set to the mean of the two cells' resistances, and the resistance between a pair of second-order (diagonal) neighbors was set to the mean resistance multiplied by the square root of 2 to reflect the

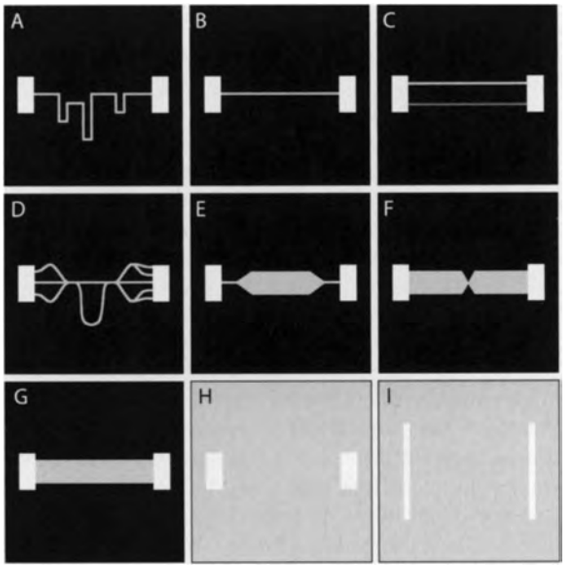

FIG. 5. Nine simple raster landscapes (A–I), consisting of 1000×1000 cells. Habitat patches (shown in white and assigned 0 resistance, or infinite conductance) are connected by different configurations of dispersal habitat (light gray, 10 ohms/cell; dark gray [lower corridor in panel C], 20 ohms/cell; black = infinite resistance or 0 conductance).

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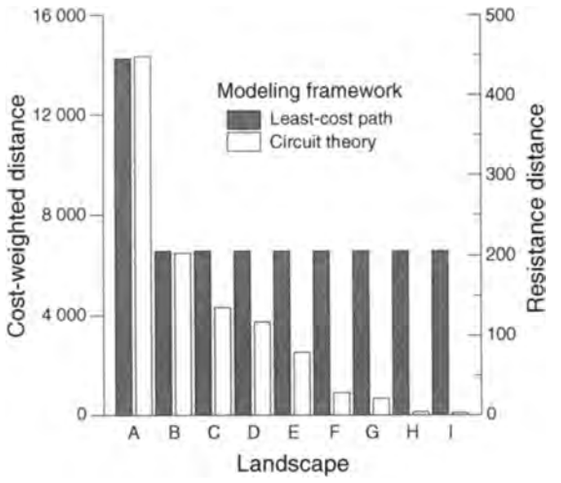

FIG. 6. Least-cost distances and resistance distances between habitat patches for the nine simple landscapes shown in Fig. 5. Least-cost distances decrease from (A) to (B) but are equivalent for all remaining maps. Effective resistances decrease not only from (A) to (B), but also from (B) to (I), reflecting the availability of more and wider pathways. Redundancy, defined here as the ratio of least-cost distance to effective resistance, would be roughly equal for cases (A) and (B) but would increase from (B) to (I). Cost-weighted distance (measured in cost units) were calculated using PATHMATRIX software. Resistance distances (measured in ohms) were calculated using Circuitscape software.

greater distance between cell centers. We converted individual cells to single nodes, except for cells in areas of zero resistance, i.e., open source/target patches; as in the simple landscape in Fig. 4, these cells were considered collectively and consolidated into a single node for the analyses. For all examples, we used the same resistance surfaces to calculate least-cost distances and map least-cost corridors using PATHMATRIX software (Ray 2005).

We started with nine simple landscapes (Fig. 5) meant to illustrate different properties of circuit models. The landscapes consisted of 1000 × 1000 cells each and contained two primary habitat patches, which were always the same distance from one another and always occupied the same total area. Least-cost and resistance distances calculated between habitat patches in the nine simple landscapes illustrate some advantages of the resistance distance (Fig. 6). Although least-cost distances correctly identify decreased isolation between habitat patches in landscape B relative to A, they were identical in landscapes B through I. Resistance distances show a similar decrease from landscape A to B, but they also decrease from B to I, reflecting the availability of additional, or wider, pathways. Note that between landscapes H and I, only the shape of the primary habitat patches has changed, and not their area or the distance separating them. Yet the resistance distance differs because the greater surface area of each habitat patch in landscape *I* acts as a "drift fence" to better intercept or release dispersers.

Commute times ranged from 1.2 million steps (landscapes B, C, and G) to 6.2 million steps (landscape A). They were intermediate for landscapes D, E, F, H, and I, which had commute times of 2.6, 3.0, 1.6, 2.7, and 2.0 million steps, respectively. Lower commute times reflect configurations in which dispersers are efficiently channeled between habitat patch pairs, minimizing wandering time.

These same simple landscapes also demonstrate how current maps (Fig. 7) can highlight connective elements in raster frameworks. As the availability of multiple pathways increases, current density—indicating cells through which dispersers are likely to pass moving from one patch to the other—decreases. Pinch points are highlighted in landscapes D–F, and the "drift fence" effect resulting from the more linear shape of the habitat patches in landscape I is evident as well. Fig. 7J shows a least-cost path map for the "braided stream" corridor configuration. The technique identifies the route with the lowest cumulative cost, but gives no information about the contribution of alternative pathways. By contrast, the current map (Fig. 7D) clearly indicates the importance of different corridor segments, with current densities at their highest in the two critical linkages and at their lowest in segments that are most redundant.

We can now illustrate how these models can be used to analyze connectivity in more realistic landscapes. Fig. 8A shows a complex landscape, with patches of high-quality habitat, lower quality "matrix" habitat, corridors, and complete barriers. Fig. 8B shows cumulative travel cost mapped between two high-quality patches using standard least-cost path techniques. The map highlights the most efficient pathway between the two patches, as well as low-cost detours that do not actually contribute to connectivity, e.g., into habitat cul-de-sacs or along "corridors to nowhere." By contrast, the current map between the same two habitat patches (Fig. 8C) highlights critical pinch points between the two patches. Habitat cul-de-sacs and corridors that do not contribute to connectivity have minimal current flow. The current map also indicates two broad routes linking the habitat patches, whereas only one is highlighted in the least-cost map. The current map thus gives important insight into the redundancy that would be lost if the second route were to be blocked.

Often it will be useful to summarize connectivity between many habitat patches or protected areas in a single map. Fig. 9A shows the result of adding 10 pairwise current maps calculated among all pairs of five habitat patches. These maps show which landscape elements are most important for overall connectivity among the five habitat patches, indicating the net number of times random walkers are expected to move through raster cells if one random walker moves from each patch to each other patch.

We could also extend the analyses of our raster maps in much the same way as the analyses in Fig. 2A were extended in Figs. 2B and 3. Ground resistors could be added to incorporate mortality or finite probabilities of

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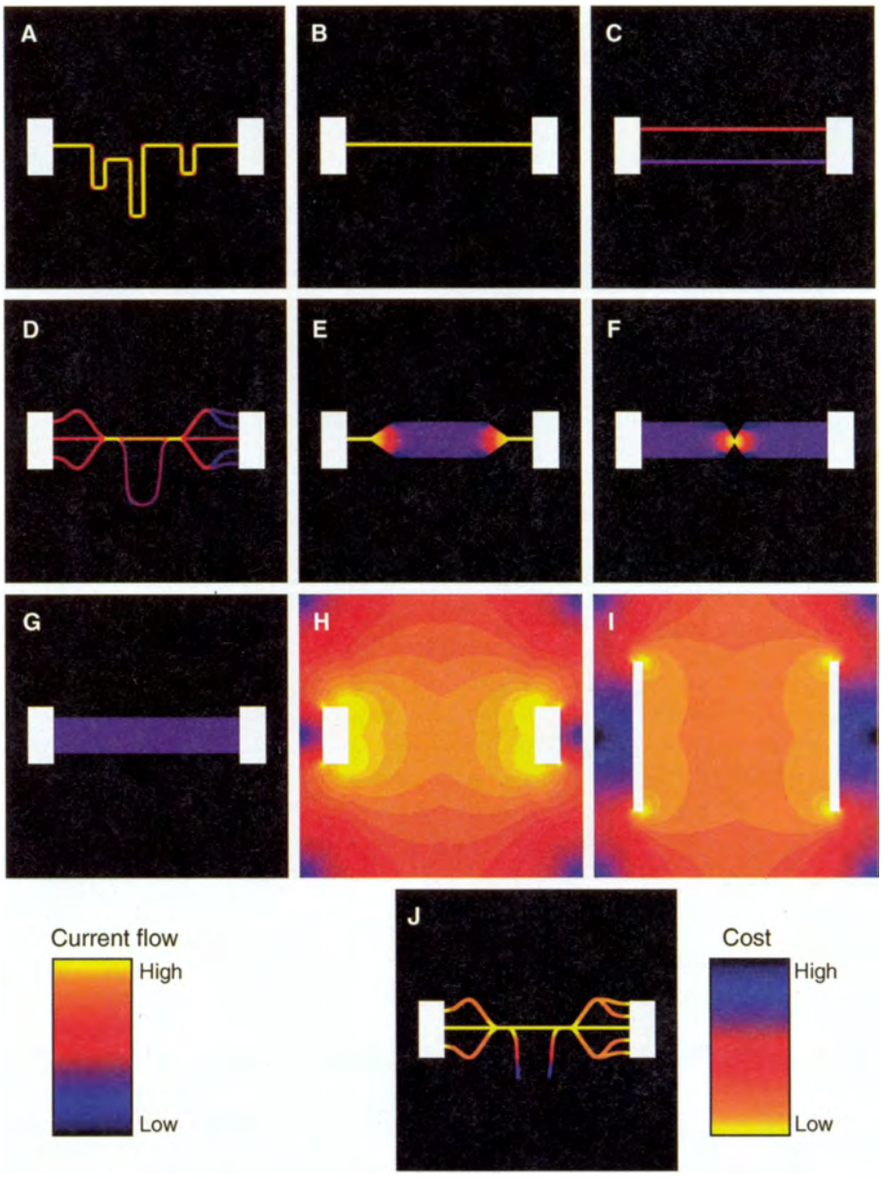

FIG. 7. Current flow through landscapes shown in Fig. 5 when 1 A (ampere) of current is injected into one habitat patch and the other is connected to ground. Current maps were log-transformed to facilitate display. Among the nine panels, three different quantitative scales are applied to the color schemes in order to most clearly illustrate differences in current densities. The three schemes are applied in panels (A)–(D), (E)–(G), and (H)–(I). Highest maximum current densities (indicating the greatest impact of habitat cell removal or conversion) are observed in (A), (B), and (D)–(E), where connectivity depends on single, narrow corridor segments. The lowest maximum current densities are observed in landscape (I), which provides the most redundancy and lowest effective resistance. This landscape also exhibits a drift-fence effect, in which the linear shapes of the habitat patches act to intercept dispersing individuals. (J) The least-cost path solution of the "braided stream" landscape shown in Fig. 5D. Whereas this technique highlights the most efficient travel path, it gives no indication of pinch points or effects of multiple parallel corridors.

settling once a disperser reaches a habitat patch or protected area. With multiple destination patches, a matrix of asymmetrical dispersal rates between all patch pairs could be generated. Or, target patches could be set to 1 V and probabilities of successful dispersal (or dispersal to one patch vs. others) from any point on the landscape could be mapped. Finally, additive maps (such as the one shown in Fig. 9A) could be adjusted to give greater weight to important source or destination patches, with more current released or absorbed by larger or higher quality habitat patches.

Model sensitivity to landscape scale

Representing a landscape as a raster grid always involves choosing an appropriate scale of analysis (cell size and map extent). Because different species respond

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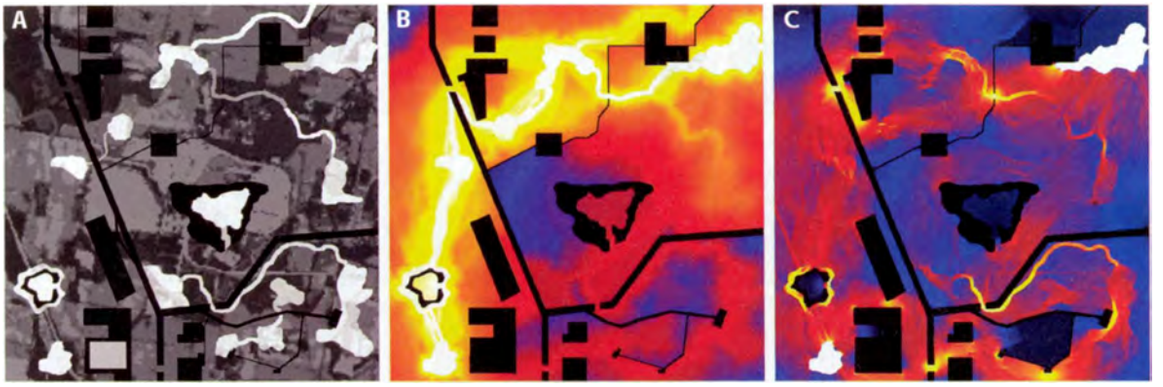

FIG. 8. Connective elements identified using least-cost path and circuit models in a complex landscape. (A) Map of the landscape, with resistances and costs for circuit and least-cost path analyses ranging from 1 (light gray) to 100 (dark gray) to infinite (black). (B) Results from least-cost modeling between habitat patches in lower left and upper right corners of the map. The value assigned to each cell indicates the cost accumulated moving along the most efficient possible route that passes through the cell from one habitat patch to the other; brighter areas indicate cells along the route of lowest cumulative cost. Some habitat cul-de-sacs are highlighted because the most efficient path connecting one patch to the other via the cul-de-sac has a low cost relative to most other features in the landscape. For the same reason, some "corridors to nowhere" are highlighted, such as the one leading off of the top of the map. (C) Current map between the same two habitat patches. Higher current densities indicate cells with higher net passage probabilities for random walkers moving from one patch to the other. The map highlights "pinch points," or critical habitat connections, between the two patches. Habitat cul-de-sacs have minimal current flow because they do not contribute new, independent pathways between habitat patches.

to landscape structure at different scales (Wiens 1985, Wiens and Milne 1989; Beier et al., *in press*), there will be no single correct approach to this. The extent of an analysis will obviously have important consequences, since map edges will constrain potential movement routes. Cell size is also important, but our analyses indicate that as long as it remains fine enough to capture relevant landscape elements, such as narrow corridors and barriers, there is considerable robustness in the technique to changes in cell size. Fig. 9B shows the same landscape as in Fig. 9A, but analyzed using cell sizes that are an order of magnitude larger. Notably, current densities and resistance distances calculated among habitat patches are highly correlated between the two scales, a consistent result in our analyses in a wide range of natural and artificial landscapes. However, these analyses also show that it is particularly important to capture absolute barriers to movement that may not easily be detected at coarser cell sizes. Such barriers (such as the narrow roads in Fig. 9A) were automatically

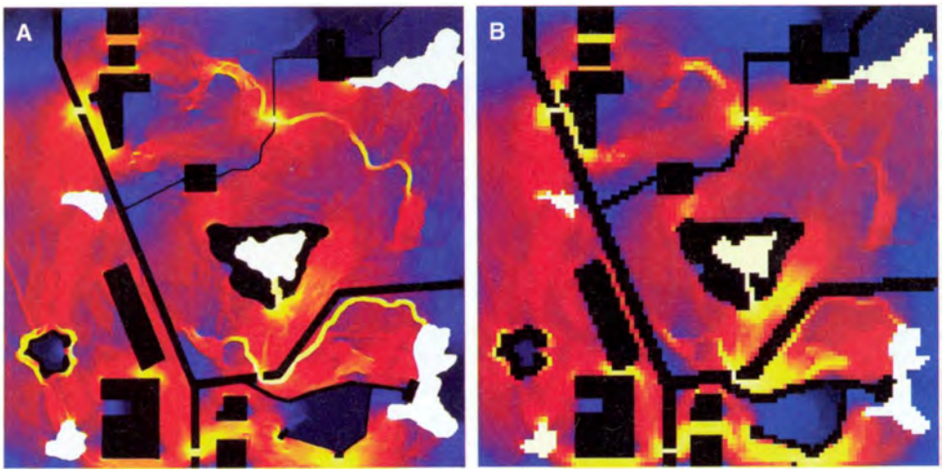

FIG. 9. Summed current from all pairwise current maps between five habitat patches, each shown in white. Calculations were performed (A) at the original 1000 × 1000 cell resolution and (B) at a reduced 100 × 100 cell resolution. To produce the coarser resolution habitat map, blocks of 10 × 10 cells were converted to single cells, with the resistance of each new cell set equal to the mean resistance of the 100 cells it contained. The current maps at the two resolutions identify the same pinch points and important corridors, and pairwise effective resistances measured between all habitat patch pairs at the two scales are highly correlated ($R^2 = 0.963$), illustrating the method's robustness to scale.

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PLATE 1. Puma mother and kitten in Caspers Wilderness Park, Orange County, California. Cirtuit theory is being applied to inform efforts to conserve connectivity for pumas in the region. Photo credit: Donna Krucki.

incorporated into our analyses in Fig. 9B because we averaged resistances among consolidated cells, with infinite resistances "trumping" all others.

DISCUSSION

Although a wide variety of methods exists for predicting connectivity across landscapes, circuit-theoretic models provide some distinct advantages. First, the precise relationships between circuit theory and random walks lend theoretical justification to these models and mean that the metrics they generate can genuinely be considered to be process based. Second, these relationships also mean that circuit models will often be more straightforward to parameterize than other connectivity models because conductances and resistances assigned to edges or raster cells have clear interpretations in terms of movement probabilities. Third, unlike commonly applied least-cost path approaches, circuit methods incorporate multiple pathways, not only in generating metrics of connectivity and isolation, but also in identifying corridors and other important landscape elements connecting habitat patches or protected areas. An advantage of this property is that when dispersal pathways are lost, the predicted importance of remaining pathways increases. Finally, circuit models have an intuitive appeal in that the idea of using resistance and current to model connectivity across landscapes is readily understood by both practitioners and nonscientists. In effect, we find that the method objectively identifies important connective elements similar to those identified by the human eye, replicating expert opinion but removing potential sources of bias once relative resistance values and scales of analysis have been defined.

Niches for circuit models

We envision several roles for circuit theory in evolution, ecology, and conservation. Circuit theory has already been shown to be useful for predicting patterns of gene flow in heterogeneous landscapes, particularly when data on absolute population sizes and migration rates are lacking, but relative population densities or permeabilities to movement are hypothesized for different landscape features (McRae 2006, McRae and Beier 2007). As discussed in the section below, the theory underlying gene flow modeling is similar to that described here, but relates resistance distances to random walks of genes over multiple generations rather than to random walks of individuals within single lifetimes.

In ecology, circuit models can be used as simple movement models, e.g., when data or time required for simulations are lacking or when the comparison of simple and complex model predictions is desirable. An example application would be to predict dispersal rates between populations based on simple landscape data in order to parameterize metapopulation models. Additionally, just as it can be used to predict gene flow, circuit theory may be useful in modeling other emergent

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processes that depend on dispersal. Some ecological phenomena, e.g., community similarity and diversity, may respond to dispersal not of one species, but of several species with only somewhat similar dispersal abilities or habitat requirements. Here, simulations may be prohibitive or inappropriate because of the large number of species involved. However, analytic approaches like ours may be able to adequately capture these processes without imposing prohibitive data or computational requirements.

Measurements of resistance distances, commute times, and current densities have clear applications in conservation planning, such as corridor design or predicting the effects of different land use practices on connectivity. Circuit theory should provide an especially powerful tool for designing robust reserve networks, i.e., those that still provide for connectivity in the face of uncertainty in species distribution data and/or future habitat loss (Moilanen et al. 2006*a*, O'Hanley et al. 2007; Pinto and Keitt, *in press*). Importantly, circuit methods can be applied to the same resistance surfaces that are commonly employed in least-cost path analyses, and with little added computational expense.

In this paper, we limited our examples of circuit-based analyses to accessible interpretations of resistance, voltage, and current. However, there should be a large number of tools that could be derived from these basic properties. For example, metrics that combine predictions of efficient travel paths, pinch points, and mortality risks could allow practitioners to map landscape features that most effectively contribute to connectivity while minimizing mortality rates. Or, metrics derived from shortest path or least-cost distances, such as the Harary index (Ricotta et al. 2000, Jordán et al. 2003) or the integral index of connectivity (Pascual-Hortal and Saura 2006) could be modified by substituting resistance distances for least-cost distances in their calculation. Additionally, algorithms like edge and node thinning, used to evaluate impacts to connectivity of habitat loss in graph theory (Urban and Keitt 2001), can also be applied using circuit-based measures.

A note about ecological vs. evolutionary applications

It is important to be aware of subtle differences in assumptions behind applications of circuit theory to different processes. So far we have identified two distinct frameworks, one which models gene flow across population networks and the other focused on individual movement across habitat networks. The former assumes nodes (or cells) represent subpopulations (or occupied habitat for continuously distributed populations), with resistors representing numbers of migrants exchanged between adjacent nodes per generation (McRae 2006). By contrast, applications focused on individual movement will typically be implemented at finer temporal and spatial scales, with nodes (cells) mapped at the scale at which individual movement decisions are made. Thus, the two will often be applied at different scales and with (at least somewhat) different habitat models. Similarly, predictions from the two frameworks must also be interpreted differently. For example, in applications where nodes or cells represent occupied habitat exchanging migrants, a decrease in the resistance distance between two nodes corresponds to a proportional increase in gene flow predicted between them; however, when nodes represent dispersal habitat rather than subpopulations, a decrease in the resistance distance corresponds only to an increase in available dispersal pathways, and not necessarily a commensurate increase in individual movement rates or gene flow. It does, however, indicate that there will be more pathways available to dispersers, and presumably greater robustness of the network to future habitat loss. Conservation applications may be implemented using either framework, but it is important to specify the process being modeled.

Model parameterization

A critical and challenging step in applying circuit models to landscape data will be assigning relative movement, mortality, and/or settlement probabilities to different land cover classes. Many of the same strategies for parameterizing least-cost path models using expert opinion, literature review or data on species occurrences, animal movement paths, or interpatch movement rates (reviewed by Beier et al., *in press*) will be useful in circuit modeling, particularly when viewed in light of the concrete interpretations of resistances in terms of random walk probabilities outlined here. Practitioners should also consider approaches taken to parameterize other models that consider habitat heterogeneity, such as diffusion and simulation models (e.g., Dunning et al. 1995, Schumaker 1996, Ovaskainen 2004; Arellano et al., *in press*; Ovaskainen et al., *in press*).

Connections between resistance distances and gene flow (McRae 2006, McRae and Beier 2007) should facilitate the use of genetic data to estimate relative resistances of different habitats. Still, because assumptions differ between evolutionary and ecological applications of circuit theory (as discussed here), using data from one to parameterize the other must be done with care.

Regardless of the method used to assign them, there will always be uncertainty in resistance values. We encourage uncertainty analyses to address how decisions at each modeling step affect results; Beier et al. (*in press*) reviewed strategies for conducting uncertainty analysis in least-cost path modeling, and these should be equally applicable to circuit theory. Additionally, for corridor and reserve designs, uncertainty in landscape resistances could be incorporated in much the same way as proposed by Moilanen et al. (2006*b*), with penalties that reflect modeled error incorporated into landscape resistance input maps.

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Limitations and alternatives

As with other methods for describing connectivity in complex landscapes, there are limitations to our approach that should be considered when deciding if it is appropriate for a given problem. First, because resistors are isotropic, i.e., their resistance to current flow is the same in both directions, the methods described here cannot accommodate movement that is biased in one direction (as in directed graphs). This will limit applications in some systems, e.g., marine environments, where directional currents play a large role in determining dispersal rates. Second, circuit models are restricted to Markovian random walks, i.e., random walks in which each step is independent of previous moves. Random walkers thus have no "memory," and our framework cannot incorporate correlated random walks, changes in movement behavior with time, or mortality rates that increase with an organism's age. Even when the assumption of constant mortality with time is reasonable, incorporating mortality into circuit models must be done with care. Because they have no memory or long distance perception, random walkers can retrace their steps over and over, inflating mortality rates because travel time and exposure to mortality risks are increased (Fig. 2B).

Several other connectivity modeling frameworks provide complements to ours. The conceptually and computationally simplest are based on Euclidean distances, and can be quickly calculated on grids with millions of cells (e.g., Moilanen et al. 2005, Moilanen and Wintle 2007). Least-cost path models have been applied for over a decade in connectivity analyses and have proven useful in conservation planning efforts (e.g., Beier et al. 2006, Rouget et al. 2006). Although they do not have the theoretical foundation in random walk theory that circuit models do, their intuitive appeal and ability to identify efficient movement pathways make them useful counterparts to the applications we have described here. Recently, variants on these approaches have been developed that identify and rank the importance of multiple pathways across landscapes (Theobald 2006; Pinto and Keitt, *in press*).

More sophisticated analytical and simulation models can be used to derive results similar to those produced by circuit theory, with some advantages. Markov chain models use the same data structures as those described here, but can accommodate directionality in movement along edges, providing more flexibility for modeling, e.g., effects of directed dispersal, prevailing winds, or ocean currents. Still, although Markov chain models have been available for decades, ecologists and conservationists have been slow to adopt them, whereas simpler, more intuitive least-cost path models have been widely employed. Spatially structured diffusion models (Ovaskainen 2004) are promising because they also integrate over all movement paths and can approximate correlated random walks in their long-term behavior, but their mathematical formulation can be quite challenging. Of course, individual-based movement simulations (e.g., Schumaker 1998, Hargrove et al. 2005) offer much more flexibility than analytic models, can incorporate subtle effects of dispersal behavior and other aspects of life history, and can simulate transient effects of landscape characteristics that evolve over time. However, the data and computational requirements of such models will likely continue to limit their use in many applications (Minor and Urban 2007). Our hope is that circuit models will fill a niche between simpler Euclidean or least-cost path analyses and more powerful analytic and simulation approaches.

Future prospects

Our focus has been on measuring connectivity in heterogeneous landscapes using models from circuit theory. Even in this context, there remain many exciting applications to explore. Nonequilibrium circuit analyses may be applicable to ecological problems (McRae and Beier 2007), and nonlinear circuit elements show promise as well (for example, diodes would allow incorporation of movement probabilities with directional bias). Additionally, analytical techniques developed to minimize effective resistances across networks (Ghosh et al. 2006) may be useful in designing optimal networks for connectivity conservation. More broadly, circuit theory will likely benefit other areas of ecology that deal with networks, such as the analysis of community interactions, food web structure, exotic invasion, or disease transmission. In the meantime, circuit models are being actively applied to conservation planning for species of concern in rapidly developing landscapes, including pumas (*Puma concolor*; see Plate 1) in southern California.

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Where to Restore Ecological Connectivity? Detecting Barriers and Quantifying Restoration Benefits

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Abstract

Landscape connectivity is crucial for many ecological processes, including dispersal, gene flow, demographic rescue, and movement in response to climate change. As a result, governmental and non-governmental organizations are focusing efforts to map and conserve areas that facilitate movement to maintain population connectivity and promote climate adaptation. In contrast, little focus has been placed on identifying barriers—landscape features which impede movement between ecologically important areas—where restoration could most improve connectivity. Yet knowing where barriers most strongly reduce connectivity can complement traditional analyses aimed at mapping best movement routes. We introduce a novel method to detect important barriers and provide example applications. Our method uses GIS neighborhood analyses in conjunction with effective distance analyses to detect barriers that, if removed, would significantly improve connectivity. Applicable in least-cost, circuit-theoretic, and simulation modeling frameworks, the method detects both complete (impermeable) barriers and those that impede but do not completely block movement. Barrier mapping complements corridor mapping by broadening the range of connectivity conservation alternatives available to practitioners. The method can help practitioners move beyond maintaining currently important areas to restoring and enhancing connectivity through active barrier removal. It can inform decisions on trade-offs between restoration and protection; for example, purchasing an intact corridor may be substantially more costly than restoring a barrier that blocks an alternative corridor. And it extends the concept of centrality to barriers, highlighting areas that most diminish connectivity across broad networks. Identifying which modeled barriers have the greatest impact can also help prioritize error checking of land cover data and collection of field data to improve connectivity maps. Barrier detection provides a different way to view the landscape, broadening thinking about connectivity and fragmentation while increasing conservation options.

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Introduction

Landscape connectivity, or "the degree to which the landscape facilitates or impedes movement among resource patches" [1], is crucial for many ecological and evolutionary processes, including dispersal, gene flow, demographic rescue, and movement in response to climate change [2–7]. Many research and conservation planning efforts have focused on mapping areas important for connectivity using GIS models (e.g., [8–12]). The results of these analyses are guiding investments by governmental and non-governmental organizations to promote ecological connectivity across large areas. In the USA and Canada, for example, numerous broad-scale conservation efforts such as the U.S. Department of Interior Landscape Conservation Cooperatives, the Western Governors' Association's Initiative on Wildlife Corridors and Crucial Habitat, and the Yellowstone to Yukon Conservation Initiative are working to integrate and coordinate connectivity conservation actions spanning millions of acres and crossing many political and ecoregional boundaries.

Conservation practitioners employ two primary strategies to promote connectivity. The first focuses on conserving areas that *facilitate* movement; the second focuses on restoring connectivity across areas that *impede* movement (e.g., by removing a fence or building a wildlife-friendly highway underpass). Most connectivity analyses have focused on the former strategy by modeling and mapping areas important for movement under present landscape conditions. A wide array of tools have been developed for this purpose: least-cost corridor modeling [8,13,14], circuit theory [15], individual-based movement models (e.g., [16–18]), graph theory [19,20], and centrality analyses (e.g., [21,22]) have all been used to identify areas important for movement of plants and animals. Outputs from such models are now being used as inputs to reserve selection algorithms (e.g., [23]) to optimize actions to conserve connectivity.

In contrast, there has been little effort by conservation scientists towards identifying candidate areas for the second strategy: that is detecting restoration opportunities by mapping barriers that strongly reduce movement potential. We define a barrier as a

landscape feature that impedes movement between ecologically important areas, the removal of which would increase the potential for movements between those areas. Here we are concerned with movements important for access to resources, demographic rescue, gene flow, range shifts, and other ecological and evolutionary processes. In this context, barriers are distinguished from features that are impermeable but not situated such that they block biologically relevant movement routes. Barriers are thus the inverse of corridors, which delineate pathways facilitating movement. Barriers can either be complete (impermeable) or partial (e.g., land cover types that hinder movement relative to ideal conditions, but may still provide some connectivity value). Barriers may be human-made (e.g., roads, fences, or urban areas) or natural (rivers or canyons); they may be linear (e.g., highways) or span large areas (agricultural fields). As with traditional connectivity concepts [1,24], what constitutes a barrier, the impact it has, and whether it reduces connectivity through behavioral inhibition, increased mortality, or other means will differ among species.

Detecting barriers to movement would complement traditional connectivity analyses in several important ways. First, some barriers may be restorable. Knowing where barriers have the greatest impact would help practitioners decide where and how to invest scarce conservation resources to conserve and enhance connectivity. For example, it may be cheaper to restore a barrier that blocks a movement corridor through public land than to establish permanent protection of a functioning corridor that runs through private land [25]. Quantifying such trade-offs would be necessary to integrate connectivity restoration into systematic conservation planning analyses aimed at optimizing conservation investments [26–28], but tools to incorporate connectivity conservation and/or restoration into such efforts remain rare [29–31]. Second, consider that corridor modeling often produces corridors that may not be good enough to realistically support movement [32]. Barrier detection analysis could reveal such cases, allowing practitioners to 'triage' a landscape, focusing efforts on more viable movement routes. Finally, surprising results in a barrier analysis could alert analysts to situations in which poor land cover data or incorrect model parameterization may be causing spurious results.

In this paper, we introduce a new method to identify barriers and rank them by their impact on connectivity. Our method complements existing connectivity modeling approaches, is applicable in least-cost and other connectivity modeling frameworks, and can be extended to centrality analyses. The method can be readily applied across large landscapes, efficiently analyzing barriers among many locations and at different scales corresponding to different sizes of barriers and types of restoration activities. It also quantifies the extent to which restoration can be expected to improve connectivity. We provide example applications of the method, showing that the potential for connectivity conservation is not constrained to narrow corridors, but includes options spanning much more of the landscape when restoration options are considered. We also discuss how our approach can facilitate sensitivity analyses, data quality screening, and prioritization of areas for error checking of GIS base data.

Method for Detecting Barriers and Restoration Opportunities

Our method identifies areas that most reduce connectivity between two locations on a landscape. Making these areas permeable to movement would therefore most increase connectivity between the locations. Thus, these are areas that practitioners should consider when implementing restoration to promote connectivity.

To illustrate the method, we use a least-cost corridor modeling framework [13,14,32], which is commonly used to map and prioritize areas important for connectivity conservation (e.g., [8–12]). However, our approach could also be used with other modeling frameworks capable of producing measures of effective distance, such as circuit theory and individual-based movement models (see Discussion).

As with least-cost corridor models, input data include locations to be connected (hereafter, "patches") and a raster resistance surface (Figure 1A). The former may consist of points or polygons, and typically represent natural landscape blocks, protected areas, or core habitat for a particular species or species guild [33]. The resistance surface represents the difficulty, energetic cost, or mortality risk associated with movement through each pixel (see [34] for a review of resistance surface development).

Least-cost methods calculate the cost-weighted distance (*CWD*) of all pixels to a source location, creating a raster of *CWD* values (Figures 1B and 1C). Adding together *CWD* rasters from two locations produces a corridor (Figure 1D), showing the pathways with the lowest cumulative movement cost between the locations [14]. The minimum value of the corridor raster is the least-cost distance (*LCD*); this represents the cumulative resistance encountered moving along the optimal path from one location to the other, and is a common measure of isolation in spatial ecology (e.g., [35,36]), landscape genetics (e.g., [37,38]), and related fields.

Our method is based on this simple assumption: if a certain area (the size is defined by the user) is restored such that the resistance across it is reduced, then the *LCD* of the best route connecting the patches through the restoration area will also be reduced. Systematically quantifying the potential reduction across a landscape will allow us to detect those areas where restoration would lead to the greatest reduction in least-cost distance.

The method begins with *CWD* calculations from two patches (Figures 1B and 1C). However, rather than adding the two *CWD* surfaces together to produce a corridor, we instead calculate the minimum value of each *CWD* surface within a localized area around each pixel location (e.g., within a 500 m radius). We then add the minimum values from both *CWD* surfaces to calculate the cumulative resistance that would be incurred moving between the patches and through the focal pixel assuming the area within the search window is restored:

$$LCD' = CWD1_{MIN} + CWD2_{MIN} + (L * R'), \qquad (1)$$

where LCD' is the least-cost distance of the best path between the patches passing through the focal pixel after barrier removal, $CWDX_{MIN}$ is the minimum *CWD* value from patch X within the search window, L is the length of the longest axis of the search window, and R' is the resistance value of the feature replacing (or cutting through) the barrier. We use a circular moving window to illustrate the method (Figure 2), but consider alternative search window shapes in the Discussion. Note that the longest axis of a circle is its diameter.

For each pixel, this formula yields the cost of the best corridor that would pass through that pixel if the resistance of a strip of land crossing the search window were changed to R'. Including R' and the search window length accounts for the cost of moving across the search window, assuming restoration or removal of the intervening barrier.

If LCD' is less than *LCD*, then restoration across the moving window (e.g., the circle in Figure 2) would reduce effective distance and increase connectivity between the two patches. When this is

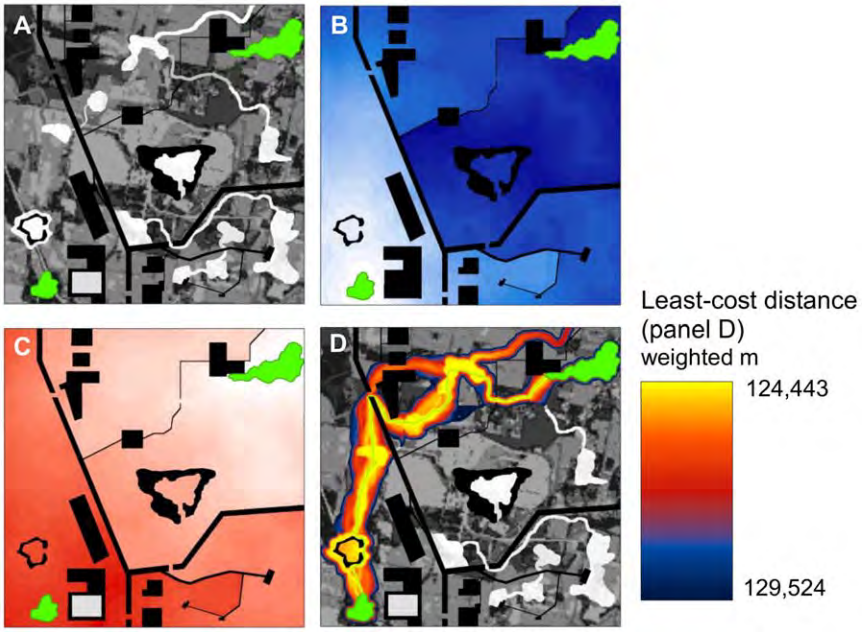

Figure 1. Cost-weighted distance modeling. (A) Example 3 km×3 km landscape with a pixel size of 3 m (from [15]). Two habitat patches (green) are embedded in a matrix of land cover types with differing resistance to movement. Resistances range from 1 (white) to 100 (dark grey); complete barriers with infinite resistance (e.g., linear features representing roads and highways) are shown in black. (B) Cost-weighted distance (*CWD*) from leftmost patch, with darker shades representing higher cumulative resistance from the patch. (C) *CWD* from rightmost patch, with darker shades representing higher cumulative resistance from the patch. (D) Modeled least-cost corridor produced by adding *CWD* surfaces shown in panels B and C (best 20% of study area shown). The least-costly path (traced in green) has a cumulative least-cost distance (*LCD*) of 124,443 weighted meters.
doi:10.1371/journal.pone.0052604.g001

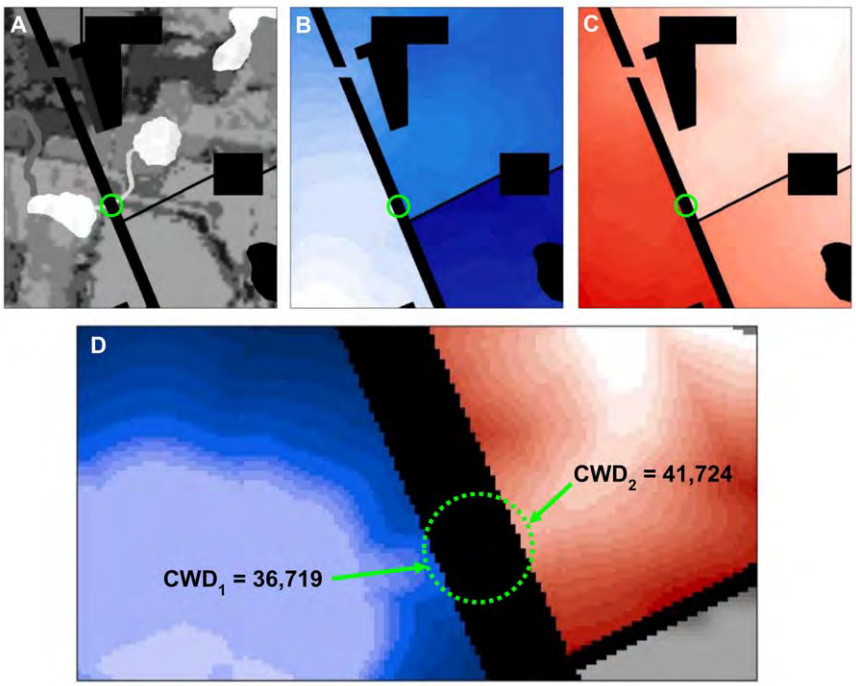

Figure 2. Detail of resistance and *CWD* surfaces with circular moving window. For a window with a diameter of 60 m (20 pixels) centered on the barrier, the arrows show the pixels in the window that have the lowest *CWD* to each patch (values shown are in weighted meters). Because the lowest *CWD* values from each patch will always be found on the edge of a moving window, only pixels on the perimeter need to be examined, increasing processing efficiency.
doi:10.1371/journal.pone.0052604.g002

the case, a simple metric of connectivity improvement that would result from restoration across the moving window is:

$$\Delta LCD = LCD - LCD' \quad (2)$$

Dividing ΔLCD by the search diameter gives the connectivity benefit per unit distance restored; dividing ΔLCD by LCD gives the proportional improvement relative to unrestored effective distance.

To illustrate the method, we first apply it to the relatively simple landscape described in Figure 1 using a search window with a diameter of 60 m (20 pixels at 3 m resolution; Figure 2). The search window size is chosen to match the size of the barrier that one is interested in detecting: a diameter of 20 pixels will fully incorporate effects of barriers up to 20 pixels across. We assign a resistance of 1 to optimal movement habitat, so that the cumulative cost of movement is identical to the Euclidean distance traversed when no barriers are encountered. For the circular window centered on the highway in Figure 2, the lowest *CWD* values from the left and right patches are 36,719 and 41,724 weighted meters, respectively. Summing these values and adding 60 (the cost of crossing the circle if it were restored to optimal movement habitat with a resistance of 1), gives the least-cost distance of the path crossing through the restored area (36,719+41,724+60 = 78,503 weighted meters). Since this is considerably lower than the least-cost distance between the patches without restoration (124,443 weighted meters), this location is a potent barrier, and the center pixel is assigned an improvement value of 45,940 weighted meters. This is repeated for every pixel on the landscape using standard GIS neighborhood analyses, resulting in a raster surface of improvement scores (Figure 3A).

The removal of the barrier where the improvement score is maximal – for example, by constructing a wildlife crossing structure – would re-route the best movement path (Figure 3B) and lower the effective distance between the two patches by 37% (45,940/124,443). Once that improvement is carried out, a second barrier analysis with the altered landscape conditions suggests that additional restorations along the highway will not further reduce the *LCD* at this point (Figure 3C). The next priority would be a road crossing in the upper right of the panel (dark orange in Figure 3C), connecting the rightmost patch to high-quality movement habitat above the road. The method is computationally efficient enough that different restoration scenarios can be tested iteratively: a barrier analysis with a 20- pixel search diameter across a landscape with 1 million pixels takes less than 2 seconds using a 2.7 GHz notebook computer.

Identifying barriers across scales and across large landscapes with multiple patches

The method described above can be extended across scales and across networks of patches, and we explore a few approaches to accomplish this here. By modifying the search diameter, the method can detect barriers of different sizes (Figure 4). Windows the width of a highway will best highlight where highways act as barriers, as in Figures 2 and 3. Larger windows will best detect barriers like agricultural fields, or cases in which narrow barriers run parallel to one another. Summary maps showing barrier effects across search window sizes may be created by first dividing improvement scores by the window size to produce maps of barrier strength per unit width, and then taking the maximum pixel score across scales (Figure 4B). This puts results from different analysis scales in the same units, allowing them to be summarized in a single map. Alternative summary metrics are possible, and we address some of them in the Discussion.

To summarize across multiple sets of patch pairs, we have implemented a similar approach in which the maximum or sum of improvement scores across all patch pairs is assigned to a pixel. Taking the maximum of improvement scores shows the features that have the greatest effect for any patch pair (Figure 4C). Summing improvement scores highlights those barriers that isolate multiple pairs of patches from one another, extending the method to quantify barrier centrality (Figure 4D).

The methods described in this paper have been implemented in Barrier Mapper software [39], freely available as a new addition to the Linkage Mapper Toolkit for ArcGIS [40].

Example application in a landscape undergoing active conservation planning

The Washington Wildlife Habitat Connectivity Working Group, a collaboration of land and resource management agencies, non-governmental organizations (NGOs), universities, and Washington treaty tribes, recently completed a connectivity analysis across the Columbia Plateau Ecoregion in Washington, Oregon, and Idaho, USA [41]. The Working Group focused on the Columbia Plateau because the ecoregion is home to a large portion of Washington's sensitive plant and animal species but is also highly fragmented by agriculture and other anthropogenic activities. The Group modeled corridors to connect habitat for 11 focal species and also to connect natural landscape blocks scoring highly on an index of landscape integrity (i.e., large areas with relatively low levels human modification). Products from the analysis are being used to inform conservation planning efforts by several state and federal agencies and NGOs. Many of the corridors identified by the analysis pass through human-dominated landscapes, where roads, agricultural fields, and other human uses likely still act as barriers to movement.

We reanalyzed results for a corridor connecting two natural landscape blocks identified by the Working Group in Douglas County, Washington (Figure 5). We chose these blocks because they have been identified as important for many species of concern; for example, the blocks contain important habitat or corridors for 8 of 11 focal species analyzed by the Working Group. Moreover, both are occupied by greater sage-grouse (*Centrocercus urophasianus*, categorized as a Species of Greatest Conservation Need in Washington and a candidate for listing under the US Endangered Species Act), and both fall within a recovery area designated for the species by Washington State [42]. In addition, this landscape contains a complex mix of native systems and agricultural lands – the latter including both annual cropland and perennial vegetation cover – and includes roads, transmission lines, and other human-made features affecting animal movement [41].

To represent species with differing degrees of sensitivity to human modification, the Working Group used different resistance surfaces for landscape integrity analyses [41]. These surfaces all contained resistance values that increased with the degrees of human modification, differing only in the range of resistances assigned. Resistance scores of 1–100, 1–1000, and 1–10,000 were used for minimum, medium, and maximum sensitivity surfaces respectively (see [41] for details). We present results from a barrier analysis using the medium sensitivity resistance surface.

The modeled least-cost corridor connecting the patches dips south from the western patch, runs east to Banks Lake, and then north along a narrow strip of native vegetation and cliffs sitting between the lake and cropland (Figure 6A). A secondary and much longer corridor follows broad swaths of native vegetation through

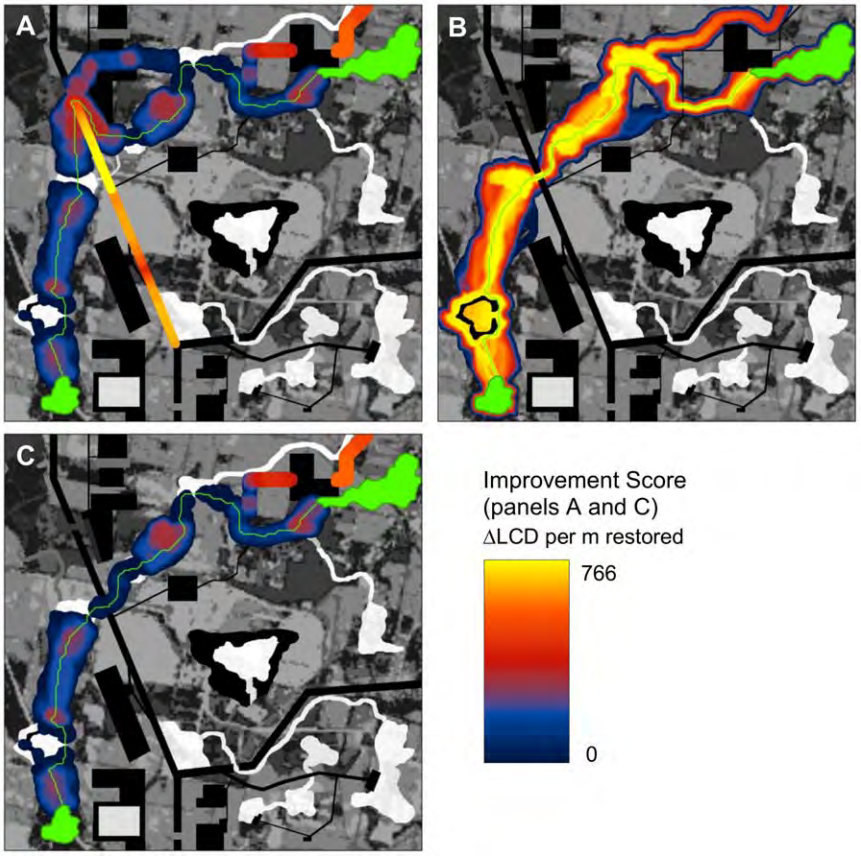

Figure 3. Barrier analysis of landscape. (A) Improvement scores (*ΔLCD*) for a 60 m search diameter using an enhanced version of Linkage Mapper software ([40]). Only positive values (indicating barriers whose removal would reduce isolation) are shown. To facilitate visualization of the barriers, scores were mapped so that they filled the search window (i.e. the maximum *ΔLCD* value within the search radius of each pixel is displayed). The greatest improvement potential was detected crossing the highway. Note that a natural corridor is bisected by the highway at the point with the highest improvement potential (see detail in Figure 2). (B) Creating a new gap in the barrier where restoration potential is highest re-routes the modeled least-cost corridor and greatly reduces resistance between the patches (*LCD* = 78,503 weighted meters compared with an *LCD* of 124,443 pre-restoration). Best 20% of study area shown. (C) Barrier detection at 60 m search diameter after restoration.
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Moses Coulee and Beezley Hills to the south. A barrier analysis indicates numerous opportunities for improving the least-cost corridor, particularly within its east-west segment (Figure 6B). There are also opportunities outside of the main corridor, occurring along the longer route to the south and to the north as well (Figure 6B). Restoring any of these latter areas would re-route the modeled least-cost corridor, causing it to occur in a different location than it did in the unrestored landscape.

Restoration of any of several barriers identified to the south would improve connectivity as measured by *LCD* (Figure 6B); however, this would result in a much longer least-cost corridor. Restoration to the north has the potential to both improve *LCD* and shorten the distance traversed by the corridor. We simulated a restoration by changing a 1 km^2 (500 m×2 km) swath of agricultural land (indicated by the arrow in Figure 6B) to a resistance of 1. We chose 2 km because the greatest improvement was detected at the 2 km scale, and we assumed 500 m was wide enough to accommodate movement. A second corridor analysis following the simulated restoration shows the new corridor to the north (Figure 6C). The corridor has 9.4% less cumulative resistance than the original (1348 weighted km *vs.* 1489 weighted km), and its least-cost path is 44% shorter in un-weighted length. A post-restoration barrier analysis indicates that the highest improvement scores now fall along the new corridor (Figure 6D); restoring a second 1 km^2 swath in this new corridor at the point indicated by the arrow would further reduce *LCD* by 50%.

Discussion

Connectivity models have provided valuable guidance to conservation planning efforts, as well as predictions of movement, gene flow, and isolation important to landscape genetics and other fields concerned with movement ecology. Yet they have almost exclusively emphasized identifying features that facilitate, rather than impede, movement; this emphasis gives an incomplete picture of how landscape features affect connectivity, what connectivity management strategies might be appropriate, and the uncertainty underlying model predictions. We see considerable potential for barrier detection analyses to help practitioners overcome these limitations. In particular, the ability to identify restoration opportunities can provide valuable alternatives to traditional conservation efforts focused on existing movement corridors.

Our reanalysis of the Columbia Plateau data (Figure 6) illustrates these points, showing how detecting barriers can increase conservation options available to practitioners, improve understanding of analysis products, and result in more robust conservation plans. Without a barrier analysis, conservation

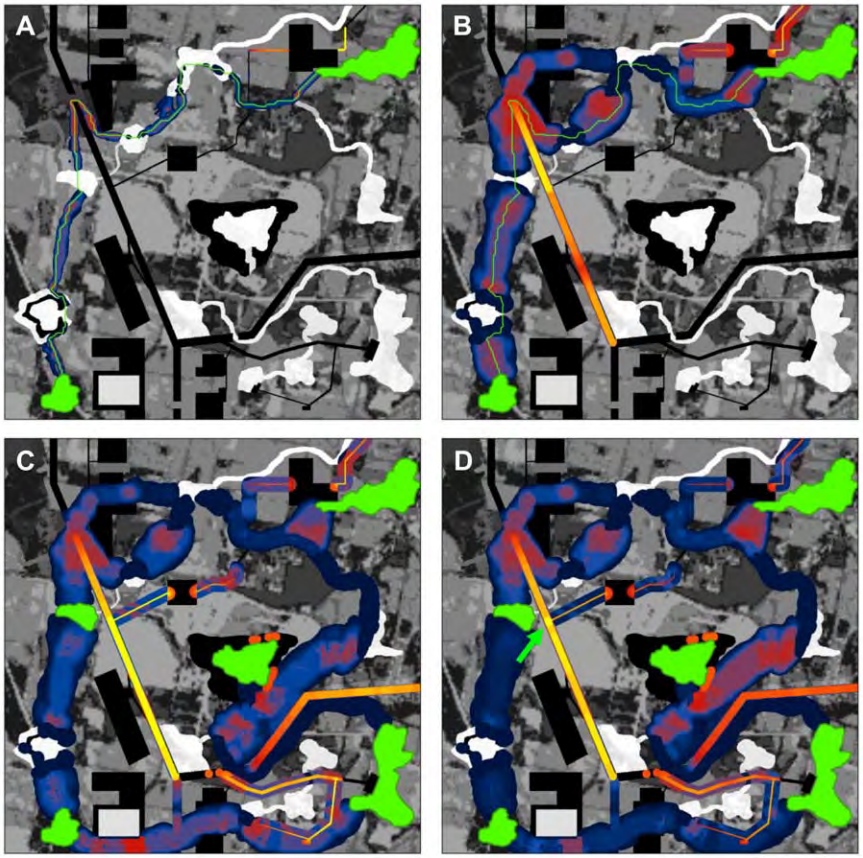

Figure 4. Barrier analyses integrating across multiple scales and patch pairs. (A) Results of barrier analysis with original patch pair at 12 m search diameter, which detects restoration opportunities equal to or less than 12 m across (e.g., local roads). (B) Maximum per-meter improvement value across 10 search window sizes (from 6 m to 60 m, with 6 m steps between search diameters). The map highlights where actions at different scales would have highest impact per meter restored. (C) Maximum per-meter improvement value across same window sizes and 5 patches, showing where greatest improvement could be achieved for any single pair of patches. (D) Sum of improvement scores among 5 patches (green). As in Panels A–C, the maximum per-meter improvement score was calculated for each patch pair at each scale. These were then summed across patch pairs to incorporate cumulative benefit for multiple patch pairs across multiple scales. The area scoring highest (bright yellow) had high improvement scores for multiple patch pairs; we interpret this area as having high 'barrier centrality,' i.e. being an important restoration opportunity for keeping the overall network connected. Note that the area occurs at a road intersection; if practical, placing a wildlife crossing structure here would re-route four corridors connecting the two leftmost patches to both the central and upper-right patch.
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planners would likely have focused on conserving land in or adjacent to the original least-cost corridor. Our analysis revealed numerous opportunities to improve this corridor, but also that restoration of a 1 km^2 swath of cropland would create a new corridor with several desirable characteristics. Specifically, the new corridor has a lower least-cost distance, is shorter in length, and appears to have fewer pinch-points (narrow sections) than the original corridor—all desirable characteristics for corridor design [15,32]. Moreover, if the two original corridors remain in place, the new, northern corridor adds redundancy to connections between the natural landscape blocks. This is important because organisms seldom follow a single optimal path [43], and because redundant connections help to ensure continued connectivity in the face of unpredictable environmental changes [15].

The analysis showed that connectivity conservation options need not be limited to a small portion of the landscape, opening up much more area for actions that could conserve or enhance connectivity and illustrating tradeoffs between different conservation strategies and target locations. Beyond the corridor quality differences cited above, we note that the original corridor runs along a narrow stretch of land bordering Banks Lake, sometimes traversing cliffs. The cliffs were assigned low resistance because the landscape integrity model used by the Working Group only quantified the degree to which pixels have been converted to human land uses. Practitioners, however, may consider cliffs to be impermeable for some species of conservation concern. The barrier analysis allows the user to quickly focus a more critical examination of corridor characteristics on areas influencing the results, and to identify options for alternative corridors that may better fit specific planning needs.

Similarly, the analysis underscored the potential sensitivity of corridor mapping to errors in GIS base data: our results show how the misclassification of a single agricultural field could have entirely altered the location of the original least-cost corridor shown in Figure 6A. The sensitivity of connectivity analysis results to landscape features at key locations has consequences for disciplines that depend on corridor maps (like conservation planning) and for disciplines that depend on connectivity measures (like landscape genetics). We discuss applicability of barrier detection methods to sensitivity analysis and error checking below.

Following the first barrier analysis and simulated restoration, a subsequent barrier analysis indicated that the restoration would

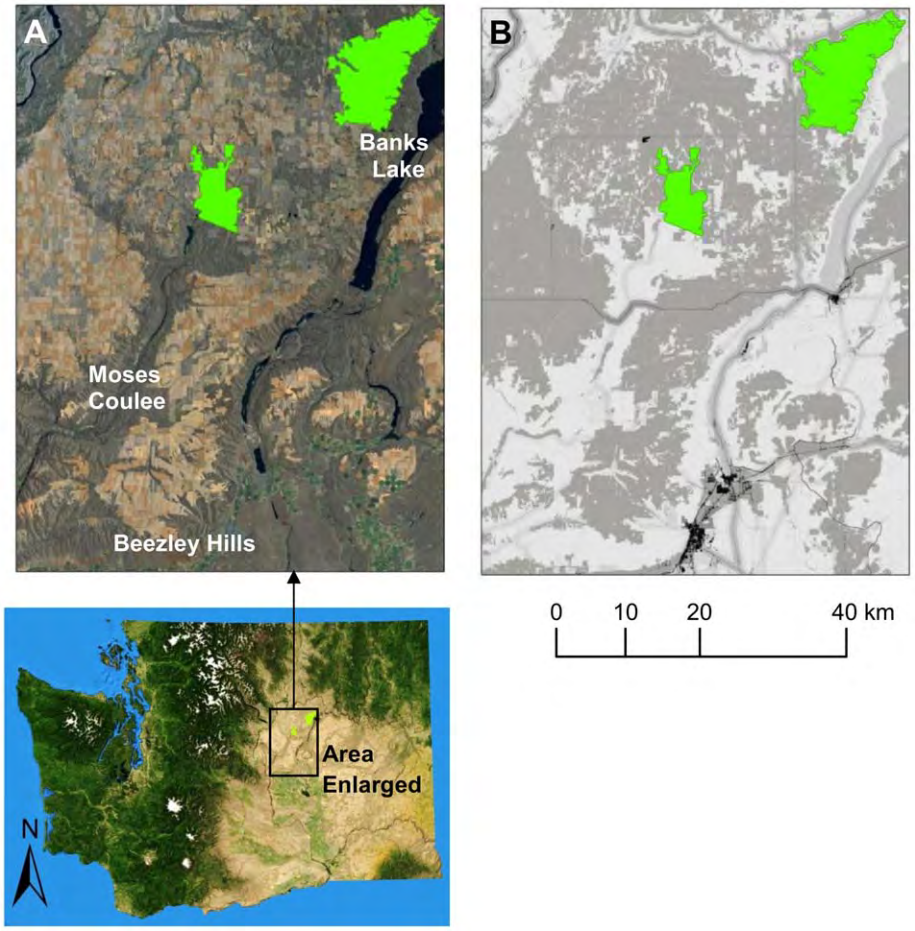

Figure 5. Corridor analysis in a landscape undergoing active conservation planning. (A) 60 km by 80 km study area in eastern Washington, USA, containing two natural landscape blocks to be connected (green). (B) Resistance map used to model corridors in a recent multi-partner connectivity analysis across the Columbia Plateau Ecoregion [41]; values range from 1 (white) to 1000 (black). Low resistance areas include native grassland and shrub-steppe, whereas high resistance areas include roads, developed areas, and agriculture.
doi:10.1371/journal.pone.0052604.g005

open up further restoration opportunities of considerable value, one of which would cut *LCD* values by half. Thus, simulating restorations and re-running corridor and barrier analyses will likely improve final conservation and restoration plans.

Although we are aware of no other efforts to automate identification of terrestrial connectivity restoration opportunities, least-cost corridor analyses have been used to guide placement of crossing structures across roads to restore connectivity for wildlife. For example, Beier et al. [44] assigned a single, finite resistance value to all segments of a highway between two protected areas, regardless of whether a segment contained wildlife crossing structures. The least-cost corridor between the areas crossed the highway at the location where a crossing structure would result in the lowest ecological cost of travel. If highway crossing structures were not located in this corridor, Beier et al. [44] recommended specific structures at particular locations. This approach is useful, but does not quantify the improvement compared to existing conditions, does not identify restoration opportunities outside of least-cost corridors, and cannot be readily applied to barriers more complex than roads.

In addition to overcoming these limitations, our method is also amenable to highlighting barriers that affect multiple corridors, introducing the concept of barrier centrality. As shown in Figure 4, barriers can be mapped across all patch pairs, and the results summed. This identifies barriers with high network centrality, similar to analyses that identify corridors or pathways with high centrality [21,22,45,46].

Applications for error checking and sensitivity analyses

GIS land cover data used to develop resistance layers for connectivity analyses are typically based on satellite or aerial imagery and often suffer from high levels of classification error [34,47]. Although our method relies on these same base data, it can help to prioritize error checking of the data by highlighting mapped features that strongly influence corridor locations. If a permeable feature is misclassified as impermeable and identified as a barrier, the misclassification could entirely alter a corridor's location. We recommend examining detected barriers, either by manually checking aerial imagery or conducting field surveys. Similarly, impermeable features misclassified as permeable that occur along least-cost paths can change corridor locations as well. Examining features along least-cost paths in tandem with barriers could thus further reduce the effects of classification error in connectivity analysis products.

Barrier detection can also be applied to parameter sensitivity analyses, important because resistances are often assigned based on expert opinion, which can be unreliable [34,47,48]. For example, if a given land cover type fell along a corridor's least-cost

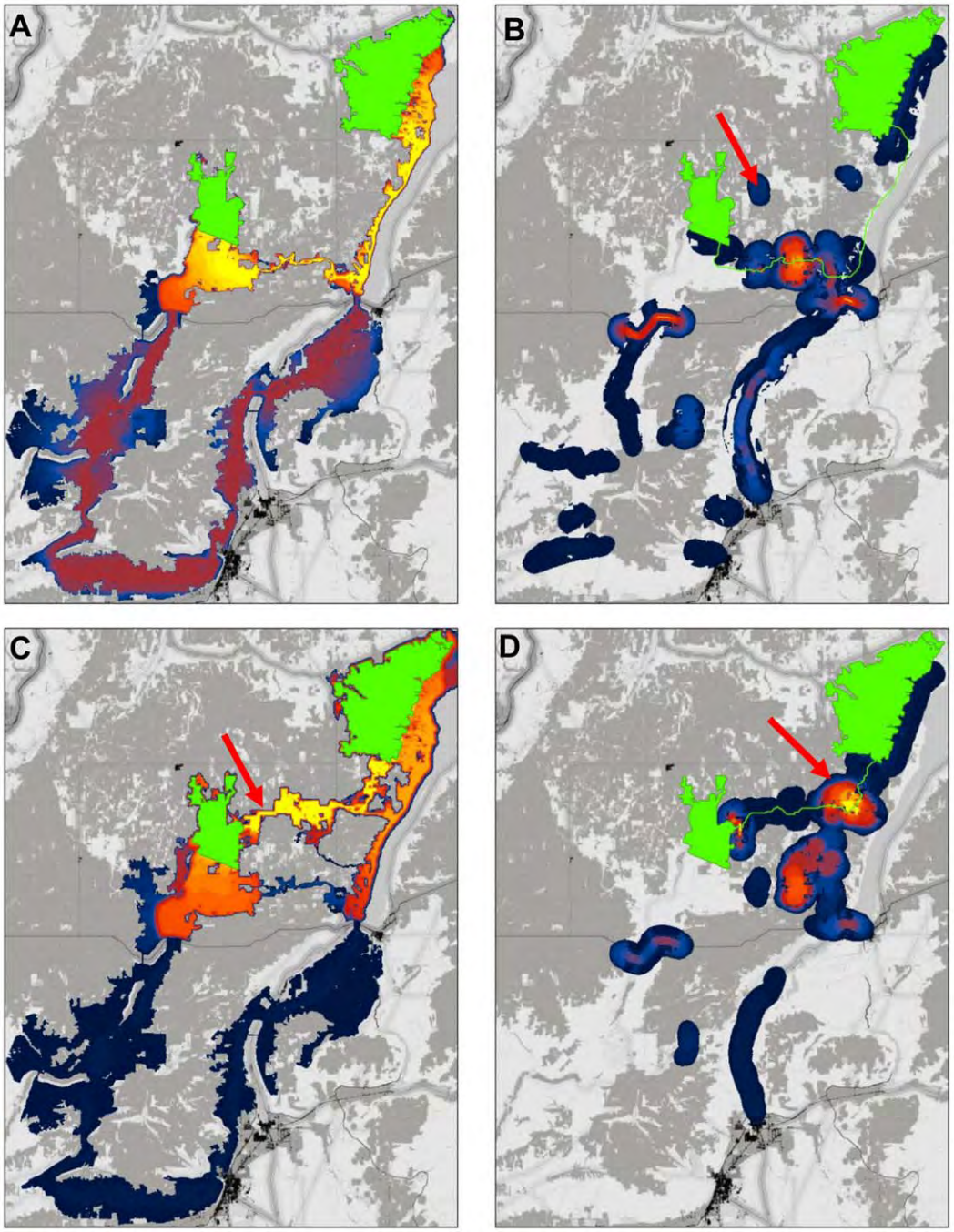

Figure 6. Reanalysis of connectivity modeling results using barrier detection algorithm. (A) Corridor connecting natural landscape blocks, showing least-cost movement routes. Best 20% of study area shown. (B) Barriers detected at diameters from 200 m to 2 km, with original least-cost path shown in green for reference. Mitigating barriers along the least-cost path (i.e., intersecting the green line) would improve the existing corridor without changing its location; mitigating barriers away from the path would re-route the best modeled corridor. (C) Restoring a 1 km^2 (500 m $\times$2 km) swath spanning the barrier indicated by the arrow establishes a new least-cost corridor to the North. (D) A barrier analysis incorporating the simulated restoration indicates opportunities to substantially improve the new corridor with additional restorations.
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path or encompassed an influential barrier outside of the corridor, the resistance assigned to that land cover type would be known to influence the corridor's location. The sensitivity of the corridor's location to the resistance value assigned the land cover type could then be analyzed using alternative parameterization methods as described by Beier et al. [47]. As with connectivity models, our method will depend on the grain size of the resistance raster; to adequately resolve features that potentially impede movement, we recommend pixels no larger than ½ the width of barriers one is interested in detecting.

Potential enhancements

Directionality of barrier effects. Our methods could be improved to more precisely pinpoint barriers. For example,

elongated moving windows (search polygons) could perform better than circles to identify the best path for an improved corridor design. Measuring ΔLCD along elongate polygons placed at different angles, although more computationally complex than measuring across circles, would allow the attribution of directionality to barrier effects as well as adjustment of improvement scores at large search distances to reflect improvement achievable at smaller (nested) distances. New procedures to select the best orientation and width of such polygons could obviate the need to subjectively orient restoration polygons, like the 500 m×2 km polygon in our simulated restoration (Figure 6).

Restoration cost. We measured barrier strength by conservation improvement per meter restored because it was the simplest way to illustrate our approach. An alternative metric would be conservation improvement per restoration dollar; this would reflect, for example, that the cost per meter of a 10 m road crossing structure exceeds the cost per meter of a 50 m crossing structure, which in turn exceeds the cost per meter of restoring agricultural land. This enhancement would facilitate incorporation of connectivity restoration into return-on-investment analyses [49,50], helping managers to balance improvement potential, corridor importance, costs, and risk of conversion or degradation when deciding which parts of a landscape should be conserved or restored. The disadvantage, or course, is that this metric would require more data to calculate.

Restoration efficacy. Different R' resistance values could be applied to different land cover types to reflect the fact that some barriers would be more permeable to movement following restoration than others. For example, a highway underpass installed to allow animal movement may still have considerable resistance, whereas a restored forest stand may have resistance similar to undisturbed forest.

Other enhancements. Just as areas that cannot be conserved can be removed from reserve selection algorithms [51], unremovable barriers, such as urban areas, could be excluded from barrier analyses. The metrics described in equation (2) could be modified to incorporate restoration costs that vary by feature type, or land prices mapped using parcel data. Metrics of corridor importance (e.g., link centrality) could be integrated by multiplying improvement scores by such metrics, which would highlight opportunities to restore the most potent barriers in the most important corridors. Or, rather than focusing on pairs of patches, the method could be altered to focus on the connectedness of each patch by summing barriers detected between each patch and all others. Lastly, improvement scores may be expressed in terms of absolute improvement or percent improvement relative to unrestored corridor resistance. An advantage of the latter approach is that it would favor restoration in corridors in which *LCD* values are already low, presumably meaning they are more viable.

Which of these enhancements are most valuable will depend on the objectives of individual users and projects.

Application in other connectivity modeling frameworks

Although least-cost corridor models are by far the most commonly applied connectivity planning tool, they rely on simple assumptions about animal movement and other processes [43,48,52,53]. However, our approach can be applied in any connectivity modeling framework that produces measures of effective distance. For example, circuit-based connectivity analyses can model the relative proximity of each pixel to two patches by setting the voltage of one patch to 1 and the other to ground (see [15] for details on applying circuit modeling to landscapes). The resulting voltage surface gives the probability that a random walker will reach one patch before reaching the other [15,54]. Strong gradients in voltage indicate barriers that separate areas relatively accessible to one patch from areas relatively accessible to the other. If removed, such barriers would reduce effective resistance between the patches, an analog to *LCD* that takes into account the availability of multiple, parallel connections. A similar approach is widely used in microchip design: simulated voltage levels reveal areas with strong voltage gradients (known as IR drops) where electrical connectivity must be enhanced [55]. Thus barrier analysis using circuit theory can identify opportunities to provide valuable redundant connections even when *LCD* would not be reduced. In contrast, barrier analysis using least-cost methods will not identify these opportunities.

Individual-based movement models provide a more complex but also more powerful framework for modeling connectivity, capable of incorporating more biological realism and behavioral information than least-cost or circuit analyses [56]. As long as an individual-based model can produce maps of effective distance (e.g., based on the probability of, or energetic expenditure associated with, reaching different locations from a source patch), the approach described here could be applied to the model. Models such as PATH [16] and HexSim [17] can be used to derive such measures.

Potential for integration with systematic conservation planning

Our method is not a substitute for algorithms like Marxan [57] or Zonation [51], which are designed to optimize selection of reserves or sets of conservation actions. Although our method identifies and ranks candidate areas for restoration actions, it does not select optimal *sets* or portfolios of conservation actions to achieve given conservation goals while minimizing cost. The same can be said for algorithms designed to map areas that most facilitate movement and connectivity (e.g., [22,40,46,58–60]); rather than incorporating optimization routines, such algorithms instead produce maps that must be interpreted by practitioners, who then make conservation decisions in light of costs, benefits, and other management objectives.

Although it has long been recognized as important to reserve network design [61], incorporating connectivity directly into optimization algorithms has proven difficult. Most such efforts can be characterized as minimizing local fragmentation by either considering the geographic proximity of candidate areas to other areas (e.g., [62–64]) or maximizing the compactness and contiguity of reserves by favoring selection of adjacent cells or using boundary quality or length penalties (e.g., [29,57,65,66]). Because these algorithms favor conserving or restoring contiguous natural areas, they may neglect areas that, although fragmented, contribute to connectivity between natural areas. Thus, relying solely on maximizing the proximity or contiguity of protected areas could lead to elimination of movement routes that cross human-dominated landscapes.

Progress toward synthesizing connectivity and optimization algorithms has likely been hampered by the 'network' nature of connectivity planning: conservation in one area can affect the function and value of distant areas, contingent upon the conservation status and characteristics of the intervening landscape. Incorporating this complexity into optimization algorithms becomes computationally prohibitive with large numbers of planning units [67]. Still, practitioners are beginning to use outputs of multi-species connectivity models as inputs to optimization algorithms like Zonation [23,68]. Such examples are promising, and should be equally applicable with restoration-oriented algorithms such as ours.

An alternative to our approach that would seek to develop a near-optimal set of conservation actions would be to employ a routine similar to that used by Zonation software, which begins with an intact landscape and iteratively removes grid cells with low conservation value [51,69]. Starting with a landscape in which all restorable barriers have been removed, different sets of barriers could be added back in and connectivity metrics recalculated at each iteration. As with traditional connectivity models, however, this would be computationally prohibitive with large numbers of patches or restoration sites because of the computational time required for recalculating connectivity metrics. A promising hybrid approach could be to use the method described in this paper to identify sets of pre-screened restoration opportunities, which could then be removed from a resistance surface and added back in using an algorithm like Zonation's.

Practical considerations for improving conservation and restoration decisions

Managing for connectivity to facilitate gene flow, climate adaptation, and other processes is challenging without reliable maps to guide practitioners [33]. Connectivity analyses have provided valuable implementation guidance in the past; barrier mapping can increase the rigor of such analyses and the range of conservation options they reveal. It can help practitioners a) decide if connectivity conservation is a worthy investment in a landscape; b) identify opportunities to restore vs. conserve different areas; c) reduce uncertainty due to errors in GIS base data; and d) balance potential improvement against costs so that investments can be prioritized.

The goals of managers and planners can be used to guide applications of barrier detection methods. For example, if a transportation agency is interested in determining which highway segments are likely to have the greatest impact on wildlife movement, the search window should correspond to the width of highways, with outputs clipped to highways and the R' value determined based on the estimated resistance of the kind of crossing structure (or alternative structures) being considered. If a land management agency is prioritizing restoration of degraded native vegetation, the search window should relate to the size of appropriate restoration projects, and outputs should be clipped to the eligible land base (e.g., limited to the type of vegetation the restoration would target). If an NGO is identifying landowners interested in obtaining voluntary incentive payments for wildlife-friendly management, the window should reflect the scale of such management. Summarizing barrier analyses across multiple scales will be desirable for collaborations among organizations with differing goals and mandates. As noted above, iterative application of the model with simulated restorations will likely provide the most informative results and most robust conservation plans.

Similarly, the method may have potential to help adapt results from coarse-filter connectivity assessments, such as landscape integrity/human modification-based connectivity maps, to more fine-filter objectives (see [70] for a review of coarse- and fine-filter conservation planning). Alternative corridors revealed by the method could be assessed for their suitability under different planning constraints (e.g., corridors for species that must avoid cliffs, as in the Columbia Plateau example). While not a replacement for species-specific connectivity analyses, such an approach could help land managers evaluate alternatives if a mapped corridor is deemed unsuitable for their particular needs.

Connectivity maps do not always identify functioning routes that need to be maintained and protected; rather, they frequently map routes that may not be currently viable, but appear to provide the best opportunities for future work toward enhancing connectivity. In this sense connectivity maps often represent visions and goals for desired future conditions [71]. Barrier detection can add insight into the practicality of these goals, and identify specific options for achieving them. It can also help practitioners to 'triage' a connectivity plan, identifying corridors that traverse numerous barriers – and therefore would require significant investment to fully restore – so that efforts may be focused on more viable movement routes.

Perhaps most importantly, the ability to detect options to re-route corridors also opens up a broader suite of potential actions to improve connectivity. It can help managers identify new corridors that add additional movement pathways in areas important to the overall connectivity of a landscape (i.e. linkages with high centrality). Combined with spatially explicit land cost data, the method could help to improve conservation efficacy while reducing costs.

We hope barrier analyses will expand conservation options available to managers, and broaden conversations about restoration of connectivity more generally. By identifying new ways to improve connectivity in a particular area, the method can allow managers to consider different suites of strategies, or engage with new sets of stakeholders with interests in different areas. Both from the perspective of entities mandated to carry out conservation actions, and from the perspective of stakeholders with interests in the lands that are the focus of such actions, broadening the suite of alternatives and tools can only increase the opportunities for finding common ground in pursuit of multiple objectives.

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Author Contributions

Conceived and designed the experiments: BHM. Performed the experiments: BHM. Analyzed the data: BHM. Contributed reagents/materials/analysis tools: BHM. Wrote the paper: BHM SAH PB DMT. Suggested refinements to methods and analyses: SAH, PB, DMT.

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IMPROVING THE SUCCESS OF WETLAND CREATION AND RESTORATION WITH KNOW-HOW, TIME, AND SELF-DESIGN[1,2]

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Abstract. The creation and restoration of new wetlands for mitigation of lost wetland habitat is a newly developing science/technology that is still seeking to define and achieve success of these wetlands. Fundamental requirements for achieving success of wetland creation and restoration projects are: understanding wetland function; giving the system time; and allowing for the self-designing capacity of nature. Mitigation projects involving freshwater marshes should require enough time, closer to 15–20 yr than 5 yr, to judge the success or lack thereof. Restoration and creation of forested wetlands, coastal wetlands, or peatlands may require even more time. Ecosystem-level research and ecosystem modelling development may provide guidance on when created and restored wetlands can be expected to comply with criteria that measure their success. Full-scale experimentation is now beginning to increase our understanding of wetland function at the larger spatial scales and longer time scales than those of most ecological experiments. Predictive ecological modelling may enable ecologists to estimate how long it will take the mitigation wetland to achieve steady state.

Key words: achieving successful wetland mitigation; creating wetlands; ecological engineering; ecological modelling; freshwater marshes; functional analysis of wetlands; mitigation of wetland loss; Olentangy River Wetland Research Park, Ohio; wetland succession.

INTRODUCTION

The way in which we measure "success" of created or restored wetlands and our ability to achieve success are two issues that have come under increased discussion in recent years by wetland scientists and managers. Success in the general sense here means the establishment of a biologically viable and sustainable wetland ecosystem. Some call a wetland a success when it replaces the functions lost in a wetland that is being replaced; others would gauge success of a created or restored wetland against natural reference wetlands in the region. Unfortunately, there has been little formal published follow-up of the poorly named (see Renner 1994) "mitigation wetlands" that are constructed to replace wetlands that are unavoidably lost and there are few satisfactory methods for assessing replacement of the functions lost with the original wetland (Mitsch and Gosselink 1993). Regulators and consultants have chosen to use simple indicators of "success" to expedite the process and to keep monitoring costs low. Normally 3–5 yr of simple once- or twice-per-year monitoring is required, with easily measured parameters such as plant lists, animals witnessed, and percentage vegetation cover as the overall indicators. Assessing success is then based on comparing these easily measured parameters with a relatively simple set of criteria that were stipulated in the original permit for the project; these criteria may or may not accurately reflect wetland function.

After reviewing pertinent literature, we discuss three fundamental requirements for achieving success of wetland creation and restoration projects: understanding wetland function, giving the system time, and appreciating the idea of self-design. Our hypothesis is that most attempts to measure and achieve success of created and restored wetlands—caused by a lack of application of good wetland science to the problem and compounded by the existing construction-schedule-driven process—are flawed because of misunderstanding or misapplication of these factors. We then argue that ecosystem-level research and ecosystem modelling may provide better guidance on when created and restored wetlands can be expected to comply with criteria that measure their success.

STUDIES ON WETLAND MITIGATION SUCCESS

Most studies suggest that there is much room for improvement in the building of wetlands. Maguire (1985) used area, vegetative cover, and implementation of permit conditions to estimate mitigation success in Virginia and found that only 50% of 23 mitigation wetlands were "successful." In most unsuccessful cases, the mitigation project had not been implemented. An additional study by Reimold and Cobler (1985) conducted for the U.S. Environmental Protection Agency (EPA) gave similar results. Glubiak et al. (1986) and Quammen (1986) both suggested the need for better management of mitigation wetlands. Additionally Glubiak et al. (1986) predicted that while the protection

[1] Manuscript received 10 June 1994; revised 3 April 1995; accepted 12 April 1995.

[2] For reprints of this group of papers on wetland mitigation, see footnote 2, page 33.

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of wetlands through a permit process—Section 404 of the Clean Water Act enacted by the U.S. Congress in 1972—was somewhat effective, it would not prevent wetland area losses as effectively as it should.

In the mid-1980s some scientists involved in wetland restoration and mitigation believed that mitigation was working (Harvey and Josselyn 1986), while others suggested that more research needed to be done and that, if not properly conducted, a wetlands mitigation project could easily fail (Race 1986). Kusler and Groman (1986) raised concerns about the granting of Section 404 permits to contractors when alternative sites are available. Many questions and issues were raised by Kusler and Groman (1986) and Golet (1986) regarding permitting processes and the actual success of wetland mitigation projects. Their major issues were: When should destruction/damage and subsequent creation/restoration be permitted? How is the damage to the original system measured and how is the creation/restoration deemed sufficient? Golet (1986) suggested that under no circumstances should damage to a wetland be allowed unless there is absolutely no alternative.

While there are many factors that could be used to monitor progress of mitigation wetlands, observing vegetation has often been the easiest and probably the most common method (see, e.g., Wentworth et al. 1988, Jarman et al. 1991, Atkinson et al. 1993). This concept has already been codified in several parts of the country. For example, in Massachusetts, vegetation cover of $\geq 75\%$ is the major success criterion, even if vegetation composition is very different from that of the original wetland (Jarman et al. 1991). Reinartz and Warne (1993) argue that while vegetation cover may be an easy measure of success, it is a poor indicator of function.

Recent investigations of wetland mitigation projects, as a greater number of mitigation sites have become available for scrutiny, generally reinforce the early concerns. For example, Erwin (1991) found that, of 40 mitigation projects in south Florida involving wetland creation and restoration, only about half of the required 430 ha of wetlands had been constructed and that 24 of the 40 projects (60%) were judged to be incomplete or failures. The most significant problems identified with created wetlands were improper water levels and hydroperiod. Sifneos et al. (1992) collected information from permits on Louisiana, Alabama, and Mississippi wetland mitigation projects and found that in Louisiana (their primary area of interest) only 8% of areas impacted by dredge-and-fill activity was compensated for, and >50% of the areas receiving permits covered <0.4 ha. Additionally, only 10% of the mitigation wetlands were monitored by at least one site visit. The lack of standardized record-keeping from state to state made the study difficult. The study suggests that follow-up monitoring and information on wetland functions be required in future permit decisions. Kentula et al. (1992) investigated several mitigation wetlands in Oregon and Washington and found a net loss in wetland area of 43% for Oregon and 26% for Washington. Data were either incomplete or of poor quality and up-to-date standardized databases were recommended. In a similar study, but without field checks, Holland and Kentula (1992) examined >300 Section 404 permits issued in California from 1971 to 1987 and found that while 1260 ha of compensatory mitigation (wetland creation, restoration, or preservation) had been required for impacts to 1180 ha of wetlands over that period, there was little follow-up of the permits and fewer than one-third (31.5%) required any field monitoring. Confer and Niering (1992) found that when comparing five created freshwater marshes with five nearby natural ones, the created marshes generally had greater water depth and thus more open water. They state that most of their created wetlands were highly dependent on highway runoff as a water source. Roberts (1993), quoting several ecologists, summarizes the skepticism by calling wetland trading "a loser's game."

Improving the Odds of Wetland Success

We propose three general concepts that will need attention of those involved in wetland mitigation if we are truly going to address the issue of creating and restoring viable wetland ecosystems: (1) Understand wetland function; (2) Give the system time; and (3) Allow for the self-designing capacity of nature. These points are discussed in detail below.

Understand wetland function

Mitsch and Cronk (1992) proposed that the "know-how" of building and restoring wetlands is based on an empiricism with little scientific backing, and is learned and relearned every time a new wetland is built. Wetland restoration and creation are relatively new fields and few engineers are trained in ecology and few ecologists have any experience in engineering methods. Engineers, consultants, scientists, and landscape architects can, and frequently do, claim to be experts with little experience or little knowledge of wetland ecology; without any certification standards for individuals involved in wetland creation and restoration, projects are often carried out by organizations and individuals not well versed in wetland ecology. A relatively high number of "failures" of mitigation wetlands can be attributed to a general lack of understanding of first principles of wetland science.

For example, an understanding of wetland hydrology as the fundamental forcing function of wetlands is well understood conceptually (Mitsch and Gosselink 1993) yet not always put into practice by many of those involved in wetland mitigation. The importance of hydrology is discussed in detail in a companion paper by Bedford (1996). Erwin (1991) pointed out that a number of Florida wetlands were considered failures in his Florida study because they lacked suitable hydrology. In so-called "on-site mitigation," wetlands are devel-

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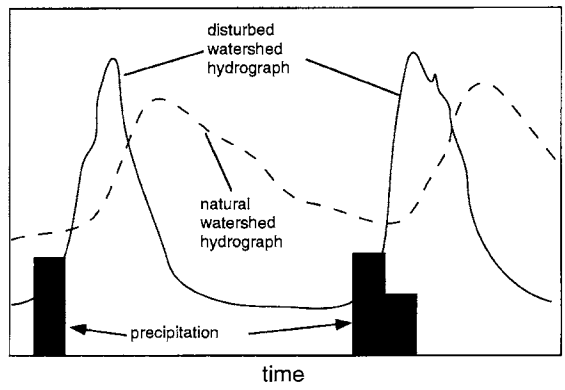

FIG. 1. Comparison of a hypothetical stream hydrograph in a natural watershed vs. one from a highly disturbed urban or suburban watershed. Placing the wetland in either of these two watersheds would probably lead to significantly different wetland structure and function.

oped in watersheds near the wetlands being drained or lost; their success is often problematic because of the usual proximity of the mitigation project to a human-altered landscape and the accompanying changes in hydrologic conditions. In these settings, created and restored wetlands can be subjected to "flashy" streams and human-regulated hydrologic conditions. In urban and suburban settings, floods are often greater and occur more quickly after precipitation; low-flow conditions are drier than in a "natural" hydrology (Dunne and Leopold 1978). Both of these conditions lead to generally greater water level fluctuations compared to those in more natural settings (Fig. 1). Unpredictable and rapidly fluctuating hydrology can lead to washouts, scouring, planting failure, and animal and macroinvertebrate emigration, leading to decreased biodiversity and even loss of water quality function.

Give the system time

A flaw in the measurement of mitigation wetland success is the limited amount of time that regulators and the land development process allow for newly created wetlands to develop before passing judgment. The legal and economic necessities seem to dictate the ecological patterns of nature, encouraging "quick-fix" wetlands while not allowing for the stochasticity of nature. Engineers have long recognized the probabilistic nature of hydrologic events (e.g., precipitation and streamflow) yet relatively deterministic indicators such as wetland plant viability, open water area, endangered species, and waterfowl are expected to develop in a relatively short time span, usually 5 yr. The very best that we can have after 5 yr of monitoring a mitigation wetland is a general idea of the wetland's ecological trajectory and even less understanding of its function.

In one of the longest-running documentations of a constructed wetland in this country, an 8-ha freshwater tidal marsh (Windmill Point), was constructed in 1974–1975 within dikes in the James River in eastern Virginia, USA. Early indications, from 1978 to 1982, considered the wetland a success as it supported a diversity of herbaceous vegetation typical of tidal freshwater marshes (Newling and Landin 1985). At that time the monitoring was referred to as "long-term." But the dikes were breached in 1986 due to flooding on the James River, eliminating the vegetation and submersing the wetland in the river (Landin 1994, *personal communication*). Sixteen years after construction the project could be termed by some as a hydrologic and ecologic failure if long-term survival of the wetland was one if its goals.

Because of the stochastic nature of hydrologic events and the slow development of ecosystems, sometimes in spurts, sometimes in the slow process of recruitment and growth, the 5-yr time horizon can be viewed as arbitrary and probably much too short. As ecological models show (see e.g., Jørgensen 1994), the further initial conditions are from steady-state, the longer it will take for that system to reach or approach steady state (Fig. 2). Short monitoring times favor measuring success with transplanted vegetation and pioneer organisms; long-term success is less dependent on these initial conditions.

Allow self-design

There are two general approaches for introducing vegetation (and other organisms) in wetland creation and restoration projects. One is the "designer" approach of introducing species and expecting their survival in Gleasonian zones, akin to gardening or landscape architecture. The other emphasizes the "self-design" or "self organization" capacity of Nature to both recruit species on its own and to make choices from those species introduced by humans (Odum 1989, Mitsch 1993). In self-design the emphasis is on the introduction of as many species as possible, knowing that natural forces will help in the ultimate design by choosing the most appropriate species. Self-design also recognizes the importance of natural colonization of species in wetlands.

In one of the few studies to make a preliminary comparison of these two general approaches, Reinartz and Warne (1993) compared 11 created wetlands in southeastern Wisconsin that were naturally colonized with 5 wetlands in the same region where 22 species were

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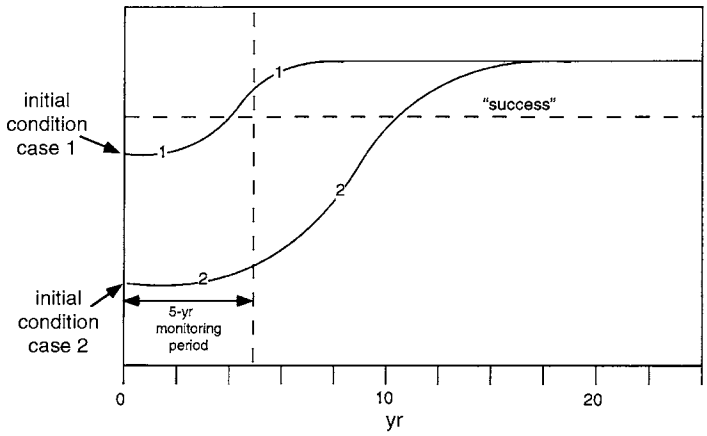

FIG. 2. Hypothetical comparison of the pattern of one wetland criterion for "success," e.g., percentage vegetation cover, for two different initial conditions at the same hypothetical wetland site. In Case 1 the wetland would be considered a "success" after 5 yr, while in Case 2 the wetland would be considered a "failure." Each wetland case could end up eventually at the same level, but well after 5 yr. In reality, a multiplicity of criteria would be used in this comparison.

introduced by seeding. The diversity and richness of plants in the colonized wetlands increased with age, size, and proximity to the nearest wetland source even though *Typha* spp. comprised 15% of the vegetation for 1-yr-old wetlands, and 55% for 3-yr-old wetlands. Seeded wetlands had a high species diversity and richness after 2 yr and *Typha* cover in the seeded sites was lower than in the naturally colonized sites after a 2-yr period.

Many studies to date (e.g., Confer and Niering 1992, McKnight 1992), especially those on restoration of non-coastal wetlands, have probably over-predicted—because of short time horizons and small spatial scales—the survivability of transplanted species in "designer" wetlands. (An exception to this short time horizon is the long-term observation of Frenkel and Boss [1988], through aerial photography, of the spread of *Spartina patens* in areas along Oregon's coastal wetlands.) With enough time and space, introduced species may be less successful than we initially believed. A better idea is to give the wetland system many possibilities through multiple-seeding, multiple-transplanting, and establishment of hydrologically open systems; this allows nature to participate in the wetland design.

PROVIDING THE NEEDED RESEARCH TOOLS

In addition to the above suggestions for wetland managers and ecological engineers who are attempting to design and monitor wetlands, there are some important approaches that wetland scientists can use to reduce the uncertainty of wetland mitigation.

Select the proper experimental scale

The limited ability of science as we generally practice it to both understand and solve our dilemmas in natural resource conservation was argued by Ludwig et al. (1993) and debated in the pages of *Ecological Applications* (Levin 1993). Taking the cue from Holling (1993) and Costanza (1993) in that discussion, we question whether reductionistic experimental science, with its short time scales (often the time required for a Ph.D. dissertation) and its small spatial scales (often in laboratories or small field plots) can correctly prescribe how to build large wetlands. A holistic systems approach, with the appropriate time and space scales, should at least have equal emphasis.

As one example, a number of studies of wetland function were carried out with four full-scale constructed wetlands at the Des Plaines River Wetland Demonstration Project in northeastern Illinois (Sanville and Mitsch 1994). Hydrologic conditions were varied for high- and low-flow conditions for entire wetlands (average size: 2.4 ha), not just experimental plots; the studies were carried out over 3 yr. Researchers had important findings in estimating detention and mixing (Kadlec 1994), water quality function (Hey et al. 1994, Phipps and Crumpton 1994), sedimentation (Brueske and Barrett 1994, Fennessy et al. 1994*a*), vegetation development (Fennessy et al. 1994*b*), aquatic metabolism (Cronk and Mitsch 1994*a*, *b*), and avian success (Hickman 1994) in created wetlands, most as a function of hydrology.

In a comparison of two natural tidal marshes with a 0.65-ha constructed marsh in coastal Virginia 5 yr after construction, Havens et al. (1995) found seasonal differences in fish and shellfish abundances between natural and constructed marshes, with lower numbers in the latter. They attribute the differences to relative lack of organic carbon and less morphometric heterogeneity (e.g., stream rivulets, microtopography) in the created marsh.

We recently initiated a full-scale comparison of "self-design" and "designer" approaches to wetlands at the Olentangy River Wetland Research Park at The Ohio State University (Fig. 3; Mitsch and Wu 1995, Mitsch 1995). In one newly constructed wetland basin (1 ha), we planted, in approximately the stratification that we would find in nature, ≈2500 individuals representing 14 species of wetland plants. In an identical constructed wetland basin nearby, we planted nothing. Hydrologic conditions are being maintained as similar as possible in the two basins and there is no predeter-

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FIG. 3. The Olentangy River Wetland Research Park at The Ohio State University in Columbus, Ohio, USA, is a whole-ecosystem long-term experiment begun on 14 May 1994 with the planting of one of the deep-water marshes shown in foreground (right basin) with ≈2500 plants representing 15 wetland species. The second deep-water marsh (left basin) remains unplanted. Each basin is 1 ha in size and water is supplied by pumps in the lower right-hand corner of the site to create a similar hydrology for each basin. The Olentangy River, shown flowing from bottom right to the top of the picture (with the university ≈0.5 km downstream of the site on the horizon of the picture), is the source of the water, which is pumped in proportion to the river flow in the same patterns for each wetland basin. The photo was taken in November 1993 prior to the introduction of water to the wetlands (photo by Mark Myers, Apex, Columbus, Ohio).

mined completion date to our experiment. We believe that our "experiment" is closer to the scale necessary for documenting the forces, e.g., plant recruitment, geese and muskrat invasions, etc., that influence ecosystem development. Working at this full scale precludes extensive replication because of land and construction costs, yet our understanding of ecosystem development and other wetland functions will come only

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from studying spatial scales and longer time scales to supplement traditional ecological experiments.

Develop predictive modelling

Little attention has been paid to ecological modelling—the one tool that can expand the time horizon—in predicting success of created and restored wetlands. While this approach must be used with caution and proper qualifications, it enables ecologists to project into the future and estimate how long it will take the mitigation wetland to achieve some type of steady state. A few publications (Costanza and Sklar 1985, Mitsch et al. 1988, Mitsch 1994) have reported on the state of the art of simulation modelling in wetland ecology, but this powerful "systems" tool has rarely been used to predict mitigation success. Stochastic inputs, adaptive model structure (Jørgensen 1994), higher-order modelling languages (e.g., STELLA) and spatially dynamic models are useful advances in ecological modelling, but simple-structure models that aggregate components into overall variables such as "vegetation" or "nutrients" can be just as effective (Mitsch et al. 1995). In an application of modelling for a mitigation project in central Ohio, Niswander and Mitsch (1995) used simulation models both to "fill in" information to make calculations about ecosystem function (phosphorus retention) of a created freshwater marsh and to "enhance the time horizon" by predicting one structural aspect of this project well into the future—the survival of planted wetland trees over the next 50 yr. Modelling, of course, will not provide an exact prediction of conditions well into the future but, when used with good wetland ecology and sufficient field monitoring, it can provide another tool for those interested in predicting the future of created and restored wetlands.

Conclusions

There is optimism that wetlands can be created and restored and that wetland function can be replaced, despite a recent spotty record in the United States with the mitigation of wetland loss. The spotty record is due, in our opinion, to little understanding of wetland function by those constructing the wetlands, insufficient time for the wetlands to develop, and a lack of recognition or underestimation of the self-design capacity of nature. Understanding wetlands enough to be able to create and restore them requires a substantial training in plants, soils, wildlife, hydrology, water quality, and engineering. We should give mitigation projects involving freshwater marshes enough time, closer to 15–20 yr rather than 5 yr, before judging their success. Restoration and creation of forested wetlands, coastal wetlands, or peatlands may require even more time. For example, the restoration of certain coastal salt marshes has been suggested to require at least 50 yr (Frenkel and Morlan 1991). Finally, we should recognize that Nature remains the chief agent of both self-design and ecosystem development; humans are not the only participants in the design process.

Science will need to make significant contributions to the process of reducing our uncertainty about predicting wetland success. Wetland mitigation needs to become part of an applied ecological science, not a technique that is relearned each time without theoretical underpinnings. Scientists need to make the connections between structural measures (e.g., vegetation density, diversity, productivity) and functions such as wildlife use, organic sediment accretion, or nutrient retention in quantitative and carefully designed experiments. Simply having a list of plant species is inadequate for regulators or managers to estimate ecosystem function. Simulation models and experimentation at the proper spatial and temporal scales should be able to help us predict the behavior of these wetlands and estimate proper designs.

Acknowledgments

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Special Report 4: Impact of COVID-19 Mitigation on Wildlife-Vehicle Conflict

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6/24/2020

Impact of COVID-19 Mitigation on Wildlife-Vehicle Conflict

"Temporary respite for wildlife with reduced traffic"

Using traffic and collision data from California, Idaho, and Maine, **we found that wildlife-vehicle conflict (WVC), including for mountain lions in CA, has declined by ~21-58% following the various government stay-at-home orders.** From early March to mid-April, these orders have resulted in up to 71%, 63% and 73% reduction in driving, as measured by vehicle miles traveled (VMT), in CA, ID, and ME respectively. We used carcass and crash reports to calculate the change in daily collision rates from the 4 weeks prior to stay-at-home orders going into effect, to the 4 weeks after. Although rates of WVC naturally vary by season, the change from 1 month pre-stay-at-home orders to 1 month post-order only occurred in 2020 and not 2015, 2016, 2017, 2018, or 2019, suggesting that the reduction was associated with the reduction in traffic. In the three states, this could amount to 5,700 to 13,000 fewer large mammals killed on roads per year and in CA 50 fewer mountain lion mortalities on roads per year. **This represents the first evidence of reduced rates of WVC in response to the reduced travel by many Americans in response to COVID-19 related mitigation efforts.**

This report and other tools are available on the Road Ecology Center website: https://roadecology.ucdavis.edu. For more information, contact Fraser Shilling (fmshilling@ucdavis.edu).

We would like to **acknowledge** the hard work and data collection efforts of the California Highway Patrol officers; Caltrans Districts, MaineDOT (especially Eric Ham), and IDT Maintenance and Environmental staff (especially Alissa Salmore); volunteers in the California Roadkill Observation System and Idaho Fish and Wildlife Information System; the Idaho Department of Fish and Game (especially Matt Pieron); the California Department of Fish and Wildlife (especially Justin Dellinger); and Winston Vickers. We recognize the trauma, pain, and losses that the Covid-19 pandemic has brought to the US and other countries and by pointing out the benefits from reduced traffic, we are not making light of Covid-19 impacts.

Cover photo credit. Coyote, California Roadkill Observation System

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Special Report on Impact of COVID19 Mitigation on Wildlife-Vehicle Conflict

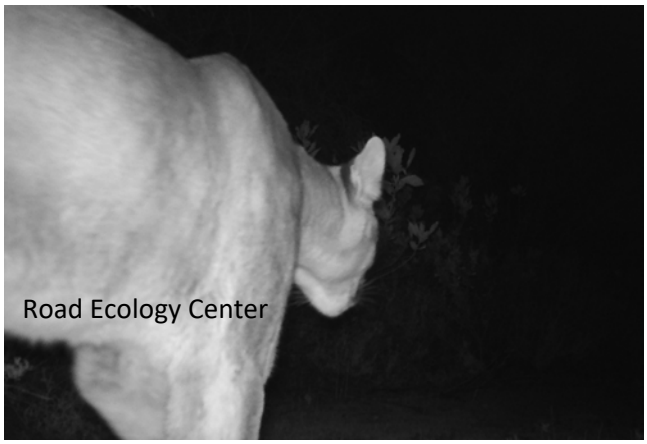
Top 4 Talking Points

1) **Nationwide traffic data suggests that most residents in all states significantly reduced their travel in response to "stay-at-home" orders.** We used data from Caltrans' Performance Monitoring System (PeMS) for CA state highways and from Streetlightdata.com to estimate changes in travel in CA, ID and ME. State highway travel in CA and ME declined 20-60% between early March and mid-April and travel on all roads in CA , ID, and ME declined by up to 71%, 63%, and 73%, respectively, suggesting that the majority of people were taking guidance about staying at home seriously.

2) **Traffic reduction in US states was accompanied by statistically-significant reductions in the number of WVC.** We found that for CA, ID, and ME, the number of WVC recorded as crashes or carcasses in statewide WVC-reporting systems declined statistically between the 4 weeks prior to the stay-at-home order and the 4 weeks after the order. This is contrast to previous years, where WVC rates in this time period usually either stays constant or increases, due to transition from winter to spring.

3) **Mountain lions in CA experienced a 58% reduction in mortality on roads at a time when the state is considering legal protection for the species, in part because of lion-vehicle collisions.** Mountain lions are reported hit on California roads and highways up to twice per week. In a typical year, this rate either stays constant or increases slightly in the transition from winter to summer. We found that the rate of mountain lion mortality declined 58% between the 10 weeks prior to the state order and the 10 weeks after.

4) **The distribution of WVC generally did not change between the period before and after the order.** The density of WVC per unit area was calculated for the pre- and post-order periods for each state. Generally, there was no obvious difference between patterns and distribution of WVC density before and after state stay-at-home orders, suggesting an evenly-distributed benefit to wildlife across the states.



Introduction to Study

Mitigation of the spread of COVID-19 has been implemented by cities, counties, and governors' offices through "shelter-in-place" and "stay-at-home" orders and related actions (e.g., closure of non-essential businesses). In previous reports, we have pointed to the potential unintended impact of reduced traffic: 1) reduced traffic crashes and thus injuries and fatalities for people involved in the incidents; 2) reduced costs associated with crashes for society (e.g., emergency response, medical costs, vehicle repair/replacement, lost time at work); 3) reduced fuel use and corresponding fuel tax revenue for state and local government; and 4) reduced greenhouse gas emissions due to reduced driving and fuel use. This mixture of silver linings (e.g., reduced crashes) and potential impacts (e.g., reduced tax revenue) are an ongoing and dynamic consequence of stay-at-home orders and these reports represent a type of "real-time" policy analysis. The reports are available on the Road Ecology Center website: https://roadecology.ucdavis.edu).

In the current report, we investigated potential changes in impacts to wild and domestic animals from reduced traffic in 3 US states with advanced systems for tracking wildlife-vehicle conflict (WVC): California, Idaho and Maine. There are several important caveats to keep in mind with this report: a) WVC can be under-reported by 5 to 9-fold (Donaldson, 2017; Olson et al., 2014); b) despite the massive impact that transportation has on wildlife, there is no systematic monitoring of WVC involving large, medium and small animals (mammals, reptiles, amphibians, and birds) in any US state; and c) animal responses to roadways and changes in traffic volumes is likely to vary substantially among species. Traffic volumes are tied to rates of WVC, though not in a linear way. In other words, intermediate traffic volumes may result in higher rates of WVC than large traffic volumes because wildlife may be more willing to attempt to cross roads/highways with moderate traffic than highways with frequent vehicles (Seiler, 2003). For any given highway, it is possible that if traffic volumes are radically reduced, say by 75% for weeks, as has been the case for many US roads and highways, then rates of WVC may be proportionally reduced. Given that it is possible that 100s of millions of vertebrates (birds, reptiles, amphibians, and mammals) are killed per year on US roadways, then such a reduction could be equivalent to millions of animals not being killed during periods of low traffic volumes.

In past reports, we have examined the impact of reduced traffic on traffic crashes affecting people. We continue that thread here by examining the possibility that reduced traffic has resulted in reduced rates of wildlife mortality on US state highways and roadways. For CA, we used data collected by the Road Ecology Center's California Highway Incident Processing System (CHIPS) from California Highway Patrol reports. For ID, we downloaded data from the Idaho Fish and Wildlife Information System (IFWIS) and communicated the use of the data to Idaho Department of Fish and Game. For ME, we requested and received data from the Maine Department of Transportation. We compared total numbers and rates of WVC before and after the respective stay at home orders for each state. For mountain lion mortalities, we used a "consensus" dataset developed by the Road Ecology Center, Winston Vickers (UC Davis) and California Department of Fish and Wildlife.

Findings

1) Reduction in Travel

Using daily travel data from Streetlightdata.com, we calculated the change in daily "vehicle miles traveled" for every county in the US from early March to mid-April. Streetlightdata uses custom algorithms with cell-phone tracking data to estimate how many miles people drive per day. The total miles traveled in the first week of March in the US was 103 billion miles, whereas the total miles traveled in the second week of April was 29 billion miles. This 71% reduction in total miles traveled was reflected in the range of reductions seen across each state. The date of the stay-at-home order, or similar guidance, varied among states. For California, it was March 20th, for Idaho March 26th and for Maine March 31st. We calculated the drop in average weekly travel from the first week of March to the second week of April as reasonable pre- and post- order timeframes. Travel on all roads decreased by 75%, 63% and 73% for CA, ID and ME between early March and mid-April (Figure 1). The decrease in VMT for all travel on all roads for CA, 75%, is greater than the estimated change in traffic volumes on 12 state highways, 37%, suggesting that driving patterns may be quite different on local roads and state highways. A caveat to the finding for ME is that traffic engineers in

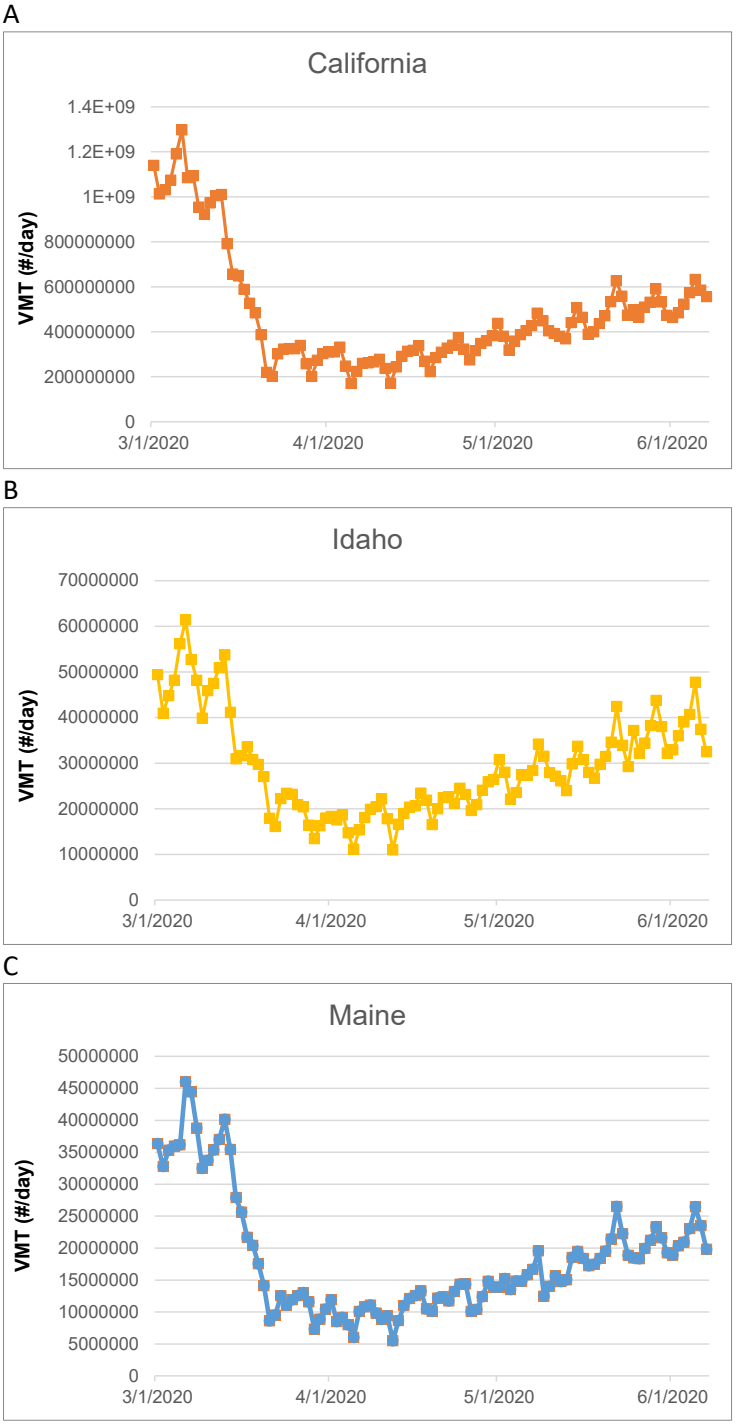


Figure 1. Vehicle miles traveled (VMT) for CA, ID, and ME between March 1, 2020 and June 10, 2020 for (A) CA, (B) ID, and (C) ME.

MaineDOT have reported only a 20% reduction in traffic on state roads following the stay-at-home guidance. This suggests that resolution is needed of the true reduction in traffic volumes has been and whether there are differences in reductions between state and minor roads.

States have seen a return of traffic similar to before the stay-at-home guidance, but it is not clear that this is consistent among states or that it has stabilized at some new rate. In CA, there has been a 3-fold increase in traffic, to a level about 50% of pre-order (Figure 1A). In ID, a similar 2-3 fold increase in traffic has resulted in traffic level about 75% of pre-order (Figure 1B). In ME, traffic has increased 3-fold and is now about 50% of pre-order traffic (Figure 1C).

2) Reduction in Impacts to Wildlife

Co-occurring with and possibly because of the reduction in VMT were statistically-significant reductions in collisions with wild animals of 21%, 38% and 44% for CA, ID and ME (Table 1). We compared the number of animals found dead on state highways, or involved in a collision reported to emergency response, in the 4 week period prior to each state's stay at home order with the number killed in the 4 week period after each state's order. In the case of California's order, we used 28 days prior to the San Francisco Bay region's order on 3/16/2020 because this region represents a large portion of California's WVC. There were similar statistically-significant ($p<0.05$) reductions in impacts to domestic animals, including cows, horses, sheep, goats, dogs, and cats for CA. For all 3 states, we also analyzed rates of WVC in previous years (2015, 2016, 2017, 2018, & 2019) and for the same time periods, there were either significant increases or no change in numbers of WVC before and after the date of each state's order in any of these previous years. An important point is that these numbers represent the numbers of large wildlife reported killed in collisions (e.g., mule deer, white-tailed deer, moose, elk, black bear, coyote, mountain lion) and does not represent all collisions with large wild animals, or with all wild animals of any size. However, in every case, we confirmed that the effort of reporting carcasses or crashes had not changed before and after the order suggesting the reductions are not due to less people reporting carcasses or crashes with wild animals.

Table 1. Number of large wildlife killed per day on California, Idaho and Maine state highways and significance of the change. P-values less than 0.05 indicate statistical significance.

State	Number/day Pre-Order	Number/day Post-Order	Decrease/Statistical Significance
CA	8.4	6.6	21%/P=0.04
ID	8.7	5.4	38%/P=0.01
ME	15.2	8.4	45%/P<0.001

Previous research has shown that collisions with deer and other large wildlife can be under-reported to police and others by 5 to 9 fold (Donaldson, 2017; Olson et al., 2014). In 2019, CA, ID, and ME recorded at least 5,443 (mule deer only), 4,530, and 5,808 collisions with large mammals per year, respectively. This suggests that 27,000 – 49,000 large mammals are killed per year on CA roads and highways, as well as an unknown number of other species. This is supported by the State Farm Insurance Co estimate of >23,000 claims/year for collisions with deer resulting claims in California (https://newsroom.statefarm.com/download/234883/allstates2015-16deerstats-finalpdf.pdf).

It is likely that there are also collisions that do not result in insurance claims. If we used a conservative under-reporting rate of 5-fold, then it is possible that the reported collisions represent 27,200, 22,650, and 29,040 deer and other large mammals killed on roads and highways per year in CA, ID, and ME, respectively. The reduction we observed would represent 5,712, 8,607, and 13,068 fewer deer and other large mammals killed per year in CA, ID and ME, respectively. Obviously, as traffic increases again, these reductions may be reversed.

3) Reduction in Impacts to Mountain Lions

Mountain lions are proposed for legal listing in CA as state-threatened. There are three primary threats to the species: 1) state-permitted killing of mountain lions that may have attacked domestic animals, 2) mortality from road and highway traffic, and 3) population fragmentation by busy highways. We found that the rate of mountain lion mortality declined 58% (P=0.030) from the 10-week period pre-order to the 10 week period post-order. A longer period was used than for all wildlife because the number of mountain lions killed per day is low in comparison to all large wildlife. The rate of mortality during the post-order period in 2020 was also significantly lower than rates for the same period during the preceding two years (P<0.04).

Table 2. Rate of mountain lion mortality on CA roads and highways in 2020, 2019, 2018, 2017, and 2016, before and after the dates of the Bay Area and state stay-at home orders. P-values of <0.05 are considered statistically-significant, P-values >0.05 are not significant. "n.s." refers to non-significant differences.

Year	Mortality/day pre-order	Mortality/day post-order	% Change	P-value/ significance
2020	0.27	0.11	- 58%	0.030/significant
2019	0.19	0.26	--	0.40/n.s.
2018	0.21	0.23	--	0.88/n.s.
2017	0.17	0.21	--	0.57/n.s.
2016	0.11	0.1	--	0.79/n.s.

One significant impact of this finding is the clear link between traffic and rates of mountain lion death. This means that to reduce mountain lion mortality, populations must be protected from traffic, especially in the Bay Area and Southern California where isolated and small populations of mountain lions are at risk of extinction. Protection from traffic has been accomplished in CA and other places by building wildlife crossings associated with fencing. For example, SR 241, a state highway operated by the Transportation Corridor Agencies of Orange County as a toll-road, is punctuated with large bridge under-crossings and is protected along much of its length with 10'-high fencing. This combination of large crossings and 10'-high fencing has eliminated wildlife entry onto the highway, including by the endangered mountain lion population of the Santa Ana Mountains. A proposed wildlife over-crossing on US 101 in the San Fernando Valley would become California's second wildlife over-crossing and the largest in the world. Its primary goal is to reduce the isolation of the mountain lion population of the Santa Monica Mountains.

4) No Change in Distribution of WVC

In general, there were no major changes in the distribution of WVC across the states. In other words, the number of animals killed by vehicles seemed to decrease uniformly across all highways. In California, areas around the San Francisco Bay, Sacramento region, and Southern California that usually have higher densities of WVC than surrounding areas continued to have higher densities (Figure 1 A,B). Similarly in Maine, areas along the I-95 corridor around Portland, Augusta, Bangor and Houlton continued to have higher densities of WVC than surrounding areas, but with lower overall numbers (Figure C,D). These results are consistent with the idea that there was proportionally less driving among areas between the pre and post-order periods.

A B

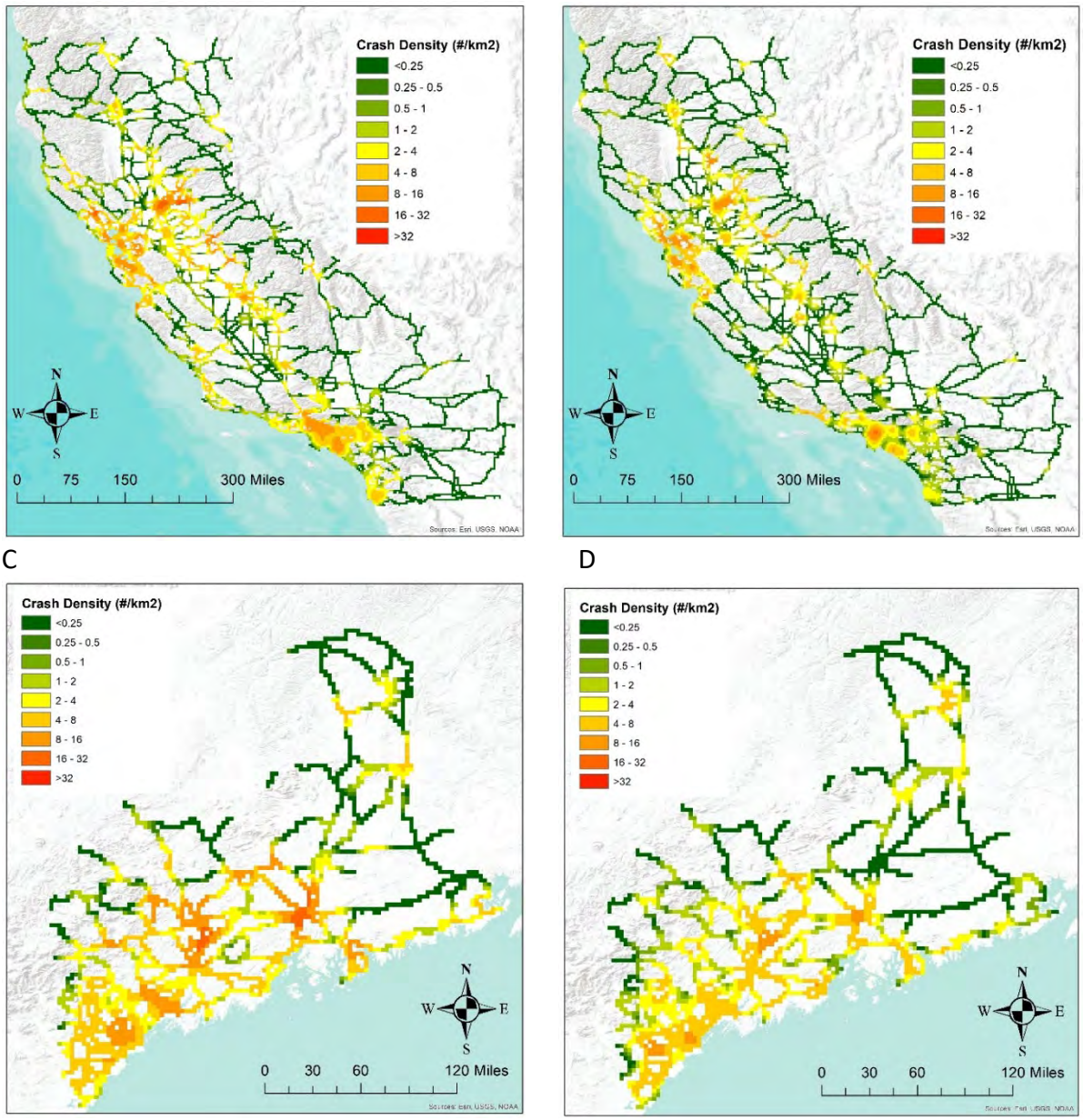


Figure 1. Distribution of AVC density before and after stay-at-home orders in California, A and B, respectively, and in Maine, C and D, respectively.

Conclusions

Our previous reports have highlighted the various unintended consequences of COVID-19 mitigation through state and regional stay-at-home and shelter-in-place guidance (available here: https://roadecology.ucdavis.edu). We show here that there was a statistically-significant reduction in the number of large wild animals killed per day on CA, ID, and ME state highways that coincided with the reduced traffic following state stay-at-home guidance. It seems likely that the reduction was due to reduced driving and further that this positive impact occurred in other states and for other animals besides large mammals. Given the five to 9-fold under-reporting of large animals involved in collisions with vehicles and the lack of systematic reporting of smaller animals killed on roads, the positive impacts we report are likely to be just the tip of the iceberg of reduced deaths of wildlife on U.S. roads and highways. This unintended positive consequence of COVID-19 mitigation on wildlife joins the growing group of "silver", "gold" and "green" linings: reduced injury/fatal crashes for drivers/passengers, reduced costs associated with crashes, and reduced greenhouse gas emissions.

Citations

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Geometry of Forest Landscape Connectivity: Pathways for Persistence

Deanna H. Olson and Kelly M. Burnett

Abstract

Streamside areas may be dispersal funnels or runways for a variety of species. For over-ridge dispersal, headwaters offer the shortest distance links among riparian zones in adjacent drainages. We summarize landscape designs for connectivity of habitats using headwater riparian linkage areas as the foundation for a web of landscape-scale links. We developed management considerations for placement of headwater linkage areas including: 1) providing connections between larger basins; 2) maintaining habitat connectivity in the face of climate change; 3) incorporating place-based disturbance regimes such as headwater debris-flow-prone areas; 4) targeting connectivity areas to address sensitive species conservation strongholds; and 5) accounting for geometry at the forest-stand scale of a single project or proposed timber sale, including managing habitats to connect lands on adjacent federal ownerships, by means of connecting corners of checkerboard landscape blocks along diagonals. Although our proposed linkage areas are designed to target headwater species, the resulting web of connections across the landscape is expected to benefit many forest-dependent species.

Keywords: watersheds, forest, headwaters, biodiversity, linkage areas, dispersal.

Introduction

Biodiversity retention and restoration is an emerging priority for global ecosystems. Astounding losses within major taxonomic groups have been reported nationally and internationally (41 percent of amphibians, 25 percent of mammals, 15 percent of bony fishes, 13 percent of birds: Hoffmann et al. 2010; 50–60 percent of turtles: Kiester and Olson 2011). In particular, protection and restoration of forests and forest biodiversity has become a paramount concern worldwide (e.g., Convention on Biological Diversity: *www.cbd.int/forest/*). A toolbox of management approaches has been developed to conserve forest biodiversity, largely through a mixture of fine- and coarse-grained habitat protections (e.g., United States Northwest Forest Plan: USDA and USDI 1993, 1994; Cissel et al. 1998; Lindenmayer and Franklin 2002; Raphael and Molina 2007; Lindenmayer et al. 2007) and site-specific designs to maintain or restore forest structural heterogeneity (McComb 2001; Lindenmayer and Franklin 2002; Brockerhoff et al. 2008).

Development of landscape designs to manage habitat connectivity for multiple species is an especially active research topic in forest biodiversity conservation, due to continuing trends of forest fragmentation and to an upswing

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in world reforestation efforts. Managing forested landscapes for connectivity functions benefiting biodiversity requires incorporating several fundamental conservation concepts. These basic conservation tenets include identifying the critical habitats used throughout species' life histories (breeding, foraging, overwintering, and dispersal habitats), and commensurate habitat protections to ensure that these biotic functions are retained. If an organism uses different habitats through its life cycle, then maintaining connectivity among these habitats is essential to ensure its persistence. Of particular relevance is the characterization and retention or restoration of dispersal habitat. This includes the home ranges of individuals and the broader dispersal of offspring or individuals that tie sub-populations and populations together over larger areas. This broader-scale dispersal function maintains genetic variation within natural populations, which may foster resiliency needed to adapt to changing environmental conditions. The future of species may rely on our careful attention to managing for connectivity now.

Defining the adequacy of dispersal habitat in forests is a complex topic (Noss et al. 1997) and may address a variety of elements, including habitat condition, corridor sizes (length, width), and corridor redundancy (Pinto and Keitt 2008). Redundancy is especially relevant because multiple connectivity pathways can assist dispersal across landscapes by organisms in different locations and increase the probability of movement in the face of many interacting site-specific factors (microsite features, disturbances). Redundancy of habitat connectivity hedges against catastrophe, uncertainty, and stochastic processes that can affect individuals and sub-populations that vary in their movement propensities, possibly related to patch size, habitat quality, and population demography.

Low-mobility species may merit special attention devoted to the placement and redundancy of connectivity corridors, because barriers to dispersal may arise as a result of their basic biology and ecology (Raphael and Molina 2007). These species may move slowly and require refugia along corridors because it may take them years to move between optimum habitat patches. Due to a potentially longer residency time within connectivity corridors, low-mobility species may be particularly vulnerable to sub-optimal corridor conditions and stochastic processes. Hence, redundancy of connections may be critically important to increase their likelihood of successful movement across landscapes for such low-mobility species. Patches of higher-quality habitat within dispersal corridors may be used as stepping stones for such species and may be an essential aspect of their long-term persistence (e.g., Grant et al. 2010). Such stepping stones may function as habitat refugia or "stopover reserves" (Dobson et al. 1999), which promote survival of individual organisms as they move through the environment. Stepping stones may have more suitable physical habitat conditions than the surrounding area, or may allow individuals to forage to replenish energy reserves or survive harsh seasons (summer, winter) in localized refugia, from which they may disperse again later.

Herein, we synthesize our ongoing studies of the utility of headwater riparian areas as proposed connectivity corridors, or linkage areas, for dispersal of riparian-associated and low-mobility species in Pacific Northwest forests. Once designed, such headwater linkage areas may benefit many taxa. Our studies also conceptually integrate aquatic network and upland-forest habitats, functions, and processes. The combination of protections for aquatic and upland systems is providing new insights into forest ecosystem management approaches. We summarize the key considerations for the geometric orientation of connectivity pathways to assist migration of species across watersheds and across webs of connections, to maintain linked aquatic-terrestrial populations at landscape scales. Our goal here is to provide

a summary of these conceptual designs, while research continues to address these issues and advance design effectiveness.

Utility of Watersheds as Redundant Landscape-scale Linkage Units

Watersheds are widely accepted units for monitoring and evaluating the effects of land use on aquatic resources (Omernik and Bailey 1997). Where their boundaries can be clearly mapped, watersheds are increasingly common units for forest management planning and conservation designs. For example, in the U.S., the Aquatic Conservation Objectives of the federal Northwest Forest Plan (USDA and USDI 1994: p. B-11), address connectivity among watersheds:

> *"Maintain and restore spatial and temporal connectivity within and between watersheds. Lateral, longitudinal, and drainage network connections include floodplains, wetlands, upslope areas, headwater tributaries, and intact refugia. These network connections must provide chemically and physically unobstructed routes to areas critical for fulfilling life history requirements of aquatic and riparian-dependent species."*

Hydrologic units (HUs), delineated by the U.S. Geological Survey (Seaber et al. 1987), are also a convenient and widely used basis for forest assessment and planning (e.g., Maxwell et al. 1995; Suring et al. 2011). The HU coding describes a hierarchical system of units nested by drainage area; larger code numbers designate smaller drainage areas. Watersheds or segments of watersheds comprise HUs. Even though the majority of HUs at each level of the hierarchy are not true topographic watersheds, such a perspective can aid biodiversity conservation designs, especially as smaller headwater basins are delineated and used for replicating protected areas (e.g., 6t^{h}-code HUs: Suzuki et al. 2008) and creation of redundant connections across landscapes (via 6th- and 7th-code HUs: Olson and Burnett 2009).

The value of using headwater basins as the premise for establishing connectivity corridors across forested landscapes is due to their habitat conditions, potential use by a variety of organisms, frequency of occurrence on the landscape, and minimization of dispersal distances (fig. 1). Olson et al. (2007) summarized some of the merits of headwater riparian habitats for species in the northwest, including providing cool, moist microclimates for interior-forest dependent organisms and aquatic-riparian associated species such as amphibians. Some taxa may use these areas due to their habitat suitability; others may respond to streams as movement barriers, and then move along banks parallel to such barriers. Streamside areas may be dispersal funnels or runways for a variety of species. For example, we have seen terrestrial salamanders (species that do not use stream or pond habitats for breeding or other life-history functions) moving predominantly through near-stream areas (D. Olson and M. Kluber, unpubl. data). Additional taxa that use riparian corridors in northwestern forests include a variety of lichens, bryophytes, fungi, vascular plants, mollusks, mammals (e.g., ground-dwelling mammals: Wilk et al. 2010), birds, and general forest-obligates that may occur in legacy forest attributes such as wolf trees along riparian buffer zones. As a minimum estimate across taxonomic groups, over 100 species were identified as likely to benefit by habitat protections of combined intermittent and perennial streams provided by riparian reserves in federal forest lands in the range of the Northern Spotted Owl (*Strix occidentalis caurina*) (table 1) (USDA and USDI 1997). Species with restricted dispersal abilities were identified for special consideration relative to utility of riparian reserves during watershed analyses under the Northwest Forest Plan (USDA and USDI 1997).

Furthermore, the high density of small streams in upland northwest forests has been widely recognized over the last 20 years, as our basic

Table 1—Species benefitting from interim riparian reserves developed for the federal Northwest Forest Plan (from table B1 in USDA and USDI 1997). Riparian reserve protection includes a one site-potential tree-height or 30.5 m (100 ft) buffer, whichever is greater, as an interim measure along all intermittent streams, and a two site-potential tree-height buffer as an interim measure along perennial streams (see USDA and USDI 1993, page III-9).

Taxonomic group	Species
Bryophytes	*Antitrichia curtipendula, Douinia ovata, Kurzia makinoana, Scouleria marginata, Tritomaria exectiformis*
Fungi	
Rare chanterelles	*Polyozellous multiplex*
Rare gilled mushrooms	*Clitocybesubditopoda, C. senilis, Neolentinus adherens, Rhodocybe nitida, Rhodocybe speciosa, Tricholomposis fulvenscens*
Rare cup fungi	*Helvella compressa, H. crassitunicata, H. elastica, H. maculata*
Jelly mushroom	*Phlogiotis helvelloides*
Moss-dwelling mushrooms	*Cyphellostereum leave, Galerina atkinsoniana, G. cerina, G. hetrocysis, G. sphagnicola, G. vittaeformis, Rickenella setipes*
Lichens	
Riparian lichens	*Certelia cetrarioides, Collema nigrescens, Leptogium burnetiae var. hirsutum, L. cyanescens, L. saturninum, L. teretiusculum, Platismatia lacunose, Ramalina thrausta, Usnea longissima*
Aquatic lichens	*Dermatocarpon luridum, Hydrothyria venosa, Leptogium rivale*
Vascular plants	*Bensoniella oregano, Botrychium minganense, B. montanum, Coptis trifolia*
Mollusks	*Ancotrema voyanum, Crypotmastix devia, C. henersoni, Monadenia fidelis salmonensis, Verspericola depressa, V. sierranus, Fluminicola* spp. nov. 1-20, *F. seminalis, Helisoma newberryi newberryi, Juga (C.) acutifilosa, J. (C.) occata, J (O.)* spp. nov. 2-3, *J. (Oreobasis) orickensis, Lanx alta, Lyogyrus* sp. nov. 1, 3, *Pyrgulopsis intermedia, Vorticifex klamathensis sintsini, V.* sp. nov. 1
Amphibians	
Riparian	*Aneides flavipunctatus, Rhyacotriton cascadae, R. kezeri, R. variegatus, Dicamptodon copei, Plethodon vandykei, Ascaphus truei*
Fish	Coho Salmon (*Oncorhynchus kisutch*), fall and spring Chinook Salmon (*O. tshawytscha*), resident and sea-run Cutthroat Trout (*O. clarkii clarkii*), resident Rainbow Trout (*O. mykiss*), summer and winter Steelhead (anadromous *O. mykiss*)
Birds	Common Merganser (*Mergus merganser*) [Marbled Murrelet, *Brachyramphus marmoratus*; Northern Spotted Owl, *Strix occidentalis caurina*]
Bats	Fringed, Long-eared, and Long-legged Myotis (*Myotis thysanodes, M. evotis, M. volans*), Hoary Bat (*Lasiurus cinereus*), Pallid Bat (*Antrozous pallidus*), Silver-haired Bat (*Lasionycteris noctivagans*)
Other mammals	Fisher (*Martes pennanti*), Marten (*Martes americana*), Red Tree Vole (*Arborimus longicaudus*)

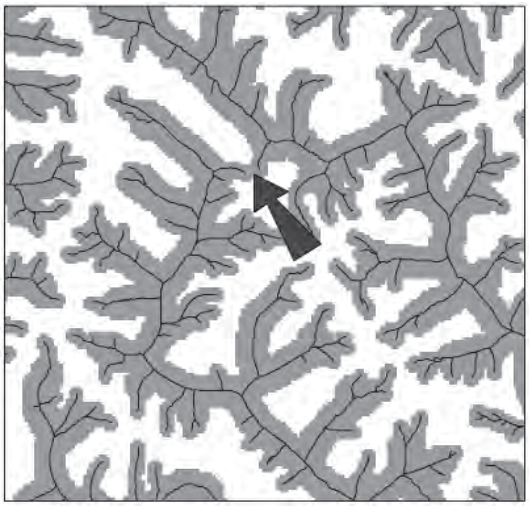

Figure 1—Example interim riparian reserve network from the US federal Northwest Forest Plan implemented in the Pacific Northwest, showing frequency of headwater streams on the landscape and the resulting one and two site-potential tree-height buffers along streams (upper left quadrant). Arrow indicates example over-ridge area where the distance between headwater riparian reserves in different watersheds is small and over-ridge connectivity may be more easily achieved. These headwater riparian areas can be used to facilitate landscape linkage area designs for organism dispersal and aquatic-terrestrial habitat connectivity functions.

knowledge of stream and forest ecology has expanded. In some areas, headwaters comprise 80 percent of a stream network (Gomi et al. 2002). This realization intersected with forest management practices when mapping of Northwest Forest Plan scenarios revealed that large percentages of watersheds were being incorporated into interim riparian reserves due to the high density of headwater stream networks (fig. 1). An additional value of using headwater drainages to plan landscape connectivity designs is that the distance from headwater streams to ridgelines is the shortest within a watershed, hence reducing travel distances for overland dispersal to neighboring stream-riparian areas or forest reserve blocks. Distance analysis tools, such as for "least-cost path" in landscape modeling (e.g., ArcGIS, Environmental Systems Research Institute, Inc., Redlands, CA), have been developed to assess distances between habitat patches. These tools would be useful for designing least-distance headwater linkage areas. Least "cost" path is a relevant term applied to the economics of animal movements, to minimize the distance moved—especially for mobility-restricted organisms. This term may also apply to the economics of forest management if identification of a dispersal corridor results in a financial cost for on-the-ground implementation or affects revenue from resource extraction in a managed forest context.

Northwest Forest Plan riparian reserves were intended as major contributors to the maintenance and restoration of aquatic conservation objectives, including aquatic network connectivity (USDA and USDI 1994). The importance of linking headwater stream functions and processes to those of downstream stream networks has been a focus of much work in the last two decades. Welsh (2011) captured many elements of the developing history of stream network theory and the role of aquatic connectivity in summarizing the conceptual frameworks of geomorphic channel processes (transfer and depositional zones), nutrient cycling (upstream marine influence via salmonid migration, downstream nutrient spiraling via down wood movements), aquatic-riparian linkages via reciprocal subsidies, and the intersection of herpetofaunal distributions with the classic stream continuum concept of taxonomic patterns that vary with stream order. As we look up the aquatic network into headwater streams and beyond, we summarize how extending riparian buffers up drainages and connecting them over ridgelines can both maintain terrestrial connectivity and functionally link aquatic-terrestrial systems.

Several conceptual designs of riparian buffer widths and patch reserves have been proposed to assist over-ridge migration of organisms within forests (fig. 2; Olson et al. 2007). Over-ridge connectivity considerations were further developed by Olson and Burnett (2009), and modeled for the Oregon Coastal Province. This model of connectivity linked every 6th- and 7th-code HU to each neighboring HU. Focusing on the Siuslaw River basin, a 4th-code HU within

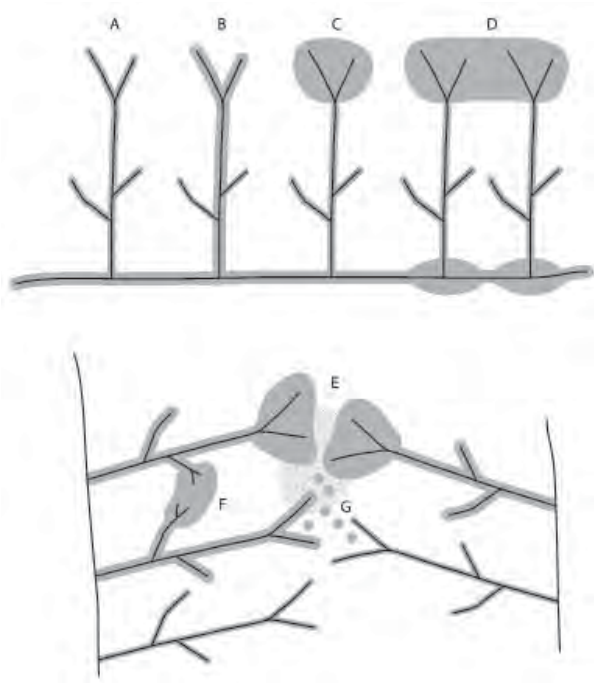

Figure 2—Headwater management considerations to retain aquatic-riparian biodiversity by stream buffers of different widths (A, B) and provide linkage areas between adjacent basins (C-G) using alternative forest management practices including uncut blocks (C, D, F), thinning (E), and leave islands (E, G) (from Olson et al. 2007).

that area, the linkage design illustrated where one over-ridge link could connect each adjacent HU (fig. 3). At the 7th-code HU scale, one link between each adjacent 7th-code watershed resulted in roughly 15 percent of headwater streams being extended and connected For the Oregon Coastal Province, this resulted in over 5,000 links, with about one link per 4.6 km^2. This is an example of redundant connectivity, essentially creating a web of connections across the landscape. Using the 6th-code HU scale, the amount of connectivity created is approximately halved, with one link per 9.3 km^2 for the Oregon Coastal Province.

There are no defined guidelines for how many links or how much habitat connectivity is necessary to maintain populations. The amount of dispersal habitat that might be needed to sustain even highly researched species, such as

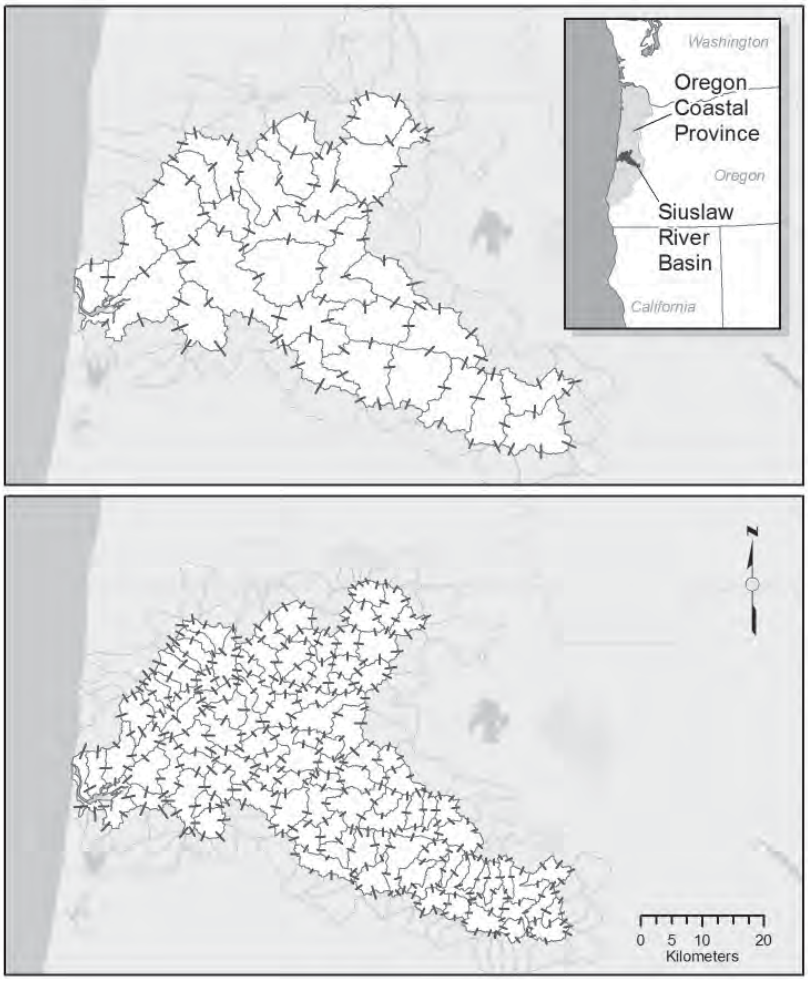

Figure 3—Linkage areas between watersheds can provide connectivity of headwater habitats across landscapes. In the Oregon Coast Range Province, the Siuslaw River basin, a 4th-code Hydrologic Unit (HU), is used to illustrate: A) a single connection between adjacent 6th-code HUs; and B) a single connection between adjacent 7th-code HUs, which results in 376 connections across the basin and if expanded to the entire province, about 5000 links within 23 000 km^2 (from Olson and Burnett 2009).

the northern spotted owl, is unknown; a "more is better" attitude prevails in the face of this uncertainty. Nevertheless, research is accruing about how much dispersal may be needed to maintain genetic diversity within and among populations. The "one migrant per generation" rule has been offered as a minimum level to reduce genetic isolation, inbreeding, and bottlenecks (e.g., Mills and Allendorf 1996). However, such a rule has many underlying assumptions that may not be supported when the complexities of natural systems are considered (e.g., Wang 2004).

Furthermore, relating effective migration rates to habitat protections in managed systems is not a straightforward exercise: if we build corridors, will they be used? Ongoing mark-recapture, radio tracking, and genetic studies are helping us to answer this question. For example, genetic connectivity analyses of stream-associated Rocky Mountain Tailed Frogs (*Ascaphus montanus*) in Idaho supported this species' affiliation with intact forested habitats: their path of connectivity followed riparian corridors in managed forests (Spear and Storfer 2010). This pattern supports the "riparian corridors as funnels" concept, but it contrasted with Coastal Tailed Frog (*A. truei*) genetic connectivity pathways in the Olympic Peninsula, Washington, which were primarily overland in areas that had timber harvest activities (Spear and Storfer 2008). Precipitation and population differences between these areas were hypothesized as accounting for these differences, as the more mesic conditions that prevail in northwestern Washington may facilitate the upland dispersal of moisture-reliant tailed frogs. Other studies (Wahbe et al. 2004; Johnston and Frid 2002; Dupuis and Steventon 1999; Nauman and Olson 2004) also found differences in riparian-corridor associations of various amphibian species in response to climate and forest conditions, generally supporting their ability to respond to microsite gradients with an apparent affiliation to cool, moist local conditions (e.g., riparian "funnels") (Olson et al. 2007). Furthermore, Spear et al. (2012) reported that Coastal Tailed Frogs track remnant tree patches in their migration pathways after the volcanic blast at Mount St. Helens, Washington. So, if we build it, will they come? The early answer is "yes, but…" —meaning that a variety of organisms appear to be occurring in or moving along pathways of retained habitats, but with geographic, taxonomic, and population-specific contexts being important considerations. A similar conclusion has recently been supported for hedgerows as corridors between woodland fragments (Davies and Pullin 2007). More research on the design of effective linkage areas will be needed. In the interim, conceptual priorities for landscape connectivity designs can be identified, and these relate directly to emerging research priorities.

Priority Areas for Habitat Connectivity

Prioritizing linkage area placement may be important to address connectivity objectives under economic constraints, and to advance research into the effective design of linkage areas. Because linking all adjoining watersheds at small HU scales may be difficult for land managers to plan and implement in the face of myriad conflicting resource objectives, priorities may guide the first steps in connecting habitats. Olson and Burnett (2009) itemized linkage area considerations at two spatial scales, landscape and drainage area (table 2). Here, we further develop five of these priority considerations:

1. "Triads," where three large basins, with limited or no aquatic connectivity, converge at their headwaters;
2. Climate change considerations including north-south, east-west, and altitudinal linkages;
3. Landslide-prone areas;
4. Species conservation strongholds; and
5. Diagonal considerations.

Table 2—Design considerations for placement of headwater linkage areas to assist migration of forest-dependent species in the Pacific Northwest (Olson and Burnett 2009). **Bold-face type** indicates new concepts discussed further in text.

Linkage Area Design Considerations	Priorities
Landscape scale	
1. Connections across large basins	**"Triads"** – headwater locations that link three adjoining basins having no aquatic connectivity.
2. Climate change migration corridors	North-south (latitudinal) dispersal routes. Altitudinal dispersal routes. Migration across ecoregion boundaries. **East-west dispersal routes.**
3. Linking landscape fragments	Connecting remnant late-successional and old-growth (LSOG) forest patches to other patches or restored habitats may aid dispersal of LSOG-associated species, especially those with dispersal limitations such as lichens, bryophytes, and mollusks; creation of connected archipelagos of patches.
4. Disturbance frequency	Correlating frequency of connections with rates of landscape-scale disturbances, natural or anthropogenic; i.e., more linkage areas in more-disturbed places.
5. **Redundancy**	Planning for multiple paths across landscapes will improve dispersal probabilities.
Drainage-basin scale	
6. Known sites for target species	Low-mobility species. LSOG-associated species. Species with status of concern. **Biodiversity hotspots** – communities. **Species "strongholds"** – priority species management areas such as key watersheds
7. Existing protections	Co-location of linkages on current set-asides (e.g., federal late-successional reserves, owl "cores", Survey and Manage species sites, botanical set asides, landslide-prone areas included in riparian reserves)
8. Short connections	For economy of space, with economic and ecological benefits, shorter connectivity corridors are preferred; ecologically, shorter distances for dispersal may reduce energetic costs for individual movements and time needed for propagules to disperse.
9. Paths of least resistance	Easier dispersal routes may be lower-gradient or lower-elevation "saddles" across ridgelines. Wind-dispersers may have least resistance in paths that follow wind directions during seasons of dispersal.
10. Risk of disturbance	Use hazard models for disturbances such as landslides, debris flows, ice/wind damage, and fire in placement of linkage areas, or in decisions about the need for redundant linkages. For example, debris-flow-prone areas may be headwater set-asides during riparian reserve delineation, and such areas may be co-located with dispersal corridors; redundant links may be considered in fire-prone areas. Mapped overlays of roads, recreation areas, human development, and mining might be avoided during linkage area delineation, when alternative locations exist.
11. Land ownership patterns	Co-location of links on federal and state lands, where possible. **Diagonal linkage areas across checkerboard ownerships.**

Each of these five considerations results in a geometric view of how connectivity webs may be arranged across landscapes.

These five considerations are not mutually exclusive; how they may interact during prioritization exercises also is developed briefly here. Although they were derived for northwest forest landscapes, these concepts may have broader utility worldwide.

1. "Triads"

In the Oregon Coastal Province, Olson and Burnett (2009) highlighted the potential importance of linking larger river basins, which have no freshwater connectivity, through existing riparian buffer networks. Over-ridge forest habitat linkages may be absent unless reserves are placed in the area. Streams in such basins may flow directly to the Pacific Ocean or into a much larger river without a forested riparian area, and so have headwaters that are functionally disconnected. Here, we examined 4th-code HUs for the Oregon Coastal province, the scale of the Siuslaw River basin highlighted above. We then looked for locations where three of these 4th-code HUs joined at their headwaters: we call this a "triad" location. For example, headwaters of the Siuslaw River, Yaquina River, and Marys River converge at Marys Peak (between Corvallis, Newport, and Waldport, OR), which would be one such triad. Only 18 of these headwater triads exist for the Oregon Coastal Province (fig. 4). We suggest that such triads be considered priorities for habitat linkage areas because these would be spatially economical for land managers to implement and potentially ecologically efficient as connections across three watershed boundaries simultaneously.

A current research priority is to empirically assess the proposed linkage-area function of landscape locations such as headwater triads. Using a genetic approach, we have sampled northwestern amphibians from headwater streams of adjacent drainages that are potentially connected across ridgelines in the Oregon Coast Range, including three adjoining headwaters in triads (such as Marys Peak). Preliminary genetic analyses of the Coastal Giant Salamander, *Dicamptodon tenebrosus*, generally support our contention of over-ridge connectivity among drainages (L. Knowles and M.R. Marchán-Rivadeneira, Univ. Michigan, unpubl. data). Previous studies have supported overland connectivity of stream-breeding amphibians (e.g., Spear and Storfer 2008, 2010), and such animals have been found up to 400 m from streams (Olson et al. 2007), but no previous published study has designed

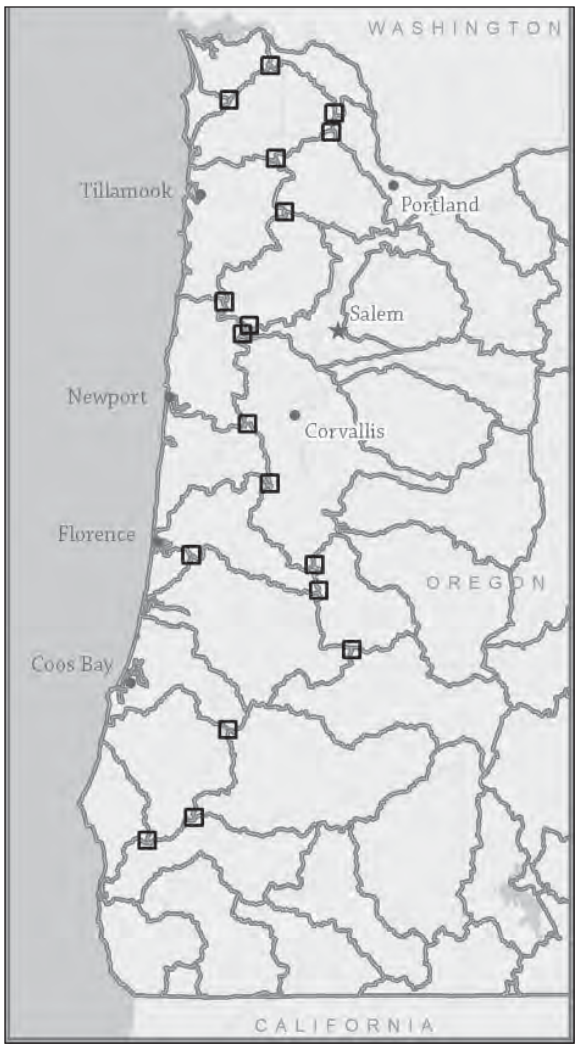

Figure 4—"Triads" are indicated (squares) where three 4th-code Hydrologic Units in the Oregon Coast Range Province meet at their headwaters. Triads are priority locations for linkage area or 'species stronghold' placement to effectively manage for species dispersal simultaneously across three distinct watershed boundaries.

sampling to specifically address headwater over-ridge connectivity among discrete drainages. This remains an information gap that could be addressed for all forest taxonomic groups, and would aid the adaptive management of the triad connectivity concept.

2. Climate Change

A second priority consideration for northwest forest connectivity is assisting migration in the face of climate change (Olson and Burnett 2009). Predicted climate change effects on northwest forest habitats include drought, insect, and fire effects on forest stands, with large conifers and high-elevation trees being vulnerable to losses (Spies et al. 2010). Aquatic habitat changes in forested landscapes are anticipated in cold-water mountain streams (Spies et al. 2010) and in headwaters (Olson and Burnett 2009). Increasing stream temperatures, with negative implications for cold-water fauna, are already apparent across the northwest (Isaak et al. 2011). Given uncertainty in the geographic specificity of climate change trajectories due to complex El Niño and Pacific Decadal Oscillation cycles, "dynamic and adaptive thinking" (Spies et al. 2010) is needed. A prudent course for linkage area placement may be to consider connected routes in north-south, east-west, and altitudinal directions within and among watersheds (fig. 5). Such consideration may allow multiple potential pathways of movement for species facing changing conditions. Pockets of suitable microhabitats for species persistence may be related to local conditions, and may occur as "stepping stones" along these linear trajectories, like beads along a string. Providing connectivity paths adjoining both riparian areas and north-facing slopes is one such example, with both near-stream areas and hill shading resulting from topographic relief providing cool, moist conditions for target species such as some late-successional and old-growth (LSOG)-associated salamanders (e.g., Suzuki et al. 2008). Landscape-scale monitoring of forest conditions and species distributions may inform adaptive management of likely climate change refugia for different taxa.

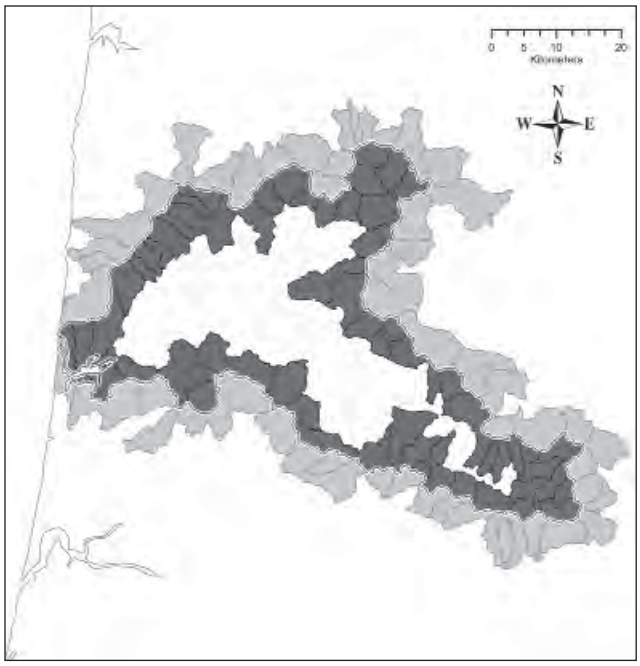

Figure 5—Designs for assisted migration of species in the face of climate change might include prioritizing headwater linkage area placement across north-south and east-west watershed boundaries. The Siuslaw River basin, a 4th-code Hydrologic Unit in the Oregon Coast Range Province, is shown highlighting perimeter sub-drainages (dark grey) where linkage areas could be made to discrete drainages to the north, south, and east.

3. Managing Disturbances: Landslide-Prone Areas

A third priority consideration for the design of linkage areas is to integrate their placement with local disturbance regimes. Landslides and debris flows can be dominant disturbance processes affecting headwater streams in forested, mountainous regions (e.g., Benda 1990; Iverson et al. 1997). The Northwest Forest Plan directs that riparian reserves incorporate landslide-prone areas to reduce the probability that activities associated with timber harvest will alter wood and sediment inputs to streams by changing the rate, magnitude, composition, or timing of debris flows. Co-locating linkage areas with existing riparian reserves, where these include steep areas prone to landsliding, can provide

economic efficiency and conservation synergy for land and resource managers. Burnett and Miller (2007) modeled differences among hill slopes and headwater channels in probabilities of initiating and transporting debris flows that deliver to fish-bearing channels for the Oregon Coastal Province (fig. 6). Those headwaters with the highest likelihood of affecting downstream areas important for fish might be high priorities for extending riparian reserves over ridgelines. Because debris flows can be important sources of large wood (May and Gresswell 2003; Hassan et al. 2005), a fundamental component of stream habitat complexity (Bilby and Bisson 1998; Gregory et al. 2003), managing these expanded riparian reserve areas to accelerate tree growth could be an additional consideration. Redundancy of connections would be important when planning ground-disturbing activities for linkage areas with a high probability of landsliding. To aid identification and adaptive management of landslide-prone areas, these areas have been mapped for many northwest forests by the NetMap interactive web-tool developed by Earth Systems Institute (*http://netmaptools.org/*).

4. Species Strongholds

"Species strongholds" are areas where biodiversity conservation is a priority, and where thriving populations can occur to anchor species persistence in the region. Retaining connectivity among species strongholds enhances the likelihood of persistence under the uncertainty of stochastic events (catastrophic fire, disease outbreaks) or emerging patterns of disturbance (climate change) that may affect any particular stronghold. Managing stronghold-to-stronghold connectivity is a fourth priority to consider in developing linkage area designs across forest landscapes. Species strongholds may be created for communities of diverse taxa at larger spatial scales by land-use allocations such as

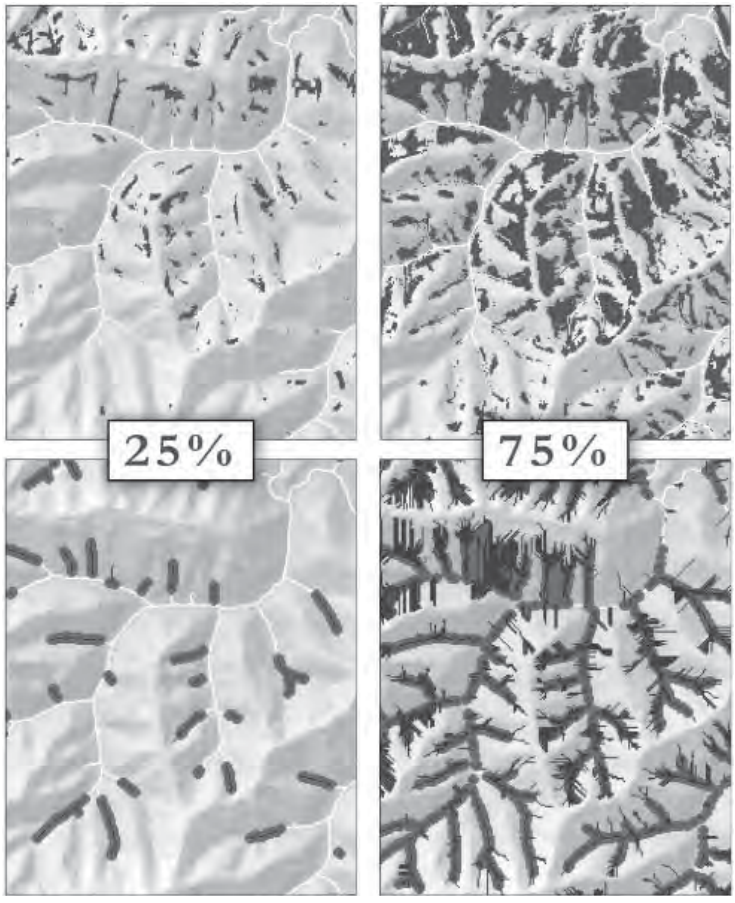

Figure 6—Placement of between-drainage links might consider other landscape-scale provisions such as management scenarios to retain the natural disturbance regime, including landslide-prone areas managed to deliver wood and sediment to streams. Top figures show models of 25 percent and 75 percent of the landslide-prone hillslopes in an example forest landscape, and bottom figures show their likely traversal paths to streams (Burnett and Miller 2007). Headwater riparian buffers of these areas provide long-term wood and sediment inputs for stream biota. From Olson and Burnett 2009.

Congressionally reserved lands (wilderness areas, national parks), or the Northwest Forest Plan late-successional reserves or key watersheds (USDA and USDI 1993, 1994). At smaller spatial scales, strongholds for a targeted species of concern may be critical habitat areas, such as caves, ponds, meadows, botanical set-asides, or areas managed for Survey and Manage species under the federal Northwest Forest Plan (USDA and USDI 1993, 1994). Riparian buffers themselves might be considered as strongholds, but here, we expand that perspective to other areas.

Developing new species strongholds is particularly important when considering connectivity issues. Three examples follow. First, areas with high "intrinsic potential," the capacity to support high-quality habitats for salmon (Burnett et al. 2007), may serve as nuclei for designing linkage areas. Intrinsic potential models have been developed and broadly applied for salmonids in the Pacific Northwest and elsewhere (e.g., Mollot and Bilby 2008; Sheer et al. 2009; Busch et al. 2011; Barnett and Spence 2011). Streams with high intrinsic potential can be identified and then targeted, as appropriate, for salmon conservation across a landscape. Such areas of high intrinsic potential are essentially "species strongholds" from which aquatic-terrestrial linkage areas can originate. Areas of high intrinsic potential for some salmonid species may occur in larger streams, but tools exist to easily identify headwater streams that feed into these both laterally and from upstream (Clarke et al. 2008).

Second, criteria for Priority Amphibian and Reptile Conservation Areas (PARCAs) are under development for nationwide application (Riley et al. 2011). PARCAs are being discussed for integration into the landscape planning processes of other entities, such as the U.S. Department of Interior Landscape Conservation Cooperatives (*http://www.doi.gov/lcc/index.cfm*), which is a partnership network to sustain America's land, water, wildlife, and cultural resources. Once established, PARCAs would function as species strongholds. Similarly, the International Union for the Conservation of Nature (IUCN) is developing criteria to identify sites of global significance for biodiversity conservation, called Key Biodiversity Areas. Such areas are synonymous with the concept of species strongholds. The additional element that we suggest is to provide connectivity among such areas.

Third, triads, as we previously described, could be ideal locations for species strongholds, as these occur at the ridgeline junction of three large basins. However, we note that triads are not established biodiversity hotspots, and are proposed here as a conceptual design.

Development of landscape-scale linkage webs from either new or existing species strongholds is needed to reduce isolation of those areas, and as possible to allow them to function as potential "source" habitats with optimal conditions that can anchor species over time and also connect to adjoining areas, in a metapopulation context. Linking dispersal pathways from strongholds up and over ridgelines to adjacent watersheds and neighboring strongholds is a direct approach that may offer a least-cost path. Relevant to our proposed headwater linkage areas concept, connecting such species strongholds to headwaters which then extend and connect over ridgelines is another consideration. Additionally, strongholds may be linked to protected riparian areas along larger streams that are subsequently extended upstream into headwaters and connected over ridgelines. Multiple connectivity pathways may be conceived. As a web of connections is considered relative to species stronghold connectivity, the previous priorities discussed above and outlined in table 2 can be overlain, including large basins and triads, linear trajectories to address for climate change gradients, and occurrence of landslide-prone areas.

Adaptive management of strongholds may need to be addressed over the long term as future conditions unfold. As applied here, the concept of a stronghold evokes less of an immovable fortress than an anchor. A species stronghold intended

to anchor habitat may need to function as do real anchors on occasion, and be repositioned or "drag" across landscapes in response to changing conditions or management priorities (Olson et al. 2007). The temporal scale of strongholds can be addressed at the time of their development, and interact with the spatial scale of stronghold designs and the frequency of strongholds. For example, habitat anchors designed to drag across landscapes may be implemented more easily if they are smaller and more numerous. Olson et al. (2007) suggested considering 6th-code watersheds (HUs) as a spatial scale for amphibian habitat anchors. The anchor concept warrants testing, with a sufficient timeframe to weigh success at the landscape scale, in addition to replication. It may have greater success if it were to be implemented in areas with more resilient ecosystems.

5. Thinking Diagonally: Funnels and Chains

The geometry and land-management context of land-use and land-ownership parcels on the landscape is a final set of priority considerations for linkage-area placements that we will develop briefly here. The northwest forest landscape is a patchwork of land ownerships and land-use allocations, each with differing management priorities, which creates a complex challenge for biodiversity conservation (Suzuki and Olson 2007). During planning for large blocks of forest land, and during planning of individual projects at smaller spatial scales, managing for connectivity within and among ownership areas can be difficult due to differing priorities across boundaries. To diminish the dilemma of achieving effective biodiversity conservation in such a multi-ownership landscape, it may help to think of streams as dispersal "funnels" that serve to channel organisms along protected riparian areas, and connectivity corridors or linkage areas as "chains" functionally moving animals up and over ridgelines (Olson and Kluber, unpubl. data). Overlaying many of the previously discussed priorities can provide an integrated perspective for addressing the challenges of land-ownership/allocation geometries.

Diagonal linkage areas are of specific relevance in a landscape with a checkerboard ownership pattern (fig. 7), and in other landscape geometries that abut at corners or other edge types (Olson and Kluber, unpubl. data). Species dispersal along such diagonals might be promoted by forest management actions that retain habitat elements toward the corners of such lands. For example, weighted green-tree retention, leave islands, and directional felling of down wood (recruitment of large logs, in particular) from corners may assist migration of species along the diagonal by providing chains or stepping stones of suitable microhabitats for species refugia. Linking chains of habitat elements from corners to stream- and riparian-protected areas, especially headwaters (fig. 7B), may functionally extend and connect riparian buffers. Organisms that are funneled along riparian areas may venture through corners via these habitat chains. A chain of habitat need not extend from headwaters, but could extend from any part of a riparian buffer, or from a species stronghold, as discussed above.

It may be neither feasible nor desirable to address habitat connectivity at all corners of adjacent lands within an ownership. Similarly, when land parcels are in close proximity but do not adjoin, it may not be possible to consider linkage areas along their entire boundaries. Several additional design concepts arise and interface with ideas presented above.

First, linkage areas among land parcels might be "stream-lined" if streams align through corners (fig. 8), or connect nearby land blocks. When streams follow diagonals in a checkerboard landscape, riparian protection may more effectively promote multi-species diagonal dispersal: funnels without the added chains linking across diagonals. Streams that loosely follow diagonals, not intersecting exactly at corners, could be quite functional to assist species

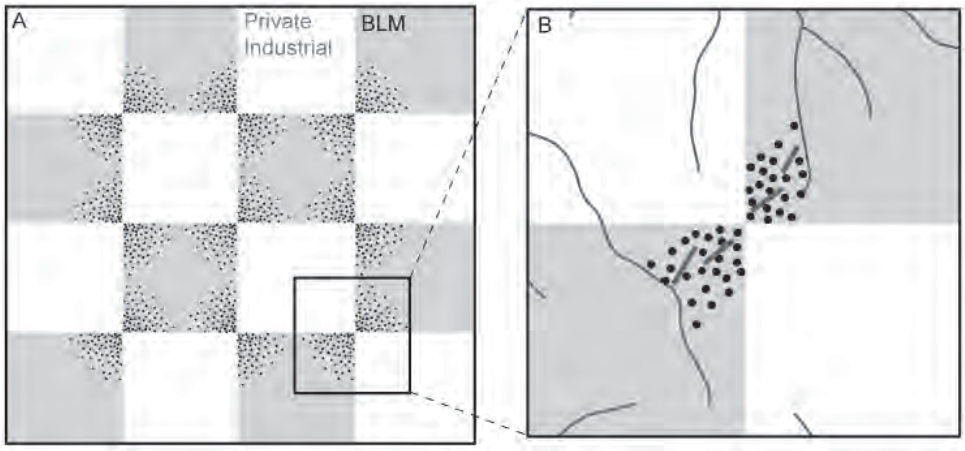

Figure 7—In a checkerboard ownership pattern, such as that created by the Oregon and California Lands Act (1937) where US Bureau of Land Management (BLM) and private industrial forestlands are intermixed, management for connectivity along diagonals may improve likelihood of species dispersal within ownerships. A: Corners are shaded to show linkage area considerations. However, routes along selected diagonals to species strongholds, reserves, or triads might be used to prioritize which corners are chosen for connectivity emphasis. B: Forest management options to facilitate species dispersal from stream corridors (which may serve to funnel species movements) to corners might include chains of habitat structures provided by green tree retention, directional log placement from corners to streams, or both. Concepts could be applied to other ownership geometries with corners or edges in proximity.



Figure 8—Connectivity designs to aid species dispersal among ownership blocks may overlay on streamside riparian management zones. This US Bureau of Land Management study site for the Density Management and Riparian Buffer Study of western Oregon (Cissel et al. 2006) shows riparian buffers extending along the full diagonal (A) as well as laterally toward an opposing corner (B), with leave islands and dispersed tree retention aiding habitat connectivity, and to a neighboring private land block (C). "Stream-lined" connectivity (A) may aid within-watershed dispersal, but overland connectivity designs (B and C) may warrant consideration to link or "chain" habitats overland between watersheds. Photo provided by Oregon Bureau of Land Management.

migration, in this regard. Streams that link disconnected parcels may similarly function to funnel organisms' movements. The context of the adjoining lands may need to be assessed, however. Managing such a stream-line to promote its potential connectivity function is a consideration, but such stream-lined connectivity does not address overland dispersal. Chains from streams to ridgelines are needed to fully integrate aquatic and terrestrial landscape connectivity functions. Collaborative management of such stream-lines and overland chains among ownerships and

across land-use allocations within ownerships, remains a challenge.

Second, in multi-ownership landscapes, road densities may be higher than in single owner landscapes. An assessment of the effects of roads on species connectivity designs may be particularly important in these landscapes. In particular, paved roads or high-use unpaved roads may be barriers to low-mobility species. As roads intersect streams, aquatic organism passage may be affected, with consequences for overland connectivity. Site-specific designs can include these considerations.

Third, as hazard models of disturbances are developed for a landscape, it may be helpful to ask how hazards align with land-ownership boundaries, land-use allocations, and existing connectivity webs. For example, how are landslide-prone areas arranged relative to the geometry of lands by ownership and land-use allocation? As discussed above, can priority linkage areas be designed to overlay on landslide-prone areas that are already set-asides for riparian reserve management, and now also serve "to chain" habitats to adjoin land-ownership blocks?

Fourth, in a larger landscape context, it may be useful to know how larger basins, climate change projections, and species strongholds are arranged and whether these be used to prioritize connectivity area pathways. Can dispersal routes be conceived from streams and then through land-ownership diagonals or between ownership blocks to foster connections relative to these issues?

Multiple overlapping considerations are emerging, and a stepwise process may be needed to integrate them. Limitations may emerge due to topography, geometry of land configurations at local scales, or pre-existing conditions. For example, a dispersal barrier such as a road may need to be considered first. The existence of under-road culverts may create spatially explicit bottlenecks for connectivity planning. Routing linkage area pathways to those stream corridors and culverts may be needed to increase the odds of dispersal across the road. Culverts that act as dispersal nodes in this way could be prioritized for enhancement to provide passage for non-aquatic species. Similarly, triads and species strongholds, as discussed above, are essentially dispersal nodes. Routing dispersal routes via headwater linkage area pathways to triads and strongholds could increase the overall effectiveness of these conservation measures.

Conclusions

Forest biodiversity conservation is an ecosystem service that will continue to be addressed at local-to-landscape scales in the coming century. Retaining organisms across managed forest landscapes requires a toolbox of approaches including fine- and coarse-scale habitat protections and restoration practices, retaining or creating structural elements that are critical habitats for species, and development and management of connectivity pathways to allow gene flow. Renewed efforts to address communities of organisms as well as species of concern are called for as emerging stressors need evaluation, new knowledge is accrued, and adaptive management of existing forest plans are needed.

We review the numerous benefits of forest connectivity designs that rely on headwater linkage areas, and emphasize priorities for their placement at landscape scales. The benefits of headwater linkage areas include their likely functional role in integrating aquatic and terrestrial systems, their potential use by multiple taxonomic groups, their utility for creating webs of connections across forested lands to increase their effectiveness for biodiversity conservation, and their efficiency in minimizing both the distances that animals must move overland and the financial burdens of forest manager.

Placement of headwater linkage areas may include consideration of a variety of factors (table 2). Prioritizing linkage areas can provide a starting point for managing connectivity among

critical habitat areas, suggest directional routes for dispersal among areas, or identify dispersal nodes as anchors for connectivity webs. The five priority considerations that we developed include triads that effectively link three larger basins, north-south and east-west directional routes to address climate change scenarios, linkages overlaid on management of disturbances such as landslide-prone areas, links among species strongholds, and diagonal links that route dispersal across management boundaries. These five concepts can be integrated into an overall geometry of landscape connectivity designs. Our conceptualization of headwater linkage area utility and these priority considerations are posed as hypotheses warranting further study and development. We offer these ideas with the caveat that they will not benefit all taxa in forested landscapes. Extremely rare or patchily distributed organisms with low mobility may need a finer-grained, site-by-site conservation approach (Raphael and Molina 2007).

Acknowledgments

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POLICY PERSPECTIVE

Protected areas are now the last strongholds for many imperiled mammal species

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Abstract

The global network of terrestrial protected areas (PAs) has experienced a fourfold expansion since the 1970s. Yet, there is increasing debate around the role of the global PA estate in covering and sustaining threatened species, with serious ramifications for current PA financing and the setting of post-2020 global conservation targets. By comparing "past" (1970s) and current distribution range of 237 mammals, and measuring the proportion of range covered by PAs in the past and in the present, we show that a small number of PAs have now become the last bastions of hope for ensuring the persistence of many mammal species. For 187 species (~79% of those analyzed) the proportion of range covered by PAs has doubled over the time period, with 10% of all species now having most of their current range protected. This increase in proportional protection over time is largely due to a retreat of species distribution (outside existing PAs) and, in smaller part, to PA expansion. It is clear that adequately resourcing those PAs critical in sustaining mammal species is now essential, to avert a worldwide rapid mammal loss.

KEYWORDS
extinction, mammal conservation, population loss, protected areas, range collapse

1 | INTRODUCTION

A fourfold expansion in the global network of terrestrial protected areas (PAs) has occurred since the 1970s, and today PAs cover ~15% of the terrestrial planet (UNEP-WCMC & IUCN, 2016). Recent works have shown the number of threatened vertebrates included in PAs is increasing as a consequence of an expanding PA estate (Venter et al., 2014) and there is evidence that some PAs have been effective at maintaining, or even enhancing wildlife populations (Geldmann et al., 2013; Walston, Stokes, & Hedges, 2016). For example, species like the tiger (*Panthera tigris*) and lion (*Panthera leo*) have clearly benefited from the use of fences and antipoaching measures employed within PAs (Geldmann et al., 2013; Karanth, Nichols, Kumar, & Hines, 2006). Yet, there is increasing conjecture around the role of the global PA estate in covering and sustaining imperiled species, as PA coverage is biased toward locations that are less expensive to protect and sometimes of limited importance for biodiversity (Visconti et al., 2019; Venter et al., 2014)).

Signatory nations of the Convention of Biological Diversity (CBD) are now focusing on generating a new, post-2020 PA target that includes a further increase of global PA coverage (Convention on Biological Diversity, 2020). But the uncertainty of how effective PAs have been in saving

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imperiled species has serious ramifications for current PA financing (Watson, Dudley, Segan, & Hockings, 2014), and is likely to impact international debate on the best post-2020 strategy for PAs (Visconti et al., 2019). As such, assessments around the effectiveness of the PA estate to conserve biodiversity are increasingly important for policy discussions and financing (Coad et al., 2019).

We collected data on past (1970s) distribution ranges for a total of 237 mammal species (Table S1) by combining a public database on past distribution maps for terrestrial non-volant mammals (Pacifici et al., 2019) with literature-based information on bat distributions. We measured species' range changes, and the past and present overlay of the ranges with PAs at different spatial resolutions for sensitivity testing (see Supporting Methods). Due to the 50-year timeframe considered, the changes in distribution we observed are related to relatively recent human activities (Pacifici et al., 2020) and may underestimate historical contractions in species' ranges.

Our results show that many imperiled species have now become almost completely dependent on PAs for their persistence. We chose mammals because they are a well-studied taxon which has highly suffered from human impact in recent years despite having a crucial role in providing and maintaining services and functions associated with sustaining balanced ecosystems (Di Marco, Venter, Possingham, & Watson, 2018; Pacifici et al., 2020). Our analysis represents all major taxonomic mammal orders and biogeographic regions, with the exception of the Palearctic region for which we have a relatively lower number of species (Figure S1). Although large-bodied orders are usually better represented in mammal distribution analyses as they are more studied (Monsarrat & Kerley, 2018), we improved the Pacifici et al. (2019) database—which did not include volant mammals—so as to balance the number of large charismatic species and small less-known mammals and obtain more generalizable results (Figure S2, Table S4). Small mammals (< 3 kg) represent 53% of the species in our database, although our data might underrepresent those species that live in very small areas and for which local extinctions are not realistically contemplated

2PROTECTED AREAS ARE ESSENTIAL FOR MANY IMPERILED MAMMALS

There have been clear increases in PA coverage for 224 (i.e., 94%) of the mammal species in our analysis (Figure 1a, Table S2), with an average 12% additional coverage since 1970s. For 187 species (~79%) the proportion of range covered by PAs has at least doubled in the last 50 years, with 10% of all species now having more than half of their distribution range protected (Figures 1a, 2). This pattern of increased protection relative to range size was especially true in the tropics (Figure S3), with some areas, like the Sunda Islands and Central-Eastern Africa, standing out for the high number of charismatic species surviving now almost exclusively in PAs (Figure 2).

Importantly, the majority of species ($n = 147$, 62%) experienced contractions of their distribution range alongside an increase in percentage PA cover (Table S2). Large-bodied mammals (here defined as those species with body mass >20 kg, following MacDonald & Willis, 2013) are the most significant examples of the trend of net loss of distribution range and proportional increase in PA coverage (Figure 1b, c). The increased in percentage coverage of PAs was only due to a net increase in the extent of PAs within the range of the species (i.e., no range reduction) in 33% of cases, while for 53% of species, the increase in proportional protection over time is almost entirely due to a net decline of their distribution outside existing PAs (Table S2). For example, ~80% of the range of the Indian rhinoceros (*Rhinoceros unicornis*) is currently protected compared to 3% in the 1970s, after the species has lost a dramatic 99.7% of its distribution in just 50 years (Table S1); about 87% of the remaining individuals currently occur in just two PAs (Kaziranga National Park in India and Chitwan National Park in Nepal; Walston et al., 2016). Likewise, the percentage range protection of the Addax in Africa (*Addax nasomaculatus*) has increased from 3% in the 1970s up to 59% today, after a 97% range contraction (Figure 2).

For 26 other mammal species, we found no reduction in species' distribution and an increase in range protection from PA expansion (Table S2). An example is the puma (*Puma concolor*), a widespread species that occurs from Canada to Chile. This species showed no significant changes in its distribution but a 17% increase in PA coverage (Table S2). Puma is a very adaptable species, found in every major habitat type of the Americas (Nielsen, Thompson, Kelly, & Lopez-Gonzalez, 2015), and it widely occurs in Brazil, the country where annual rate of land protection is the highest in the world (UNEP-WCMC et al., 2018). There were also a few ($n = 14$) species that had no change in percentage range protected, mostly located in eastern and Midwestern United States and Mexico (Figure S1); these are some of the areas with the lowest PA expansion over the past two decades (UNEP-WCMC et al., 2018).

3 | AN URGENT NEED TO IDENTIFY THOSE JEWELS IN THE PROTECTED AREA ESTATE

We did not set out to prove PAs are effective at preventing future extinctions, but to simply assess if (and why) mammal species are increasingly found in protected land and

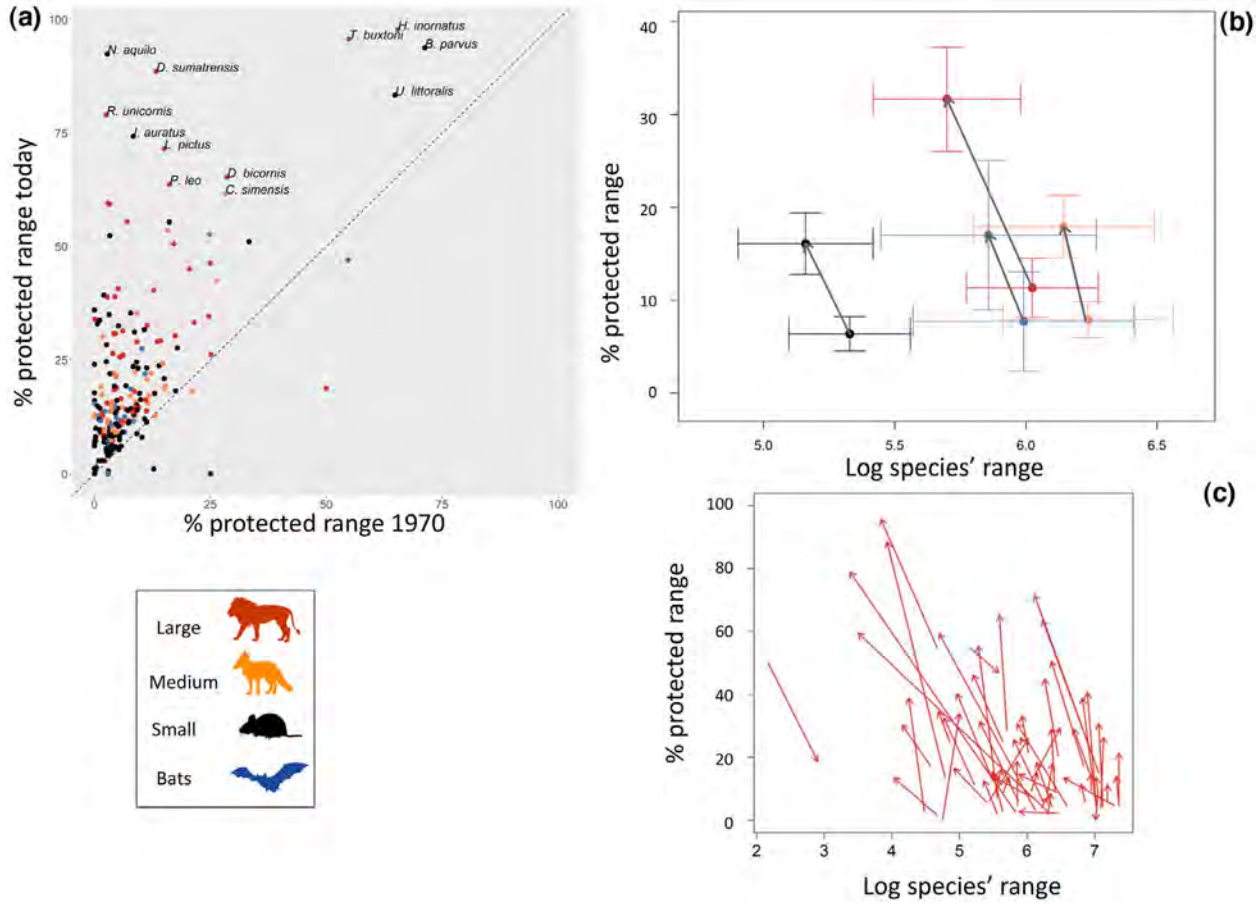

FIGURE 1 Changes in protected area coverage within mammal ranges since the 1970s. (a) Comparison between current and past protected area coverage within species ranges divided by body mass and locomotion: large-bodied non-volant mammals, ≥20 kg, in red; medium-bodied nonvolant species, 3–15 kg, in orange; small-bodied nonvolant species, ≤3 kg, in black; bats in blue. (b) Past and present relationship between species' range size and protected area coverage; arrows direction goes from past to current data, with error bars representing 95% confidence intervals. (c) Trends of large-bodied species (arrows direction goes from past to current data)

to explore the policy consequences of this. Our results are unequivocal, and supported also by a sensitivity analysis (Figure S4)—there are clear increases in PA coverage for 94% of the mammal species, and for 79% of species the proportion of range covered by PAs has at least doubled in the last 50 years (Table S2). The most likely explanation is that PAs, especially when well resourced, managed, and well-placed within the wider landscape, have every chance in halting the threatening processes causing mammal decline (Coad et al., 2019; Edgar, Stuart-Smith, Willis, & Nature, 2014; Watson et al., 2014). Another key aspect that emerged from our work is that when dealing with spatial analysis on species distribution and PAs, the resolution and resampling technique must be carefully selected. We found for those species with very small, fragmented distributions, simply resampling polygons at a coarser resolution may lead to a loss of ecological signal (Table S3, Figure S4).

There is growing body of species-specific evidence around why PAs are effective at maintaining mammal populations. For example, despite a disastrous 82% reduction in global distribution (Table S1), the tiger population in Rajiv Gandhi (Nagarahole) National Park in India has increased by 400%, due to improved reserve management aimed at maintaining high prey densities (Karanth et al., 2006). Likewise, South-African lions subpopulations showed an overall 12% increase since 1993, with a peak of +1,400% in the well-budgeted Tembe Elephant Park (South Africa, Bauer et al., 2015), despite a global species decline of 43%.

In Latin America, the amount of range under protection of the white-lipped peccary (*Tayassu pecari*), a declining species classified as Vulnerable by the International Union for Conservation of Nature (IUCN), has increased sevenfold since the 1970s (Suárez et al., 2009; Figure 1c). In the Yasuni Biosphere Park and Reserve in Ecuador, the species has been the subject of an intensive commercial bushmeat trade in the last 3 decades, with peaks in the years 2005–2007 (Suárez et al., 2009). A successful collaboration between TRAFFIC, the Ministry of Environment and local communities planned targeted actions for the

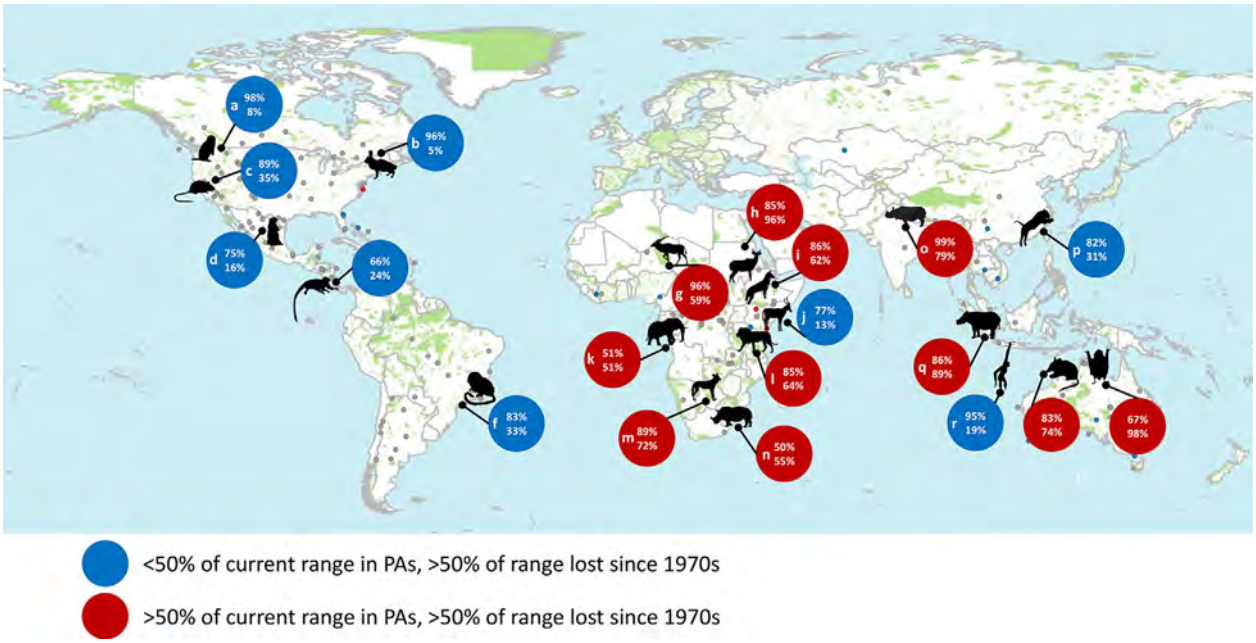

FIGURE 2 Top 20 species of mammals threatened by range reduction. The figure highlights species with the highest percentage range contraction since 1970s. Red circles represent species for which protected areas represent the last bastions (> 50% range is protected). Blue circles show species with very high rates of range decline, and relatively small portions of the current distribution protected (< 50%). In each big circle, percentage values at the top indicate range loss, while those at the bottom represent the amount of range currently protected. Protected areas are represented in green. Small dots represent the centroid of the range of the other species in the original sample. A full species list of the top 20 mammals threatened by range reduction (big circles) is provided in Table S1

different consumer groups, targeted to reducing the consumption of wild meat while providing alternative sources of protein to local populations (Phelps, Biggs, & Webb, 2016).

The saiga antelope (*Saiga tatarica*) lost > 70% of its range (Table S2) and is currently listed as Critically Endangered by the IUCN. Population estimates for Mongolia, where animals are mostly concentrated in two PAs (Sharga Nature Reserve and Mankhan Nature Reserve), suggest that the population is growing (Milner-Gulland, 2015), probably due to rigorous conservation efforts since 1993 when reserves have been established to protect most of the remaining distribution range of the species (IUCN SSC Antelope Specialist Group, 2018). What these examples show is identifying those PAs that play a vital role for highly threatened species is a priority: they should get appropriate levels of funding to ensure effective management and be upsized and upgraded if needed. Our analysis, while not claiming to be comprehensive across all threatened species, indicates that many PAs in East and South-East Asia and Sub-Saharan Africa are a priority for conservation investment, as they contain enormous percentages of threatened terrestrial mammals ranges. Efforts should be made to systematically identify PAs across every continent which play a disproportionally important role in maintaining species current distributions; this should be taken into account when threatened species belonging to any taxonomic group are strictly related to PAs management and effectiveness, as these PAs are essential to these species' long-term security.

For those international policy forums that deal with PAs, greater clarity must be made in specific protected area text that showcases the roles different PAs play in abating the conservation crisis. This is especially timely, given the world's governments will soon adopt a post-2020 biodiversity framework. This plan will likely contain biodiversity targets that define the global conservation agenda for at least the next decade and, while it is still unknown what the actual targets will be (and still the subject of much debate; Visconti et al., 2019), it is clear that PAs will play an important role in this wider conservation agenda. Our research provides more evidence that conservation policy development and implementation must be built on a platform that is clear on the overall goals of conservation (Visconti et al., 2019). This is because some PAs play more of a critically important role for mammal conservation than others, and these must be identified and targeted for resources. Therefore, policy makers must be clear on the different roles PAs will play in achieving these goals. By clearly specifying the different roles PAs play within the wider conservation agenda, there will be a shift in focus toward objective assessments on PAs through the world,

focusing on which ones need more resourcing and what are the best ways to identify key funding gaps and priorities (Coad et al., 2019). At the same time, it will lead to more effective monitoring and reporting of PAs by nations, including states and trends of threatened species, which should underpin the adaptive management of PAs.

4 | PROTECTED AREAS ARE NECESSARY BUT NOT SUFFICIENT TO HALT MAMMAL DECLINE

PAs are not the one-and-only panacea when it comes to effective conservation for imperiled mammals. The Earth surface has been drastically altered and fragmented by human activities, with natural lands usually converted into other land cover types (Haddad et al., 2015). This has led wildlife to be increasingly confined in evermore rare and sparse habitat patches, often only found in PAs, facing problems of isolation, increased vulnerability to stochastic events—for example, genetic drift, environmental and demographic stochasticity—and higher probability of local extinction due to the reduction of their populations (Newmark, 1995; Pacifici et al., 2020). For example, the Cape buffalo (*Syncerus caffer caffer*) populations inhabiting smaller isolated parks in Kenya and Uganda showed signs of genetic erosion, presumably because of the lower ecological carrying capacities of these reserves, hence restricting the effective population size of animals, and the small ratio between the size of the PA and the surrounding human-dominated landscape which reduces gene flow (Heller, Okello, & Siegismund, 2010).

Large carnivores isolated in small PAs have proven to be more vulnerable to human-induced mortality rather than to stochastic processes. For these mammals, conflicts with humans on reserve borders are the main cause of mortality, and species with relatively larger home ranges have a higher probability of going locally extinct (Woodroffe & Ginsberg, 1998). Conservation measures that aim only to combat stochastic events are therefore unlikely to avert extinction for these species with large area requirements. Instead, actions that seek to maximize PA size and connectivity between PAs are essential, as are efforts to mitigate carnivore persecution on PA borders and in buffer zones.

5 | WITHOUT WELL-FUNDED PROTECTED AREAS, THE FUTURE LOOKS GRIM FOR MAMMALS

Our research provides clear evidence of dramatic range declines for many mammal species, with distribution shrinkage toward PAs. The rate at which species have disappeared from their past (1970s) range has largely surpassed the rate by which PAs have been created, pointing to the obvious fact that we are running out of time to save these species. As the global community comes together and debates new post-2020 conservation goals (where protected area targets and future financing will play a central role), it is vital that the role that those well-placed PAs play in ensuring many mammal species persist in the wild is formally recognized. As species like the African wild dog (*Lycaon pictus*), dhole (*Cuon alpinus*), lion, and tiger face continuing conflict with people even inside well cited PAs (Woodroffe & Ginsberg, 1998; respectively 14%, 3%, 12%, 4% of their range losses have been inside PAs; Table S2), it is critical that PAs must be well financed and managed. This is the only chance for highly threatened, exploited species to survive

Many of the species we found retreating toward PAs are heavily affected by illegal trade, a market worth US $7–$23 billion a year (Nellemann et al., 2016). Mountain Nyalas (*Tragelaphus buxtoni*), for example, are widely persecuted for their meat and horns (Sillero-Zubiri, 2013) and today survive almost exclusively within PAs. Mountain Nyala is one of the few species in our list that lost vast portions of its range also within PAs (63%; Table S2). The situation is similar for white rhinoceros (*Ceratotherium simum*), black rhinoceros (*Diceros bicornis*), Indian rhinoceros, and Sumatran rhinoceros, whose horns are mainly used for traditional medicine and dagger handles in Asia (Biggs et al., 2013), with the vast majority of their current distributions (65–89%) being in PAs (Table S1). To ensure the long-term survival of mammals, global conservation policies must focus on securing those critically important PAs and, at the same time, reward those efforts that ensure reexpansion and recolonization of wildlife populations on territories beyond protected area boundaries. This means focusing on retaining Earth's remaining intact ecosystems that contain key PAs and prioritizing efforts to restore habitat corridors between isolated reserves that best provide opportunities movement and genetic exchange.

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AUTHORS' CONTRIBUTIONS

MP, MDM, and JEMW designed the study. MP analyzed the data. All authors discussed the results and wrote the paper.

DATA ACCESSIBILITY STATEMENT

Data sources for past ranges are available at https://onlinelibrary.wiley.com/doi/10.1002/ecy.2747/suppinfo. IUCN current ranges are available upon request at https://www.iucnredlist.org/. Current ranges not taken from the IUCN Red List for sensitive species are available from the corresponding author upon reasonable request.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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A globally coherent fingerprint of climate change impacts across natural systems

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Causal attribution of recent biological trends to climate change is complicated because non-climatic influences dominate local, short-term biological changes. Any underlying signal from climate change is likely to be revealed by analyses that seek systematic trends across diverse species and geographic regions; however, debates within the Intergovernmental Panel on Climate Change (IPCC) reveal several definitions of a 'systematic trend'. Here, we explore these differences, apply diverse analyses to more than 1,700 species, and show that recent biological trends match climate change predictions. Global meta-analyses documented significant range shifts averaging 6.1 km per decade towards the poles (or metres per decade upward), and significant mean advancement of spring events by 2.3 days per decade. We define a diagnostic fingerprint of temporal and spatial 'sign-switching' responses uniquely predicted by twentieth century climate trends. Among appropriate long-term/large-scale/multi-species data sets, this diagnostic fingerprint was found for 279 species. This suite of analyses generates 'very high confidence' (as laid down by the IPCC) that climate change is already affecting living systems.

The Intergovernmental Panel on Climate Change[1] (IPCC) assessed the extent to which recent observed changes in natural biological systems have been caused by climate change. This was a difficult task despite documented statistical correlations between changes in climate and biological changes[2–5]. With hindsight, the difficulties encountered by the IPCC can be attributed to the differences in approach between biologists and other disciplines, particularly economists. Studies in this area are, of necessity, correlational rather than experimental, and as a result, assignment of causation is inferential. This inference often comes from experimental studies of the effects of temperature and precipitation on the target species or on a related species with similar habitats. Confidence in this inferential process is subjective, and differs among disciplines, thus resulting in the first divergence of opinion within the IPCC.

The second impasse came from differences in perspective on what constitutes an 'important' factor. Anyone would consider a currently strong driver to be important, but biologists also attach importance to forces that are currently weak but are likely to persist. In contrast, economic approaches tend to discount events that will occur in the future, assigning little weight to weak but persistent forces. Differences of opinion among disciplines can therefore stem naturally from whether the principal motivation is to assess the magnitude of immediate impacts or of long-term trajectories. Most field biologists are convinced that they are already seeing important biological impacts of climate change[1–4,6–9]; however, they have encountered difficulty in convincing other academic disciplines, policy-makers and the general public. Here, we seek to improve communication, provide common ground for discussion, and give a comprehensive summary of the evidence.

How should a 'climate fingerprint' be defined? A straightforward view typical of an economist would be to conclude that climate change was important if it were principally responsible for a high proportion of current biotic changes. By this criterion a climate fingerprint appears weak. Most short-term local changes are not caused by climate change but by land-use change and by natural fluctuations in the abundance and distribution of species. This fact has been used by non-biologists to argue that climate change is of little importance to wild systems[10]. This approach, however, effectively ignores small, systematic trends that may become important in the longer term. Such underlying trends would be confounded (and often swamped) by strong forces such as habitat loss. Biologists have tended to concentrate on studies that minimize confounding factors, searching for trends in relatively undisturbed systems and then testing for significant associations with climate change. Economists have viewed this as biased (nonrandom exclusion of data) whereas biologists view this as reducing non-climatic noise. Thus, economists focus on total direct evidence and apply heavy time discounting; biologists apply a 'quality control' filter to available data, accept indirect (inferential) evidence and don't apply time discounting.

The test for a globally coherent climate fingerprint does not require that any single species show a climate change impact with 100% certitude. Rather, it seeks some defined level of confidence in a climate change signal on a global scale. Adopting the IPCC 'levels of confidence'[11] and applying the economists' view of a fingerprint, we would have "very high confidence" in a fingerprint if we estimated that more than 95% of observed changes were principally caused by climate change, "high confidence" between 95% and 67%, "medium confidence" between 33% and 67%, and "low confidence" below 33%. In contrast, the biologists' confidence level comes from the statistical probability that global biotic trends would match climate change predictions purely by chance, coupled with supporting experimental results showing causal relationships between climate and particular biological traits.

Here, we present quantitative estimates of the global biological impacts of climate change. We search for a climate fingerprint in the overall patterns, rather than critiquing each study individually. Using the biologists' approach, we synthesize a suite of correlational studies on diverse taxa over many regions to ask whether natural systems, in general, have responded to recent climate change. Furthermore, we attempt a cross-fertilization by applying an economists' measure—the estimated proportion of observed changes for which climate trends are the principal drivers—to data sets chosen using biologists' criteria. We call this a 'global coherence' approach to the detection of climate change impacts.

First, we explore a biologists' confidence assessment with two types of analyses of observed change: statistical meta-analyses of effect size in restricted data sets and more comprehensive categorical analyses of the full literature. Second, we present a probabilistic model that considers three variables: proportion of observations matching climate change predictions, numbers of competing explanations for each of those observations, and confidence in causal

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attribution of each observation to climate change. These three variables feature equally in a model that explores an economists' 'confidence' assessment. Finally, we explore diagnostic 'sign-switching' patterns that are predicted uniquely by climate change.

The evidence

A few studies indicate evolutionary responses of particular species to climate change[12–14], but the generality of evolutionary response remains unknown. Here, we focus on phenological (timing) shifts, range boundary shifts, and community studies on species abundances (Table 1).

Meta-analyses

We developed databases suitable for meta-analysis[15] on two phenomena: range-boundary changes and phenological shifts. To control for positive publishing bias, we used only multi-species studies that reported neutral and negative results as well as positive (see Methods).

For range boundaries, suitable data spanned 99 species of birds[16], butterflies[17] and alpine herbs[18,19] (see Methods). The meta-analysis showed that the range limits of species have moved on average 6.1 ($\pm$2.4) km per decade northward or m per decade upward, significantly in the direction predicted by climate change (bootstrapped 95% confidence interval of the mean (CI_{mean}) = 1.3–10.9 km m^{-1} per decade; one-sample *t*-test, degrees of freedom (d.f.) = 98, $t = 2.52$, $P = 0.013$; Table 2).

For phenologies, suitable data were reported for herbs[20–23], shrubs[20–25], trees[20,23–25], birds[20,21], butterflies[26] and amphibians[27,28], a total of 172 species (see Methods). There was a mean shift towards earlier spring timing of 2.3 days per decade, with a bootstrapped 95% CI of 1.7–3.2 days advancement per decade (significant at $P < 0.05$).

Categorical analyses

The remaining studies were not included in the meta-analyses, either because they were on single species or because they did not present data in the raw form of *x* unit change per *y* time units per species. These less-detailed data were simplified into four categories: changed in accord with or opposite to climate change predictions, changed in some other fashion or stable (see Methods).

As with previous studies[17], analyses ignore species classified as 'stable'. This category does not represent a single result, as apparent stability could arise from a diversity of situations[17] such as: 1) the phenology, abundance or distribution of the species is not driven by climatic factors; 2) the species is actually changing, but poor data resolution could not detect small changes; and 3) the phenology, abundance or distribution of the species is driven by climatic factors, but fails to respond to current climate change. Such failure could stem from anthropogenic barriers to dispersal (habitat fragmentation) or from a lag in response time. Lags are expected when limited dispersal capabilities retard poleward/upward colonization[29], or when a necessary resource has slower response time than the focal species[17].

Phenological shifts. We quantitatively assessed 677 species reported in the literature (Table 1). Over a time period range of 16–132 years (median 45 yrs), 27% showed no trends in phenologies, 9% showed trends towards delayed spring events, whereas the remaining 62% showed trends towards spring advancement. Observed trends include earlier frog breeding[27,28], bird nesting[30–32], first flowering[20–25], tree budburst[23–25], and arrival of migrant birds and butterflies[20,21,26,33] (Table 1). Shifts in phenologies that have occurred are overwhelmingly (87%) in the direction expected from climate change ($P < 0.1 \times 10^{-12}$; Table 2).

Distribution/abundance shifts. In a quantitative assessment covering >1,046 species, we were able to categorize 893 species, functional

Table 1 **Summary of data studying phenological and distributional changes of wild species**

Taxon	Ref. number	Total no. of species (or species groups)	Spatial scale			Time scale (range years)	Change in direction predicted (*n*)	Change opposite to prediction (*n*)	Stable (*n*)	No prediction (*n*)
			L	R	C					
Phenological changes										
Woody plants	20,23,24*,25*	*n* = 38 sp		2	1	35–132	30	1	7	–
Herbaceous plants	20,21*	*n* = 38 sp	1	1		63–132	12	–	26	–
Mixed plants	22*	*n* = 385 sp	1			46	279	46	60	–
Birds	20,21*,30,31,32,33	*n* = 168 sp	2	3	1	21–132	78	14	76	–
Insects	26	*n* = 35 sp		1		23	13	–	22	–
Amphibians	27,28	*n* = 12 sp	2			16–99	9	–	3	–
Fish	20	*n* = 2 sp		1		132	2	–	–	–
Distribution/abundance changes										
Tree lines	54,55,56*	*n* = 4 sp + 5 grps	2	1		70–1,000	3 sp + 5 grps	–	1	–
Herbs and shrubs	18,19,41*,42*	*n* > 66 sp, 15 detailed		3		28–80	13	2	–	–
Lichens	36	4 biogeographic grps (*n* = 329 sp)	1			22	43	9	113	164
Birds	8*	*n* = 3 sp		1		50	3	–	–	–
	16,57*	N sp (*n* = 46 sp)		2		20–36	13	15	18	
		S sp (*n* = 73 sp)		2		20–36	36	16	21	6
	43*	Low elevation (>91 sp)	1			20	71	11	9	–
		High elevation (>96 sp)	1			20	37	27	32	–
Mammals	37	*n* = 2 sp		1		52	2	–	–	–
Insects	17,49*	*n* = 36 sp		1	1	98–137	23	2	10	1
	17	N boundaries (*n* = 52 sp)		1		98	34	1	17	–
		S boundaries (*n* = 40 sp)		1		98	10	2	28	–
Reptiles and amphibians	43*	*n* = 7 sp	1			17	6	–	1	–
Fish	39	*4* biogeographic grps (*n* = 83 sp)	1			–	2 grps	–	1 grp	1 grp
	40*	N sp (*n* > 1 sp)		1		70	>1	–	–	–
		S sp (*n* > 1 sp)		1		70	>1	–	–	–
Marine invertebrates	34*,40*	N sp (*n* > 21)	1	1		66–70	>19	2	–	>1 sp not classified
		S sp (*n* > 21)	1	1		66–70	>20	1	–	
		Cosmopolitan sp (*n* = 28 sp)	1			66	–	–	–	28
Marine zooplankton	40*	Cold water (*n* > 10 sp)		1		70	>10	–	–	>8 sp not classified
		Warm water (*n* > 14 sp)		1		70	>14	–	–	
	35	6 biogeographic grps (*n* ≥ 36 sp)			1	39	6 grps	–	–	–

N, species with generally northerly distributions (boreal/arctic); S, species with generally southerly distributions (temperate); L, local; R, regional (a substantial part of a species distribution; usually along a single range edge); C, continental (most or the whole of a species distribution). No prediction indicates that a change may have been detected, but the change was orthogonal to global warming predictions, was confounded by non-climatic factors, or there is insufficient theoretical basis for predicting how species or system would change with climate change.

*Study partially controlled for non-climatic human influences (for example, land-use change). Studies that were highly confounded with non-climatic factors were excluded. (See Supplementary Information for details of species classification.)

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groups or biogeographic groups (Table 1). Less than one-third (27%) of these have exhibited stable distributions during the twentieth century. Others (24%) show changes that are impossible to relate to climate change predictions. These two types of result neither support nor refute a climate change signal, although it will be important for predictive biological models to eventually determine what proportion of these are truly stable systems.

Some range shifts have been measured directly at range boundaries, whereas others have been inferred from abundance changes within local communities. Over all of the range and abundance shift data, 434 species were categorized as changing over time periods of 17–1,000 years (median 66 years) (Table 1). Of these, 80% have shifted in accord with climate change predictions (see Methods) ($P < 0.1 \times 10^{-12}$; Table 2). New species have colonized previously 'cool' regions, including sea anemones in Monterey Bay[34] and lichens and butterflies in Europe[17,36], whereas some Arctic species have contracted in range size[35,37]. Over the past 40 years, maximum range shifts vary from 200 km (butterflies[17]) to 1,000 km (marine copepods[34]).

Probabilistic coherence

How strong is the climate change signal in the light of confounding factors and lack of experimentation? We investigate this argument in a probabilistic context. We formulated a probabilistic model to ask whether a climate change fingerprint exists in a disparate set of n observed biological changes. Let n'/n indicate the proportion of observations counter to climate change predictions and p indicate the probability that climate change is the only possible causal agent of the observed biological change in any of the $n - n'$ species that do conform to climate change predictions. In practice, this can be estimated across a set of species by assigning each species a 0 or a 1, depending on whether or not competing explanations exist; p then is the proportion of species that have no competing explanations.

Competing (non-climatic) explanations can, therefore, be expected in $\{(1 - p)(n - n')\}$ of the reported analyses. Finally, for any of the $n - n'$ climate-conforming species, let π indicate the probability, determined from previous empirical study, that climate change is the principal causal agent of a particular biological change (independent of p).

These three variables, each varying from 0 to 1, are inputs to a binomial probability model whose output estimates the proportion of all species that are, in truth, being impacted by climate change. In practice, confounding factors can never be eliminated completely from observational studies; therefore, p would normally have a low value. Here, we consider only the conservative case where $p = 0$; that is, we assume that non-climatic alternative explanations exist for every species. In the Supplementary Information, we present modelling schemes where p varies from 0 to 1.0.

The importance of non-climatic explanations should decrease with increasing scale. Most local changes are idiosyncratic and consist of noise when scaled up; however, atmospheric carbon dioxide levels have risen nearly uniformly across the globe. Increased CO_2 can directly cause earlier flowering[38], as does increased temperature, making these effects difficult to separate. However, these two effects can be viewed as different aspects of global warming, legitimizing discussion of their joint impacts.

The variable π reflects the extent to which previous study and experimentation provides clear mechanistic understanding of the links between climate variables and a species' behaviour and ecology. To understand the importance of π, consider the case of the silver-spotted skipper butterfly (*Hesperia comma*) that has expanded its distribution close to its northern boundary in England over the past 20 years. Possible ecological explanations for this expansion are regional warming and changes in land use. Comparing the magnitudes and directions of these two factors suggests that climate change is more likely than land-use change to be the cause of expansion[29]. Deeper support was provided by previous empirical studies documenting strong thermal limitation. At the northern boundary, development of offspring was restricted to the hottest microclimates (south-facing chalk slopes). Range expansion coincided with colonization of non-southern slopes. Simulation models based solely on previously measured thermal tolerances (that is, without land-use change) closely matched the observed expansion of 16.4 km (model prediction 14.4 km)[12]. Thus, mechanistic understanding of the system generates a high estimate for π.

Figure 1 shows relationships between the n'/n proportions and the minimum value of π that would be required to sustain different degrees of confidence for $p = 0$. For example, the medium confidence region shows minimum values of π that would be required across the displayed range of n'/n proportions to guarantee that about half of the observed species impacts were in truth being driven principally by climate change. Claiming a climate fingerprint with high confidence would require high minimum values for π (>0.67) regardless of n'/n.

Applying the probabilistic model

Using all of the data from Table 2 to parameterize the model, $n' = 147$ and $n = 770$, making $n'/n = 0.16$ (16% of species changing opposite to climate change predictions). We now consider π. The extent to which climate change can be isolated as the predominant driving force is extremely variable among species and systems. Such attribution results from a subjective synthesis of experimental and observational research, often conducted well before and independently of any study of long-term trends. The species for which π is high are those with a history of basic biological research, especially where research has been conducted along several axes (controlled laboratory/greenhouse experiments, field manipulations and observations).

Table 2 **Summary statistics and synthetic analyses derived from Table 1**

Type of change	Changed as predicted	Changed opposite to prediction	*P*-value
Phenological ($N = 484/(678)$)	87% ($n = 423$)	13% ($n = 61$)	$<0.1 \times 10^{-12}$
Distributional changes			
At poleward/upper range boundaries	81%	19%	–
At equatorial/lower range boundaries	75%	25%	–
Community (abundance) changes			
Cold-adapted species	74%	26%	–
Warm-adapted species	91%	9%	–
$N = 460/(920)$	81% ($n = 372$)	19% ($n = 88$)	$<0.1 \times 10^{-12}$
Meta-analyses			
Range-boundaries ($N = 99$)	6.1 km m^{-1} per decade northward/upward shift*		0.013
Phenologies ($N = 172$)	2.3 days per decade advancement*		<0.05

Data points represent species, functional groups or biogeographic groups. *N*, number of statistically or biologically significant changes/(total number species with data reported for boundary, timing, or abundance processes). The no prediction category is not included here.
*Bootstrap 95% confidence limits for mean range boundary change are 1.26, 10.87; for mean phenological shift the limits are −1.74, −3.23.

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This sort of biological detail reveals that climate and extreme weather events are mechanistically linked to body size, individual fitness and population dynamics for diverse species[3–9] (but not for all). Species for which confidence in climate as the primary driving mechanism is low are those for which long-term observational records exist, but not detailed empirical research on target species or on ecologically similar species. The black line in Fig. 1 suggests that medium confidence can be claimed for $n'/n = 0.16$ if $0.35 < \pi < 0.7$. Other contingencies, such as complications from a positive publishing bias or non-independence among confounding factors, can be considered through variations of the model (see Supplementary Information).

Differentiating diagnostic patterns

Predictions of the impacts of climate change are not unidirectional, but may show opposite trends within communities and across long time spans or large spatial scales. Alternative causal agents would therefore have to be able to switch the sign of their impacts within a study if they were to form credible competing explanations. Such differentiating patterns greatly reduce the likelihood of hidden, non-climate competing explanations, thereby increasing P and decreasing the value of π necessary to achieve a given confidence level (see Supplementary Information). High confidence could be obtained under this scheme with existing patterns ($n'/n \leq 0.33$) and poor mechanistic understanding (low π). Sufficient data to quantify the differential impacts on species' distributions or phenologies across time periods or geographic regions were available for 334 species, among which 84% showed a sign-switching diagnostic of climate change response ($P < 0.1 \times 10^{-12}$; Table 3).

Community representation sign switching

Community studies in regions of overlapping 'polar' and 'temperate' species base their climate change attribution on differential responses of these two categories. Among marine fish and intertidal invertebrates (for example, snails, barnacles, anemones, copepods and limpets) off the Californian coast[34,39] and in the North Atlantic[35,40], lichens in the Netherlands[36], foxes in Canada[37] and birds in Great Britain[16], polar species have tended to be stable or decline in abundance, whereas temperate species at the same site have increased in abundance and/or expanded their distributions. Analogous shifts are occurring even within the Arctic and Antarctic among penguins[8], woody plants[41] and vascular plants[42]. Similar patterns exist for lowland compared with highland birds in the tropics[43]. Most of these studies are local, with high variability of individual species' population dynamics. Even so, 80% of changes in community representation are in accord with climate change predictions (Tables 2 and 3).

Temporal sign switching

Long-term studies encompass periods of climate cooling as well as warming. If the distributions of species are truly driven by climate trends, these species should show opposite responses to cooling and warming periods. Such sign switching has been documented in the United Kingdom for marine fish, limpets, barnacles and zooplankton[40], in the United Kingdom and Estonia for birds[20,31,44,45], and in the United Kingdom, Finland and Sweden for butterflies[17,46–48] (see also Table 3 legend). A typical pattern includes northward range shifts during the two twentieth-century warming periods (1930–45 and 1975–99), and southward shifts during the intervening cooling period (1950–70). No species showed opposing temporal trends (Table 3).

Spatial sign switching

Whole-range, continental-scale studies, by encompassing the extremes of a species' distribution, allow testing for differential spatial impacts. In North America and Europe, detailed temporal data spanning the twentieth century were compiled for 36 butterfly species at both northern and southern range extremes[17,49]. Eight species (22%) exhibited a diagnostic pattern of northward expansion (new colonizations) and southern contraction (population extinctions). No species showed opposing range shift trends (northward contraction and southward expansion) (Table 3).

Discussion

The logic of a global focus on biological change is analogous to that for climate change itself. With climate change, attribution of recent warming trends to changes in atmospheric gases comes from analysis of global patterns, not from detailed data from individual meteorological stations. Similarly, when assessing biological

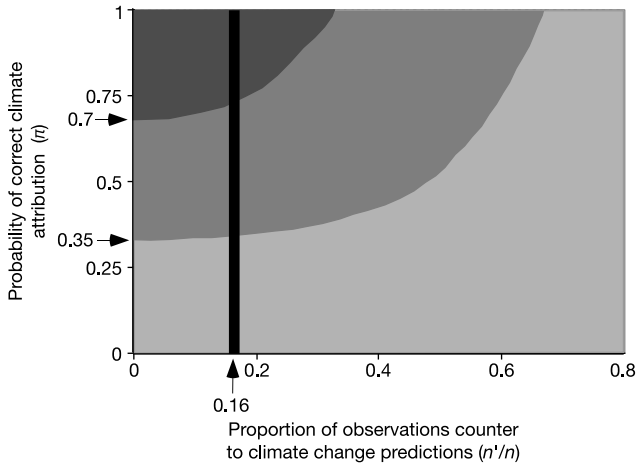

Figure 1 Probabilistic model based on parameter estimates from a review of the literature. Levels of confidence in the linkage of biological changes to global climate change are: high (dark grey), medium (mid-grey) and low (light grey). Confidence regions assume $p = 0$ (competing explanations exist for all studies). The black line indicates the region of confidence possible using the probabilistic model on the basis of the parameter estimate of n'/n from the literature review, and allowing π to vary freely.

Table 3 **Biological fingerprint of climate change impacts**

Sign-switching pattern	Percentage of species showing diagnostic pattern
Community	
Abundance changes have gone in opposite directions for cold-adapted compared with warm-adapted species. Usually local, but many species in each category. Diverse taxa, $n = 282$*.	80%
Temporal	
Advancement of timing of northward expansion in warm decades (1930s/40s and 1980s/90s); delay of timing or southward contraction in cool decades (1950s/60s), 30–132 years per species. Diverse taxa, $n = 44$*.	100%
Spatial	
Species exhibit different responses at extremes of range boundary during a particular climate phase. Data are from substantial parts of both northern and southern range boundaries for each species. All species are northern hemisphere butterflies, $n = 8$*.	100%

Differential sign-switching patterns diagnostic of climate change as the underlying driver.
*Numbers of species represent minimum estimates, as not all species were described in sufficient detail in each study to classify. A few species showed two types of sign switching, and so are included in more than one cell. Data are from references in text and from raw data provided by L. Kaila, J. Kullberg, J. J. Lennon, N. Ryrholm, C. D. Thomas, J. A. Thomas and M. Warren.

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impacts, the global pattern of change is far more important than any individual study.

The approach of biologists selects study systems to minimize confounding factors and deduces a strong climate signal both from systematic trends across studies and from empirically derived links between climate and biological systems. This deduction is made even if climate explains only a small part of the observed biological change. The meta-analyses of 334 species and the global analyses of 1,570 species (or functional/biogeographic groups) show highly significant, nonrandom patterns of change in accord with observed climate warming in the twentieth century, indicating a very high confidence (>95%) in a global climate change fingerprint (Table 2).

The approach of economists takes a broader view. In its purest form, applied to all existing data and incorporating time discounting, this approach would conclude that climate change has little total impact on wild species. We argue that this approach misses biologically important phenomena. Here we hybridize the two approaches by applying an economists' model to data that biologists would consider reasonable, and forego time discounting. A total of 74–91% of species that have changed have done so in accord with climate change predictions (Table 2) giving an estimate of $n'/n = 0.16$ for the hybrid model. Assessment of π, the probability of correct attribution to climate, is subjective and relies on the level of confidence in inferential evidence. Such evidence comes from empirical analyses and experimental manipulations, which have documented the importance of climatic variables to the dynamics, distributions and behaviour of species[3,5,8,9]. From these studies, biologists infer that expected values of π are often high. We show that moderate values of π (0.35–0.70) are consistent with medium confidence in a global climate change fingerprint.

The different approaches raise two distinct questions of the data and result in different levels of confidence in a climate change fingerprint. The questions are: (1) whether climate change can be shown to be an over-riding factor currently driving natural systems; and (2) whether there is sufficient evidence to implicate climate change as a common force impacting natural systems on a global scale. In an absolute sense, land-use change has probably been a stronger driver of twentieth century changes in wild plants and animals than has climate change (question 1). From a biological view, however, finding any significant climate signal amidst noisy biological data is unexpected in the absence of real climate drivers (question 2). Such small, persistent forces are inherently important in that they can alter species interactions, de-stabilize communities and drive major biome shifts.

A review of the literature reveals that the patterns that are being documented in natural systems are surprisingly simple, despite the real and potential complexity of biotic change. Change in any individual species, taxon or geographic region may have a number of possible explanations, but the overall effects of most confounding factors decline with increasing numbers of species/systems studied. Similarly, uncertainty in climate attribution for any particular study does not prevent the development of a global conclusion on the basis of a cumulative synthesis. In particular, a clear pattern emerges of temporal and spatial sign switches in biotic trends uniquely predicted as responses to climate change. With 279 species (84%) showing predicted sign switches, this diagnostic indicator increases confidence in a climate change fingerprint from either viewpoint.

The published IPCC conclusion stated high confidence ($P > 0.67$) in a climate signal across observed biotic and abiotic changes. Analyses presented here support that conclusion. Furthermore, a driver of small magnitude but consistent impact is important in that it systematically affects century-scale biological trajectories and ultimately the persistence of species. The climate fingerprint found here implicates climate change as an important driving force on natural systems. □

Methods

Climate change predictions

Expected phenological shifts for regions experiencing warming trends are for earlier spring events (for example, migrant arrival times, peak flight date, budburst, nesting, egg-laying, and flowering) and for later autumn events (for example, leaf fall, migrant departure times, and hibernation)[50,51]. Response to climate warming predicts a preponderance of polward/upward shifts[50,51]. Dynamics at the range boundaries are expected to be more influenced by climate than are dynamics within the interior of a species range. Thus, community level studies of abundance changes are used best to infer range shifts when they are located at ecotones involving species having fundamentally different geographic ranges: higher compared with lower latitudes, or upper compared with lower altitudes. Response to climate warming predicts that southerly species should outperform northerly species at the same site[50,51].

Selection of studies for review

This was not an exhaustive review. The studies listed in Table 1 comprise the bulk of wild species studied with respect to climate change hypotheses. Selection of papers was aimed at those with one or more of the following attributes: long temporal span (>20 years), data covering a large geographic region, and/or data gathered in an unbiased manner for a multi-species assemblage (typically species abundance data of locally well-documented communities). We excluded several high-quality studies of single species performed at local scale or highly confounded by non-climatic global change factors. The stable category represents species for which any observed changes are indistinguishable from year to year fluctuations, either from a statistical test for trend using very long time series data or from comparing net long-term movement to expected yearly variation on the basis of basic biological knowledge of dispersal/colonization abilities.

Meta-analyses

To create databases, studies were combined that made similar types of measurements and that reported quantitative estimates of change over a specified time period. All species were used; that is, even species that are categorized as stable in Table 1 were included in the meta-analysis. We treated phenological and distributional changes separately. To minimize positive publishing bias, only multi-species studies were included.

We considered each species as an independent data point, rather than each study. Only data reported in terms of change per individual species were included. This precluded use of studies that only report mean change across a set of species.

We used only distributional studies at range boundaries. We excluded equatorial and lower elevational boundaries because of a paucity of data combined with theoretical reasons for treating these boundaries separately from poleward/upper elevational boundaries[52]. Three studies met the criteria for data detail, covering 9 alpine herbs[18,19], 59 birds[16] and 31 butterflies[17]. The geographic locations of these boundaries were non-overlapping, reducing the likelihood of correlated confounding variables. Altitude was converted to latitudinal equivalent (for temperature clines, 1 km northward = 1 m upward). The United Kingdom bird data compared mean northern boundary in 1999 to that in 1972 using the ten northernmost occupied grid cells (on 10 km^2 grids) from published atlases. The Swedish butterfly data compared mean northern boundary in the period 1971–97 to mean northern boundary in 1900–20 using the five northernmost records per year. The Swiss herb data showed changes in species assemblages over the twentieth century in fixed plots up altitudinal gradients on 26 mountains.

The effect size per species was the absolute magnitude of range boundary shift, standardized across species to be in units of km m^{-1} per decade, with northward/upslope shifts positive and southward/downslope shifts negative. Data were not skewed, and n was large. Therefore, a one-sample t-test was used to evaluate the null hypothesis of no overall trends (that is, $H_ø$: mean boundary change across all species is zero). Variances were not available for all species, so we used an unweighted analysis. We performed an additional bootstrap analysis of 95% confidence limits on the mean boundary shift (10,000 iterations)[53].

The phenological meta-analysis was on spring timing events—there were insufficient studies on autumn phenology to warrant analysis. Nine studies published magnitudes of shift over a given time period (17–61 years). They included 11 trees[20,23–25], 6 shrubs[20,21,23–25], 85 herbs[20–23], 35 butterflies[26], 21 birds[21], 12 amphibians[27,28] and 2 fish[20]. This data set was inappropriate for the t-test owing to skew, but bootstrapped confidence limits provided an estimate of the probability that the true mean shift includes zero.

For both analyses, geography and taxa are confounded. For the range boundary analysis, all bird data are from the United Kingdom, all butterfly data from Sweden, and all herb data from Switzerland. For the phenological analysis, most shrub and bird data are from the United States, butterfly data from Great Britain, and trees from Europe. Therefore, it is not meaningful to split the analyses further.

Categorical analyses

Reported data from all studies listed in Tables 1 and 3 were included in the categorical analyses. The predicted direction is a change predicted by global warming scenarios[50,51]. All studies were conducted in temperate Northern Hemisphere, except for 194 species in Costa Rica[43] and 5 species in Antarctica[8,42]. Two categories showing changes either predicted by or opposite to predictions of climate change theory were tested against the random expectation of an equal probability of observing changes in either direction. Analyses were by binomial test with $H_ø$: $P = 0.5$.

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Ecological and Evolutionary Responses to Recent Climate Change

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Key Words

aquatic, global warming, phenology, range shift, terrestrial, trophic asynchrony

Abstract

Ecological changes in the phenology and distribution of plants and animals are occurring in all well-studied marine, freshwater, and terrestrial groups. These observed changes are heavily biased in the directions predicted from global warming and have been linked to local or regional climate change through correlations between climate and biological variation, field and laboratory experiments, and physiological research. Range-restricted species, particularly polar and mountaintop species, show severe range contractions and have been the first groups in which entire species have gone extinct due to recent climate change. Tropical coral reefs and amphibians have been most negatively affected. Predator-prey and plant-insect interactions have been disrupted when interacting species have responded differently to warming. Evolutionary adaptations to warmer conditions have occurred in the interiors of species' ranges, and resource use and dispersal have evolved rapidly at expanding range margins. Observed genetic shifts modulate local effects of climate change, but there is little evidence that they will mitigate negative effects at the species level.

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INTRODUCTION

Historical Perspective

Climate change is not a new topic in biology. The study of biological impacts of climate change has a rich history in the scientific literature, since long before there were political ramifications. Grinnell (1917) first elucidated the role of climatic thresholds in constraining the geographic boundaries of many species, followed by major works by Andrewartha & Birch (1954) and MacArthur (1972). Observations of range shifts in parallel with climate change have been particularly rich in northern European countries, where observational records for many birds, butterflies, herbs, and trees date back to the mid-1700s. Since the early part of the twentieth century, researchers have documented the sensitivity of insects to spring and summer temperatures (Bale et al. 2002, Dennis 1993, Uvarov 1931). Ford (1945) described northward range shifts of several butterflies in England, attributing these shifts to a summer warming trend that began around 1915 in Britain. Ford noted that one of these species, *Limenitis camilla*, expanded to occupy an area where attempted introductions prior to the warming had failed. Kaisila (1962) independently documented range shifts of Lepidoptera (primarily moths) in Finland, using historical data on range boundaries dating back to 1760. He showed repeated instances of southward contractions during decades of "harsh" climatic conditions (cold wet summers), followed by northward range expansion during decades with climate "amelioration" (warm summers and lack of extreme cold in winter). Further corroboration came from the strong correlations between summer temperatures and the northern range boundaries for many butterflies (Dennis 1993).

Similar databases exist for northern European birds. A burst of papers documented changed abundances and northerly range shifts of birds in Iceland, Finland, and Britain associated with the 1930s–1940s warming period (Gudmundsson 1951; Harris 1964; Kalela 1949, 1952; Salomonsen 1948). A second wave of papers in the 1970s described the subsequent retreats of many of these temperate bird and butterfly species following the cool, wet period of the 1950s–1960s (Burton 1975, Heath 1974, Sevenrty 1977, Williamson 1975).

Complementing this rich observational database is more than 100 years of basic research on the processes by which climate and extreme weather events affect plants and animals. As early as the 1890s, Bumpus (1899) noted the differential effects of an extreme winter storm on the introduced house sparrow (*Parus domesticus)*, resulting in stabilizing selection for intermediate body size in females and directional selection for large body size in males (Johnston et al. 1972). The first extensive studies of climate variability as a powerful driver of population evolution date back to the 1940s, when Dobzhansky (1943, 1947) discovered repeated cycles of seasonal evolution of temperature-associated chromosomal inversions within *Drosophila pseudoobscura* populations in response to temperature changes from spring through summer.

In summary, the history of biological research is rich in both mechanistic and observational studies of the impacts of extreme weather and climate change on wild species: Research encompasses impacts of single extreme weather events; experimental studies of physiological tolerances; snapshot correlations between

climatic variables and species' distributions; and correlations through time between climatic trends and changes in distributions, phenologies, genetics, and behaviors of wild plants and animals.

Anthropogenic Climate Change

In spite of this wealth of literature on the fundamental importance of climate to wild biota, biologists have been reluctant to believe that modern (greenhouse gas-driven) climate change is a cause of concern for biodiversity. In his introduction to the 1992 *Annual Review of Ecology, Evolution, and Systematics* volume on "Global Environmental Change," Vitousek wrote, "ultimately, climate change probably has the greatest potential to alter the functioning of the Earth system . . . . nevertheless, the major effects of climate change are mostly in the future while most of the others are already with us." Individual authors in that volume tended to agree—papers were predominantly concerned with other global change factors: land use change, nitrogen fertilization, and the direct effects of increased atmospheric CO_2 on plant ecophysiology.

Just 14 years later, the direct impacts of anthropogenic climate change have been documented on every continent, in every ocean, and in most major taxonomic groups (reviewed in Badeck et al. 2004; Hoegh-Guldberg 1999, 2005b; Hughes 2000; IPCC 2001a; Parmesan 2005b; Parmesan & Galbraith 2004; Parmesan & Yohe 2003; Peñuelas & Filella 2001; Pounds et al. 2005; Root & Hughes 2005; Root et al. 2003; Sparks & Menzel 2002; Thomas 2005; Walther et al. 2002, 2005). The issue of whether observed biological changes can be conclusively linked to anthropogenic climate change has been analyzed and discussed at length in a plethora of syntheses, including those listed above. Similarly, complexity surrounding methodological issues of detection (correctly detecting a real trend) and attribution (assigning causation) has been explored in depth (Ahmad et al. 2001; Dose & Menzel 2004; Parmesan 2002, 2005a,b; Parmesan & Yohe 2003; Parmesan et al. 2000; Root et al. 2003, Root & Hughes 2005, Schwartz 1998, 1999; Shoo et al. 2006). The consensus is that, with proper attention to sampling and other statistical issues and through the use of scientific inference, studies of observed biological changes can provide rigorous tests of climate-change hypotheses. In particular, independent syntheses of studies worldwide have provided a clear, globally coherent conclusion: Twentieth-century anthropogenic global warming has already affected Earth's biota.

Detection: ability to discern long-term trends above yearly variability and real changes from apparent changes brought about by changes in sampling methodology and/or sampling intensity

Attribution: teasing out climate change as the causal driver of an observed biological change amid a backdrop of potential confounding factors

Globally coherent: a common term in economics, a process or event is globally coherent when it has similar effect across multiple systems spread across different locations throughout the world

Scope of This Review

This review concentrates on studies of particularly long time series and/or particularly good mechanistic understanding of causes of observed changes. It deals exclusively with observed responses of wild biological species and systems to recent, anthropogenic climate change. In particular, agricultural impacts, human health, and ecosystem-level responses (e.g., carbon cycling) are not discussed. Because they have been extensively dealt with in previous publications, this review does not repeat discussions of detection and attribution, nor of the conservation implications of climate

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change. Rather, some of the best-understood cases are presented to illustrate the complex ways in which various facets of climatic change impact wild biota. The choice of studies for illustration attempts to draw attention to the taxonomic and geographic breadth of climate-change impacts and to the most-recent literature not already represented in prior reviews.

Researchers have frequently associated biological processes with indices of ocean-atmosphere dynamics, such as the El Niño Southern Oscillation and the North Atlantic Oscillation (Blenckner & Hillebrand 2002, Holmgren et al. 2001, Ottersen et al. 2001). However, the nature of the relationship between atmospheric dynamics, ocean circulation, and temperature is changing (Alley et al. 2003, IPCC 2001b, Karl & Trenberth 2003, Meehl et al. 2000). Therefore, there is large uncertainty as to how past relationships between biological systems and ocean indices reflect responses to ongoing anthropogenic climate change. Although I use individual examples where appropriate, this complex topic is not fully reviewed here.

OVERVIEW OF IMPACTS LITERATURE

An extensive, but not exhaustive, literature search revealed 866 peer-reviewed papers that documented changes through time in species or systems that could, in whole or in part, be attributed to climate change. Some interesting broad patterns are revealed. Notably, the publication rate of climate-change responses increases sharply each year. The number of publications between 1899 and January 2003 (the date of two major syntheses) was 528. Therefore, approximately 40% of the 866 papers compiled for this review were published in the past three years (January 2003 to January 2006).

The studies are spread broadly across taxonomic groups. Whereas distributional studies concentrated on animals rather than plants, the reverse is true of phenological time series. This may simply be because historical data on species range boundaries have higher resolution for animals than for plants. Conversely, local records of spring events are much more numerous for plants (e.g., flowering and leaf out) than for animals (e.g., nesting).

Although there is still a terrestrial bias, studies in marine and freshwater environments are increasing in proportional representation. The largest gaps are geographic rather than taxonomic. In absolute numbers, most biological impact studies are from North America, northern Europe and Russia. Few biological studies have come from South America, and there are large holes in Africa and Asia, with most of the studies from these two continents coming from just two countries: South Africa and Japan. In past decades, Australia's impact studies have stemmed predominantly from the coral reef community, but in recent years scientists have dug deep to find historical data, and terrestrial impact studies are now emerging. Similarly, the Mediterranean/North African region (Spain, France, Italy, and Israel) has recently spawned a spate of studies. Antarctica stands out as a region where impacts (or lack of impacts) on most species and systems have been documented, even though data often have large geographic or temporal gaps.

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Few studies have been conducted at a scale that encompasses an entire species' range (i.e., a continental scale), with only a moderate number at the regional scale (e.g., the United Kingdom or Germany). Most have been conducted at local scales, typically at a research station or preserve. Continental-scale studies usually cover most or all of a species' range in terrestrial systems (Both et al. 2004, Burton 1998a,b, Dunn & Winkler 1999, Menzel & Fabian 1999, Parmesan 1996, Parmesan et al. 1999). However, even a continental scale cannot encompass the entire ranges of many oceanic species (Ainley & Divoky 1998, Ainley et al. 2003, Beaugrand et al. 2002, Croxall et al. 2002, Hoegh-Gulberg 1999, McGowan et al. 1998, Reid et al. 1998, Spear & Ainley 1999). Terrestrial endemics, in contrast, can have such small ranges that regional, or even local, studies may represent impacts on entire species (Pounds et al. 1999, 2006).

Meta-analysis: set of statistical techniques designed to synthesize quantitative results from similar and independent experiments

Meta-Analyses and Syntheses: Globally Coherent Signals of Climate-Change Impacts

A handful of studies have conducted statistical meta-analyses of species' responses or have synthesized independent studies to reveal emergent patterns. The clear conclusion across global syntheses is that twentieth-century anthropogenic global warming has already affected the Earth's biota (IPCC 2001a; Parmesan 2005a,b; Parmesan & Galbraith 2004; Parmesan & Yohe 2003; Peñuelas & Filella 2001; Pounds et al. 2005; Root & Hughes 2005; Root et al. 2003; Thomas 2005; Walther et al. 2002, 2005).

One study estimated that more than half (59%) of 1598 species exhibited measurable changes in their phenologies and/or distributions over the past 20 to 140 years (Parmesan & Yohe 2003). Analyses restricted to species that exhibited change documented that these changes were not random: They were systematically and predominantly in the direction expected from regional changes in the climate (Parmesan & Yohe 2003, Root et al. 2003). Responding species are spread across diverse ecosystems (from temperate grasslands to marine intertidal zones and tropical cloud forests) and come from a wide variety of taxonomic and functional groups, including birds, butterflies, alpine flowers, and coral reefs.

A meta-analysis of range boundary changes in the Northern Hemisphere estimated that northern and upper elevational boundaries had moved, on average, 6.1 km per decade northward or 6.1 m per decade upward ($P < 0.02$) (Parmesan & Yohe 2003). Quantitative analyses of phenological responses gave estimates of advancement of 2.3 days per decade across all species (Parmesan & Yohe 2003) and 5.1 days per decade for the subset of species showing substantive change (>1 day per decade) (Root et al. 2003).

A surprising result is the high proportion of species responding to recent, relatively mild climate change (global average warming of 0.6°C). The proportion of wild species impacted by climate change was estimated at 41% of all species (655 of 1598) (Parmesan & Yohe 2003). This estimate was derived by focusing on multispecies studies that reported stable as well as responding species. Because responders and

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stable species were often sympatric, variation of response is not merely a consequence of differential magnitudes of climate change experienced.

PHENOLOGICAL CHANGES

By far, most observations of climate-change responses have involved alterations of species' phenologies. This is partly a result of the tight links between the seasons and agriculture: Planting and harvest dates (and associated climatic events such as day of last frost) have been well recorded, dating back hundreds of years for some crops. But the plethora of records also stems from the strong sociological significance of the change of the seasons, particularly in high-latitude countries. Peoples of Great Britain, the Netherlands, Sweden, and Finland have been keen on (some might say even obsessed with) recording the first signs of spring—the first leaf on an oak, the first peacock butterfly seen flying, the first crocus in bloom—as a mark that the long, dark winter is finally over. Fall has not captured as much enthusiasm as spring, but some good records exist, for example, for the turning of leaf color for trees.

The longest records of direct phenological observations are for flowering of cherry trees *Prunus jamasakura* and for grape harvests. Menzel & Dose (2005) show that timing of cherry blossom in Japan was highly variable among years, but no clear trends were discerned from 1400 to 1900. A statistically significant change point is first seen in the early 1900s, with steady advancement since 1952. Recent advancement exceeds observed variation of the previous 600 years. Menzel (2005) analyzed grape-harvest dates across Europe, for which April-August temperatures explain 84% of the variation. She found that the 2003 European heat wave stands out as an extreme early harvest (i.e., the warmest summer) going back 500 years. Although such lengthy observational records are extremely rare, these two unrelated plants on opposite sides of the world add an important historical perspective to results from shorter time series.

Several lines of evidence indicate a lengthening of vegetative growing season in the Northern Hemisphere, particularly at higher latitudes where temperature rise has been greatest. Summer photosynthetic activity (normalized difference vegetation index estimates from satellite data) increased from 1981–1991 (Myneni et al. 1997), concurrent with an advance and increase in amplitude of the annual CO_2 cycle (Keeling et al. 1996). White et al. (1999) modeled meteorological and satellite data to estimate actual growing season length each year from 1900–1987 in the United States. Growing season was unusually long during the warm period of the 1940s at all 12 sites. However, patterns have recently diverged. Since 1966, growing season length has increased only in four of the coldest, most-northerly zones (42°–45° latitude), not in the three warmest zones (32°–37° latitude). Across the European Phenological Gardens (experimental clones of 16 species of shrubs and trees at sites across Europe), a lengthening of the growing season by 10.8 days occurred from 1959–1993 (Menzel 2000, Menzel & Fabian 1999). Analysis of climatological variables (e.g., last frost date of spring and first frost date of fall) mirrors this finding, with an estimated lengthening of the growing season of 1.1–4.9 days per decade since 1951 (Menzel et al. 2003).

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Bradley et al. (1999) built on Aldo Leopold's observations from the 1930s and 1940s on the timing of spring events on a Wisconsin farm. Of 55 species resurveyed in the 1980s and 1990s, 18 (35%) showed advancement of spring events, whereas the rest showed no change in timing (with the exception of cowbirds arriving later). On average, spring events occurred 7.3 days earlier by the 1990s compared with 61 years before, coinciding with March temperatures being 2.8°C warmer.

Another long-term (100-year) study by Gibbs & Breisch (2001) compared recent records (1990–1999) of the calling phenology of six frog species in Ithaca, New York, with a turn-of-the-century study (1900–1912). They showed a 10–13-day advance associated with a 1.0–2.3°C rise in temperature during critical months. Amphibian breeding has also advanced in England, by 1–3 weeks per decade (Beebee 1995). Ecophysiological studies in frogs have shown that reproduction is closely linked to both nighttime and daytime temperatures (Beebee 1995).

In the United Kingdom, Crick et al. (1997), analyzing more than 74,000 nest records from 65 bird species between 1971 and 1995, found that the mean laying dates of first clutches for 20 species had advanced by an average 8.8 days. Brown et al. (1999) found a similar result for the Mexican jay (*Aphelocoma ultramarina*) in the mountains of southern Arizona. In the North Sea, migrant birds have advanced their passage dates by 0.5–2.8 days per decade since 1960, with no significant difference between short- and long-distance migrants (Hüppop & Hüppop 2003). In contrast, Gordo et al. (2005) found that three of six long-distance migrant birds had significantly delayed arrival to breeding grounds in Spain, with arrival date highly correlated with climatic conditions in their overwintering grounds in the southern Sahara.

Butterflies frequently show a high correlation between dates of first appearance and spring temperatures, so it is not surprising that their first appearance has advanced for 26 of 35 species in the United Kingdom (Roy & Sparks 2000) and for all 17 species analyzed in Spain (Stefanescu et al. 2003). Seventy percent of 23 species of butterfly in central California have advanced their first flight date over 31 years, by an average of 24 days (Forister & Shapiro 2003). Climate variables explained 85% of variation in flight date in the California study, with warmer, drier winters driving early flight.

There are only two continental-scale studies of bird phenology. Dunn & Winkler (1999) analyzed changes in breeding for tree swallows (*Tachycineta bicolor*) from 1959 to 1991 over the entire breeding range in the contiguous United States and Canada. Laying date was significantly correlated with mean May temperature and had advanced by an average of nine days over the 32-year period. In a complementary study, Both et al. (2004) analyzed the pied flycatcher (*Ficedula hypoleuca*) at 23 sites across Europe and found a significant advance in laying date for nine of the populations, which also tended to be those with the strongest warming trends. Continental-scale studies of both lilac (*Syringa vulgaris*) and honeysuckle (*Lonicera tatarica* and *L. korolkowii*) in the western United States have shown an advance in mean flowering dates of 2 and 3.8 days per decade, respectively (Cayan et al. 2001).

Aquatic systems exhibit similar trends to those of terrestrial systems. In a lake in the northwestern United States, phytoplankton bloom has advanced by 19 days from

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1962 to 2002, whereas zooplankton peak is more varied, with some species showing advance and others remaining stable (Winder & Schindler 2004). The Arctic seabird Brunnich's guillemot, *Uria lomvia*, has advanced its egg-laying date at its southern boundary (Hudson Bay) with no change at its northern boundary (Prince Leopold Island); both trends are closely correlated with changes in sea-ice cover (Gaston et al. 2005).

Roetzer et al. (2000) explicitly quantified the additional impacts of urban warming by comparing phenological trends between urban and rural sites from 1951 to 1995. Urban sites showed significantly stronger shifts toward earlier spring timing than nearby rural sites, by 2–4 days. An analysis of greening across the United States via satellite imagery also concluded that urban areas have experienced an earlier onset of spring compared with rural areas (White et al. 2002).

Researchers generally report phenological changes as a separate category from changes in species' distributions, but these two phenomena interplay with each other and with other factors, such as photoperiod, to ultimately determine how climate change affects each species (Bale et al. 2002, Chuine & Beaubien 2001).

INTERACTIONS ACROSS TROPHIC LEVELS: MATCHES AND MISMATCHES

Species differ in their physiological tolerances, life-history strategies, probabilities of population extinctions and colonizations, and dispersal abilities. These individualistic traits likely underlie the high variability in strength of climate response across wild species, even among those subjected to similar climatic trends (Parmesan & Yohe 2003). For many species, the primary impact of climate change may be mediated through effects on synchrony with that species' food and habitat resources. More crucial than any absolute change in timing of a single species is the potential disruption of coordination in timing between the life cycles of predators and their prey, herbivorous insects and their host plants, parasitoids and their host insects, and insect pollinators with flowering plants (Harrington et al. 1999, Visser & Both 2005). In Britain, the butterfly *Anthocharis cardamines* has accurately tracked phenological shifts of its host plant, even when bud formation came two to three weeks early (Sparks & Yates 1997). However, this may be the exception rather than the rule.

Visser & Both (2005) reviewed the literature and found only 11 species' interactions in which sufficient information existed to address the question of altered synchrony. Nine of these were predator-prey interactions, and two were insect–host plant interactions. In spite of small sample size, an important trend emerged from this review: In the majority of cases (7 of 11), interacting species responded differently enough to climate warming that they are more out of synchrony now than at the start of the studies. In many cases, evidence for negative fitness consequences of the increasing asynchrony has been either observed directly or predicted from associated studies (Visser & Both 2005).

In one example, Inouye et al. (2000) reported results of monitoring between 1975 and 1999 at Rocky Mountain Biological Laboratory in Colorado, where there has been a 1.4°C rise in local temperature. The annual date of snowmelt and plant flowering did

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not change during the study period, but yellow-bellied marmots (*Marmota flaviventris*) advanced their emergence from hibernation by 23 days, changing the relative phenology of marmots and their food plants. In a similar vein, Winder & Schindler (2004) documented a growing asynchrony between peak phytoplankton bloom and peak zooplankton abundances in a freshwater lake.

More complex phenomena resulting from trophic mismatches have also been documented. For example, phenological asynchrony has been linked to a range shift in the butterfly *Euphydryas editha*. Warm and/or dry years alter insect emergence time relative to both the senescence times of annual hosts and the time of blooming of nectar sources (Singer 1972, Singer & Ehrlich 1979, Singer & Thomas 1996, Thomas et al. 1996, Weiss et al. 1988). Field studies have documented that butterfly-host asynchrony has resulted directly in population crashes and extinctions. Long-term censuses revealed that population extinctions occurred during extreme droughts and low snowpack years (Ehrlich et al. 1980, Singer & Ehrlich 1979, Singer & Thomas 1996, Thomas et al. 1996), and these extinctions have been highly skewed with respect to both latitude and elevation, shifting mean location of extant populations northward and upward (Parmesan 1996, 2003, 2005a).

Van Nouhuys & Lei (2004) showed that host-parasitoid synchrony was influenced signficantly by early spring temperatures. Warmer springs favored the parasitoid wasp *Cotesia melitaearum* by bringing it more in synchrony with its host, the butterfly *Melitaea cinxia*. Furthermore, they argue that because most butterfly populations are protandrous (i.e., males pupating earlier than females), temperature-driven shifts in synchrony with parasitoids may affect butterfly sex ratios.

Intergovernmental Panel on Climate Change: a scientific panel formed under the auspices of the United Nations and the World Meteorological Organization for the purpose of synthesizing literature and forming scientific consensus on climate change and its impacts

OBSERVED RANGE SHIFTS AND TRENDS IN LOCAL ABUNDANCE

Expected distributional shifts in warming regions are poleward and upward range shifts. Studies on these shifts fall mainly into two types: (*a*) those that infer large-scale range shifts from small-scale observations across sections of a range boundary (with the total study area often determined by a political boundary such as state, province, or country lines) and (*b*) those that infer range shifts from changes in species' composition (abundances) in a local community. Studies encompassing the entire range of a species, or at least the northern and southern (or lower and upper) extremes, are few and have been concentrated on amphibians (Pounds et al. 1999, 2006), a mammal (Beever et al. 2003), and butterflies (Parmesan 1996, Parmesan et al. 1999). The paucity of whole-range studies likely stems from the difficulties of gathering data on the scale of a species' range—often covering much of a continent.

Shifts at Polar Latitudes

Broad impacts of climate change in polar regions—from range shifts to community restructuring and ecosystem functioning—have been reviewed by the Intergovernmental Panel on Climate Change (Anisimov et al. 2001), the Arctic Climate Impact Assessment (2004) and the Millenium Ecosystem Assessment (Chapin et al. 2006).

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SST: sea surface temperature

Antarctic. Plant, bird, and marine life of Antarctica have exhibited pronounced responses to anthropogenic climate change. These responses have been largely attributed to extensive changes (mostly declines) in sea-ice extent, which in turn appears to have stimulated a trophic cascade effect in biological systems. Declines in sea-ice extent and duration since 1976 have apparently reduced abundances of ice algae, in turn leading to declines in krill (from 38%–75% per decade) in a large region where they have been historically concentrated, the southwest Atlantic (Atkinson et al. 2004). Krill (*Euphausia superba*) is a primary food resource for many fish, seabirds, and marine mammals. Interestingly, McMurdo Dry Valleys, which actually cooled between 1990 and 2000, also showed declines in lake phytoplankton abundances and in soil invertebrate abundances (Doran et al. 2002).

Penguins and other seabirds in Antarctica have shown dramatic responses to changes in sea-ice extent over the past century (Ainley et al. 2003, Croxall et al. 2002, Smith et al. 1999). The sea-ice dependent Adélie and emperor penguins (*Pygoscelis adeliae* and *Aptenodytes forsteri*, respectively) have nearly disappeared from their northernmost sites around Antarctica since 1970. Emperors have declined from 300 breeding pairs down to just 9 in the western Antarctic Peninsula (Gross 2005), with less severe declines at Terre Adélie (66° S), where they are now at 50% of pre-1970s abundances (Barbraud & Weimerskirch 2001). Adélies have declined by 70% on Anvers Island (64°–65° S along the Antarctic peninsula (Emslie et al. 1998, Fraser et al. 1992), whereas they are thriving at the more-southerly Ross Island at 77° S (Wilson et al. 2001)—effectively shifting this species poleward. In the long-term, sea-ice-dependent birds will suffer a general reduction of habitat as ice shelves contract [e.g., as has already occured in the Ross Sea (IPCC 2001b)] or collapse [e.g., as did the Larsen Ice Shelves along the Antarctic Peninsula in 2002 (Alley et al. 2005)].

In contrast, open-ocean feeding penguins—the chinstrap and gentoo—invaded southward along the Antarctic Peninsula between 20 and 50 years ago, with paleological evidence that gentoo had been absent from the Palmer region for 800 years previously (Emslie et al. 1998, Fraser et al. 1992). Plants have also benefited from warming conditions. Two Antarctic vascular plants (a grass, *Deschampsia antarctica*, and a cushion plant, *Colobanthus quitensis*) have increased in abundance and begun to colonize novel areas over a 27-year period (Smith 1994).

Arctic. Nearly every Arctic ecosystem shows marked shifts. Diatom and invertebrate assemblages in Arctic lakes have shown huge species' turnover, shifting away from benthic species toward more planktonic and warm-water-associated communities (Smol et al. 2005). Across northern Alaska, Canada, and parts of Russia, shrubs have been expanding into the tundra (Sturm et al. 2005). Field studies, experimentation, and modeling link this major community shift to warming air temperatures, increased snow cover, and increased soil microbial activity (Chapin et al. 1995; Sturm et al. 2001, 2005). Populations of a pole-pole migrant, the sooty shearwater (*Puffinus griseus*), have shifted their migration routes by hundreds of kilometers in concert with altered sea surface temperature (SST) in the Pacific (Spear & Ainley 1999).

Sea-ice decline in the Arctic has been more evenly distributed than in the Antarctic. Because of differing geology, with an ocean at the pole rather than land, Arctic species

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that are sea-ice dependent are effectively losing habitat at all range boundaries. Polar bears have suffered significant population declines at opposite geographic boundaries. At their southern range boundary (Hudson Bay), polar bears are declining both in numbers and in mean body weight (Stirling et al. 1999). Climate change has caused a lengthening of ice-free periods on Hudson Bay, periods during which the bears starve and live on their reserves because an ice shelf is necessary for feeding. Furthermore, researchers have also linked warming trends to reductions of the bears' main food, the ringed seal (Derocher et al. 2004, Ferguson et al. 2005). At the bears' northern range boundaries off Norway and Alaska, sea ice has also been reduced, but poorer records make it is less clear whether observed declines in body size and the number of cubs per female are linked to climate trends or to more basic density-dependent processes (Derocher 2005, Stirling 2002).

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Shifts in Northern-Hemisphere Temperate Species

On a regional scale, a study of the 59 breeding bird species in Great Britain showed both expansions and contractions of northern range boundaries, but the average boundary change for 12 species that had not experienced overall changes in density was a mean northward shift of 18.9 km over a 20-year period (Thomas & Lennon 1999). For a few well-documented bird species, their northern U.K. boundaries have tracked winter temperatures for over 130 years (Williamson 1975). Physiological studies indicate that the northern boundaries of North American songbirds may generally be limited by winter nighttime temperatures (Burger 1998, Root 1988).

Analogous studies exist for Lepidoptera (butterflies and moths), which have undergone an expansion of northern boundaries situated in Finland (Marttila et al. 1990, Mikkola 1997), Great Britain (Hill et al. 2002, Pollard 1979, Pollard & Eversham 1995, Warren 1992), and across Europe (Parmesan et al. 1999). Depending on the study, some 30% to 75% of northern boundary sections had expanded north; a smaller portion (<20%) had contracted southward; and the remainder were classified as stable. In a study of 57 nonmigratory European butterflies, data were obtained from both northern and southern range boundaries for 35 species (Parmesan et al. 1999). Nearly two thirds (63%) had shifted their ranges to the north by 35–240 km, and only two species had shifted to the south (Parmesan et al. 1999). In the most-extreme cases, the southern edge contracted concurrent with northern edge expansion. For example, the sooty copper (*Heodes tityrus*) was common in the Montseny region of central Catalonia in the 1920s, but modern sightings are only from the Pyrenees, 50 km to the north. Symmetrically, *H. tityrus* entered Estonia for the first time in 1998, by 1999 had established several successful breeding populations, and by 2006 had reached the Baltic Sea (Parmesan et al. 1999; T. Tammaru, personal communication).

Another charismatic insect group with good historical records is Odonata (dragonflies and damselflies). In a study of all 37 species of resident odonates in the United Kingdom, Hickling et al. (2005) documented that 23 of the 24 temperate species had expanded their northern range limit between 1960–1995, with mean northward shift of 88 km.

Nondiapausing (i.e., active year-round) butterfly species are also moving northward with warmer winters. The northern boundary of the sachem skipper butterfly has expanded from California to Washington State (420 miles) in just 35 years (Crozier 2003, 2004). During a single year—the warmest on record (1998)—it moved 75 miles northward. Laboratory and field manipulations showed that individuals are killed by a single, short exposure to extreme low temperatures (–10°C) or repeated exposures to –4°C, indicating winter cold extremes dictate the northern range limit (Crozier 2003, 2004). The desert orange tip (*Colotis evagore*), which historically was confined to northern Africa, has established resident populations in Spain while maintaining the same ecological niche. Detailed ecological and physiological studies confirm that *C. evagore* has remained a specialist of hot microclimates, needing more than 164 days at greater than 12°C to mature. It has not undergone a host switch in its new habitat, and it has not evolved a diapause stage (Jordano et al. 1991).

In the Netherlands between 1979 and 2001, 77 new epiphytic lichens colonized from the south, nearly doubling the total number of species for that community (van Herk et al. 2002). Combined numbers of terrestrial and epiphytic lichen species increased from an average of 7.5 per site to 18.9 per site. An alternate approach to documenting colonizations is to document extinction patterns. Comparing recent censuses across North America (1993–1996) with historical records (1860–1986), Parmesan (1996) documented that high proportions of population extinctions along the southern range boundary of Edith's checkerspot butterfly (*E. editha*) had shifted the mean location of living populations 92 km farther north (Parmesan 1996, 2003, 2005a).

Shifts of Tropical Species Ranges

Warming trends at lower latitudes are associated with movements of tropical species into more-temperate areas. The rufous hummingbird has undergone a dramatic shift in its winter range (Hill et al. 1998). Thirty years ago it wintered mainly in Mexico, and between 1900 and 1990, there were never more than 30 winter sightings per year along the Gulf Coast of the United States. In the early 1990s, sightings increased to more than 100 per year in the southern United States. The number of sightings has increased steadily since then—up to 1,643 by 1996, with evidence that, by 1998, resident populations had colonized 400 km inland (Howell 2002). Over this same period, winter temperatures rose by approximately 1°C (IPCC 2001b). In Florida, five new species of tropical dragonfly established themselves in 2000, an apparently natural invasion from Cuba and the Bahamas (Paulson 2001).

Similarly, North African species are moving into Spain and France, and Mediterranean species are moving up into the continental interior. The African plain tiger butterfly (*Danaus chrysippus*) established its first population in southern Spain in 1980 and by the 1990s had established multiple, large metapopulations (Haeger 1999).

Elevational Shifts

Montane studies have generally been scarcer and less well documented (lower sampling resolution), but a few good data sets show a general movement of species upward

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in elevation. By comparing species compositions in fixed plots along an elevational gradient in Monteverde National Park, Costa Rica, Pounds et al. (1999, 2005) documented that lowland birds have begun breeding in montane cloud-forest habitat over the past 20 years. A similar study across 26 mountains in Switzerland documented that alpine flora have expanded toward the summits since the plots were first censused in the 1940s (Grabherr et al. 1994, Pauli et al. 1996). Upward movement of treelines has been observed in Siberia (Moiseev & Shiyatov 2003) and in the Canadian Rocky Mountains, where temperatures have risen by 1.5°C (Luckman & Kavanagh 2000).

The few studies of lower elevational limits show concurrent contractions upward of these warm range boundaries. Because warm boundaries generally have data gaps through time, these studies have conducted recensuses of historically recorded (sedentary) populations and looked for nonrandom patterns of long-term population extinctions.

A 1993–1996 recensus of Edith's checkerspot butterfly (*E. editha*) populations recorded 1860–1986 throughout its range (Mexico to Canada) documented that more than 40% of populations from 0–2400 m were extinct (in spite of having suitable habitat), whereas less than 15% were extinct at the highest elevations (2400–3500 m) (Parmesan 1996). Over the past 50–100 years, snowpack below 2400 m has become lighter by 14% and melts 7 days earlier, whereas higher elevations (2400–3500 m) have 8% heavier snowpack and no change in melt date (Johnson et al. 1999). In concert with altered snow dynamics, the mean location of *E. editha* populations has shifted upward by 105 m (Parmesan 1996, 2003, 2005a).

In southern France, metapopulations of the cool-adapted Apollo butterfly (*Parnassius apollo*) have gone extinct over the past 40 years on plateaus less than 850 m high but have remained healthy where plateaus were greater than 900 m high (Descimon et al. 2006). The data suggest that dispersal limitation was important, and this strong flyer can persist when nearby higher elevation habitats exist to colonize. In Spain, the lower elevational limits of 16 species of butterfly have risen an average of 212 m in 30 years, concurrent with a 1.3°C rise in mean annual temperatures (Wilson et al. 2005).

In the Great Basin of the western United States, 7 out of 25 recensused populations of the pika (*Ochotona princeps*, Lagomorpha) were extinct since being recorded in the 1930s (Beever et al. 2003). Human disturbance is minimal because pika habitat is high-elevation talus (scree) slopes, which are not suitable for ranching or recreational activities. Extinct populations were at significantly lower elevations than those still present (Parmesan & Galbraith 2004). Field observations by Smith (1974) documented that adult pika stopped foraging in the midday heat in August at low elevation sites. Subsequent experiments showed that adults were killed within a half hour at more than 31°C (Smith 1974).

Marine Community Shifts

Decades of ecological and physiological research document that climatic variables are primary drivers of distributions and dynamics of marine plankton and fish (Hays et al. 2005, Roessig et al. 2004). Globally distributed planktonic records show strong shifts of phytoplankton and zooplankton communities in concert with regional oceanic

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climate regime shifts, as well as expected poleward range shifts and changes in timing of peak biomass (Beaugrand et al. 2002, deYoung et al. 2004, Hays et al. 2005, Richardson & Schoeman 2004). Some copepod communities have shifted as much as 1000 km northward (Beaugrand et al. 2002). Shifts in marine fish and invertebrate communities have been been particularly well documented off the coasts of western North America and the United Kingdom. These two systems make an interesting contrast (see below) because the west coast of North America has experienced a 60-year period of significant warming in nearshore sea temperatures, whereas much of the U.K. coast experienced substantial cooling in the 1950s and 1960s, with warming only beginning in the 1970s (Holbrook et al. 1997, Sagarin et al. 1999, Southward et al. 2005).

Sagarin et al. (1999) related a 2°C rise of SST in Monterey Bay, California, between 1931 and 1996 to a significant increase in southern-ranged species and decrease of northern-ranged species. Holbrook et al. (1997) found similar shifts over the past 25 years in fish communities in kelp habitat off California.

Much of the data from the North Atlantic, North Sea, and coastal United Kingdom have exceptionally high resolution and long time series, so they provide detailed information on annual variability, as well as long-term trends. Over 90 years, the timing of animal migration (e.g., veined squid, *Loligo forbesi*, and flounder *Platichthys flesus*) followed decadal trends in ocean temperature, being later in cool decades and up to 1–2 months earlier in warm years (Southward et al. 2005).

In the English Channel, cold-adapted fish (e.g., herring *Clupea harengus*) declined during both warming periods (1924 to the 1940s, and post-1979), whereas warm-adapted fish did the opposite (Southward et al. 1995, 2005). For example, pilchard *Sardina pilchardus* increased egg abundances by two to three orders of magnitude during recent warming. In the North Sea, warm-adapted species (e.g., anchovy *Engraulis encrasicolus* and pilchard) have increased in abundances since 1925 (Beare et al. 2004), and seven out of eight have shifted their ranges northward (e.g., bib, *Trisopterus luscus*) by as much as 100 km per decade (Perry et al. 2005). Records dating back to 1934 for intertidal invertebrates show equivalent shifts between warm- and cold-adapted species (e.g., the barnacles *Semibalanus balanoides* and *Chthamalus* spp., respectively), mirroring decadal shifts in coastal temperatures (Southward et al. 1995, 2005).

Pest and Disease Shifts

Pest species are also moving poleward and upward. Over the past 32 years, the pine processionary moth (*Thaumetopoea pityocampa*) has expanded 87 km at its northern range boundary in France and 110–230 m at its upper altitudinal boundary in Italy (Battisti et al. 2005). Laboratory and field experiments have linked the feeding behavior and survival of this moth to minimum nighttime temperatures, and its expansion has been associated with warmer winters. In the Rocky Mountain range of the United States, mountain pine beetle (*Dendroctonus ponderosae*) has responded to warmer temperatures by altering its life cycle. It now only takes one year per generation rather than its previous two years, allowing large increases in population abundances, which, in turn, have increased incidences of a fungus they transmit (pine blister rust,

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Cronartium ribicola) (Logan et al. 2003). Increased abundance of a nemotode parasite has also occurred as its life cycle shortened in response to warming trends. This has had associated negative impacts on its wild musk oxen host, causing decreased survival and fecundity (Kutz et al. 2005).

In a single year (1991), the oyster parasite *Perkinsus marinus* extended its range northward from Chesapeake Bay to Maine—a 500 km shift. Censuses from 1949 to 1990 showed a stable distribution of the parasite from the Gulf of Mexico to its northern boundary at Chesapeake Bay. The rapid expansion in 1991 has been linked to above-average winter temperatures rather than human-driven introduction or genetic change (Ford 1996). A kidney disease has been implicated in low-elevation trout declines in Switzerland. High mortality from infection occurs above 15°–16°C, and water temperatures have risen in recent decades. High infection rates (27% of fish at 73% of sites) at sites below 400 m have been associated with a 67% decline in catch; mid-elevation sites had lower disease incidence and only moderate declines in catch; and the highest sites (800–3029 m) had no disease present and relatively stable catch rates (Hari et al. 2006).

Changes in the wild also affect human disease incidence and transmission through alterations in disease ecology and in distributions of their wild vectors (Parmesan & Martens 2006). For example, in Sweden, researchers have documented marked increases in abundances of the disease-transmitting tick *Ixodes ricinus* along its northernmost range limit (Lindgren & Gustafson 2001). Between the early 1980s and 1994, numbers of ticks found on domestic cats and dogs increased by 22%–44% along the tick's northern range boundary across central Sweden. In the same time period, this region had a marked decrease in the number of extremely cold days (<-12°C) in winter and a marked increase in warm days (>10°C) during the spring, summer, and fall. Previous studies on temperature developmental and activity thresholds indicated the observed warmer temperatures cause decreased tick mortality and longer growing seasons (Lindgren & Gustafson 2001).

Trees and Treelines: Complex Responses

A complex of interacting factors determines treeline, often causing difficulties in interpretation of twentieth-century trends. Some species are "well behaved" in that they show similar patterns of increased growth at treeline during the early warming in the 1930s and 1940s as during the recent warming of the past 20 years. In recent decades, treelines have shifted northward in Sweden (Kullman 2001) and eastern Canada (Lescop-Sinclair & Payette 1995), and upward in Russia (Meshinev et al. 2000, Moiseev & Shiyatov 2003) and New Zealand (Wardle & Coleman 1992).

However, in other studies, researchers saw a strong response to warming in the late 1930s and 1940s but a weaker (or absent) response in recent warm decades (Innes 1991, Jacoby & D'Arrigo 1995, Lescop-Sinclair & Payette 1995, Briffa et al. 1998a,b), possibly resulting from differences in rainfall between the two warm periods. In Alaska, recent decades have been relatively dry, which may have prevented trees from responding to current warming as they did before (Barber et al. 2000, Briffa et al. 1998b). In contrast, treelines in the arid southwest United States, which has

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had increased rainfall, have shown unprecedented increased tree-ring growth at high elevations (Swetnam & Betancourt 1998).

An impressive study across all of northern Russia from 1953–2002 showed a shift in tree allometries. In areas where summer temperatures and precipitation have both increased, a general increase in biomass (up 9%) is primarily a result of increased greenery (33% more carbon in leaves and needles), rather than woody parts (roots and stem). In areas that have experienced warming and drying trends, greenery has decreased, and both roots and stems have increased (Lapenis et al. 2005).

EXTINCTIONS

Amphibians

Documented rapid loss of habitable climate space makes it no surprise that the first extinctions of entire species attributed to global warming are mountain-restricted species. Many cloud-forest-dependent amphibians have declined or gone extinct on a mountain in Costa Rica (Pounds et al. 1999, 2005). Among harlequin frogs in Central and South American tropics, an astounding 67% have disappeared over the past 20–30 years. Pounds et al. (2006) hypothesised that recent trends toward warmer nights and increased daytime cloud cover have shifted mid-elevation sites (1000–2400 m), where the preponderance of extinctions have occurred, into thermally optimum conditions for the chytrid fungus, *Batrachochytrium dendrobatidis*.

Tropical Coral Reefs

Elevated sea temperatures as small as 1°C above long-term summer averages lead to bleaching (loss of coral algal symbiont), and global SST has risen an average of 0.1°–0.2°C since 1976 (Hoegh-Guldberg 1999, IPCC 2001b). A more acute problem for coral reefs is the increase in extreme temperature events. El Niño events have been increasing in frequency and severity since records began in the early 1900s, and researchers expect this trend to continue over coming decades (Easterling et al. 2000, IPCC 2001b, Meehl et al. 2000). A particularly strong El Niño in 1997–1998 caused bleaching in every ocean (up to 95% of corals bleached in the Indian Ocean), ultimately resulting in 16% of corals rendered extinct globally (Hoegh-Guldberg 1999, 2005b; Wilkinson 2000).

Recent evidence for genetic variation among the obligate algal symbiont in temperature thresholds suggests that some evolutionary response to higher water temperatures may be possible (Baker 2001, Rowan 2004). Changes in genotype frequencies toward increased frequency of high-temperature-tolerant symbiont appear to have occurred within some coral populations between the mass bleaching events of 1997–1998 and 2000–2001 (Baker et al. 2004). However, other studies indicate that many entire reefs are already at their thermal tolerance limits (Hoegh-Guldberg 1999). Coupled with poor dispersal of symbiont between reefs, this has led several researchers to conclude that local evolutionary responses are unlikely to mitigate the negative impacts of future temperature rises (Donner et al. 2005, Hoegh-Guldberg et al. 2002).

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One optimistic result suggests that corals, to some extent, may be able to mirror terrestrial range shifts. Two particularly cold-sensitive species (staghorn coral, *Acropora ceervicornis*, and elkhorn coral, *Acropora palmata*) have recently expanded their ranges into the northern Gulf of Mexico (first observation in 1998), concurrent with rising SST (Precht & Aronson 2004). Although continued poleward shift will be limited by light availability at some point (Hoegh-Guldberg 1999), small range shifts may aid in developing new refugia against extreme SST events in future.

Although impacts have not yet been observed, the fate of coral reefs may be as, or more, affected in coming decades by the direct effects of CO_2 rather than temperature rise. Increased atmospheric CO_2 since industrialization has significantly lowered ocean pH by 0.1. The more dire projections (a doubling to tripling of current CO_2 levels) suggest that, by 2050, oceans may be too acidic for corals to calcify (Caldeira & Wickett 2003, Hoegh-Guldberg 2005a, Orr et al. 2005).

Population Extinctions Leading to Range Contractions

Many species have suffered reduced habitable area due to recent climate change. For those species that have already been driven extinct at their equatorial or lower range boundaries, some have either failed to expand poleward or are unable to expand due to geographic barriers. Such species have suffered absolute reductions in range size, putting them at greater risk of extinction in the near future.

This is particularly evident in polar species, as these are already pushed against a geographical limit. Researchers have seen large reductions in population abundances and general health along the extreme southern populations of Arctic polar bears (Derocher 2005, Derocher et al. 2004, Stirling et al. 1999) and the extreme northern populations of Antarctic Adélie and emperor penguins (Ainley et al. 2003, Croxall et al. 2002, Emslie et al. 1998, Fraser et al. 1992, Smith et al. 1999, Taylor & Wilson 1990, Wilson et al. 2001). In the United Kingdom, four boreal odonates have contracted northward by an average of 44 km over 40 years (Hickling et al. 2005).

Similarly, high numbers of population extinctions have occurred along the lower elevational boundaries of mountaintop species, such as pikas in the western United States (Beever et al. 2003) and the Apollo butterfly in France (Descimon et al. 2006). For 16 mountain-restricted butterflies in Spain, warming has already reduced their habitat by one third in just 30 years (Wilson et al. 2005). Warming and drying trends on Mt. Kiliminjaro have increased fire impacts, which have caused a 400-m downward contraction of closed (cloud) forest, now replaced by an open, dry alpine system (Hemp 2005). Temperate low-elevation species are not immune: Twenty-five percent of temperate butterflies in Europe contracted northward by 35–50 km over a 30–70-year period. For one of these, its northern range boundary had not expanded, so it suffered an overall contraction of range size (Parmesan et al. 1999).

EVOLUTION AND PLASTICITY

Species ranges are dynamic. Historically, ecologists have viewed species' niches as static and range shifts over time as passive responses to major environmental changes (global climate shifts or geological changes in corridors and barriers).

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There is no doubt that climate plays a major role in limiting terrestrial species' ranges (Andrewartha & Birch 1954; Bale et al. 2002; Parmesan et al. 2000, 2005; Precht et al. 1973; Webb & Bartlein 1992; Weiser 1973; Woodward 1987). Recent physiological and biogeographic studies in marine systems also implicate temperature as a primary driver of species' ranges (Hoegh-Guldberg 1999, 2005b; Hoegh-Guldberg & Pearse 1995).

However, evolutionary processes clearly can substantially influence the patterns and rates of response to climate change. Theoretically, evolution can also drive range shifts in the absence of environmental change (Holt 2003). A prime example of this is the hybridization of two species of Australian fruit fly that led to novel adaptations, allowing range expansion with no concomitant environmental change (Lewontin & Birch 1966).

The problem of estimating the relative roles of evolution and plasticity is tractable with extensive, long-term ecological and genetic data. For example, genetic analysis of a population of red squirrels in the Arctic indicated that 62% of the change in breeding dates occurring over a 10-year period was a result of phenotypic plasticity, and 13% was a result of genetic change in the population (Berteaux et al. 2004, Réale et al. 2003).

Geneticists in the 1940s noticed that certain chromosomal inversions in fruit flies (*Drosophila*) were associated with heat tolerance (Dobzhansky 1943, 1947). These "hot" genotypes were more frequent in southern than in northern populations and increased within a population during each season, as temperatures rose from early spring through late summer. Increases in the frequencies of warm-adapted genotypes have occurred in wild populations of *Drosophila ssp* in Spain between 1976 and 1991 (Rodríguez-Trelles & Rodriguez 1998, Rodríguez-Trelles et al. 1996, 1998), as well as in the United States between 1946 and 2002 (Levitan 2003). The change in the United States was so great that populations in New York in 2002 were converging on genotype frequencies found in Missouri in 1946.

In contrast, red deer in Norway show completely plastic responses. Their body size responds rapidly to yearly variability of winter temperatures. Warmer winters cause developing males to become larger while females become smaller (Post et al. 1999). In consequence, the end result of a gradual winter warming trend has been an increase in sexual dimorphism.

A surprising twist is that species whose phenology is under photoperiodic control have also responded to temperature-driven selection for spring advancement or fall delay. Bradshaw & Holzapfel (2001) showed that the pitcher plant mosquito, *Wyeomyia smithii*, has evolved a shorter critical photoperiod in association with a longer growing season. Northern populations of this mosquito now use a shorter day-length cue to enter winter diapause, doing so later in the fall than they did 24 years ago.

The Role of Evolution in Shaping Species' Impacts

Increasing numbers of researchers use analyses of current intraspecific genetic variation for climate tolerance to argue for a substantive role of evolution in mitigating

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negative impacts of future climate change (Baker 2001, Baker et al. 2004, Davis & Shaw 2001, Rowan 2004). However, in spite of a plethora of data indicating local adaptation to climate change at specific sites, the fossil record shows little evidence for the evolution of novel phenotypes across a species as a whole. Pleistocene glaciations represent shifts 5–10 times the magnitude of twentieth-century global warming. These did not result in major evolution at the species level (i.e., appearance of new forms outside the bounds of known variation for that species), nor in major extinction or speciation events. Existing species appeared to shift their geographical distributions as though tracking the changing climate, rather than remaining stationary and evolving new forms (Coope 1994, Davis & Zabinski 1992, Huntley 1991).

Most of the empirical evidence for rapid adaptation to climate change comes from examples of evolution in the interiors of species' ranges toward higher frequencies of already existing heat-tolerant genotypes. In studies that focus on dynamics at the edge of a species' range or across an entire range, a different picture emerges. Several studies suggest that the effects of both genetic constraints and asymmetrical gene flow are intensified close to species' borders (Antonovics 1976, Garcia-Ramos & Kirkpatrick 1997, Hoffmann & Blows 1994). It is expected that a warming climate strengthens climate stress at equatorial range boundaries and reduces it at poleward boundaries. Equatorial boundary populations are often under natural selection for increased tolerance to extreme climate in the absence of climate change, but may be unable to respond due to lack of necessary genetic variance. Furthermore, gene flow from interior populations may stifle response to selection at the range limits, even when sufficient genetic variation exists (Kirkpatrick & Barton 1997).

Because of strong trade-offs between climate tolerance and resource/habitat preferences, a relaxation of selection on climate tolerance at northern boundaries may cause rapid evolution of these correlated traits. This process has been investigated in the European butterfly *Aricia agestis*, in which populations near the northern range boundary had previously adapted to cool conditions by specializing on the host genus, *Helianthemum*, which grows in hot microclimates and hence supports fast larval growth. Climate warming did not initially cause range expansion because *Helianthemum* was absent to the immediate north of the range limit. However, warming did permit rapid evolution of a broader diet at the range limit, to a host used in more southern populations, *Geranium*, which grows in cooler microclimates. Once this local diet evolution occurred, the boundary expanded northward across the band from which *Helianthemum* was absent but *Geranium* was present (Thomas et al. 2001).

This example shows how a complex interplay may occur between evolutionary processes and ecological responses to extreme climates and climate change. However, these evolutionary events did not constitute alternatives to ecological responses to climate change; they modulated those changes. Adaptive evolution of host preference occurred at the northern range boundary in response to temperature rise, but genetic variation for host use already existed within the *A. agestis* butterfly. In this case, evolutionary processes are not an alternative to range movement, but instead modulate the magnitude and dynamics of the range shift. This is not likely to be an isolated example because populations of other species near poleward boundaries

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are known to specialize on resources that mitigate the effects of cool climate. Such resources either support rapid growth or occur in the hottest available microclimates (Nylin 1988, Scriber & Lederhouse 1992, Thomas et al. 2001).

In addition to resource choice, dispersal tendency evolves at range margins in response to climate change. In nonmigratory species, the simplest explanation of northward range expansions is that individuals have always crossed the species' boundary, and with climate warming, some of these emigrants are successful at founding new populations outside the former range. When dispersal tendency is heritable, these new populations contain dispersive individuals and higher rates of dispersal will soon evolve at the expanding boundary.

Evolution toward greater dispersal has indeed been documented in several species of insect. Two species of wing-dimorphic bush crickets in the United Kingdom have evolved longer wings at their northern range boundary, as mostly long-winged forms participated in the range expansion and short-winged forms were left behind (Thomas et al. 2001). Adults of newly colonized populations of the speckled wood butterfly (*Pararge aegeria*) in the United Kingdom have larger thoraces and greater flight capability than historical populations just to the south (Hill et al. 1999). Variation in dispersal abilities can be cryptic. Newly founded populations of the butterfly *M. cinxia* contained females that were genetically superior dispersers due to increased production of ATP (Hanski et al. 2004).

Overall, empirical evidence suggests that evolution can complement, rather than supplant, projected ecological changes. However, there is little theoretical or experimental support to suggest that climate warming will cause absolute climatic tolerances of a species to evolve sufficiently to allow it to conserve its geographic distribution in the face of climate change and thereby inhabit previously unsuitable climatic regimes (Donner et al. 2005; Hoegh-Guldberg 1999, 2005b; Hoegh-Guldberg et al. 2002; Jump & Peñuelas 2005).

CONCLUDING THOUGHTS ON EVOLUTION AND CLIMATE CHANGE

For species-level evolution to occur, either appropriate novel mutations or novel genetic architecture (new gene complexes) would have to emerge to allow a response to selection. Lynch & Lande (1993) used a genetic model to infer rates of environmental change that would allow populations to respond adaptively. However, Travis & Futuyma (1993)—discussing the same question from broad paleontological, population, genetic, and ecological perspectives—highlighted the complexity of predicting future responses from currently known processes. Fifteen years later, answers still lie very much in empirical observations. These observations indicate that, although local evolutionary responses to climate change have occurred with high frequency, there is no evidence for change in the absolute climate tolerances of a species. This view is supported by the disproportionate number of population extinctions documented along southern and low-elevation range edges in response to recent climate warming, resulting in contraction of species' ranges at these warm boundaries, as well as by extinctions of many species.

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SUMMARY POINTS

1. The advance of spring events (bud burst, flowering, breaking hibernation, migrating, breeding) has been documented on all but one continent and in all major oceans for all well-studied marine, freshwater, and terrestrial groups.
2. Variation in phenological response between interacting species has already resulted in increasing asynchrony in predator-prey and insect-plant systems, with mostly negative consequences.
3. Poleward range shifts have been documented for individual species, as have expansions of warm-adapted communities, on all continents and in most of the major oceans for all well-studied plant and animal groups.
4. These observed changes have been mechanistically linked to local or regional climate change through long-term correlations between climate and biological variation, experimental manipulations in the field and laboratory, and basic physiological research.
5. Shifts in abundances and ranges of parasites and their vectors are beginning to influence human disease dynamics.
6. Range-restricted species, particularly polar and mountaintop species, show more-severe range contractions than other groups and have been the first groups in which whole species have gone extinct due to recent climate change. Tropical coral reefs and amphibians are the taxonomic groups most negatively impacted.
7. Although evolutionary responses have been documented (mainly in insects), there is little evidence that observed genetic shifts are of the type or magnitude to prevent predicted species extinctions.

FUTURE ISSUES

1. Ocean-atmosphere processes are dynamically changing in response to anthropogenic forcings. Indices such as the El Niño Southern Oscillation and the North Atlantic Oscillation may be a poor basis for projecting future biological impacts.
2. Projections of impacts will be aided by a better mechanistic understanding of ecological, behavioral, and evolutionary responses to complex patterns of climate change, and in particular to impacts of extreme weather and climate events.

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South Coast Missing Linkages Project:

A Linkage Design for the Santa Monica-Sierra Madre Connection



Prepared by:

Kristeen Penrod
Clint R. Cabañero
Dr. Paul Beier
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June 2006

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Results and information in this report are advisory and intended to assist local jurisdictions, agencies, organizations, and property owners in making decisions regarding protection of ecological resources and habitat connectivity in the area.

Produced by South Coast Wildlands: Our mission is to protect, connect and restore the rich natural heritage of the South Coast Ecoregion through the establishment of a system of connected wildlands.

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Executive Summary

Habitat loss and fragmentation are the leading threats to biodiversity, both globally and in southern California. Efforts to combat these threats must focus on conserving well-connected networks of large wildland areas where natural ecological and evolutionary processes can continue operating over large spatial and temporal scales—such as top-down regulation by large predators, and natural patterns of gene flow, pollination, dispersal, energy flow, nutrient cycling, inter-specific competition, and mutualism. Adequate landscape connections will thereby allow these ecosystems to respond appropriately to natural and unnatural environmental perturbations, such as fire, flood, climate change, and invasions by alien species.

The tension between fragmentation and conservation is particularly acute in California, because our state is one of the 25 most important hotspots of biological diversity on Earth. And nowhere is the threat to connectivity more severe than in southern California—our nation's largest urban area, and still one of its fastest growing urbanizing areas. But despite a half-century of rapid habitat conversion, southern California retains some large and valuable wildlands, and opportunities remain to conserve and restore a functional wildland network here.

Although embedded in one of the world's largest metropolitan areas, southern California's archipelago of conserved wildlands is fundamentally one interconnected ecological system, and the goal of South Coast Missing Linkages is to keep it so. South Coast Missing Linkages is a collaborative effort among a dozen governmental and non-governmental organizations. Our aim is to develop Linkage Designs for 15 major landscape linkages to ensure a functioning wildland network for the South Coast Ecoregion, along with connections to neighboring ecoregions. The Santa Monica-Sierra Madre Connection is one of the few remaining coastal connections in the South Coast Ecoregion; it is a critical landscape connection to restore and protect.

On July 29, 2002, 60 participants representing over 30 agencies, academic institutions, land managers, land planners, conservation organizations, and community groups met to establish biological foundations for planning landscape linkages in the Santa Monica-Sierra Madre Connection. They identified 20 focal species that are sensitive to habitat loss and fragmentation here, including three plants, four insects, one fish, one amphibian, two reptiles, four birds and five mammals. These focal species cover a broad range of habitat and movement requirements: some are widespread but require huge tracts of land to support viable populations (e.g., mountain lion, badger); others are species with very limited spatial requirements (e.g., harvester ant). Many are habitat specialists (e.g., cactus wren) and others require specific configurations of habitat elements (e.g. steelhead trout that uses rivers for migrating and streams for rearing and spawning). Together, these species cover a wide array of habitats and movement needs in the region, so that planning adequate linkages for them is expected to cover connectivity needs for the ecosystems they represent.

To identify potential routes between existing protected areas we conducted landscape permeability analyses for three focal species for which appropriate data were available. Permeability analyses model the relative cost for a species to move between protected core habitat or population areas. We defined a least-cost corridor—or best potential route—for each species, and then combined these into a Least Cost Union covering all three species. We then analyzed the size and configuration of suitable habitat patches within this Least Cost Union for all focal species to verify that the final Linkage Design would suit the live-in or move-through habitat needs of all. Where the Least Cost Union omitted areas essential to the needs of a particular species, we expanded the Linkage Design to accommodate that species' particular requirements to produce a final Linkage Design (Figure ES-1). We also visited priority areas in the field to identify and evaluate barriers to movement for our focal species. In this plan we suggest restoration strategies to mitigate those barriers, with special emphasis on opportunities to reduce

the adverse effects of Interstate 101, and 5, and State Routes 23, 118, 126, and14. Overall, the results and recommendations from our analyses are advisory, but can hopefully assist local jurisdictions, agencies, organizations, and property owners make planning and land use decisions that promote protection of ecological resources and habitat connectivity in the area.

The ecological, educational, recreational, and spiritual values of protected wildlands in the South Coast Ecoregion are immense. Our Linkage Design for the Santa Monica-Sierra Madre Connection represents an opportunity to protect a truly functional landscape-level connection. The cost of implementing this vision will be substantial—but the cost is small compared with the benefits. If implemented, our plan would not only permit movement of individuals and genes between the Santa Monica Mountains and the Sierra Madre Ranges, but should also conserve large-scale ecosystem processes that are essential to the continued integrity of existing conservation investments throughout the region. We hope that our biologically based and repeatable procedure will be applied in other parts of California and elsewhere to ensure continued ecosystem integrity in perpetuity.

Introduction

Nature Needs Room to Roam

Movement is essential to wildlife survival, whether it be the day-to-day movements of individuals seeking food, shelter, or mates, dispersal of offspring (e.g., seeds, pollen, fledglings) to new home areas, or migration of organisms to avoid seasonally unfavorable conditions (Forman 1995). Movements can lead to recolonization of unoccupied habitat after environmental disturbances, the healthy mixing of genes among populations, and the ability of organisms to respond or adapt to environmental stressors. Movements in natural environments lead to complex mosaics of ecological and genetic interactions at various spatial and temporal scales.

In environments fragmented by human development, disruption of movement patterns can alter essential ecosystem functions, such as predator-prey relationships, gene flow, pollination and seed-dispersal, competitive or mutualistic relationships among species, resistance to invasion by alien species, energy flow, and nutrient cycling. Without the ability to move among and within natural habitats, species become more susceptible to fire, flood, disease and other environmental disturbances and show greater rates of local extinction (Soulé and Terborgh 1999). The principles of island biogeography (MacArthur and Wilson 1967), models of demographic stochasticity (Shaffer 1981, Soulé 1987), inbreeding depression (Schonewald-Cox 1983; Mills and Smouse 1994), and metapopulation theory (Levins 1970, Taylor 1990, Hanski and Gilpin 1991) all predict that isolated populations are more susceptible to extinction than connected populations. Establishing connections among natural lands has therefore long been recognized as important for sustaining natural ecological processes and biological diversity (Noss 1987, Harris and Gallagher 1989, Noss 1991, Beier and Loe 1992, Noss 1992, Beier 1993, Forman 1995, Beier and Noss 1998, Hunter 1999, Crooks and Soulé 1999, Soulé and Terborgh 1999, Penrod et al. 2001, Crooks et al. 2001, Tewksbury et al. 2002, Forman et al. 2003).

Patterns of Habitat Conversion

As a consequence of rapid habitat conversion to urban and agricultural uses, the South Coast Ecoregion of California (Figure 1) has become a hotspot for species at risk of extinction. California has the greatest number of threatened and endangered species in the continental U.S, representing nearly every taxonomic group, from plants and invertebrates to birds, mammals, fish, amphibians, and reptiles (Wilcove et al. 1998). In an analysis that identified “irreplaceable” places for preventing species extinctions (Stein et al. 2000), the South Coast Ecoregion stood out as one of the six most important areas in the United States (along with Hawaii, the San Francisco Bay Area, Southern Appalachians, Death Valley, and the Florida Panhandle). The ecoregion is part of the California Floristic Province, one of 25 global hotspots of biodiversity, and the only one in North America (Mittermeier et al. 1998, Mittermeier et al. 1999).

A major reason for regional declines in native species is the pattern of habitat loss. Species that once moved freely through a mosaic of natural vegetation types are now confronted with a man-made labyrinth of barriers, such as roads, homes, businesses,

and agricultural fields that fragment formerly expansive natural landscapes. Movement patterns crucial to species survival are being permanently altered at unprecedented rates. Countering this threat requires a systematic approach for identifying, protecting, and restoring functional connections across the landscape to allow essential ecological processes to continue operating as they have for millennia.

A Statewide Vision

In November 2000, a coalition of conservation and research organizations (California State Parks, California Wilderness Coalition, The Nature Conservancy, Zoological Society of San Diego's Center for Reproduction of Endangered Species, and U.S. Geological Survey) launched a statewide interagency workshop at the San Diego Zoo entitled "Missing Linkages: Restoring Connectivity to the California Landscape". The workshop brought together over 200 land managers and conservation ecologists representing federal, state, and local agencies, academic institutions, and non-governmental organizations to delineate habitat linkages critical for preserving the State's biodiversity. Of the 232 linkages identified at the workshop, 69 are associated with the South Coast Ecoregion (Penrod et al. 2001).

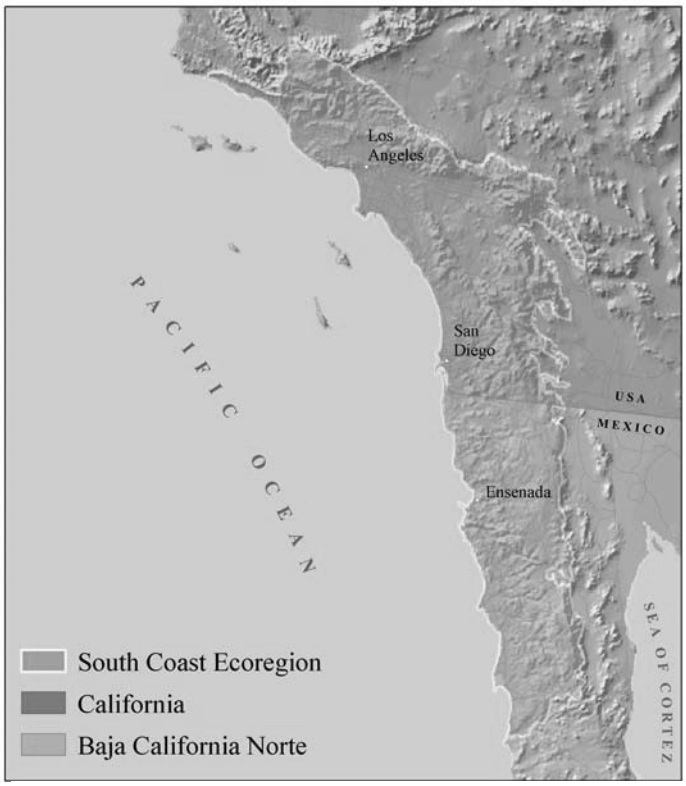


Figure 1. South Coast Ecoregion encompasses roughly 8% of California and extends 300 km (190 mi) into Baja California.

South Coast Missing Linkages: A Vision for the Ecoregion

Following the statewide Missing Linkages conference, South Coast Wildlands, a non-profit organization established to pursue habitat connectivity planning in the South Coast Ecoregion, brought together regional ecologists to conduct a formal evaluation of these 69 linkages. The evaluation was designed to assess the biological irreplaceability and vulnerability of each linkage (*sensu* Noss et al. 2002). Irreplaceability assessed the relative biological value of each linkage, including both terrestrial and aquatic criteria: 1) size of habitat blocks served by the linkage; 2) quality of existing habitat in the smaller habitat block; 3) quality and amount of existing habitat in the proposed linkage; 4) linkage to other ecoregions or key to movement through the ecoregion; 5) facilitation of seasonal movement and responses to climatic change; and 6) addition of value for aquatic ecosystems. Vulnerability was evaluated using recent high-resolution aerial



Figure 2. The South Coast Missing Linkages Project addresses habitat fragmentation at a landscape scale, and the needs of a variety of species. The Santa Monica-Sierra Madre Connection is a chain of linkages that connect the Santa Monica, Simi, Santa Susana, and Sierra Madre ranges, addressing two of the 15 landscape linkages identified as irreplaceable and imminently threatened.

photographs, local planning documents, and other data concerning threats of habitat loss or fragmentation in the linkage area. This process identified 15 linkages of crucial biological value that are likely to be irretrievably compromised by development projects over the next decade unless immediate conservation action occurs (Figure 2). The biological integrity of several thousand square miles of the very best southern California wildlands would be irreversibly jeopardized if these linkages were lost.

Identification of these 15 priority linkages launched the South Coast Missing Linkages Project. This project is a highly collaborative effort among federal and state agencies and non-governmental organizations to identify and conserve landscape-level habitat linkages to protect essential biological and ecological processes in the South Coast Ecoregion. Partners include but are not limited to: South Coast Wildlands, The Wildlands Conservancy, The Resources Agency California Legacy Project, California State Parks, California State Parks Foundation, United States Forest Service, National Park Service, Santa Monica Mountains Conservancy, The Nature Conservancy, Rivers and Mountains Conservancy, Conservation Biology Institute, San Diego State University Field Stations Program, Southern California Wetlands Recovery Project, Environment Now, Mountain Lion Foundation, and the Zoological Society of San Diego's Center for

Reproduction of Endangered Species (now called Conservation and Research for Endangered Species). Cross-border alliances have also been formed with Pronatura, Universidad Autonoma de Baja California, and Conabio to further the South Coast Missing Linkages initiative in northern Baja. It is our hope that the South Coast Missing Linkages Project will serve as a catalyst for directing funds and attention toward the protection of ecological connectivity for the South Coast Ecoregion and beyond.

To this end, South Coast Wildlands is coordinating and hosting regional workshops, providing resources to partnering organizations, conducting systematic GIS analyses for all 15 linkages, and helping to raise public awareness regarding habitat connectivity needs in the ecoregion. South Coast Wildlands has taken the lead in researching and planning for 8 of the 15 linkages; while the National Park Service at Santa Monica Mountains National Recreation Area, Santa Monica Mountains Conservancy, The Nature Conservancy, San Diego State University Field Station Programs, California State Parks, U. S. Forest Service, and Conservation Biology Institute have taken the lead on the other 7 linkages. The Santa Monica-Sierra Madre Connection addresses two of these 15 linkages, whose protection is crucial to maintaining ecological and evolutionary processes among large blocks of protected habitat within the South Coast Ecoregion.

The 15 Priority Linkages

Santa Monica Mountains-Santa Susana Mountains
Santa Susana Mountains-Sierra Madre Mountains
Sierra Madre Mountains-Castaic Ranges
Sierra Madre Mountains-Sierra Nevada Mountains
San Gabriel Mountains-Castaic Ranges
San Bernardino Mountains-San Gabriel Mountains
San Bernardino Mountains-San Jacinto Mountains
San Bernardino Mountains-Little San Bernardino Mountains
San Bernardino Mountains-Granite Mountains
Santa Ana Mountains-Palomar Ranges
Palomar Ranges-San Jacinto/Santa Rosa Mountains
Peninsular Ranges-Anza Borrego
Laguna Mountains-Otay Mountain-Northern Baja
Campo Valley-Laguna Mountains
Jacumba Mountains-Sierra Juarez Mountains

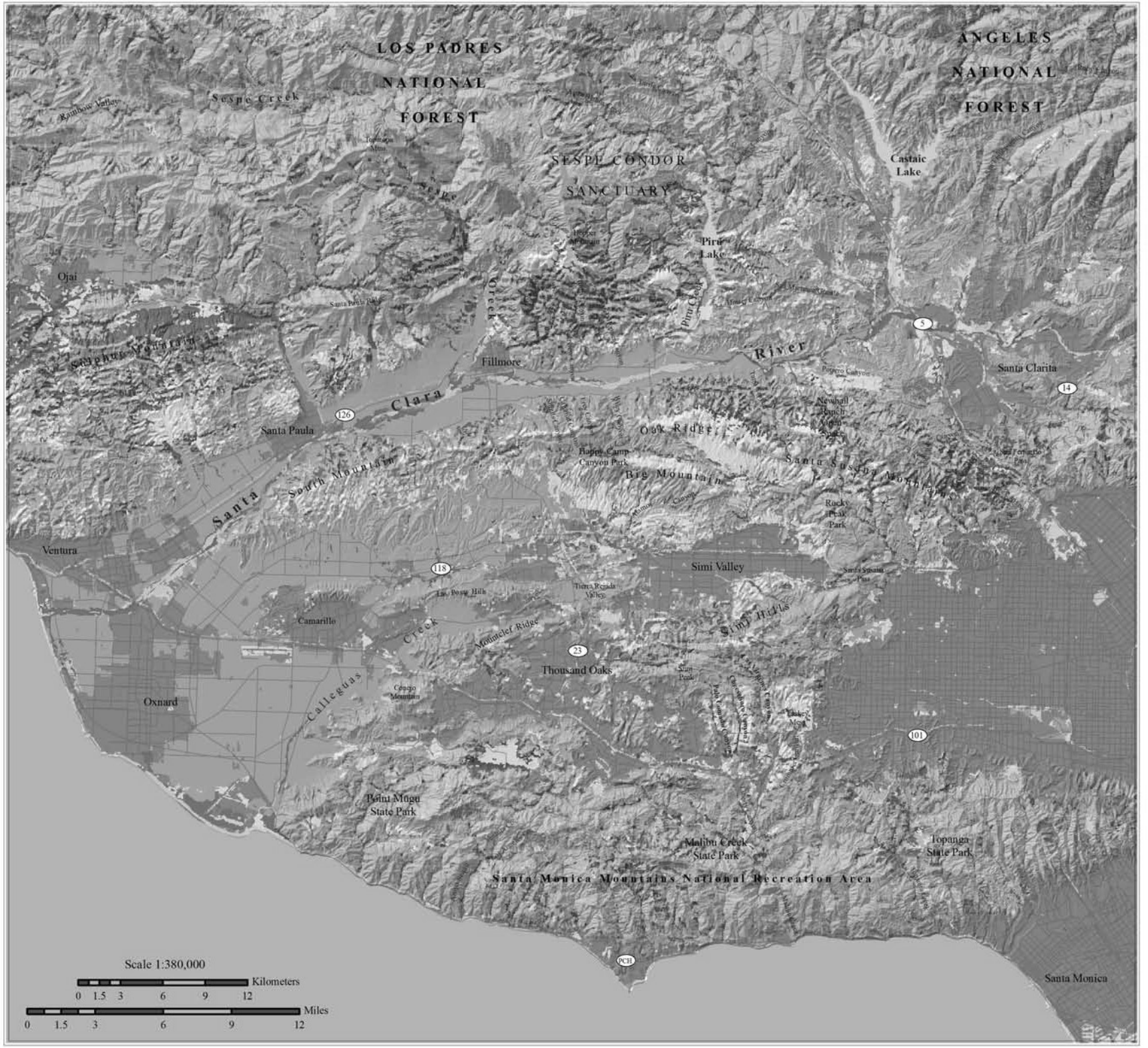
Ecological Significance of the Santa Monica-Sierra Madre Connection

The Santa Monica-Sierra Madre Connection is one of the few coastal to inland connections remaining in the South Coast Ecoregion, stretching from the rugged Santa Monica Mountains at the coast to the gently sloping Simi Hills, and on to the jagged peaks of the Santa Susana Mountains and the Sierra Madre Ranges of Los Padres National Forest. A rich mosaic of natural communities occur in this area, from coast live oak woodland, valley oak savanna, and walnut woodland, to chaparral, coastal sage scrub, grasslands, and diverse riparian forests and woodlands (Figure 3). Coastal sage scrub and chaparral are the dominant plant communities, with scattered groves of coast live oak woodland and walnut woodland on north facing slopes and in ravines, and riparian communities dominated by cottonwood, sycamore, and various willow species along drainages. A number of sensitive natural communities occur in the planning area, including valley foothill riparian, cottonwood willow riparian forest, coast live oak riparian forest, valley oak woodland, and walnut woodland (CDFG 2005). These are some of the most rare vegetation communities in the United States.

This variety of habitats supports a diversity of organisms, including many species listed as endangered, threatened, or sensitive by government agencies (USFWS 1980, 1998,

Figure 3.
Vegetation Types in the Planning Area

- Annual Grassland
- Chamise-Redshank Chaparral
- Coastal Oak Woodland
- Coastal Scrub
- Mixed Chaparral
- Valley Oak Woodland
- Montane Chaparral
- Jeffrey Pine
- Montane Hardwood
- Montane Hardwood-Conifer
- Sierran Mixed Conifer
- Desert Scrub
- Juniper
- Pinyon-Juniper
- Sagebrush
- Desert Wash
- Freshwater Emergenet Wetland
- Montane Riparian
- Saline Emergent Wetland
- Valley Foothill Riparian
- Water
- Agriculture
- Barren
- Eucalyptus
- Urban



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1999, 2000, 2001, 2002, 2006, CDFG 1996, 2005a, 2005b). A number of rare species depend on the area's riparian communities, which provide breeding locations for many special status amphibians and reptiles, such as California red-legged frog (*Rana aurora draytonii*), arroyo toad (*Bufo californicus*), western pond turtle (*Emys marmorata*), and the two-striped garter snake (*Thamnophis hammondii*). The critically endangered southern steelhead trout (*Oncorhynchus mykiss mykiss*) also occurs in the planning area and both the Malibu Creek Watershed and the Santa Clara River Watershed have been identified as core watersheds for recovery efforts (CDFG 1996). The Pacific lamprey (*Lampetra tridentate*), arroyo chub (*Gila orcutti*), and the endangered tidewater goby (*Eucyclogobius newberryi*) are other native freshwater fish species known to still inhabit the planning area. The creeks and lagoons in the area are also important to resident, over wintering, and migratory birds on the Pacific Flyway, in addition to providing year round habitat and critical resources for resident species. Several riparian songbirds, such as yellow warbler (*Dendroica petechia*), and the endangered least Bell's vireo (*Vireo bellii pusillus*), southwestern willow flycatcher (*Empidonax traillii extimus*), and yellow-billed cuckoo (*Coccyzus americanus*) have the potential to occur in riparian habitats in the linkage. Sensitive reptiles that prefer drier habitats and sparser vegetative cover, such as the coast horned lizard (*Phrynosoma coronatum blainvillei*) also occur, as do a number of sensitive birds of prey, including Swainson's hawk (*Buteo swainsoni*), northern harrier (*Circus cyaneus*), and bald eagle (*Haliaeetus leucocephalus*). The planning area also provides habitat for a number of imperiled plant species, including the San Fernando Valley spineflower (*Chorizanthe parryi* var. *fernandina*), which was presumed extinct in 1929 until it was rediscovered on Ahmanson Ranch in the Simi Hills and Newhall Ranch in the Santa Susana Mountains.

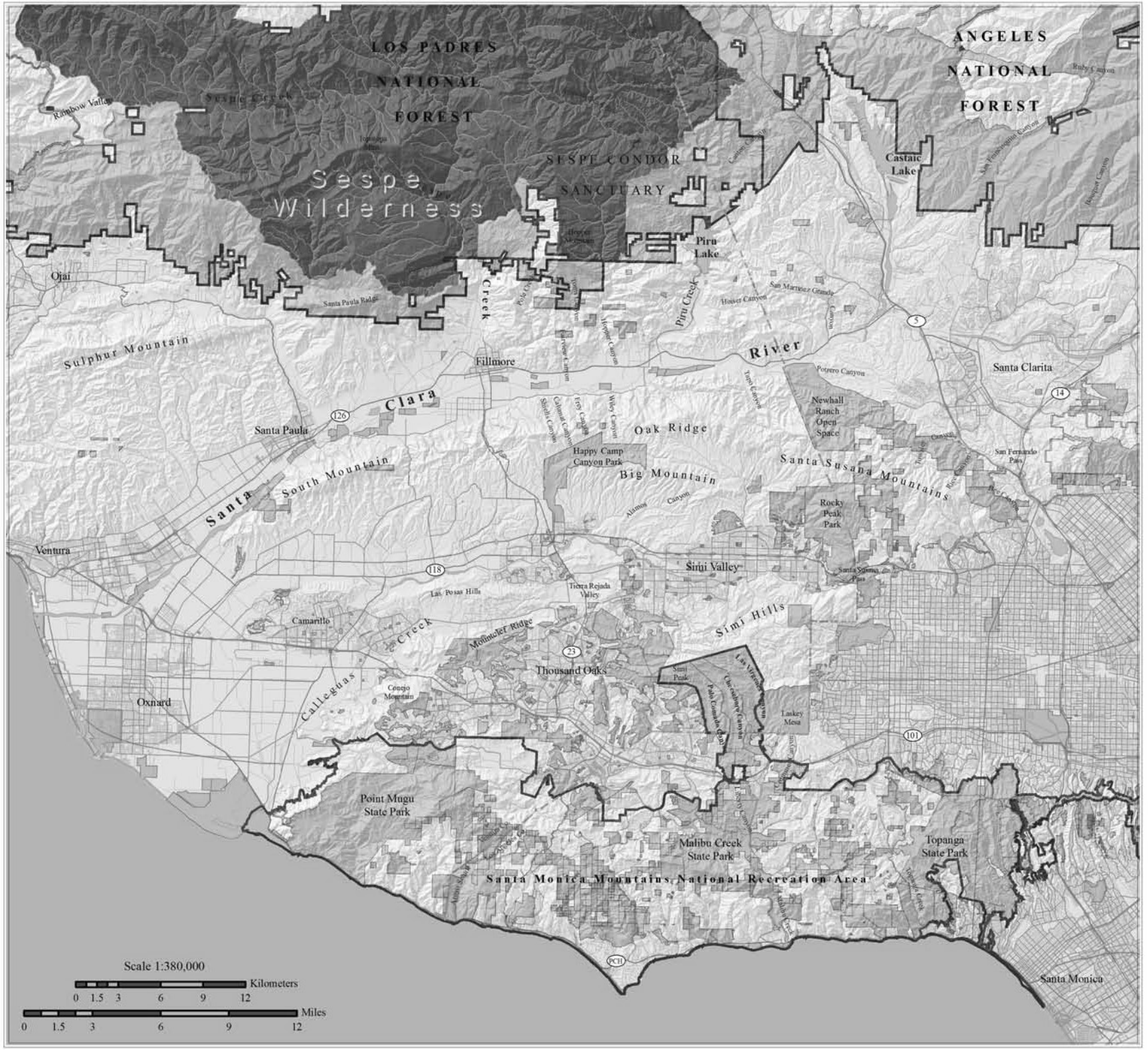
In addition to providing habitat for rare and endangered species, the linkage provides live-in and move-through habitat for numerous native species such as American badger (*Taxidea taxus*), mule deer (*Odocoileus hemionus*), and mountain lion (*Felis concolor*) that require extensive wildlands to thrive. Several peer-reviewed scientific studies have called attention to maintaining connectivity between remaining patches of natural habitat in this region (Soulé 1989, Edelman 1991, Kohn et al. 1999, Ng 2000, Sauvajot et al. 2000, Allen 2001, Riley et al. 2003, Casterline et al. 2003, Ng et al. 2004, LSA 2004, Riley et al. 2005, Riley et al. 2006 a,b).

Existing Conservation Investments

Significant conservation investments already exist in the region (Figure 4), but the resource values they support could be irreparably harmed by loss of connections between them. This linkage connects two expansive core areas that are largely conserved within the Los Padres National Forest and the Santa Monica Mountains National Recreation Area. The Sespe Wilderness Area occurs just inside the boundary of Los Padres National Forest and the California Wild Heritage Campaign (www.californiawild.org) has proposed additional Wilderness Areas in both Los Padres and Angeles National Forests.

Much of the land in the linkage has already been protected though successful conservation planning efforts undertaken by Santa Monica Mountains Conservancy, National Park Service, The Nature Conservancy, California State Parks, U.S. Forest Service, Mountain Recreation Conservation Authority, Mountain Restoration Trust, Friends of the Santa Clara River, and other county, city and local agencies, although

Figure 4.
Existing Conservation Investments in the Planning Area



- Designated Wilderness
- Proposed Wilderness
- Protected Lands
- Santa Monica Mountains National Recreation Area
- County Boundary
- Lakes & Reservoirs
- Hydrography
- Roads

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gaps in protection remain. The Santa Monica Mountains Conservancy has been working with other federal, state, county, and local agencies for over 25 years to protect the Rim of the Valley Corridor. The Los Angeles County General Plan update would establish 3 Significant Ecological Areas (SEA): the proposed Santa Monica Mountains SEA (99,430 acres) that crosses the 101 freeway at Liberty and Crummer canyons; the Santa Susana/Simi Hills SEA (26,795 ac) that covers the eastern part of these ranges within the county; and the Santa Clara River SEA which covers the portion of the river in the county (PCR Services Corporation 2000 a, b, c). The value of already protected land in the region for biodiversity conservation, environmental education, outdoor recreation, and scenic beauty is immense.

Southern California's remaining wildlands form an archipelago of natural open space thrust into one of the world's largest metropolitan area within a global hotspot of biological diversity. These wild areas are naturally interconnected; indeed, they historically functioned as one ecological system. However, recent intensive and unsustainable activities threaten to sever natural connections, forever altering the functional integrity of this remarkable natural system. The ecological, educational, recreational, and spiritual impacts of such a severance would be substantial. Certainly, restoring functional habitat connectivity to this regionally important landscape linkage is a wise investment.

The goal of linkage conservation planning is to identify specific lands that must be conserved to maintain or restore functional connections for all species or ecological processes of interest, generally between two or more protected core habitat areas. We adopted a spatially hierarchical approach, gradually working from landscape-level processes down to the needs of individual species on the ground. The planning area encompasses habitats between the Santa Monica Mountains National Recreation Area (south of the 101 Freeway) and Los Padres National Forest. We conducted various landscape analyses to identify those areas necessary to accommodate continued movement of selected focal species through this landscape. Our approach can be summarized as follows:

1) *Focal Species Selection:* Select focal species from diverse taxonomic groups to represent a diversity of habitat requirements and movement needs.

2) *Landscape Permeability Analysis:* Conduct landscape permeability analyses to identify a zone of habitat that addresses the needs of multiple species potentially traveling through or residing in the linkage.

3) *Patch Size & Configuration Analysis:* Use patch size and configuration analyses to identify the priority areas needed to maintain linkage function.

4) *Field Investigations:* Conduct fieldwork to ground-truth results of prioritization analyses, identify barriers, and document conservation management needs.

5) *Linkage Design:* Compile results of analyses and fieldwork into a comprehensive report detailing what is required to conserve and improve linkage function.

Our approach has been highly collaborative and interdisciplinary (Beier et al. 2005). We followed Baxter (2001) in recognizing that successful conservation planning is based on the participation of experts in biology, conservation design, and implementation in a reiterative process (Figure 5). To engage regional biologists and planners early in the process, we held a habitat connectivity workshop on July 29, 2002. The workshop gathered indispensable information on conservation needs and opportunities in the linkage. The workshop engaged 60 participants representing over 30 different agencies, academic institutions,

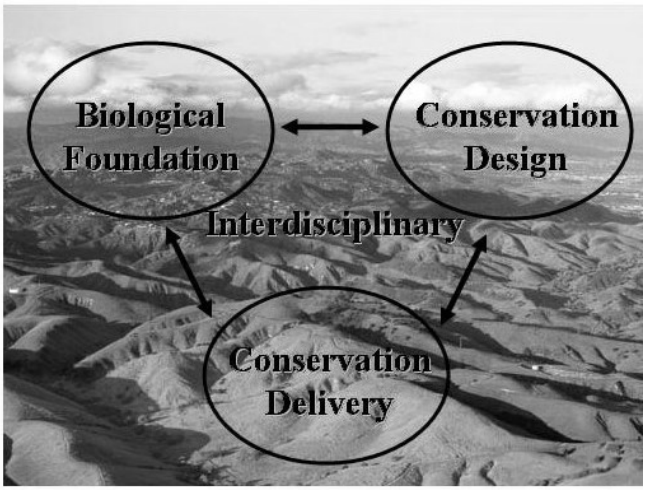


Figure 5. Successful conservation planning requires an interdisciplinary and reiterative approach among biologists, planners and activists (Baxter 2001).

conservation organizations, and community groups (Appendix A).

Focal Species Selection

The workshop participants identified a taxonomically diverse group of focal species that are sensitive to habitat loss and fragmentation (Table 1). These species represent the diversity of ecological interactions that can be sustained by successful linkage design. The focal species approach (Beier and Loe 1992) recognizes that species move through and utilize habitat in a wide variety of ways. Workshop participants divided into taxonomic working groups; each group identified life history characteristics of species that were either particularly sensitive to habitat fragmentation or otherwise meaningful to linkage design. Participants then summarized the relevant information on species occurrence, movement characteristics, and habitat preferences and delineated suitable habitat and potential movement routes through the linkage region. (For more on the workshop see Appendix B.)

Table 1. Regional ecologists selected 20 focal species for the Santa Monica-Sierra Madre Connection

Plants
Arctostaphylos glauca (Bigberry manzanita)
Quercus lobata (Valley oak)
Juglans californica (California walnut)
Invertebrates
Pogonomyrmex rugosus (Harvester ant)
Euphydryas chalcedona (Chalcedon checkerspot butterfly)
Odonata - Zygoptera spp. (Damselflies)
Anuroctonus phaiodactylus (Scorpion)
Fish
Oncorhynchus mykiss mykiss (Southern steelhead trout)
Reptiles & Amphibians
Cnemidophoris tigris stejnegeri (Western whiptail)
Lampropeltis getula (California kingsnake)
Bufo boreas (Western toad)
Birds
Melanerpes formicivorus (Acorn woodpecker)
Toxostoma redivivum (California thrasher)
Campylorhynchus brunneicapillus (Cactus wren)
Lanius ludovicianus (Loggerhead shrike)
Mammals
Neotoma lepida (Desert woodrat)
Sylvilagus bachmanni (Brush rabbit)
Odocoileus hemionus (Mule deer)
Taxidea taxus (American badger)
Puma concolor (Mountain lion)

The 20 focal species identified at the workshop capture a diversity of movement needs and ecological requirements, from species that require large tracts of land (e.g., mountain lion, badger, mule deer) to those with very limited spatial requirements (e.g., desert woodrat). They include habitat specialists (e.g., acorn woodpeckers in oak woodlands) and those requiring a specific configuration of habitat types and elements (e.g., southern steelhead trout that utilize the entire river or stream system, from the headwaters to the ocean, and require clean, cool, well-oxygenated water). Dispersal distance capability of focal species ranges from 160 m to 274 km; modes of dispersal include walking, flying, swimming, climbing, hopping, and slithering.

Landscape Permeability Analysis

Landscape permeability analysis is a GIS technique that models the relative cost for a species to move between core areas based on how each species is affected by habitat

characteristics, such as slope, elevation, vegetation composition, and road density. This analysis identifies a least-cost corridor, or the best potential route for each species between protected core areas (Walker and Craighead 1997, Craighead et al. 2001, Singleton et al. 2002). The purpose of the analysis was to identify land areas, which would best accommodate all focal species living in or moving through the linkage (Beier et al. 2005). Species used in landscape permeability analysis must be carefully chosen, and were included in this analysis only if:

- We know enough about the movement of the species to reasonably estimate the cost-weighted distance using the data layers available to our analysis.
- The data layers in the analysis reflect the species' ability to move.
- The species occurs in both cores (or historically did so and could be restored) and can potentially move between cores, at least over multiple generations.
- The time scale of gene flow between core areas is shorter than, or not much longer than, the time scale at which currently mapped vegetation is likely to change due to disturbance events and environmental variation (e.g. climatic changes).

Three of the 20 focal species were found to meet these criteria and were used in permeability analyses to identify the least-cost corridor between protected core areas: mountain lion, badger, and mule deer. Ranks and weightings adopted for each species are shown in Table 2.

The relative cost of travel was assigned for each of these three species based upon its ease of movement through a suite of landscape characteristics (vegetation type, road density, and topographic features). The following spatial data layers were assembled at 30-m resolution: vegetation, roads, elevation, and topographic features (Figure 6). We derived four topographic classes from elevation and slope models: canyon bottoms, ridgelines, flats, or slopes. Road density was measured as kilometers of paved road per square kilometer. Within each data layer, we ranked all categories between 1 (preferred) and 10 (avoided) based on focal species preferences as determined from available literature and expert opinion regarding how movement is facilitated or hindered by natural and urban landscape characteristics. Each input category was ranked and weighted, such that: (Vegetation * w%) + (Road Density * x%) + (Topography * y%) + (Elevation * z%) = Cost to Movement, where w + x + y + z = 100%.

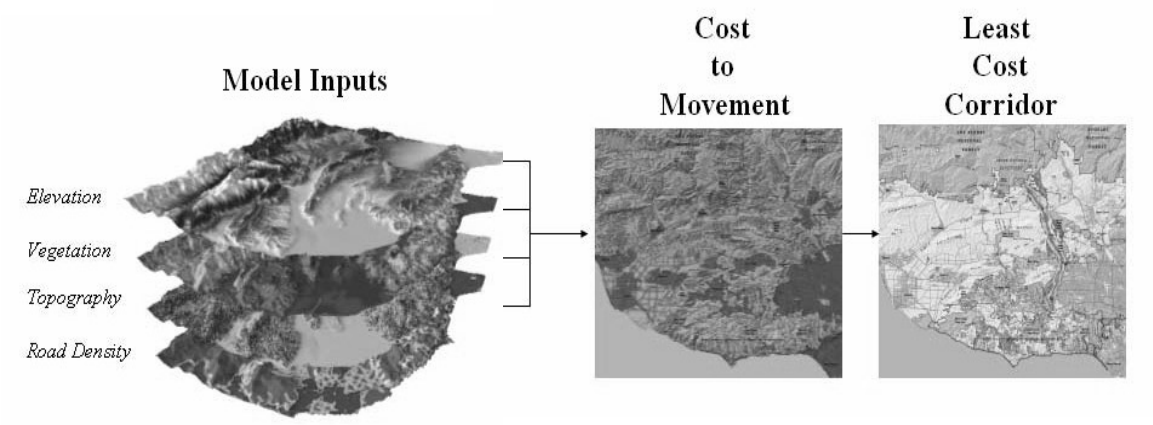


Figure 6. Permeability Model Inputs: elevation, vegetation, topography, and road density. Landscape permeability analysis models the relative cost for a species to move between core areas based on how each species is affected by various habitat characteristics.

Table 2. Model Parameters for Landscape Permeability Analyses

	Odocoileus hemionus (Mule deer)	*Taxidea taxus* (Badger)	*Puma concolor* (Mountain lion)
MODEL VARIABLES			
VEGETATION			
Alpine-Dwarf Shrub	9	4	4
Agriculture	9	7	10
Annual Grassland	9	1	7
Alkali Desert Scrub	10	2	7
Barren	10	9	10
Bitterbrush	3	3	2
Blue Oak-Foothill Pine	1	5	3
Blue Oak Woodland	1	5	2
Coastal Oak Woodland	1	5	2
Closed-Cone Pine-Cypress	3	6	5
Chamise-Redshank Chaparral	6	4	5
Coastal Scrub	3	4	2
Desert Riparian	4	3	1
Desert Scrub	9	2	7
Desert Succulent Shrub	8	2	7
Desert Wash	5	3	2
Eastside Pine	1	5	5
Estuarine	10	10	5
Freshwater Emergent Wetland	9	9	2
Jeffrey Pine	2	5	5
Joshua Tree	8	2	4
Juniper	5	3	3
Lacustrine	10	9	10
Lodgepole Pine	5	6	5
Mixed Chaparral	6	4	5
Montane Chaparral	5	4	5
Montane Hardwood-Conifer	1	6	3
Montane Hardwood	1	6	3
Montane Riparian	2	6	1
Perennial Grassland	7	1	6
Pinyon-Juniper	4	3	3
Palm Oasis	7	6	3
Ponderosa Pine	2	5	5
Riverine	9	9	1
Red Fir	4	6	5
Subalpine Conifer	6	6	5
Saline Emergent Wetland	10	10	6
Sagebrush	5	3	7
Sierran Mixed Conifer	2	6	5
Urban	10	10	10

Table 2. Continued	*Odocoileus hemionus* (Mule deer)	*Taxidea taxus* (Badger)	*Puma concolor* (Mountain lion)
MODEL VARIABLES			
Valley Oak Woodland	1	4	2
Valley Foothill Riparian	1	4	2
Water	10	10	9
White Fir	2	6	5
Wet Meadow	5	4	6
Unknown Shrub Type	5	5	5
Unknown Conifer Type	4	5	5
Eucalyptus	8	6	6
ROAD DENSITY			
0-0.5 km/sq. km	1	1	1
0.5-1 km/sq. km	1	1	3
1-2 km/sq. km	2	2	4
2-4 km/sq. km	5	2	6
4-6 km/sq.km	7	4	9
6-8 km/sq. km	10	7	10
8-10 km/sq.km	10	10	10
10 or more km/sq. km	10	10	10
TOPOGRAPHY			
Canyon bottoms	5	2	1
Ridgetops	2	7	7
Flats	8	1	3
Slopes	1	9	5
ELEVATION (feet)			
-260-0	6	1	N/A
0-500	4	1	
500-750	3	1	
750-1000	3	1	
1000-3000	3	2	
3000-5000	3	3	
5000-7000	3	3	
7000-8000	5	5	
8000-9000	5	5	
9000-11500	5	5	
>11500	8	8	
WEIGHTS			
Land Cover	0.65	0.55	0.40
Road Density	0.15	0.15	0.30
Topography	0.20	0.20	0.30
Elevation	0.00	0.10	0.00

Weighting allowed the model to capture variation in the influence of each input (vegetation, road density, topography, elevation) on focal species movements. A unique cost surface was thus developed for each species. A corridor function was then performed in GIS to generate a data layer showing the relative degree of permeability between core areas.

Running the permeability analysis required identifying the endpoints to be connected. Usually, these targeted endpoints are selected as medium to highly suitable habitat within protected core habitat areas (e.g., National Forests, State Parks) that needed to be connected through currently unprotected lands. However, since some of the land in the linkage was already protected (e.g., Ahmanson Ranch, Rocky Peak Park), and because of the complexity of ownerships in the Santa Monica Mountains, we selected endpoints for this analysis as areas supporting medium to highly suitable habitat for each species in Los Padres and Angeles National Forests within the analysis extent, and the Santa Monica Mountains National Recreation Area south of the 101 Freeway, near the far northern and southern extents of the study area. This gave the model broad latitude in interpreting functional corridors across the entire study area.

For each focal species, the most permeable area of the study window was designated as the least-cost corridor. An arbitrary definition of "most permeable" was assigned such that only the areas representing the top 1% of the least cost corridor function were included in the final output. In some instances (e.g. mountain lion), we relaxed the top 1% criteria to examine the sensitivity of mapped output to this constraint and to assess if and how least cost results would change. However, in our final analysis and in the mapped results presented in this report, the "most permeable" routes are shown for the top 1% output for each of the three focal species (and for the Least Cost Union, see below).

The least-cost corridor output for all three species was then combined to generate a Least Cost Union. The biological significance of this Union can best be described as the zone within which all three modeled species would encounter the least energy expenditure (i.e., preferred travel route) and the most favorable habitat as they move between targeted protected areas. The output does not identify barriers (which were later identified through fieldwork), mortality risks, dispersal limitations or other biologically significant processes that could prevent a species from successfully reaching a core area. Rather, it identifies the best zone available for focal species movement based on the data layers used in the analyses.

Patch Size & Configuration Analysis

Although the Least-Cost Union identifies the best zone available for movement based on the data layers used in the analyses, it does not address whether suitable habitat in the Union occurs in large enough patches to support viable populations and whether these patches are close enough together to allow for inter-patch dispersal. We therefore conducted patch size and configuration analyses for all focal species (Table 1) and adjusted the boundaries of the Least Cost Union where necessary to enhance the likelihood of movement. Patch size and configuration analyses are particularly important for species that require multiple generations to traverse the linkage. Many species exhibit metapopulation dynamics, whereby the long-term persistence of a local

population requires connection to other populations (Hanski and Gilpin 1991). For relatively sedentary species like desert woodrat and terrestrial insects, gene flow will occur over decades through a metapopulation. Thus, the linkage must be able to accommodate metapopulation dynamics to support ecological and evolutionary processes in the long term.

A habitat suitability model formed the basis of the patch size and configuration analyses. Habitat suitability models were developed for each focal species using the literature and expert opinion. Spatial data layers used in the analysis varied by species and included: vegetation, elevation, topographic features, slope, aspect, hydrography, and soils. Using scoring and weighting schemes similar to those described in the previous section, we generated a spectrum of suitability scores that were divided into five classes using natural breaks: low, low to medium, medium, medium to high, or high. Suitable habitat was identified as all land that scored medium, medium to high, or high.

To identify areas of suitable habitat that were large enough to provide a significant resource for individuals in the linkage, we conducted a patch size analysis. The size of all suitable habitat patches in the planning area were identified and marked as potential cores, patches, or less than a patch. *Potential core areas* were defined as the amount of contiguous suitable habitat necessary to sustain at least 50 individuals. A *patch* was defined as the area of contiguous suitable habitat needed to support at least one male and one female, but less than the potential core area. Potential cores are probably capable of supporting the species for several generations (although with erosion of genetic material if isolated). Patches can support at least one breeding pair of animals (perhaps more if home ranges overlap greatly) and are probably useful to the species if the patch can be linked via dispersal to other patches and core areas (Figure 7).

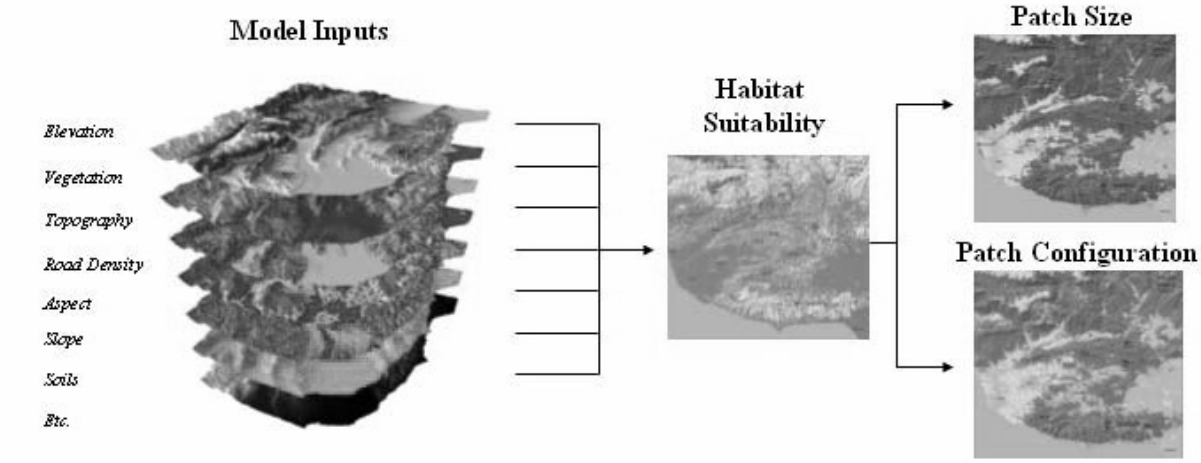


Figure 7. Model Inputs to Patch Size and Configuration Analyses vary by species. Patch size delineates cores, patches, and stepping-stones of potential habitat. Patch configuration evaluates whether suitable habitat patches and cores are within each species dispersal distance.

To determine whether the distribution of suitable habitat in the linkage supports meta-population processes and allows species to disperse among patches and core areas, we conducted a configuration analysis to identify which patches and core areas were

functionally isolated by distances too great for the focal species to traverse. Because the majority of methods used to document dispersal distance underestimate the true value (LaHaye et al. 2001), we assumed each species could disperse twice as far as the longest documented dispersal distance. This assumption is conservative in the sense that it retains habitat patches as potentially important to dispersal for a species even if it may appear to be isolated based on known dispersal distances. Groupings of core areas and patches that were greater than the adopted dispersal distance from other suitable habitat were identified using a unique color.

For each species we compared the configuration and extent of potential cores and patches, relative to the species dispersal ability, to evaluate whether the Least Cost Union was likely to serve the species. If necessary, we added additional habitat to help ensure that the linkage provides sufficient live-in or "move-through" habitat for the species' needs.

Minimum Linkage Width

While the size and distance among habitats (addressed by patch size and configuration analyses) must be adequate to support species movement, the shape of those habitats also plays a key role. In particular, constriction points—areas where habitats have been narrowed by surrounding development—can prevent organisms from moving through the Least Cost Union. To ensure that functional processes are protected, we imposed a minimum width of 2 km (1.2 mi) for all portions of the final Linkage Design.

For a variety of species, including those we did not formally model, a wide linkage helps ensure availability of appropriate habitat, host plants (e.g., for butterflies), pollinators, and areas with low predation risk. In addition, fires and floods are part of the natural disturbance regime and a wide linkage allows for a semblance of these natural disturbances to operate with minimal constraints from adjacent urban areas. A wide linkage should also enhance the ability of the biota to respond to climate change, and buffer against edge effects.

Field Investigations

We conducted field surveys to ground-truth existing habitat conditions, document existing barriers and potential passageways, and describe restoration opportunities. All location data were recorded using a mobile GIS/GPS with ESRI's ArcPad. Because paved roads often present the most formidable potential barriers, biologists drove or walked each accessible section of paved road that transected the linkage. All types of potential crossing structures (e.g., bridge, underpass, overpass, culvert, pipe) were photo documented and measured. Data taken for each crossing included: shape; height, width, and length of the passageway; stream type, if applicable (perennial or intermittent); floor type (metal, dirt, concrete, natural); passageway construction (concrete, metal, other); visibility to other side; light level; fencing; and vegetative community within and/or adjacent to the passageway. Existing highways and crossing structures are not considered permanent landscape features. In particular, crossing structures can be added or improved during projects to widen and realign highways and interchanges. Therefore, we also identified areas where crossing structures could be improved or installed, and opportunities to restore vegetation to improve road crossings and minimize roadkills.

Identify Conservation Opportunities

The Linkage Design serves as the target area for linkage conservation opportunities. We provided biological and land use summaries, and identified implementation opportunities for agencies, organizations, and individuals interested in helping conserve the Santa Monica-Sierra Madre Connection. Biological and land use summaries include descriptions and maps of vegetation, land cover, land use, roads, road crossings, and restoration opportunities. We also identified existing planning efforts addressing the conservation and use of natural resources in the planning area. Finally, we developed a flyover animation using aerial imagery, satellite imagery, and digital elevations models, which provides a visualization of the linkage from a landscape perspective (Appendix C).

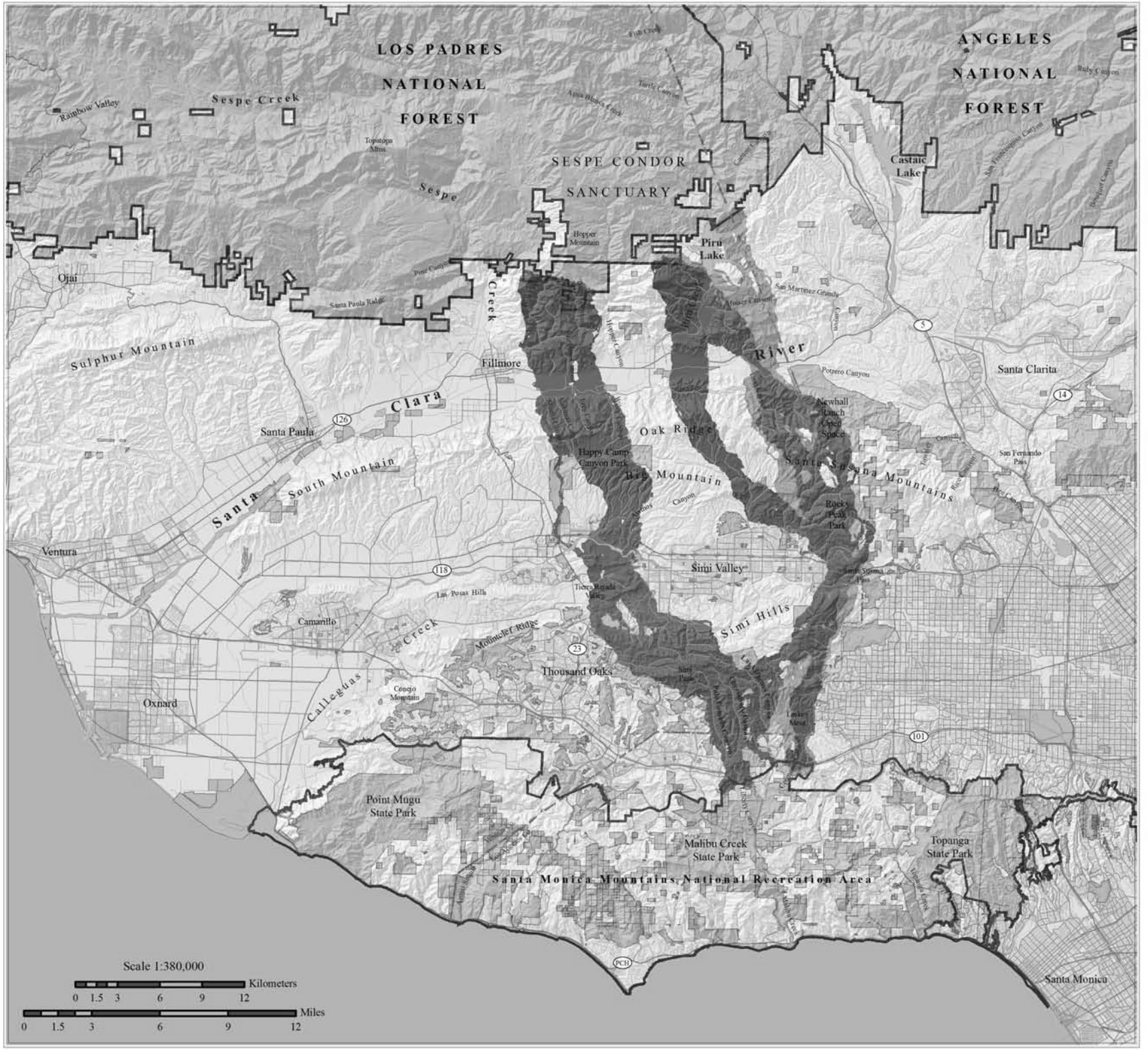
We conducted landscape permeability analyses for three focal species (mountain lion, badger, and mule deer). The least cost corridors for these species were quite similar despite their diverse ecological and movement requirements (see following species accounts in this section and Table 2 in the previous section). The most permeable paths for these focal species converged and overlapped considerably in the eastern part of the linkage, with two species, mule deer and badger, diverging to generate additional routes that also contain highly suitable habitat for mountain lions (Figure 8).

The Least Cost Union (i.e., the union of the top 1% of the least cost corridors for all three species) stretches about 40 km (25 mi) between the Santa Monica Mountains National Recreation Area and the Sierra Madre Range of Los Padres National Forest (Figure 9). It encompasses diverse vegetation and physiographic zones to account for the needs of the focal species, including coastal sage, chaparral, grassland, oak woodland, riparian woodlands and forests, and conifer habitats.

The branches of the least cost union identify the areas best suited to facilitate species movement between core areas based on model assumptions and available GIS data. All branches of the Union extend from the Santa Monica Mountains in the same general vicinity, crossing the 101 Freeway at Liberty and Crummer canyons, and then merging north of the freeway to take in most habitats in the Simi Hills. From the Simi Hills, all three focal species took the eastern branch, crossing the 118 at the Santa Susana Pass into Rocky Peak Park. From here, mountain lion and mule deer follow the riparian habitats of Tapo and Salt canyons down to the Santa Clara River and then cross Highway 126 to take in habitat in Piru Creek, Hoiser Canyon, and upper San Martinez Grande Canyon. The permeability analysis for badger follows preferred habitat for this species to the west, taking in the grasslands over Oak Ridge and up the western bank of Piru Creek, delineating another branch to the Union in the Santa Susana Mountains. Mule deer also delineated the western branch of the linkage, which was identified as the most permeable route for this species. The western branch takes in habitat in Palo Comado, Cheeseboro, and Las Virgenes canyons in the Simi Hills, and crosses over Simi Peak and through the Tierra Rejada Valley to traverse Highway 118 at Alamos Canyon and enter the Santa Susana Mountains. From here, mule deer utilizes habitat in Happy Camp Canyon Park, and then follows Sheils, Calumat, Frey, and Wiley canyons down to the Santa Clara River, and then up Pole Creek, Fairview and Toms canyons in the Sierra Madre Ranges. The western branch of the Union ranges in width from about 3 to 6 km (1.9 to 3.7 mi), the central branch from roughly 1.5 to 3 km (0.9 to 1.9 mi), and the eastern branch from approximately 1.5 to 8 km (0.9 to 5.0 mi).

The next several pages summarize the permeability analyses for each of the three modeled species. For convenience, the narratives describe the most permeable paths from south to north, although our analyses gave equal weight to movements in both directions. The following section (Patch Size and Configuration Analyses) describes how well the Least Cost Union would likely serve the needs of all focal species, including those for which we could not conduct permeability analysis. The latter analysis expanded the Least Cost Union to provide for critical live-in and/or move-through habitat for particular focal species.

Figure 8.
Least Cost Union
Displaying Species Overlap



- Mountain lion
- Mule deer
- Badger
- Target Areas
- Protected Lands
- County Boundary
- Lakes & Reservoirs
- Hydrography
- Roads

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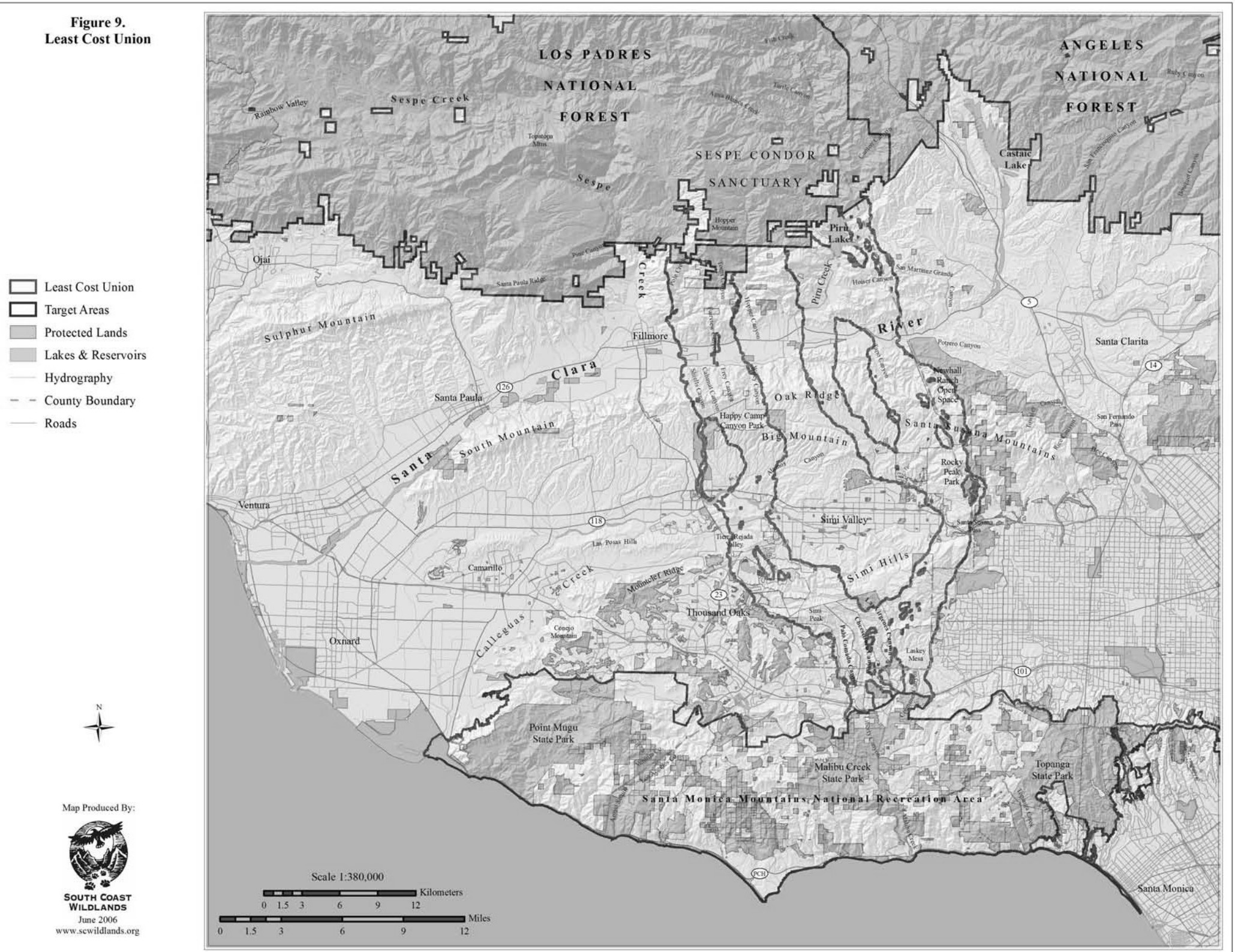
Figure 9.
Least Cost Union



Least Cost Union
Target Areas
Protected Lands
Lakes & Reservoirs
Hydrography
County Boundary
Roads

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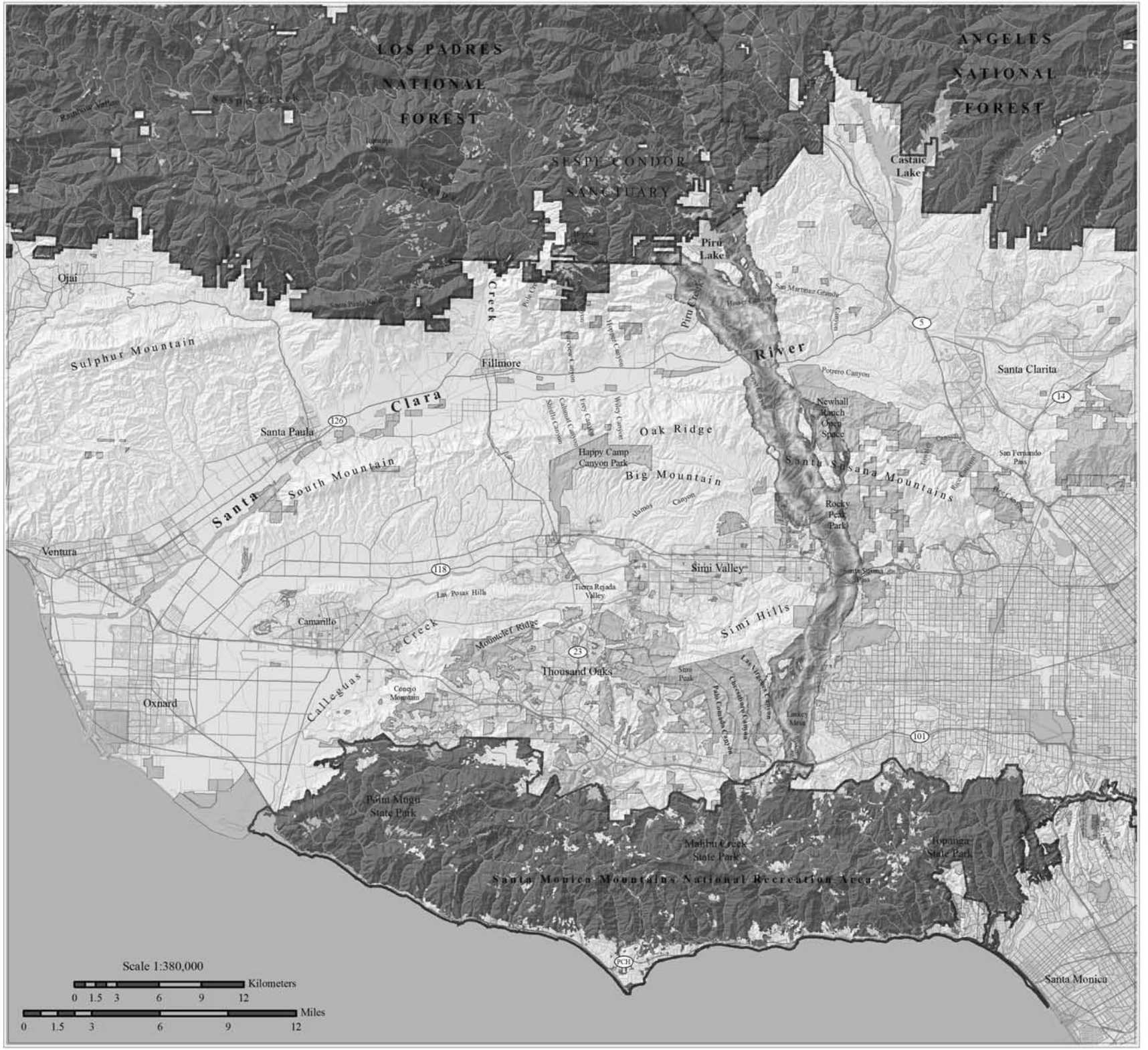
Justification for Selection: This area-sensitive species is an appropriate focal species because its naturally low densities render mountain lions highly sensitive to habitat fragmentation (Noss 1991, Noss and Cooperrider 1994). Consequently mountain lions serve as excellent indicators of broad scale landscape connectivity (Riley et al. 2006). The ecological consequences of losing large carnivores from complex ecosystems is largely unknown and difficult to predict, but may have cascading effects through the entire ecosystem (Soulé and Terborgh 1999). Regardless, loss of this species from southern California, and from the Sierra Madre-Santa Monica Mountains region in particular, would run counter to extensive public investments in parks and open spaces designed to protect biodiversity for future generations to enjoy, understand, and appreciate (Riley et al. 2005). Mountain lions have already lost a number of dispersal corridors in southern California, making them susceptible to extirpation from existing protected areas (Beier 1993). Habitat fragmentation caused by urbanization and the extensive road network has had detrimental effects on mountain lions by restricting movement, escalating mortality, and increasing contact with humans.

Conceptual Basis for Model Development: Mountain lions use brushy stages of a variety of habitat types with good cover (Spowart and Samson 1986, Zeiner et al. 1990). Within the study area, mountain lions are known to occupy a wide variety of habitat types, including within the urban interface and in parklands used extensively by recreating humans (Riley et al. 2006). Preferred travel routes are along stream courses and gentle terrain, but all habitats with cover are used (Beier and Barrett 1993, Dickson et al. 2004). In southern California, grasslands, agricultural areas, and human-altered landscapes are avoided (Dickson et al. 2004), although mountain lions can and will use these less-than-ideal habitats (Riley et al. 2006). Dirt roads do not impede movement, but highways, residential roads, and 2-lane paved roads can (Beier and Barrett 1993, Beier 1995, Dickson et al. 2004). Juvenile dispersal distances average 32 km (20 mi) for females, with a range of 9-140 km (6-87 mi), and 85 km (53 mi) for males, with a range of 23-274 km (14-170 mi; Anderson et al. 1992, Sweanor et al. 2000). The somewhat shorter dispersal distances reported in southern California (Beier 1995) reflect the fragmented nature of Beier's study area. Please see Table 2 for model variable scorings for this species. Cost to movement for mountain lion was defined by weighting the inputs as follows:

(Vegetation * 40%) + (Road Density * 30%) + (Topography * 30%)

Results & Discussion: The least cost corridor for mountain lion movement between the Santa Monica and Sierra Madre ranges (Figure 10) varies in width from about 1.5 to 6 km (0.9 to 3.7 mi). The most permeable path extends from the Santa Monica

Figure 10.
Least Cost Corridor
for
Mountain lion
(Puma concolor)



Least Cost Corridor

- Highly Permeable
- Less Permeable
- Suitable Habitat*
- Target Areas
- Protected Lands
- Lakes & Reservoirs
- Hydrography
- County Boundary
- Roads

*This analysis was run from medium to high suitable habitat within targeted protected areas.

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Mountains, crosses the 101 Freeway at Las Virgenes and Crummer Canyons to enter the Simi Hills, heads toward Chatsworth Peak, and crosses the 118 Freeway at Santa Susana Pass into Rocky Peak Park, where both an overpass and bridged underpass are located. From there, the route follows Tapo and Salt Canyons in the Santa Susana Mountains down to the Santa Clara River, and traverses the river and Highway 126 to enter Hoiser Canyon. It then branches to encompass habitat on either side of Piru Lake Reservoir, with the most permeable path following the riparian habitats of Piru Creek to Lime Canyon toward Hopper Mountain in the Sespe Condor Sanctuary, and another route taking in habitat in upper San Martinez Grande Canyon to the east of the reservoir. The analysis captured medium to highly suitable habitat for puma moving between the Santa Monica and Sierra Madre Mountains along their preferred travel routes.

To evaluate the sensitivity of constraining the least cost corridor to the top 1% of the model output, criteria were relaxed and resulting paths were assessed for mountain lion. In general, when criteria were more inclusive (e.g. top 1.5%, 2%, 2.5%, and 3% of model output), the least cost corridors largely overlapped results obtained for mule deer and, to a lesser extent, badger (Figs. 11 and 12). For example, the top 1.5% output for mountain lion adds a north-south linkage from the Los Padres National Forest near Hopper Mountain, through Happy Camp Park in the Santa Susana Mountains, across Highway 118 at Alamos Canyon, through the Tierra Rejada Valley, and ultimately into the Santa Monica Mountains through the Simi Hills via Liberty Canyon. This route is nearly entirely overlapped by the least cost path for mule deer (Fig. 12). These results likely reflect the broad habitat tolerances of all three focal species and the ecological relationships between mountain lion and mule deer. Because of the observed interspecific overlap when criteria were relaxed for mountain lion and our desire to maintain quantitative consistency among the three focal species, we adhered to a definition of “most permeable” as only the top 1% of modeled results. It should be noted, however, that even small increases in the output percentage criteria leads to inclusions of additional paths for each species, with all “least cost paths” broadly overlapping.

American badger (*Taxidea taxus*)

Justification for Selection: The Badger is a highly specialized species that requires open habitats with suitable soils for excavating large burrows (de Vos 1969, Banfield 1974, Zeiner et al. 1990, Sullivan 1996). Badgers require expansive wildlands to survive and are highly sensitive to habitat fragmentation. In fact, roadkill is the primary cause of mortality (Long 1973, Zeiner et al. 1990, Sullivan 1996).



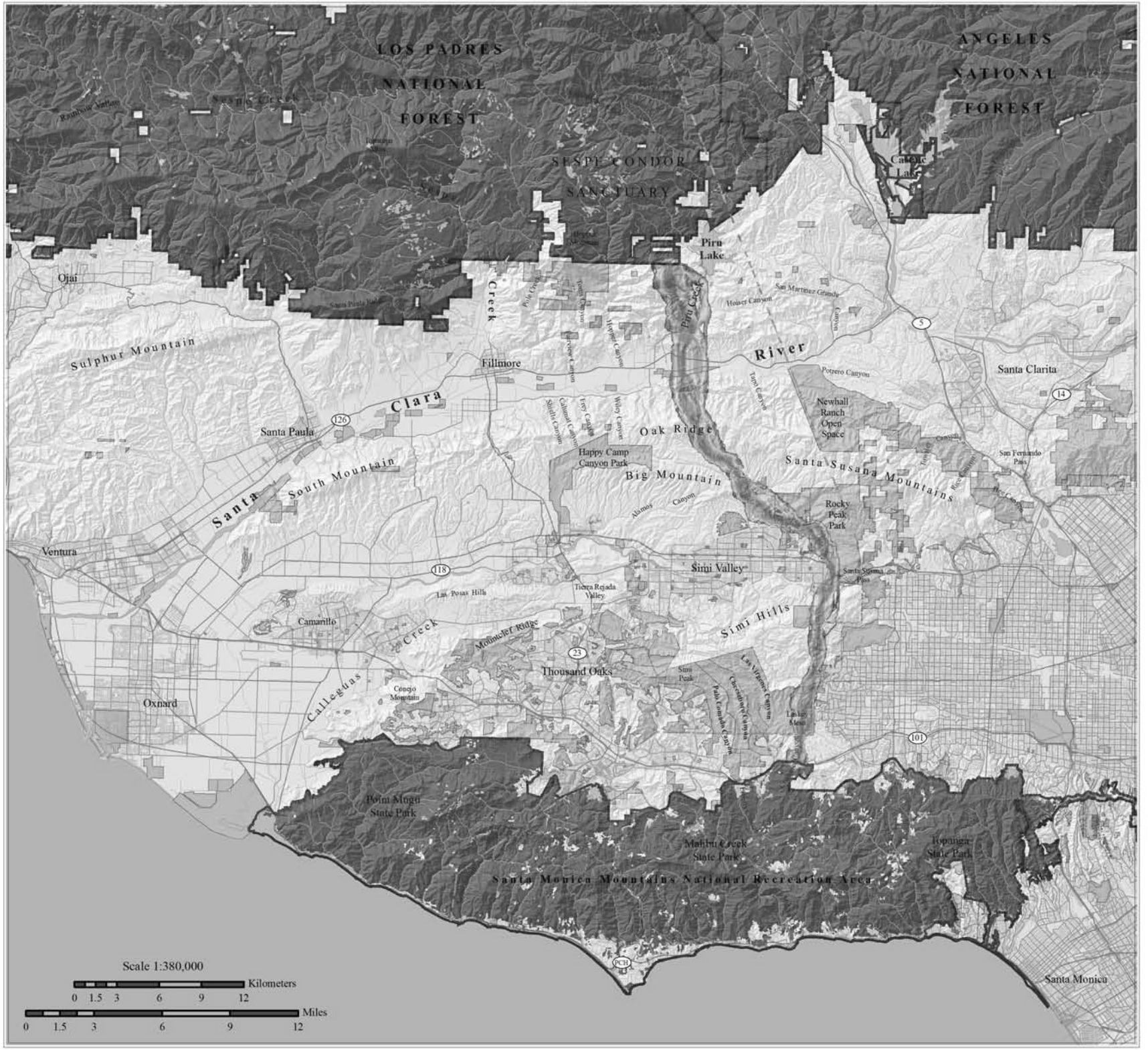
Conceptual Basis for Model Development: Badgers are associated with grasslands, prairies, and other open habitats that support abundant burrowing rodents (de Vos 1969, Banfield 1974, Sullivan 1996) but they may also be found in drier open stages of shrub and forest communities (Zeiner et al. 1990). They are known to inhabit forest and mountain meadows, marshes, riparian habitats, and desert communities including creosote bush, juniper, and sagebrush habitats (Long and Killingley 1983, Zeiner et al. 1990). The species is typically found at lower elevations (Zeiner et al. 1990) in flat, rolling or steep terrain but it has been recorded at elevations up to 3600 m (12000 ft) (Minta 1993).

Badgers can disperse up to 110 km (68 mi; Lindzey 1978), and preferentially move through open scrub habitats, fields, and pastures, and open upland and riparian woodland habitats. Denser scrub and woodland habitats and orchards are less preferred. They avoid urban and intense agricultural areas. Roads are difficult to navigate safely. Please see Table 2 for model variable scorings for this species. Cost to movement for badger was defined by weighting these inputs as follows:

(Vegetation * 0.55) + (Elevation * 0.10) + (Topography * 0.20) + (Road Density *0.15)

Results & Discussion: One strong movement route emerged from the analysis for badger (Figure 11). The least cost corridor for badger extends from the Santa Monica Mountains and traverses the 101 Freeway at Crummer Canyon; it then heads across the grassland and oak savanna habitats of Laskey Mesa in the Simi Hills to cross the 118 Freeway at Santa Susana Pass and enters Rocky Peak Park. The badger route then heads in a northwest direction to follow the grasslands around the fringes of Simi Valley, then takes Tripas Canyon over to Oak Ridge and then down Smith Canyon, which leads to the Santa Clara River; crossing Highway 126 at Piru Creek and heading up the western bank of Piru Creek toward protected habitats in Los Padres National Forest. The least cost corridor for badger varies in width from 1.5 to 3 km (0.9 to 1.9 mi). It includes the most suitable habitat for this highly specialized species moving between protected cores areas, encompassing the gently sloping topography of the grassland and oak savanna habitats wherever possible.

Figure 11.
Least Cost Corridor
for
American badger
(Taxidea taxus)



Least Cost Corridor

- Highly Permeable
- Less Permeable
- Suitable Habitat*
- Target Areas
- Protected Lands
- Lakes & Reservoirs
- Hydrography
- County Boundary
- Roads

*This analysis was run from medium to high suitable habitat within targeted protected areas.

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Mule deer (*Odocoileus hemionus*)



Justification for Selection: Mule deer were chosen as a focal species in part to help support viable populations of mountain lions, which rely on deer as their primary prey. Deer herds can decline in response to fragmentation, degradation or destruction of habitat from urban expansion, incompatible land uses and other human activities (Ingles 1965, Hall 1981, CDFG 1983). Mule deer are particularly vulnerable to habitat fragmentation by roads; in fact, nationally vehicles kill several hundred thousand deer each year (Romin and Bissonette 1996, Conover 1997, Forman et al. 2003).

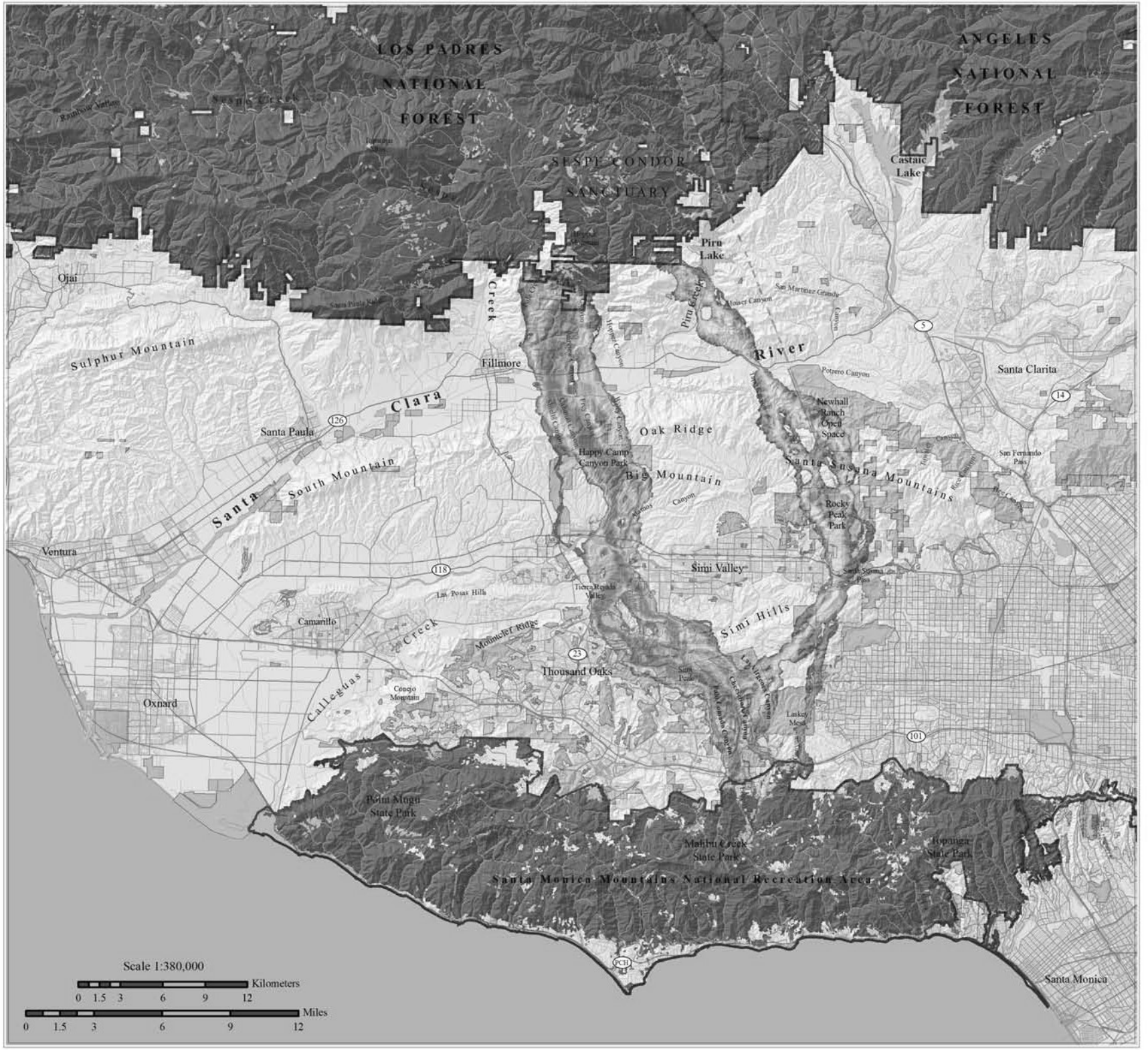
Conceptual Basis for Model Development: Mule deer use forest, woodland, brush, and meadow habitats, and reach their highest densities in oak woodlands, riparian areas, and along edges of meadows and grasslands, although they also occur in open scrub, young chaparral, and low elevation coniferous forests (Bowyer 1986, USFS 2002). Access to a perennial water source is critical in summer.

Dispersal distances of up to 217 km (135 mi) have been recorded for mule deer (Anderson and Wallmo 1984). They preferentially move through habitats that provide good escape cover, preferring ridgetops and riparian routes as major travel corridors. Varying slopes and topographic relief are important for providing shade or exposure to the sun. They avoid open habitats, agricultural and urban land cover, and centers of high human activity, even in suitable habitat. Please see Table 2 for model variable scorings for this species. Cost to movement for mule deer was defined by weighting these inputs as follows:

(Vegetation * 65%) + (Topography * 20%) + (Road Density * 15%)

Results & Discussion: Two potential routes were identified for mule deer traveling between the Santa Monica and Sierra Madre Mountains (Figure 12). The more permeable of the two paths ranges in width from 2 to 6 km (1.2 to 3.7 mi). It extends from Liberty Canyon up Palo Comado and Cheeseboro Canyons to Simi Peak, and through the Tierra Rejada Valley utilizing the coastal sage and grassland habitats between the communities of Simi Valley, Thousand Oaks, and Moorpark. It then traverses the 118 Freeway at Faulker and Alamos Canyons, crosses over Big Mountain and Oak Ridge, and then takes Sheils, Calumat, Frey and Wiley Canyons down to the river and across Highway 126 to follow Pole Creek, Fairview and Toms Canyons into the Los Padres National Forest. The least cost corridor analysis also identified another potential route for mule deer that strongly resembles the output for mountain lion and badger. Both routes encompass medium to highly suitable habitat for mule deer.

Figure 12.
Least Cost Corridor
for
Mule deer
(Odocoileus hemionus)



Least Cost Corridor

- Highly Permeable
- Less Permeable
- Suitable Habitat*
- Target Areas
- Protected Lands
- Lakes & Reservoirs
- Hydrography
- County Boundary
- Roads

*This analysis was run from medium to high suitable habitat within targeted protected areas.

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Although, the permeability models and Least Cost Union delineate swatches of habitat that based on model assumptions and available GIS data are best suited to facilitate species movement between core habitat areas, they do not address whether suitable habitat in the Union occurs in large enough patches to support viable populations or whether patches are close enough together to allow for inter-patch dispersal; and they are based on only three of the 20 focal species. We therefore perform habitat suitability, patch size and configuration analyses to evaluate the configuration and extent of potentially suitable habitat in the Least Cost Union for all 20 focal species. This helps determine whether there is sufficient habitat within the Union to support each species, and whether that habitat is distributed in a pattern that allows the species to move between patches.

Specifically, the patch size and configuration analyses for all 20 focal species addresses, 1) whether the Least Cost Union provides sufficient live-in or move-through habitat to support individuals or populations of the species; 2) whether these habitat patches are within the species' dispersal distance; 3) whether any clearly unsuitable and non-restorable habitat (e.g., developed land) should be deleted from the Union; and 4) for any species not adequately served by the Least Cost Union, whether expanding the Union to incorporate more habitat would meet the species needs. The patch size and configuration analysis does not address existing barriers to movement (such as freeways) or land use practices that may prevent species from moving through the linkage. These issues are addressed in the next section.

The Least Cost Union contains suitable habitat to support either inter- or intra-generational movements between the Santa Monica and Sierra Madre ranges for 17 of the 20 modeled focal species: mountain lion, badger, mule deer, brush rabbit, desert woodrat, loggerhead shrike, California thrasher, acorn woodpecker, western toad, California kingsnake, coastal whiptail, chalcedon checkerspot butterfly, harvester ant, scorpion, California black walnut, Valley oak, and Bigberry manzanita. Outputs from the patch configuration analyses suggest that habitat patches in the Union are not isolated by distances too great for any of the focal species to disperse.

Three focal species appear to require additional habitat outside of the Least Cost Union for the Linkage Design to serve their movement needs: southern steelhead trout, cactus wren, and damselflies. To ensure that the Linkage Design accommodates all focal species, habitat was added to the Union in six general areas (Figure 13):

Conejo Mountain & Mountclef Ridge: This connection is dominated by coastal sage scrub and extends from the western Santa Monica Mountains over Conejo Mountain and Mountclef Ridge to the Tierra Rejada Valley. This addition was necessary to accommodate cactus wren, brush rabbit, desert woodrat, and western toad movement, but the majority of other focal species will also benefit from this connection, as will many other native species not specifically addressed by our analyses. Much of this area has already been conserved, so we added contiguous natural habitats where available and agricultural lands where necessary to achieve a minimum corridor width of 2 km making it more robust to edge effects.

Santa Clara River Mainstem: The Union was also modified to include riparian and upland habitat along the mainstem of the Santa Clara River from the coast to the eastern boundary of the Linkage Design to preserve a critical migration corridor for southern steelhead trout to reach its spawning and rearing grounds in Santa Paula, Sespe, and Piru Creek. This addition also provides habitat and connectivity for western toad, California kingsnake, and damselflies, and numerous other native species will benefit from this addition. The connection includes a 2-km (1.2-mi) riparian buffer (1 km to either side of the wash) to protect water quality within the linkage and downstream.

Santa Paula Creek: To accommodate southern steelhead trout and other species that use riparian habitats, the Union was modified to include Santa Paula Creek from its confluence with the Santa Clara River to the boundary of Los Padres National Forest. We also delineated a 2-km riparian buffer along the creek where best management practices should be implemented and restoration efforts undertaken.

Sespe Creek: The Union was also modified to include Sespe Creek from its confluence with the Santa Clara River to the Los Padre National Forest boundary for southern steelhead trout. Numerous other focal species that use riparian habitats will also benefit from this addition, as will several other native species not addressed by our analyses. A 2-km wide riparian buffer was delineated to identify areas to focus habitat restoration efforts to improve habitat conditions and water quality.

Piru Creek: The Union was also modified to include the southern reaches of Piru Creek where it meets the Santa Clara River for southern steelhead trout and damselflies. Other species that use riparian habitats will also benefit from this addition.

San Fernando Pass: The San Fernando Pass is dominated by oak woodlands and savannas, coastal sage scrub, and chaparral, with walnut woodland and grasslands interspersed. This connection extends from the eastern Santa Susana Mountains, through the San Fernando Pass to the San Gabriel Mountains of the Angeles National Forest. Although our analyses were primarily focused on identifying a connection between the Santa Monica and Sierra Madre Ranges, it was evident from the results of the analyses that 18 out of the 20 focal species would benefit from maintaining connectivity through the pass. The San Fernando Pass was also previously identified as important for 11 of the 15 focal species modeled for the San Gabriel-Castaic Connection (Penrod et al. 2004). Consequently, this area was added to the Least Cost Union to provide broader regional connectivity to adjacent Missing Linkages Project study areas and remain consistent with the habitat needs of the focal species.

We deleted some areas of the Least Cost Union on the eastern side of the Tierra Rejada Valley that have already been converted to urban uses.

Figure 13.
Least Cost Union
Additions & Subtractions



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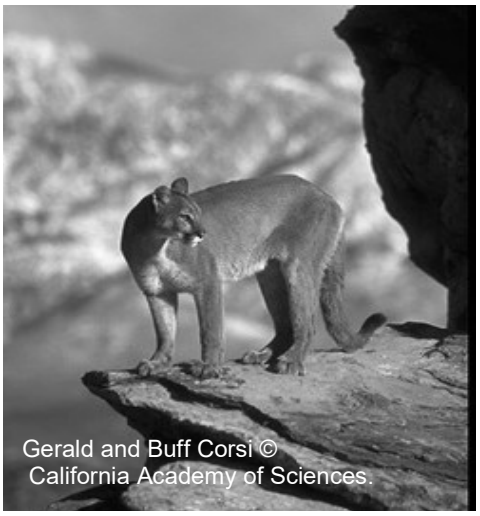
Mountain lion (*Puma concolor*)


Gerald and Buff Corsi ©
California Academy of Sciences.

Distribution & Status: Mountain lions (also known as puma or cougar) are widely distributed throughout the western hemisphere (Chapman and Feldhamer 1982, Currier 1983, Maehr 1992, Tesky 1995). The subspecies *F. c. californica* occurs in southern Oregon, California, and Nevada (Hall 1981), typically between 590-1,780 m (1,980-5,940 ft) in elevation (Zeiner et al. 1990). Since 2002, National Park Service scientists at Santa Monica Mountains National Recreation Area have been studying the ecology, behavior, and conservation of mountain lions in the Santa Monica Mountains, Simi Hills, and Santa Susana Mountains (Riley et al. 2006). Specific study objectives include determining how mountain lions use habitats across the region and specifically if mountain lions traverse between the highly fragmented habitats that remain, including across major roads and highways. To the extent that it has been possible, we have drawn upon the results from this ongoing work for information about conservation requirements for mountain lions in the planning area.

In 1990, the mountain lion population in California was estimated to be between 2,500-5,000 individuals. That same year, Proposition 117 was passed which prohibited hunting and granted puma the status of a California Specially Protected species, though depredation permits are still issued (Torres 2000).

Habitat Associations: The mountain lion is a habitat generalist, utilizing many brushy or forested habitats providing good cover (Spowart and Samson 1986, Zeiner et al. 1990). They use rocky cliffs, ledges, and vegetated ridgetops that provide cover when hunting prey (Chapman and Feldhamer 1982, Spowart and Samson 1986), especially mule deer, *Odocoileus hemionus* (Lindzey 1987). Den sites may be located on cliffs, rocky outcrops, caves, in dense thickets, or under fallen logs (Ingles 1965, Chapman and Feldhamer 1982). In southern California, most cubs are reared in thick brush (Beier et al. 1995). Mountain lions prefer vegetated ridgetops and stream courses as travel corridors and hunting routes (Spowart and Samson 1986, Beier and Barrett 1993), although movements across a variety landscape features has been documented (Riley et al. 2006).

Spatial Patterns: Home range size varies by sex, age, and the distribution of prey. A recent study in the Sierra Nevada documented annual home range sizes between 250 and 817 km^2 (61,776-201,885 ac; Pierce et al. 1999). Home ranges in southern California averaged 93 km^2 (22,981 ac) for 12 adult females and 363 km^2 (89,699 ac) for two adult males (Dickson et al. 2004). Male home ranges appear to reflect the density and distribution of females (Maehr 1992). Males occupy distinct areas and are tolerant of transients of both sexes, while the home range of females may overlap completely (Zeiner et al. 1990, Beier and Barrett 1993). Regional population counts have not been conducted but in the Santa Ana Mountain Range, Beier (1993) estimated about 1.05-1.2

adults per 100 km^2 (24,711 ac). Based on the ongoing studies of Riley et al. (2006), a small population of approximately four to eight individuals may occur in the Santa Monica Mountains south of the 101 Freeway.

Mountain lions are capable of long-distance movements, and often move in response to changing prey densities (Pierce et al. 1999). Beier et al. (1995) found mountain lions moved 6 km (3.7 mi) per night and dispersed up to 65 km (40 mi). Dispersal plays a crucial role in cougar population dynamics, because recruitment into a local population occurs mainly by immigration of juveniles from adjacent populations, while the population's own offspring emigrate to other areas (Beier 1995, Sweanor et al. 2000). Juvenile dispersal distances average 32 km (20 mi) for females and 85 km (53 mi) for males, with one male dispersing 274 km (170 mi; Anderson et al. 1992). Dispersing lions may cross large expanses of nonhabitat, though they prefer not to do so (Logan and Sweanor 2001). To allow for dispersal of juveniles and the immigration of transients, lion management should be on a regional basis (Sweanor et al. 2000, Riley et al. 2006).

Conceptual Basis for Model Development: Puma will use most habitats above 590 m (1,936 ft) elevation provided they have cover (Spowart and Samson 1986, Zeiner et al. 1990). Road density is also a significant factor in habitat suitability for mountain lions. Core areas potentially supporting 50 or more individuals were modeled using patches $\geq$ 10,000 km^2 (2,471,053 ac). Patch size was classified as $\geq$ 200 km^2 (49,421 ac) but < 10,000 km^2. Dispersal distance for puma was defined as 548 km (340 mi), or twice the maximum reported dispersal distance of 274 km (170 mi).

Results & Discussion*:* All branches of the Least Cost Union contain suitable mountain lion habitat, with the eastern branch containing the most highly suitable contiguous habitat for lions moving between protected core areas (Figure 14). The habitat suitability model predicted low to medium suitable habitat in the vicinity of Laskey Mesa. However, given that dispersing lions may cross large expanses of non-habitat (Logan and Sweanor 2001); we conclude that the Least Cost Union is likely to serve this species. All potential cores and patches of suitable habitat are within the dispersal distance of this species (figure not shown). The patch size analysis for mountain lion (Figure 15) emphasizes the importance of maintaining connectivity between these ranges, as the Santa Monica, Simi Hills, and Santa Susana Mountains combined aren't large enough to support a minimum viable population, relying on an influx of individuals from core habitats in the Sierra Madre Ranges to sustain the population.

This species requires expansive roadless areas to survive and functional connectivity between subpopulations. In October 2004, NPS scientists found that two of the mountain lions they'd been tracking (P1 and P2) had produced a litter of four kittens (Riley et al. 2006). Current NPS research is now focused on monitoring the movements and dispersal routes of these four young lions because it is expected that, for at least the two males, they will need to disperse beyond the Santa Monica Mountains in order to establish individual and non-overlapping home ranges (Riley et al. 2006). Maintaining connections between large blocks of protected habitat may be the most effective way to ensure population viability (Beier 1993, 1995, Gaona et al. 1998, Riley et al. 2003, Riley et al. 2006). To maintain and protect habitat connections for mountain lions, we recommend that:

Figure 14.
Habitat Suitability
for
Mountain lion
(Puma concolor)

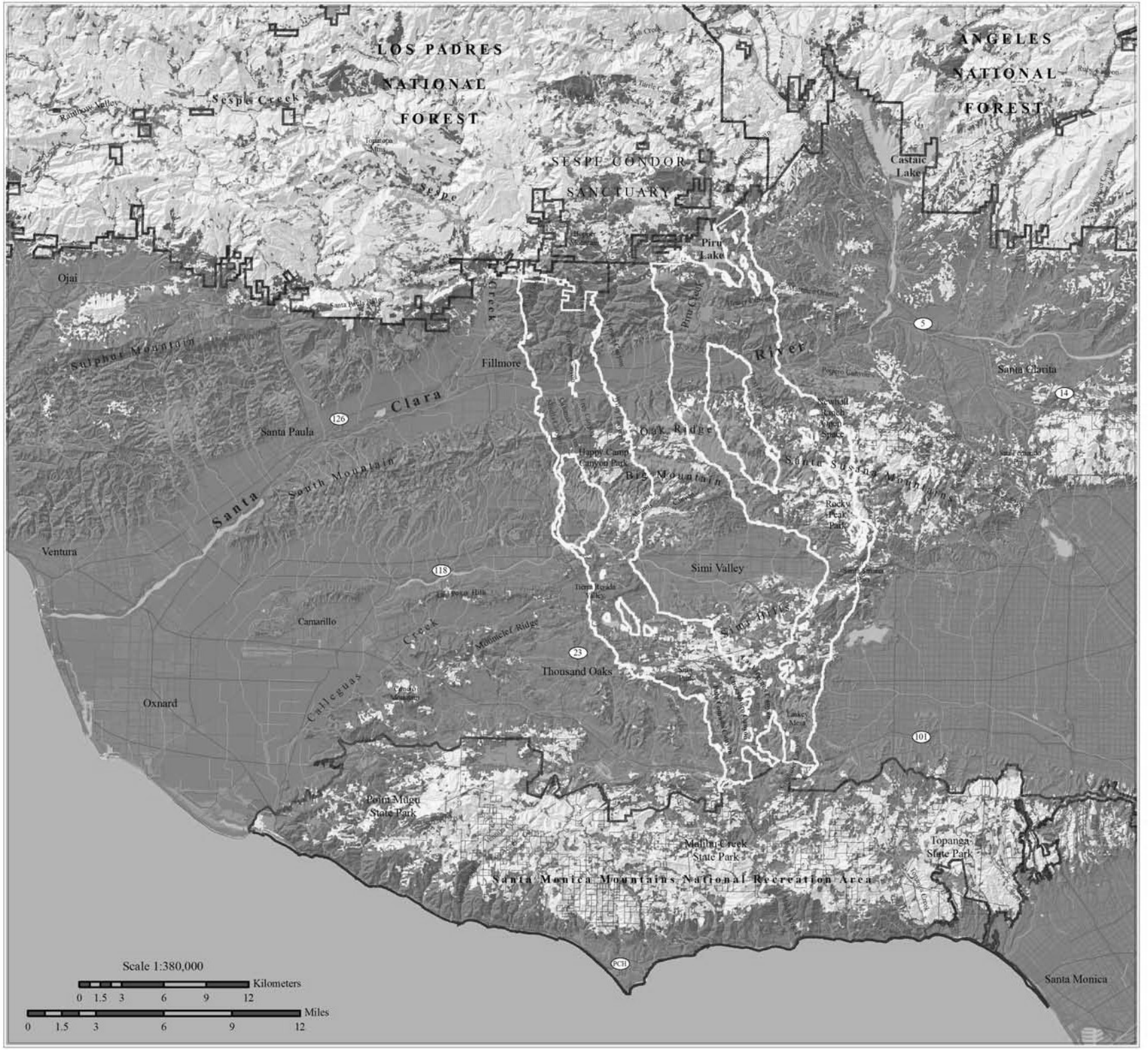


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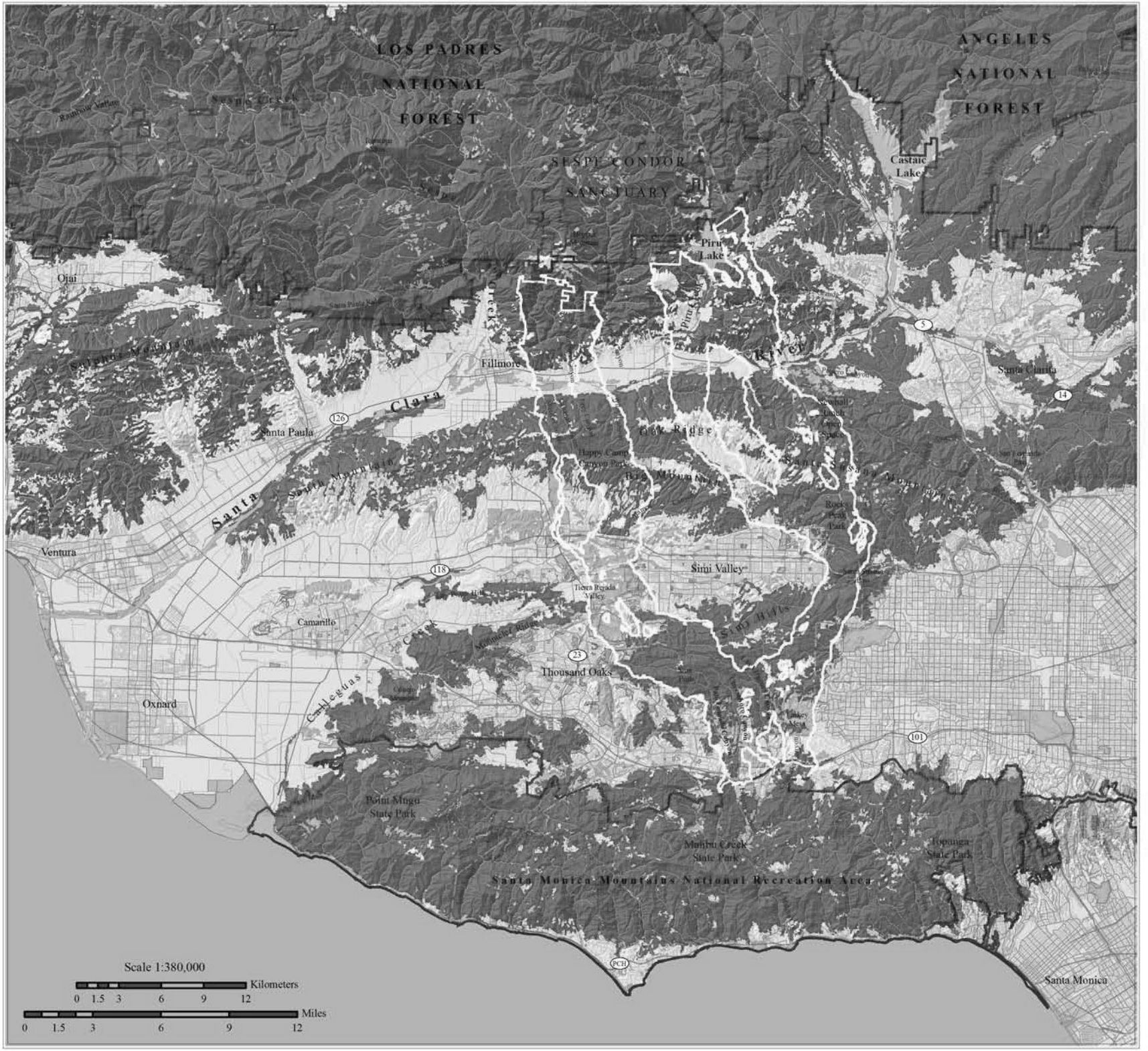
Figure 15.
Potential Cores & Patches
for
Mountain lion
(Puma concolor)



Core
Patch
< Patch
Protected Lands
Least Cost Union
Target Areas
Lakes & Reservoirs
Hydrography
County Boundary
Roads

N

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- Existing road density be maintained or reduced in the Linkage Design. When transportation improvement projects do occur, planners should incorporate crossing structures to facilitate mountain lion movement across transportation barriers, particularly for multi-lane freeways such as Highways 101 and 118 (see Linkage Design Section).

- Lighting is directed away from the linkage and crossing structures. Species sensitive to human disturbance, like puma, avoid areas that are artificially lit (Beier 1995, Rich and Longcore 2006).

- Local residents are informed about the important role of carnivores to the system, the use of predator safe enclosures for domestic livestock and pets, and the habits of being thoughtful and safe stewards of the land.

American badger (*Taxidea taxus*)


Gerald and Buff Corsi © CA Academy of Sciences

Distribution & Status: Once a fairly widespread resident in open habitats of California, the badger is now uncommon throughout the state and is considered a California Species of Special Concern (Zeiner et al. 1990, CDFG 1995).

Habitat Associations: Badgers are habitat specialists, associated with grasslands, prairies, and other open habitats (de Vos 1969, Banfield 1974, Sullivan 1996) but they may also be found in drier open stages of shrub and forest communities (Zeiner et al. 1990). They are known to inhabit forest and mountain meadows, marshes, riparian habitats, and desert communities including creosote bush, juniper, and sagebrush habitats (Long and Killingley 1983, Zeiner et al. 1990). They are occasionally found in open chaparral (< 50% cover) but haven't been documented in mature stands of chaparral (Quinn 1990, Zeiner et al. 1990). Badgers prefer friable soils for excavating burrows and require abundant rodent populations (de Vos 1969, Banfield 1974, Sullivan 1996). The species is typically found at lower elevations (Zeiner et al. 1990) in flat, rolling, or steep terrain but it has been recorded at elevations up to 3,600 m (12,000 ft; Minta 1993).

Spatial Patterns: Home range sizes for this species vary both geographically and seasonally. Depending on location, male home ranges have been estimated to vary from 240-850 ha (593-2,100 ac) while females ranged from 137-725 ha (339-1,792 ac; Long 1973, Lindzey 1978, Messick and Hornocker 1981, Zeiner et al. 1990). In northwestern Wyoming, home ranges up to 2,100 ha (5,189 ac) have been reported (Minta 1993). In Idaho, home ranges of adult females and males averaged 160 ha (395 ac) and 240 ha (593 ac) respectively (Messick and Hornocker 1981). In Minnesota, Sargeant and Warner (1972) radio-collared a female badger, whose overall home range encompassed 850 ha (2,100 ac). However, her home range was restricted to 725 ha (1,792 ac) in summer, 53 ha (131 ac) in autumn and to a mere 2 ha (5 ac) in winter. In Utah, Lindsey (1978) found fall and winter home ranges of females varied from 137-304 ha (339-751 ac), while males varied from 537-627 ha (1,327-1,549 ac). Males may double movement rates and expand their home ranges during the breeding season to maximize encounters with females (Minta 1993). Lindzey (1978) documented natal dispersal distance for one male at 110 km (68 mi) and one female at 51 km (32 mi). A short-term pilot study of five badgers using radio telemetry in the Santa Monica Mountains found similar home range sizes and spatial patterns (Lupis et al. 1999).

Conceptual Basis for Model Development: Badgers prefer grasslands, meadows, open scrub, desert washes, and open woodland communities. Terrain may be flat, rolling or steep, but below 3,600 m (12,000 ft) elevation. Core areas capable of supporting 50 badgers are equal to or greater than 16,000 ha (39,537 ac). Patch size is $\geq$ 400 ha (988 ac) but < 16,000 ha. Dispersal distance for badgers was defined as 220 km (136 mi), twice the longest recorded dispersal distance (Lindzey 1978).

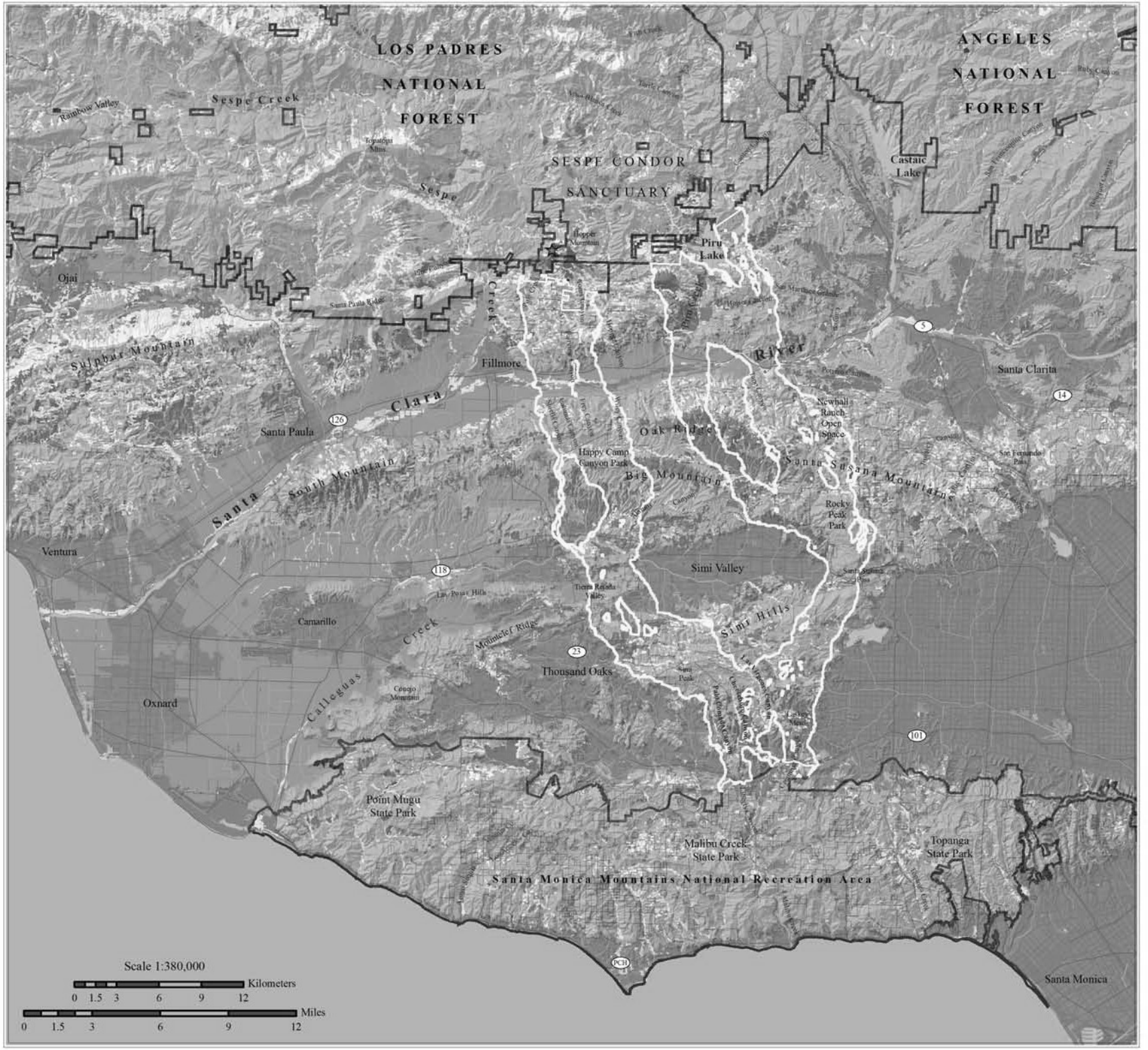
Results & Discussion: The model identified abundant suitable habitat for badger in the planning area, with the most highly suitable habitat in the central branch and the most contiguous habitat in the eastern branch of the Least Cost Union (Figure 16). The central branch contains extensive open grassland habitat that is preferred by this species and was delineated as the least cost corridor for badger (Figure 11). Although not included in the Least Cost Union, contiguous suitable habitat also extends from the western Santa Monica Mountains over Conejo Mountain and Mountclef Ridge to the Tierra Rejada Valley (Figure 16). The majority of suitable habitat within the planning area is contiguous, and thus was identified as core habitat for this species (Figure 17). All potential habitat is within badger's dispersal distance (figure not shown), although barriers to movement may exist between suitable habitat patches. The linkage is likely to serve the movement needs of this wide-ranging species.

Road mortality is the leading cause of death of badgers. Badger roadkill has been documented on Highway 118 at Santa Susana Pass (P. Edelman, pers. comm.) and along roads within the Tierra Rejada Valley (R. Sauvajot, pers. comm.). To restore and protect habitat connections for badger, we recommend that:

- Existing road density be maintained or reduced in the Linkage Design. When transportation improvement projects do occur, planners should incorporate crossing structures to facilitate badger movement across transportation barriers (see Linkage Design Section).

- Lighting is directed away from the linkage and crossing structures (Rich and Longcore 2006).

Figure 16.
Habitat Suitability
for
American badger
(Taxidea taxus)



Degree of Suitability

- High
- Medium to High
- Medium
- Low to Medium
- Low
- ★ Recorded Occurrence*
- Protected Lands
- Least Cost Union
- Target Areas
- Lakes & Reservoirs
- Hydrography
- County Boundary
- Roads

*Data Source: CNDDB

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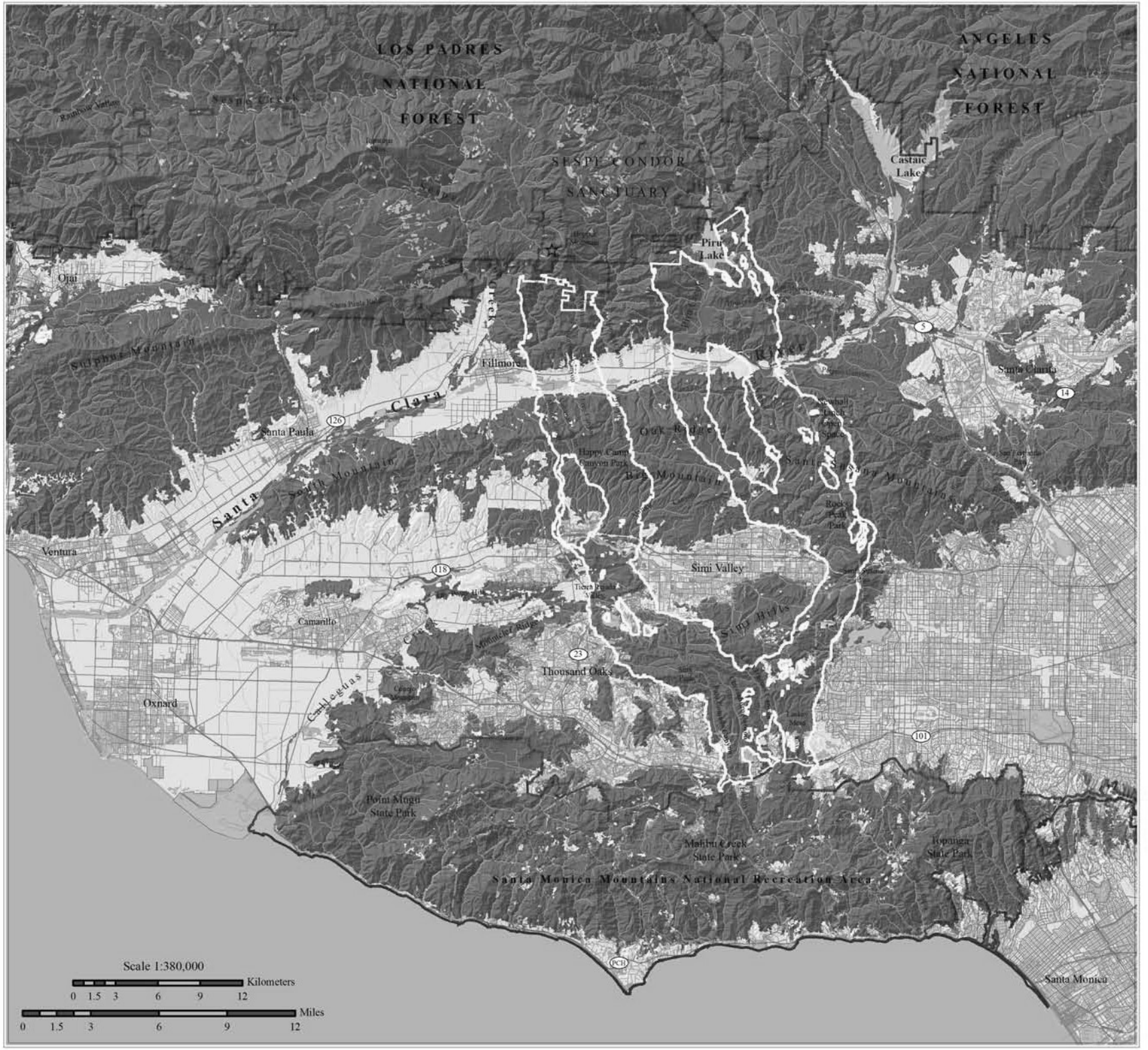
Figure 17.
Potential Cores & Patches
for
American badger
(Taxidea taxus)



- Core
- Patch
- < Patch
- ★ Recorded Occurrence*
- Protected Lands
- Least Cost Union
- Target Areas
- Lakes & Reservoirs
- Hydrography
- County Boundary
- Roads

*Data Source: CNDDB

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Mule deer (*Odocoileus hemionus*)


Photo Courtesy of USFWS

Distribution & Status: Mule deer are widespread in California and are common to abundant in appropriate habitat; they are absent from areas with no cover (Longhurst et al. 1952, Ingles 1965, Zeiner et al. 1990). Mule deer are classified by CDFG as a big game animal.

Habitat Associations: This species requires a mosaic of habitat types of different age classes to meet its life history requirements (CDFG 1983). They use forest, woodland, brush, and meadow habitats, reaching their highest densities in oak woodlands, riparian areas, and along edges of meadows and grasslands (Bowyer 1986, USFS 2002). They also occur in open scrub, young chaparral and low elevation coniferous forests (Bowyer 1981, 1986, USFS 2002). A variety of brush cover and tree thickets interspersed with meadows and shrubby areas are important for food and cover. Thick cover can provide escape from predators, shade in the summer, or shelter from wind, rain and snow. Varying slopes and topographic relief are important for providing shade or exposure to the sun. Fawning occurs in moderately dense chaparral, forests, riparian areas, and meadow edges (CDFG 1983). Meadows are particularly important as fawning habitat (Bowyer 1986, USFS 2002).

Spatial Patterns: Home ranges typically comprise a mosaic of habitat types that provide deer with various life history requirements. Home range estimates vary from 39 ha (96 ac; Miller 1970) to 3,379 ha (8,350 ac; Severson and Carter 1978, Anderson and Wallmo 1984, Nicholson et al. 1997). Harestad and Bunnell (1979) calculated mean home range from several studies as 285.3 ha (705 ac). Doe and fawn groups have smaller home ranges, averaging 100-300 ha (247-741 ac), but can vary from 50 to 500 ha (124-1,236 ac; Taber and Dasmann 1958, CDFG 1983). Bucks usually have larger home ranges and are known to wander greater distances (Brown 1961, Zeiner et al. 1990). A recent study of 5 different sites throughout California, recorded home range sizes from 49 to 1,138 ha (121-2,812 ac; Kie et al. 2002).

Where deer are seasonally nomadic, winter and summer home ranges tend to largely overlap in consecutive years (Anderson and Wallmo 1984). Elevational migrations are observed in mountainous regions in response to extreme weather events in winter, or to seek shade and perennial water during the summer (Loft et al. 1998, CDFG 1983, Nicholson et al.1997, USFS 2002). Distances traveled between winter and summer ranges vary from 8.6 to 29.8 km (5.3-19 mi; Gruell and Papez 1963, Bertram and Rempel 1977, Anderson and Wallmo 1984, Nicholson et al. 1997). Robinette (1966) observed natal dispersal distances ranging from 97 to 217 km (60-135 mi).

Conceptual Basis for Model Development: Mule deer utilize a broad range of habitats, reaching their highest densities in oak woodlands. They require access to perennial water. Core areas potentially supporting 50 or more deer are equal to or

greater than 16,000 ha (39,537 ac). Patch size was classified as ≥ 100 ha (247 ac) but < 16,000 ha. Dispersal distance was defined as 434 km (270 mi), or twice the maximum distance recorded.

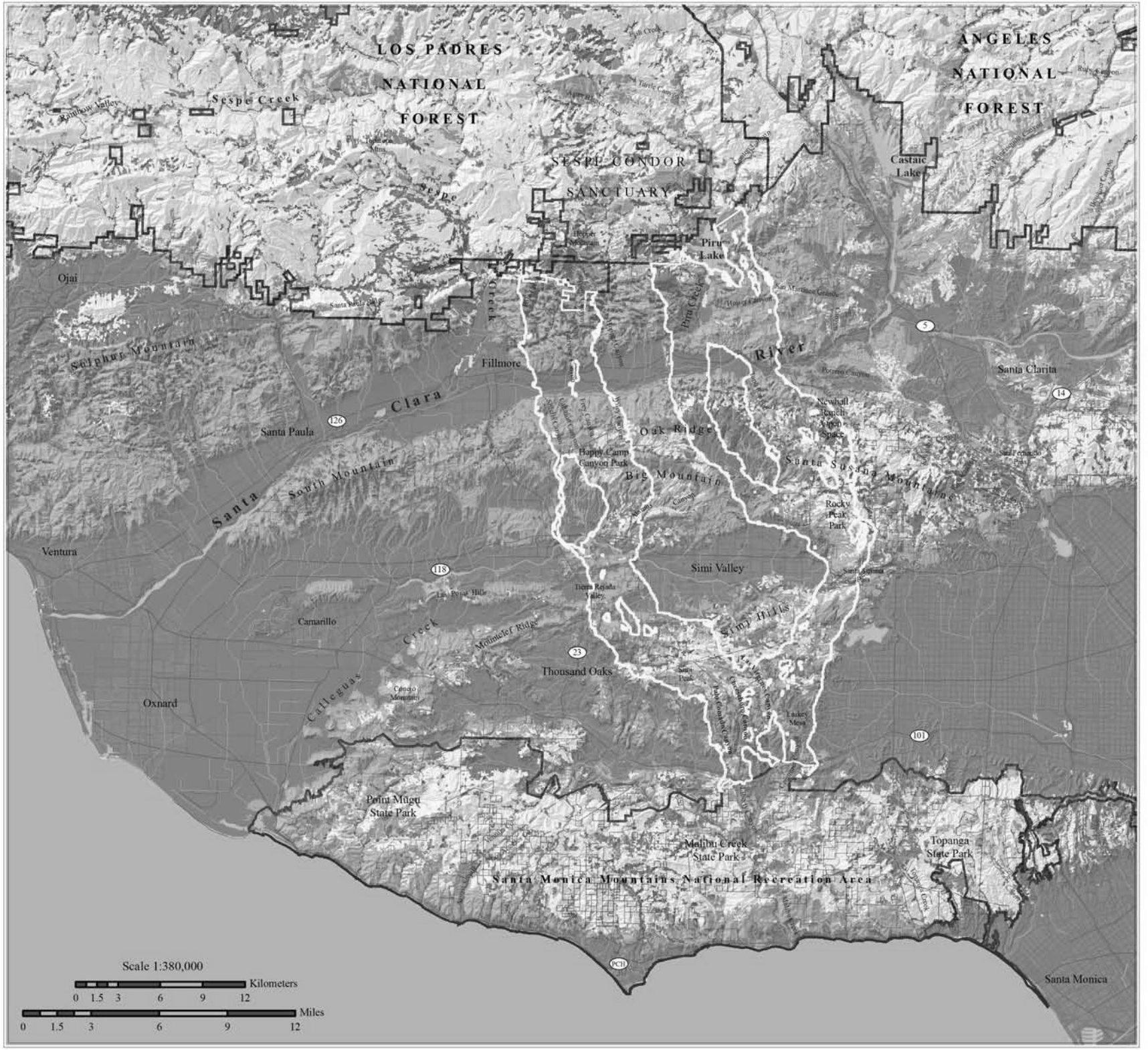
Results & Discussion: All branches of the Least Cost Union contain suitable habitat for mule deer, with the western and eastern branches providing the most contiguous connections (Figure 18). Although not included in the Union, highly suitable contiguous core habitat also extends from the western Santa Monica Mountains over Conejo Mountain and Mountclef Ridge to the Tierra Rejada Valley (Figures 18, 19). The majority of suitable habitat in the planning area was identified as potential core areas for mule deer, with all habitat in the Union identified as core areas except the area around Tierra Rejada Valley and an area along the Santa Clara River in the western branch of the Union (Figure 19). All core areas and patches of suitable habitat are within the dispersal distance of this species (figure not shown), although barriers to movement may exist between suitable habitat patches. We conclude that the linkage will likely serve the needs of mule deer traveling between these ranges.

Estimates of the number of deer killed annually on U.S. roads ranges from 720,000 to 1.5 million (Romin and Bissonette 1996, Conover 1997, Forman et al. 2003). Collisions with deer also result in the loss of human lives (Reed et al. 1975). To restore and protect habitat connections for mule deer, we make the following recommendations:

- Road barriers should be modified to accommodate mule deer movement. Though ungulates much prefer overpasses to underpasses (Gloyne and Clevenger 2001), they will utilize bridged undercrossings if they can see clearly to the other side. Crossing structures for mule deer should have natural flooring and no artificial lighting (Reed et al. 1975).

- Fencing (up to 4 m [12 feet] high) should be installed to reduce roadkill and guide deer to crossing structures. Escape ramps may also be installed in case deer get caught within road right-of-ways (Forman et al. 2003).

Figure 18.
Habitat Suitability
for
Mule deer
(Odocoileus hemionus)



Degree of Suitability

- High
- Medium to High
- Medium
- Low to Medium
- Low
- Protected Lands
- Least Cost Union
- Target Areas
- Lakes & Reservoirs
- Hydrography
- County Boundary
- Roads

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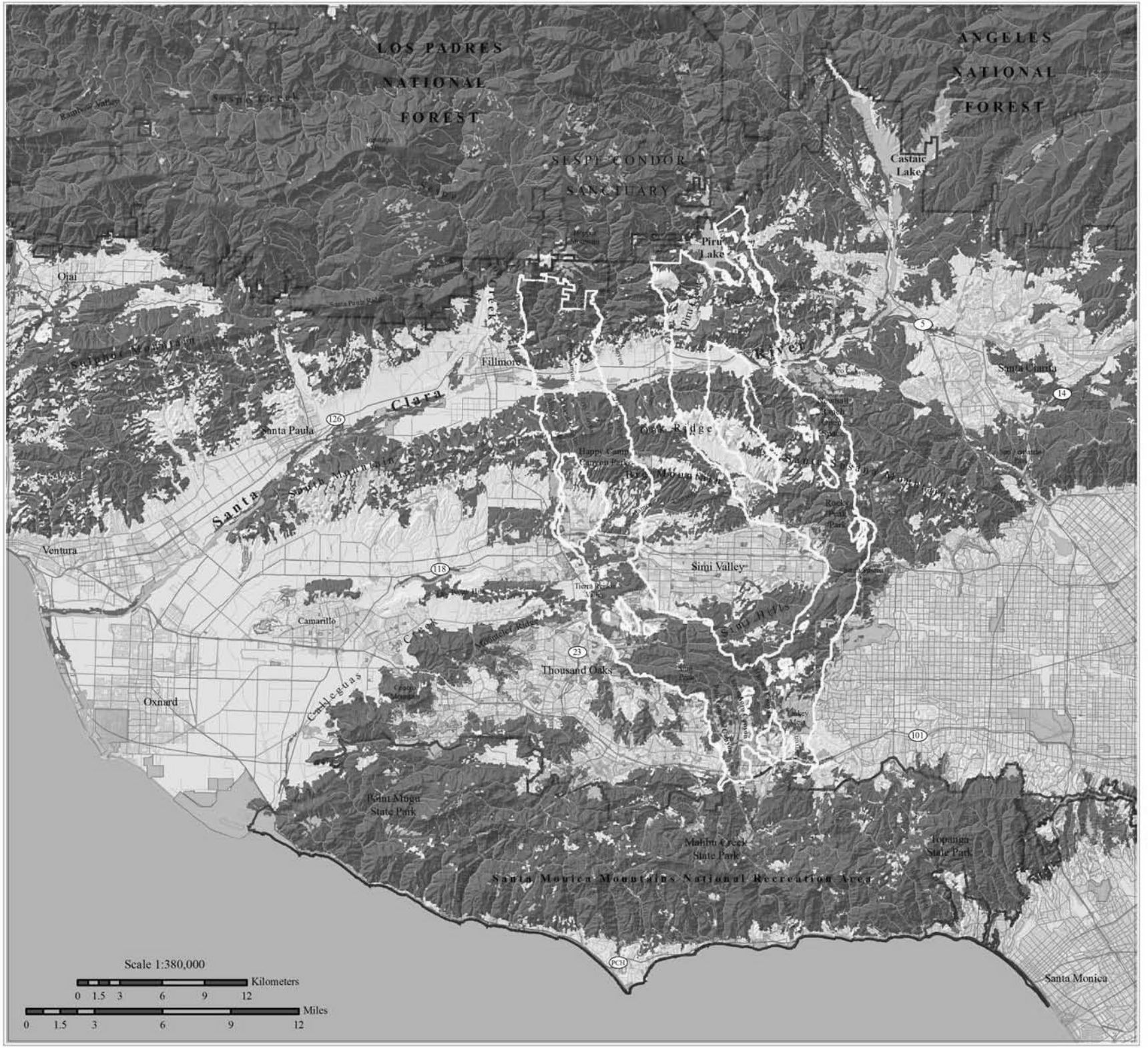
Figure 19.
Potential Cores & Patches
for
Mule deer
(Odocoileus hemionus)



Core
Patch
< Patch
Protected Lands
Least Cost Union
Target Areas
Lakes & Reservoirs
Hydrography
County Boundary
Roads

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Brush rabbit (*Sylvilagus bachmani*)



Justification for Selection: Brush rabbits are sensitive to habitat loss and fragmentation. Small, isolated habitat patches aren't likely to support viable populations of brush rabbits (Chapman 1971).

Distribution & Status: The brush rabbit occurs west of the Cascades and Sierra Nevadas from southern Oregon to Baja California, Mexico, excluding the dry Central Valley and southern arid regions (Hall 1981, Zeiner et al. 1990). Their elevational range extends from sea level to 2,070 m (6,791 ft; Chapman 1974).

The brush rabbit that occurs in the study area is not a special status species. However, the subspecies *riparius* of the San Joaquin Valley, California, is listed under the U.S. Endangered Species Act as endangered (USFWS 2000).

Habitat Associations: Brush rabbits may occur in riparian, coastal sage scrub, chaparral, grassland, and oak woodland habitats, but they are most commonly found in the dense, brushy cover of chaparral vegetation (Chapman 1974). They may also occur in early successional stages of oak and conifer habitats (Zeiner et al. 1990). They feed on a wide variety of grasses and forbs in grasslands, meadows, and riparian areas, but are never far from dense brushy cover (Orr 1940, Zeiner et al. 1990). Connell (1954) found that brush rabbits concentrate their activities at the edge of brush, suggesting that ecotonal habitat is better than continuous chaparral.

Spatial Patterns: In California, male home ranges averaged 1.5 ha (3.8 ac), and home ranges for females averaged 0.5 ha (1.3 ac; Connell 1954, Shields 1960). In Oregon, home ranges varied between .2 and .8 ha (.5 to 2.0 ac; Chapman 1971). Home ranges often conform to the size and shape of cover patches. Males apparently are not territorial; home ranges overlap. Females sometimes protect areas; Connell (1954) and Shields (1960) reported female territories 12-173 m (38-569 ft) in diameter.

Dispersal potential, though poorly documented, may be considerable. For example, a female eastern cottontail (*S. floridanus*) escaped from an enclosure and returned to its original capture site 3.7 km (2.3 mi) away (Hill 1967, Cannings and Hammerson 2004). A radio telemetry study of orientation and homing by brush rabbits in Oregon found homing ability extends up to 350 m (1,150 ft), and homing routes were largely restricted to brushy cover regardless of the direction or distance (Chapman 1971).

Conceptual Basis for Model Development: Movement in the linkage is assumed to be multigenerational. Brush rabbits may utilize a broad range of vegetation communities, reaching their highest densities in chaparral habitats. Potential core areas

are equal to or greater than 38 ha (94 ac). Patch size was classified as ≥ 1 ha (2.47 ac) but < 38 ha. Dispersal distance was defined as 700 m (2,297 ft), or twice the maximum homing distance recorded.

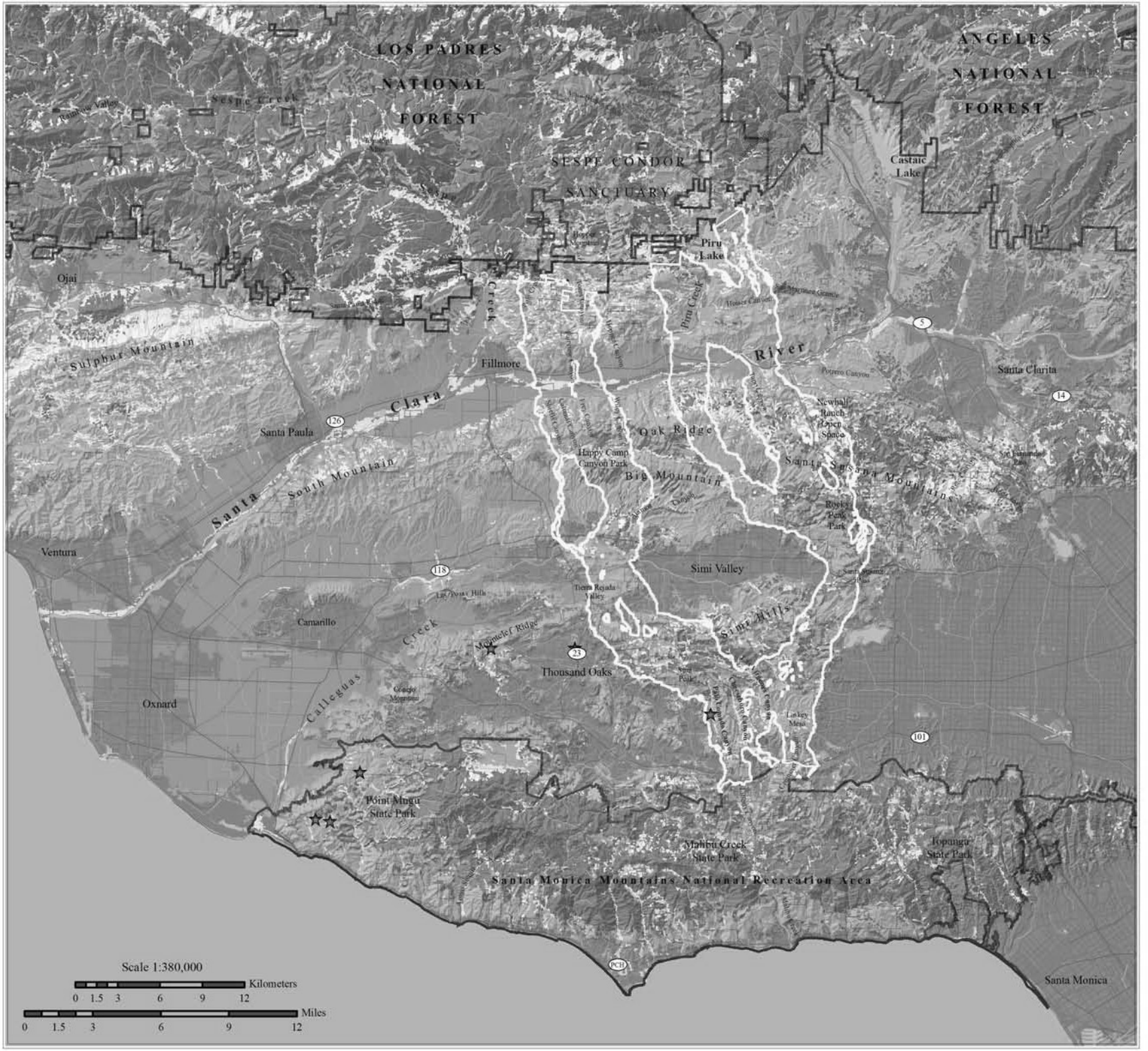
Results & Discussion: All branches of the Least Cost Union contain highly suitable habitat for brush rabbit (Figure 20). Although not included in the Union, highly suitable contiguous core habitat also extends from the western Santa Monica Mountains over Conejo Mountain and Mountclef Ridge to the Tierra Rejada Valley (Figures 20, 21). This species has been recorded in Palo Comado Canyon in the Union and on Mount Clef Ridge. The majority of suitable habitat identified in the planning area was delineated as potential core areas for brush rabbit, with all habitats in the Union identified as core habitat (Figure 21). All core areas and patches of suitable habitat are within the dispersal distance of this species (figure not shown), although barriers to movement may exist between suitable habitat patches. We conclude that the linkage will likely serve the needs of brush rabbit if habitat is added to the Union on Conejo Mountain and Mount Clef Ridge.

Little is known about the effects of habitat loss and fragmentation on the viability of brush rabbit populations. A computer simulation study of *S. transitionalis* metapopulations in response to habitat loss and environmental correlations (based on increased vulnerability to predation) showed a rapid decline or extinction of populations (Litvaitus and Villafuerte 1996). To maintain habitat connections and habitat suitability (e.g., maintaining early successional habitat) for brush rabbit, we recommend that:

- Crossing structures for small mammals be placed fairly frequently to facilitate movement across major transportation routes.

- Fire frequency is controlled to prevent type conversion of scrub habitats to nonnative annual grassland (Winter 2003).

Figure 20.
Habitat Suitability
for
Brush rabbit
(Sylvilagus bachmanni)



Degree of Suitability

- High
- Medium to High
- Medium
- Low to Medium
- Low
- ★ Recorded Occurrence*
- Protected Lands
- Least Cost Union
- Target Areas
- Lakes & Reservoirs
- Hydrography
- County Boundary
- Roads

*Data Source: National Park Service Ecological Monitoring Data

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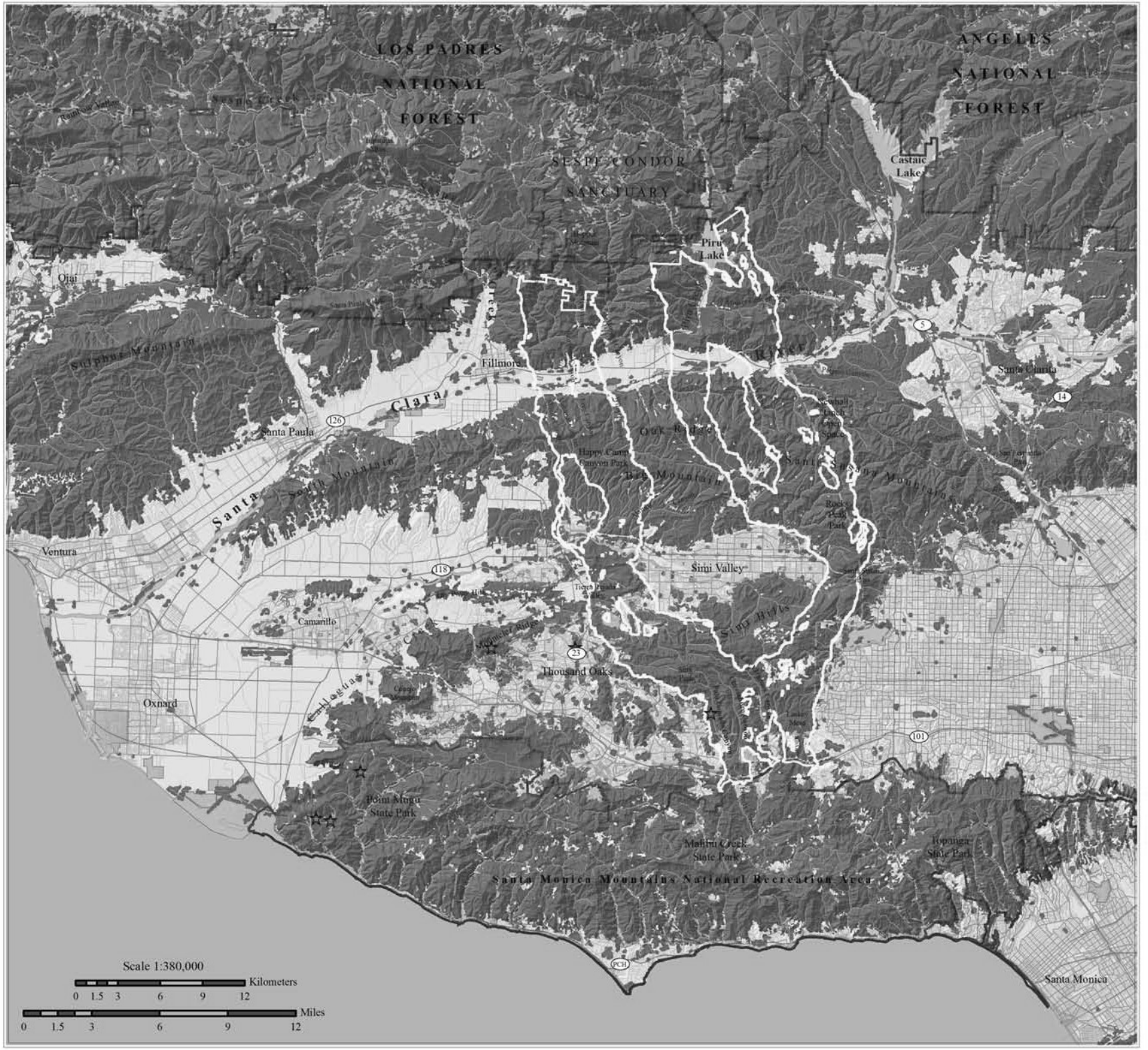
Figure 21.
Potential Cores & Patches
for
Brush rabbit
(Sylvilagus bachmanni)



- Core
- Patch
- < Patch
- ★ Recorded Occurrence*
- Protected Lands
- Least Cost Union
- Target Areas
- Lakes & Reservoirs
- Hydrography
- County Boundary
- Roads

*Data Source: National Park Service Ecological Monitoring Data

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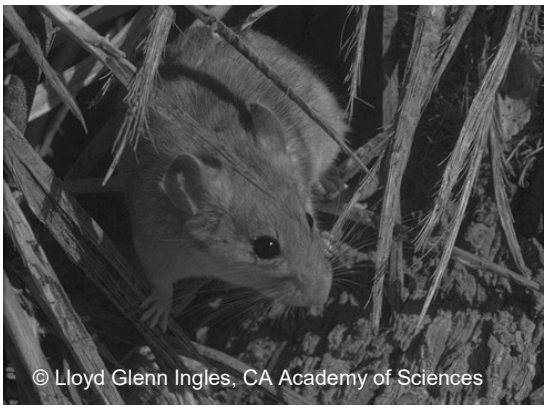
Justification for Selection: This species is sensitive to habitat fragmentation, including in coastal sage scrub habitats of southern California (Bolger et al. 1997). Movement barriers include urban developments, roadways (particularly highways with continuous solid barriers that prevent rodent passage), and major water bodies. Woodrats are also sensitive to habitat alteration and disturbance such as may occur in areas of high fire frequency, unregulated off-road vehicle use, and other activities that reduce or damage vegetative cover (Sauvajot et al. 1998).



Distribution & Status: *Neotoma lepida* inhabits virtually all of southern California, with a range extending northward along the coast to the San Francisco Bay area and inland from Inyo County south throughout the Mojave Desert and from north-central Tulare County south through the Tehachapi and San Bernardino Mountains. They also occur in extreme northeastern California, on the Baja California peninsula in Mexico, and on several islands in the Gulf of California and the Pacific Ocean near Baja, as well as in southeastern Oregon, southwestern Idaho, Nevada, and western Utah (Zeiner 1990, Verts and Carraway 2002). There are 23 subspecies, *N. l. intermedia* occurs in the study area. Desert woodrats are typically associated with elevations below 2,900 m (9,514 ft) in California (Verts and Carraway 2002) and the subspecies within this study area is notable for occurring in the southern California coastal mountain ranges.

Habitat Associations: Desert woodrats may be found in sagebrush, chaparral, Joshua tree woodland, scrub oak woodland, pinyon-juniper woodland, riparian zones, creosote bush scrub, desert scrub and rocky slopes with scattered cactus, yucca, pine-juniper, and other low vegetation, and occasionally in salt marsh habitats (Zeiner 1990, Verts and Carraway 2002). In the study area, they are common in dense coastal sage and scrub habitats, including mixed and chamise-redshank chaparral (Lee 1963, MacMillen 1964). Woodrats are known for their large, multichambered dwellings, which they depend upon for shelter, storing food items, and refuge from predators (Carraway and Verts 1991, Matocq 2002). Desert woodrats occupy elaborate dens built of vegetative debris among shrubs, along cliffs, among rocks, and occasionally in trees (Lee 1963, MacMillen 1964). Thompson (1982) observed desert woodrats actively avoiding open areas that did not provide adequate refuge sites.

Spatial Patterns: In the Little San Bernardino Mountains, Thompson (1982) reported the average home range of desert woodrats to be 0.05 ha (.13 ac), which generally included one diurnal den and foraging habitat. In coastal sage scrub, home range has been reported to range from 0.04 to .2 ha (.1 to .5 ac; MacMillen 1964, Bleich and Schwartz 1975). Populations may be limited by the availability of nest-building materials (Linsdale and Tevis 1951, Brylski 1990).

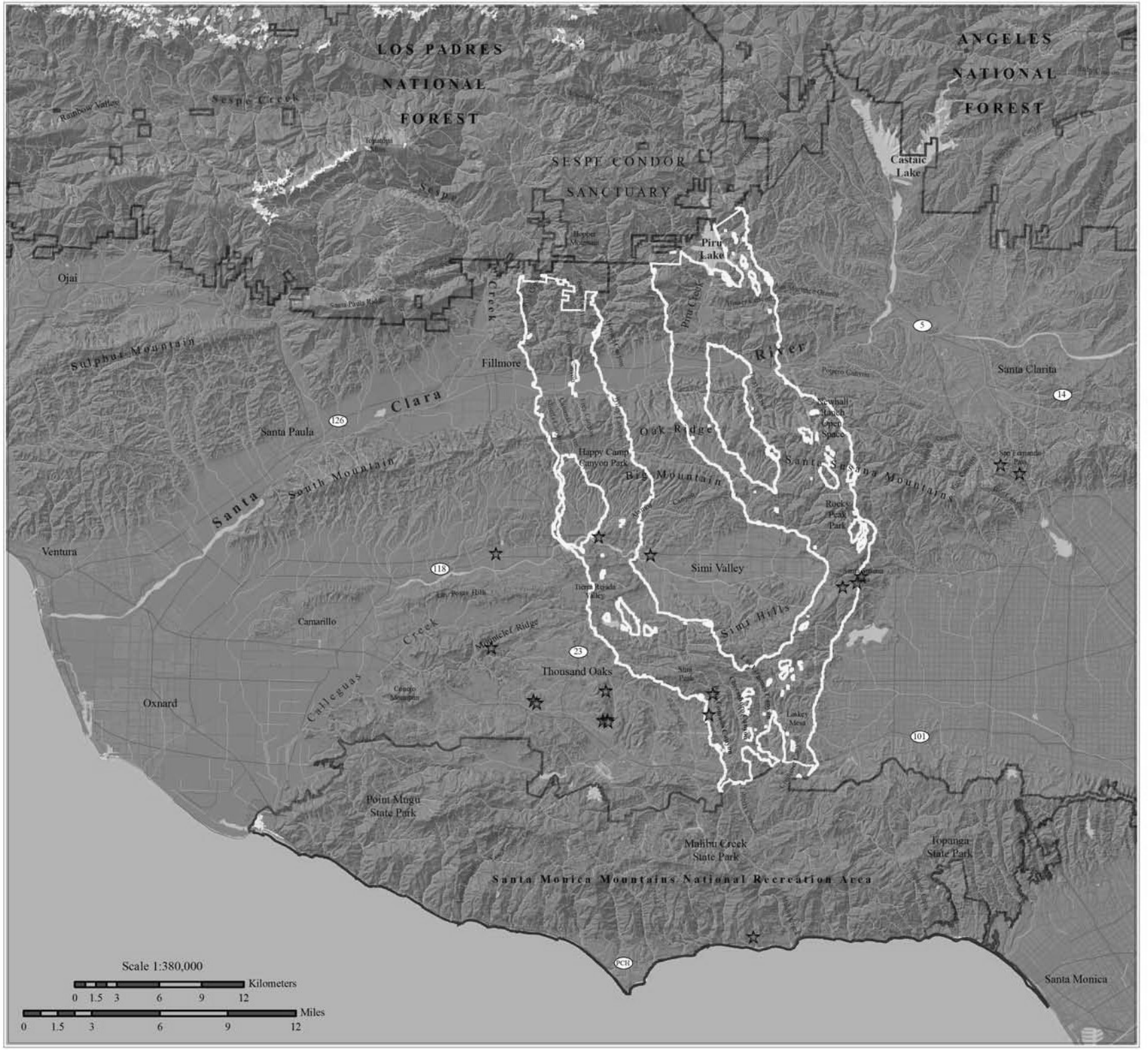
Natal site dispersal in the eastern Mojave Desert appears to be greater for male desert woodrats. Average linear movements in same habitat were about 14 m (46 ft) per night. In sagebrush-juniper habitat, males moved an average of 80 m (262 ft) per night, while female movements averaged 45 m (147 ft; Stones and Hayward 1968).

Conceptual Basis for Model Development: Movement in the linkage is assumed to be multigenerational. Desert woodrats are associated with chaparral, sagebrush, pinyon-juniper, riparian, and scrub habitats, and are typically found below 2,900 m elevation. Core areas were defined as $\geq$ 3 ha (7.41 ac). Patch size was defined as $\geq$ 0.1 ha (0.25 ac) and < 3 ha. Dispersal distance was defined as 160 m (524 ft).

Results & Discussion: Potential habitat for the desert woodrat is widespread in the planning area, with both the western and eastern branches of the Least Cost Union containing highly suitable contiguous habitat for this species (Figure 22). The desert woodrat has been recorded in Palo Comado Canyon, Santa Susana Pass, and along the Arroyo Simi near Alamos Canyon in the Union, and on Mount Clef Ridge. The majority of suitable habitat was identified as potential cores areas for this species (Figure 23). Almost all of the potential core areas and patches of suitable habitat are within the defined dispersal distance of the woodrat (figure not shown), though barriers to movement may exist between suitable habitat patches. We conclude that the linkage is likely to serve the needs of this species for movement among populations if habitat is added to Union on Mount Clef Ridge. To protect and restore habitat connectivity for the desert woodrat, we recommend that:

- Crossing structures for small mammals be placed fairly frequently to facilitate movement across transportation routes.
- Natural hydrological processes are maintained or restored.
- Lighting is directed away from the linkage and crossing structures.
- Local residents are informed about the proper use of rodenticides and pesticides to reduce the likelihood of ingestion of these lethal substances on small mammals indigenous to the area.

Figure 22.
Habitat Suitability
for
Desert woodrat
(Neotoma lepida)



Degree of Suitability

- High
- Medium to High
- Medium
- Low to Medium
- Low
- Protected Lands
- ★ Recorded Occurrence*
- Least Cost Union
- Target Areas
- Lakes & Reservoirs
- Hydrography
- County Boundary
- Roads

*Data Source: CNDDB and National Park Service Ecological Monitoring Data

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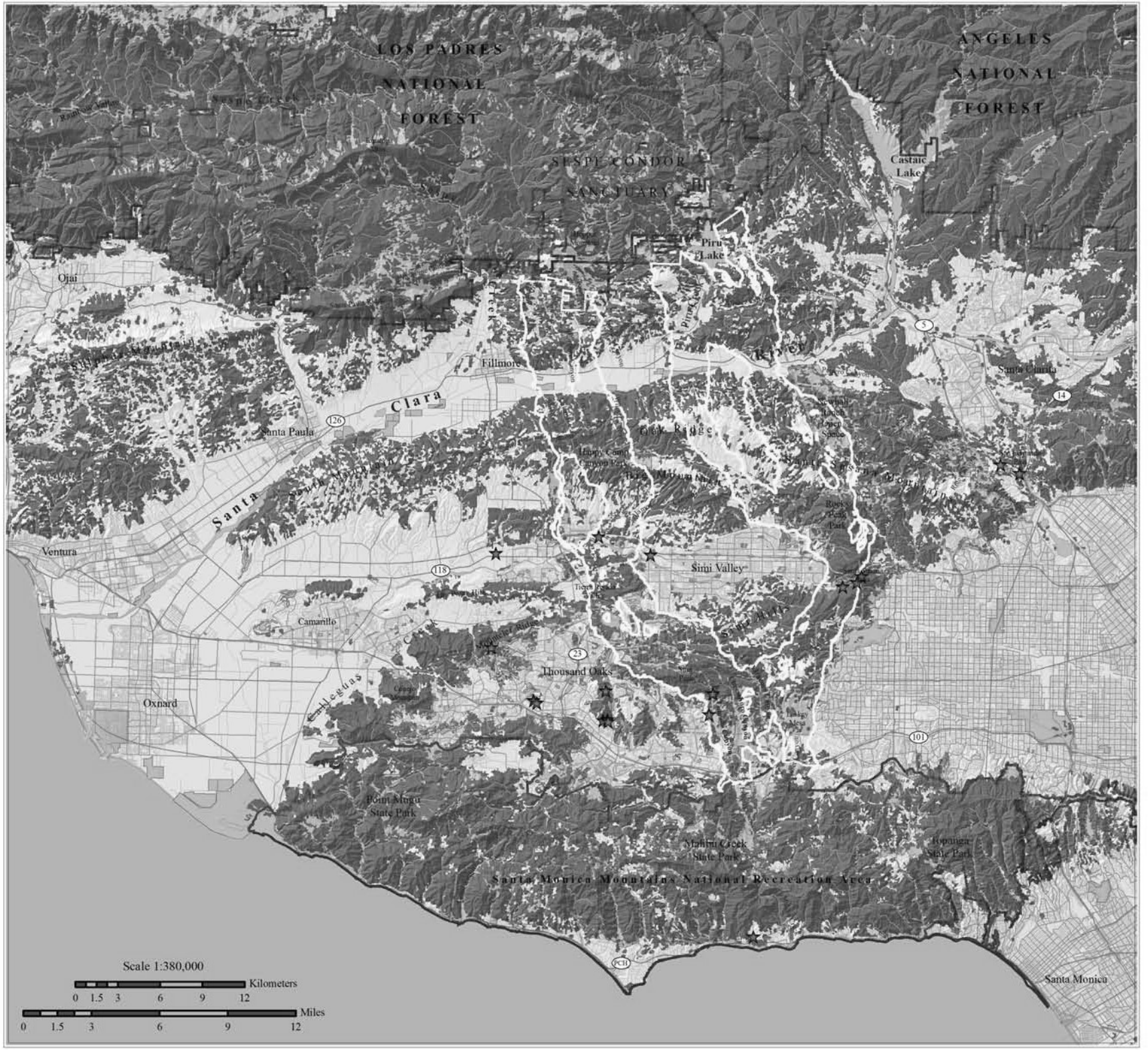
Figure 23.
Potential Cores & Patches
for
Desert woodrat
(Neotoma lepida)



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Loggerhead shrike (*Lanius ludovicianus*)


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Justification for Selection: Loggerhead shrike is a resident species that requires a mosaic of open habitats with abundant prey to persist. They have been declining throughout North America since the 1960s (Robbins et al. 1986, Sauer et al. 2001). They are sensitive to habitat loss, fragmentation, and degradation (Fraser and Luukkonen 1986, Pruitt 2000).

Distribution & Status: Loggerhead shrike ranges throughout much of North America from southern Canada to northern Mexico. They are common residents and winter visitors in the lowlands and foothills of California (Faber et al. 1989, Zeiner et al. 1990). They are absent from heavily forested areas and higher elevations in the desert ranges, typically occurring below 1,524 m (5,000 ft) in elevation (Small 1994).

North American Breeding Bird Survey (BBS) data for the period 1966-2000 indicate a 71% population decline rangewide (-3.7% annually), with a decline of 75% in the western region (Sauer et al. 2001). Loggerhead shrike is designated as a federal and state Species of Special Concern (CDFG 2005).

Known or suspected threats to loggerhead shrike populations include habitat loss and degradation, fragmentation of suitable habitat, shooting, and pesticide and other toxic contamination (Fraser and Luukkonen 1986, Pruitt 2000). While there is evidence of some eggshell thinning in Illinois, there is no apparent eggshell thinning in California and Florida (Hands et al. 1989). Pesticides may pose a greater threat in reducing food availability (Yosef 1994, Yosef 1996). Threats to the grassland habitats preferred by loggerhead shrike include conversion to agriculture, overgrazing of livestock, spread of exotic species, urbanization and disrupted fire regimes (Knopf 1994, Knight et al. 1995, Saab et al. 1995, Vickery and Herkert 1999).

Habitat Associations: Loggerhead shrike prefers open country for hunting, with perches for scanning, and fairly dense shrubs and brush for nesting (Small 1994). They may utilize grasslands, pastures, savannah, pinyon-juniper woodlands, Joshua Tree woodlands, riparian woodlands, desert oases, desert scrub and washes, and to a lesser extent, agricultural fields and orchards (Small 1994). The highest density of shrike occurs in open-canopied valley foothill hardwood, valley foothill hardwood-conifer, valley foothill riparian, savannah, pinyon-juniper, juniper, desert riparian, and Joshua tree habitats (Zeiner et al. 1990, Small 1994). Shrikes are often found in open cropland, but only rarely occur in intensive agricultural areas where pesticides have limited their prey base (Zeiner et al. 1990). Loggerhead shrike isn't found on north slopes of mountain ranges, nor in pure chaparral (Small 1994), though they may use edges of denser habitats (Grinnell and Miller 1944, McCaskie et al. 1979, Garrett and Dunn 1981).

Spatial Patterns: Loggerhead shrikes are strongly territorial and aggressive during the breeding season. Shrikes maintain relatively large territories and all activities associated with reproduction (mating, foraging, brooding) occur within the territory (Yosef 1996). In mainland California, the average size of territories was 8.5 ha (21 ac), and ranged between 4.4 ha (10.9 ac) and 16 ha (39.5 ac; Yosef 1996). In Contra Costa and Kern counties, Miller (1931) found ten territories in open shrubland that averaged 7.6 ha (18.7 ac), and varied from 4.5 to 16 ha (11-40 ac). Typically, nesting territories are smaller in areas with a greater amount of good quality habitat (Kridelbaugh 1982).

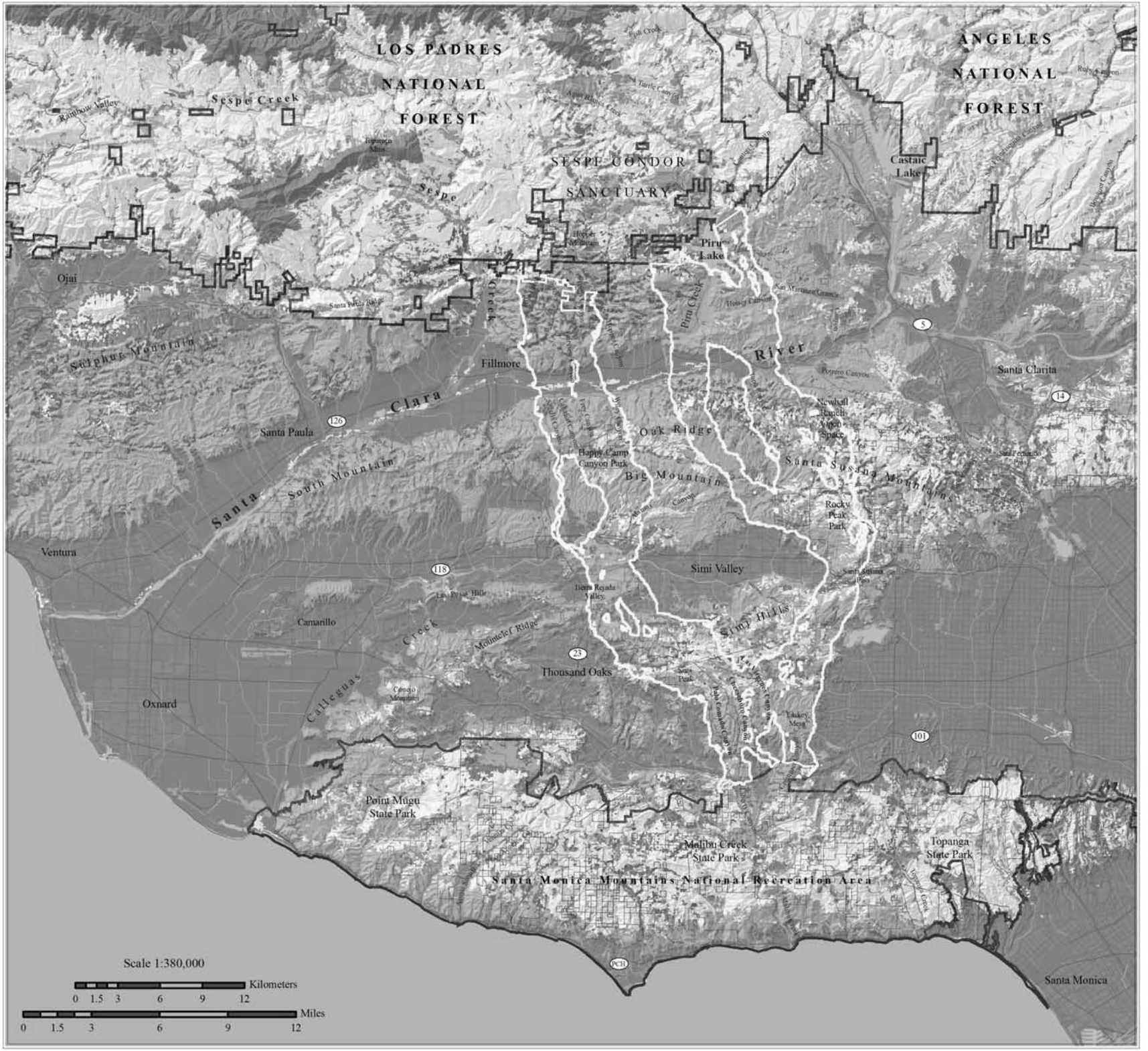
Banding studies indicate that adult loggerhead shrikes exhibit some site fidelity and juveniles disperse widely (Yosef 1996). In Alberta, the average distance of juvenile dispersal was 6.7 km (4.2 mi) between years (Yosef 1996). Over a period of 3 years from the time of banding, loggerhead shrikes dispersed up to 70 km (43.5 mi) from their natal site (Yosef 1996). In Virginia, juveniles 10-13 weeks old moved an average of 5.5 km (3.42 mi) from their parents' territory to their fall territory (Blumton et al. 1989).

Conceptual Basis for Model Development: Loggerhead shrike prefers open habitat types, such as grassland and oak savanna but they may also be encountered in riparian, desert scrub and wash communities. Potential core areas were defined as greater than or equal to 213 ha (526 ac). Patch size was classified as $\geq$ 9 ha (22.2 ac) but less than 213 ha. Dispersal distance was defined as 13.4 km (8.3 mi).

Results & Discussion: All branches of the Least Cost Union contain highly suitable habitat for loggerhead shrike, with the most contiguous habitat occurring in the eastern branch of the Union (Figure 24). The majority of suitable habitat was identified as potential cores areas for this species (Figure 25). All potential core areas and patches of suitable habitat are within the defined dispersal distance of loggerhead shrike (figure not shown), though barriers to movement may exist between suitable habitat patches. We conclude that the linkage is likely to serve the needs of this species for movement among populations. However, loggerhead shrike would also benefit from the habitat connection that extends from the western Santa Monica Mountains over Conejo Mountain and Mountclef Ridge to the Tierra Rejada Valley (Figures 24, 25).

To protect and restore habitat connectivity for loggerhead shrike, we recommend that pesticide use is restricted in shrike habitat to avoid depressing the abundance of potential prey items. Shrikes are subject to pesticide poisoning due to their position in the food chain (Hands et al. 1989).

Figure 24.
Habitat Suitability
for
Loggerhead shrike
(Lanius ludovicianus)



Degree of Suitability

- High
- Medium to High
- Medium
- Low to Medium
- Low
- Protected Lands
- Least Cost Union
- Target Areas
- Lakes & Reservoirs
- Hydrography
- County Boundary
- Roads

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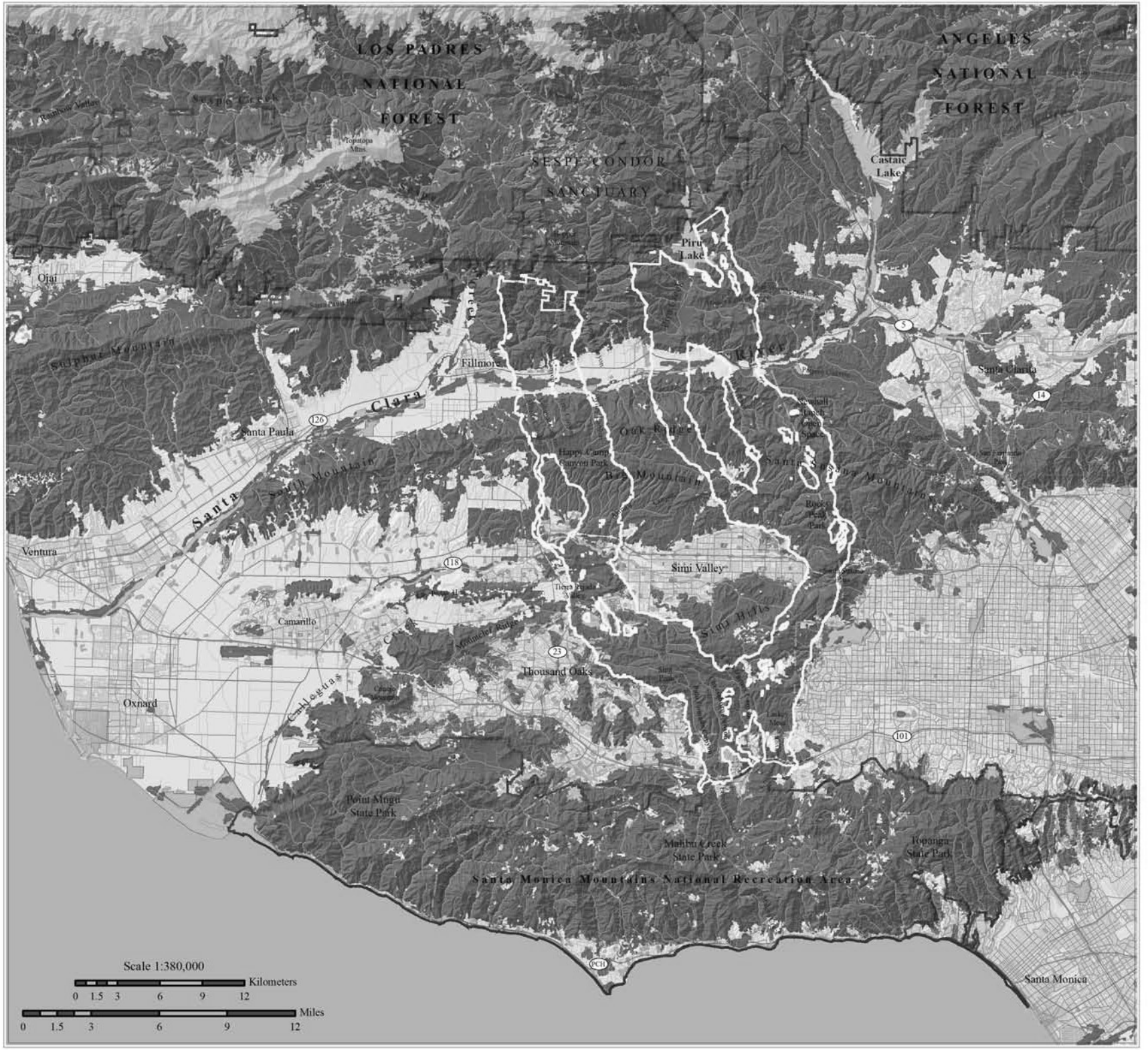
Figure 25.
Potential Cores & Patches
for
Loggerhead shrike
(Lanius ludovicianus)



Core
Patch
< Patch
Protected Lands
Least Cost Union
Target Areas
Lakes & Reservoirs
Hydrography
County Boundary
Roads

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California thrasher (*Toxostoma redivivum*)



Justification for Selection: This is one of the first species to disappear from isolated fragments (Soulé et al. 1988). Loss of habitat to urban and agricultural development constitutes the most serious threat to populations (Robertson and Tenney 1993, Cody 1998).

Distribution & Status: The California thrasher is endemic to the coastal and foothill areas of the California Floristic Province and into adjacent areas of northwest Baja California (Cody 1998). In southern California, it occurs in montane chaparral up to 2,000 m (6,000 ft; Zeiner et al. 1990). California thrasher is considered a sensitive species (CDFG 2005).

Habitat Associations: California thrasher is primarily associated with dense chaparral and sage scrub habitat though it may also occur in adjacent oak woodland and riparian habitats (Cody 1998). This species avoids oak woodland devoid of understory (Robertson and Tenney 1993), although it may use these habitats outside of the breeding season (Cody 1998). Some vegetation communities on desert slopes may also provide habitat, including pinyon-juniper and Joshua tree woodlands (Cody 1998).

Spatial Patterns: Home range size may be up to 20 ha (50 ac) in scrub oak desert habitat (Jehl 1978, Zeiner et al. 1990). In the Santa Monica Mountains, territories averaged 1.4 ha (3.5 ac) in size (Kingery 1962, Zeiner et al. 1990). California thrasher is mostly a sedentary resident species, although there may be some local movement in the nonbreeding season (Zeiner et al. 1990).

Conceptual Basis for Model Development: This species has a strong preference for chaparral and sage scrub vegetation, though it may also be found in riparian and oak woodland habitats. Core areas potentially supporting 50 or more individuals was defined as $\geq$ 300 ha (741.32 ac). Patch size was classified as $\geq$ 3 ha (7.41 ac) but < 300 ha. Dispersal distance was not estimated for this species.

Results & Discussion: All branches of the Least Cost Union contain highly suitable habitat for California thrasher, with the most highly suitable contiguous habitat occurring in the eastern branch of the Union (Figure 26). Another highly suitable habitat connection not included in the Union extends from the western Santa Monica Mountains over Conejo Mountain and Mountclef Ridge to the Tierra Rejada Valley (Figure 26). Indeed, the patch size analysis identified contiguous core habitat for this species in the area, while some potential core areas in the Union are separated by patches of suitable habitat (Figure 27). We conclude that the spatial configuration of suitable habitat within

the Union will likely allow for intergenerational movement of thrashers between targeted protected areas (Figure 27).

It seems counterintuitive that birds, because they can fly, would need movement corridors to persist in fragmented landscapes (Machtans et al.1996). However, several studies have shown gaps in habitat may form barriers to songbird movement (Whitcomb et al. 1981, Lynch and Whigham 1984, Lens and Dhondt 1994, Machtans et al. 1996, Debinski and Holt 2000, Crooks et al. 2001). Haas (1995) studied the movement ecology of brown thrashers (*T. rufum*) and found that wooded corridors channeled movements between habitat patches. To protect and maintain habitat continuity between protected cores areas for California thrasher, we recommend that:

- Existing road density be maintained or reduced in the Linkage Design.
- Suitable native vegetation is provided in the vicinity of potential crossing points to facilitate movement across barriers (e.g. roads, developments, etc.).
- Habitat restoration efforts are initiated along the Santa Clara River to provide a 2 km wide habitat connection.

Figure 26.
Habitat Suitability
for
California thrasher
(Toxostoma redivivum)

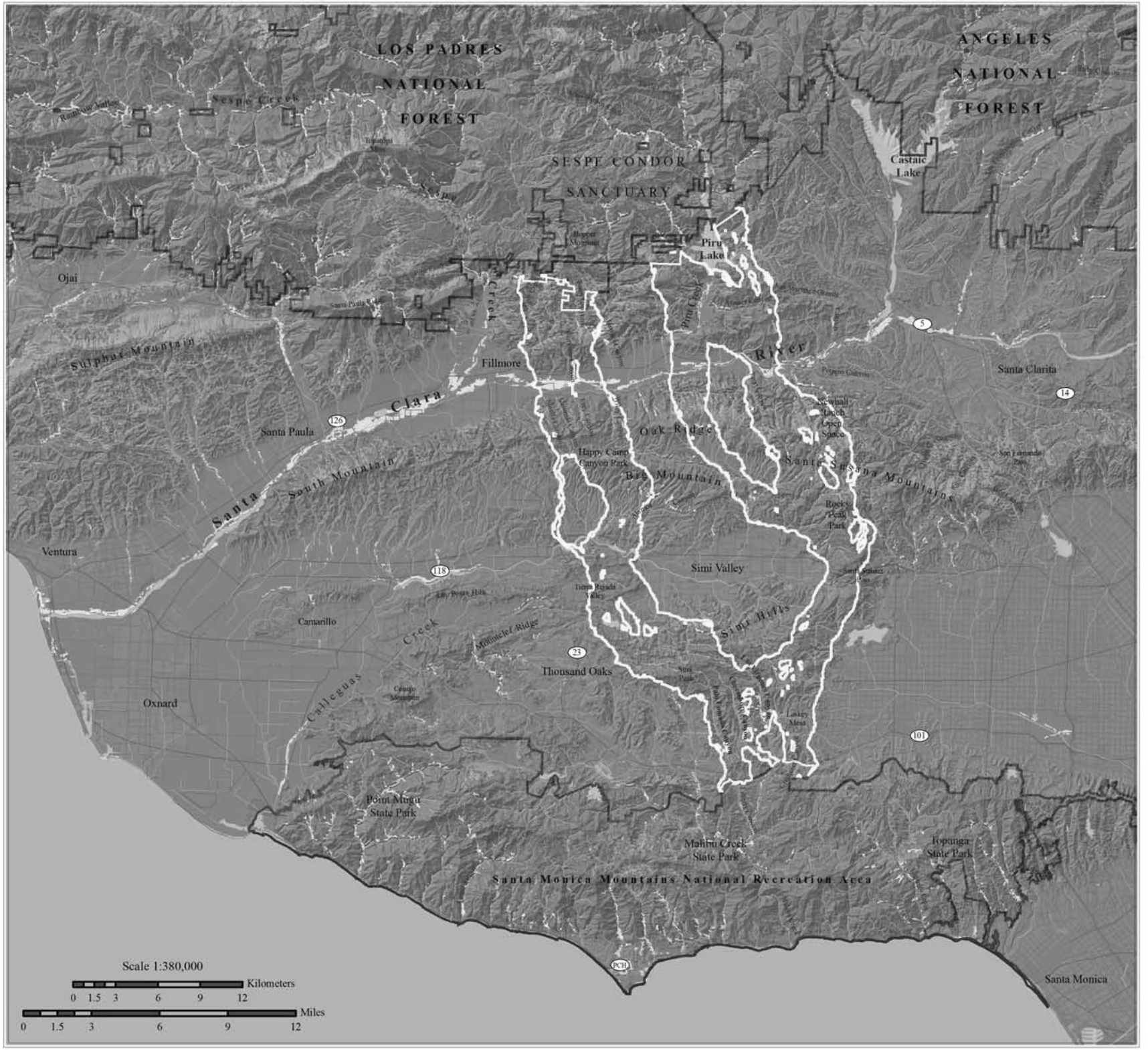

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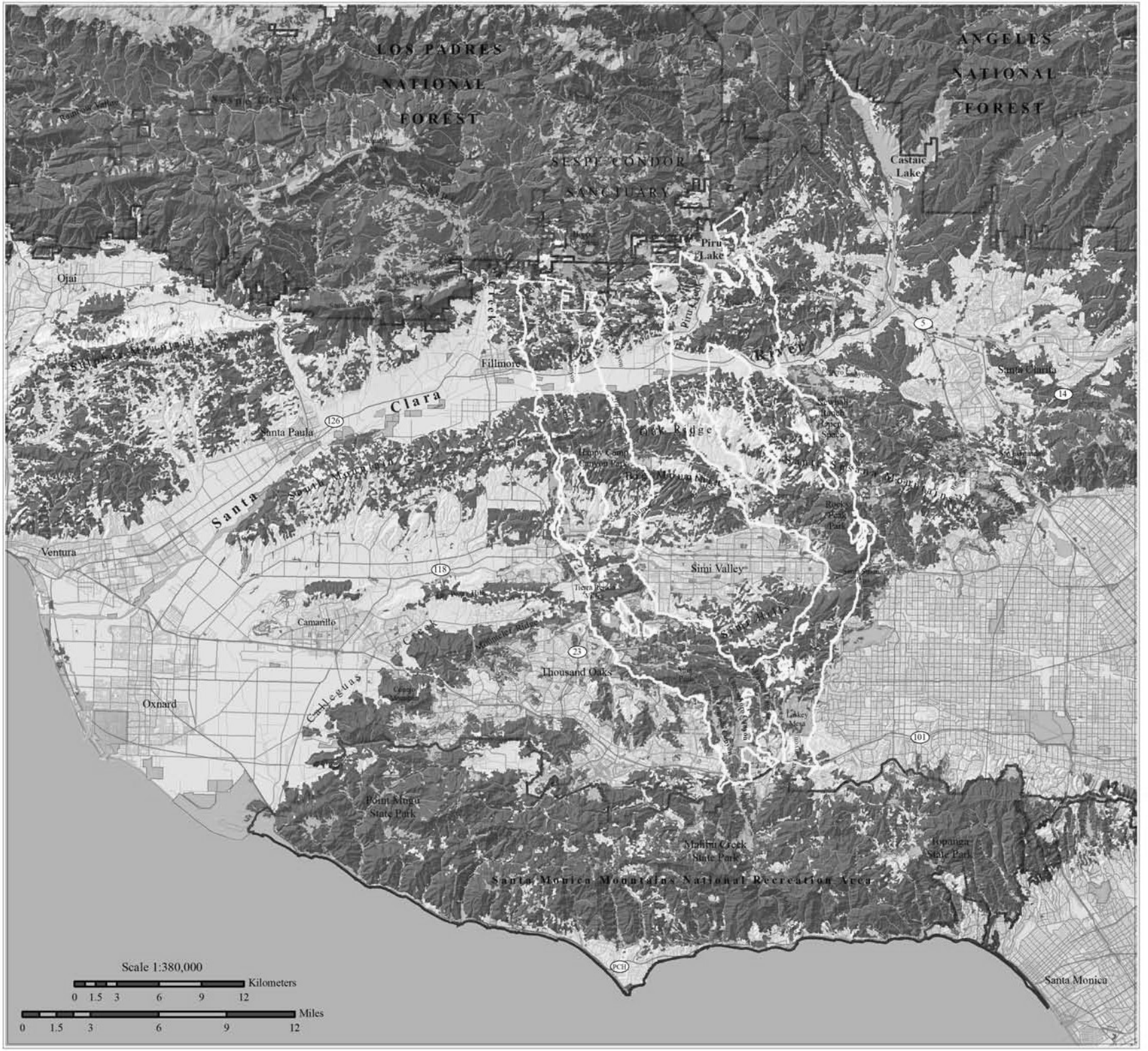
Figure 27.
Potential Cores & Patches
for
California thrasher
(Toxostoma redivivum)



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Cactus wren (*Campylorhynchus brunneicapillus*)



Justification for Selection: Habitat loss and fragmentation are a concern for this species (Soulé et al. 1988). Historically, the interior and coastal populations were connected through the San Gorgonio Pass in Riverside County, but the connection has been severed due to urbanization of the pass (Rea and Weaver 1990, Solek and Sziji 2004).

Distribution & Status: The cactus wren is widely distributed from southern California south to southern Baja, and in parts of Nevada, Utah, Arizona, New Mexico, and Texas south to Mexico (Dudek and Associates 2001). In California, the interior race is resident in the Mojave and Colorado deserts, from Mexico north to Inyo and Kern counties, while the coastal race is restricted to westward-draining slopes from Ventura County to San Diego County (Zeiner et al. 1990, Solek and Sziji 2004). Taxonomic affiliation of the coastal and interior populations is still being debated (Rea and Weaver 1990, Solek and Sziji 2004).

The coastal race is considered a California Species of Special Concern due to habitat loss, degradation, and fragmentation (Solek and Sziji 2004). Activities that are known to adversely impact the species include weed abatement projects, grading or clearing activities, and some recreational activities (Harper and Salata 1991, Solek and Sziji 2004). Overly frequent fire eliminates the dense, older cactus patches required as habitat. The domestic cat is the most dangerous predator (Anderson and Anderson 1963, Solek and Sziji 2004).

Habitat Associations: Cactus wrens may be encountered in coastal sage scrub, desert scrub, desert succulent scrub, Joshua tree, and desert wash habitats where cactus patches are present (Zeiner et al. 1990). In the planning area, cactus wrens are most often associated with relatively dense patches of prickly pear cactus (*Opuntia sp*.) They depend on thickets of xeric vegetation for cover and thermal relief. Nests are found in branching cacti, thorny scrub, and small trees (e.g., Joshua tree), with nests also used as roosts (Grinnell and Miller 1944, Anderson and Anderson 1957, Zeiner et al. 1990).

Spatial Patterns: The home range of cactus wrens may be maintained throughout the year (Anderson and Anderson 1963, Zeiner et al. 1990). In Arizona, Anderson and Anderson (1973) found an average home range size of 1.9 ha (4.8 ac), varying from 1.2-2.8 ha (2.9-6.9 ac; Zeiner et al. 1990). In San Diego County, California, Rea and Weaver (1990) found smaller home ranges from 0.8 to 2 ha, (2 to 4.9 ac) with an average of 1.3 ha (3.2 ac). On Camp Pendleton, home range size varied from 0.5-2 ha (1.2 to 4.9 ac; Solek and Sziji 2004).

Atwood (1998) found an average dispersal distance of 1.59 km (0.98 mi) for juvenile cactus wrens on the Palos Verdes Peninsula, but this isolated coastal population has

limited dispersal options. In Arizona, Anderson and Anderson (1973) found juvenile females dispersed farther away from their natal territories than juvenile males (Solek and Sziji 2004).

Conceptual Basis for Model Development: Cactus wrens prefer coastal sage scrub, desert scrub, desert succulent scrub, Joshua tree, and desert wash and alluvial habitats in the vicinity of cactus plants. Potential core areas were defined as greater than or equal to 33 ha (81.5 ac). Patch size was classified as $\geq$ 2 ha (4.9 ac) but less than 33 ha. Dispersal distance was defined as 3.18 km (2 mi).

Results & Discussion: The most highly suitable habitat for cactus wren closely follows the distribution of coastal sage scrub habitat in the planning area, particularly where coastal sage scrub co-occurs with cactus (Figure 28). The western branch of the Least Cost Union provides the most highly suitable habitat (in large part due to the presence of extensive cactus stands), while the eastern branch provides the most contiguous habitat (Figure 28). The western branch of the Union is likely to serve this species if the highly suitable core habitat that extends from the western Santa Monica Mountains over Conejo Mountain and Mountclef Ridge to the Tierra Rejada Valley is added to the Union to serve the needs of this species (Figure 29). Distances among all cores and patches of suitable habitat are within the dispersal distance of this species (figure not shown), but barriers may exist between suitable habitat patches.

To protect and restore habitat connectivity for cactus wren, we recommend that fire frequency be controlled to prevent type conversion of scrub habitats to nonnative annual grassland (Winter 2003) and that important cactus scrub areas be protected and maintained. Suitable native vegetation should be provided in the vicinity of potential crossing points to facilitate movement across barriers (e.g. roads, developments, etc.).

Figure 28.
Habitat Suitability
for
Cactus wren

(Campylorhynchus brunneicapillus)

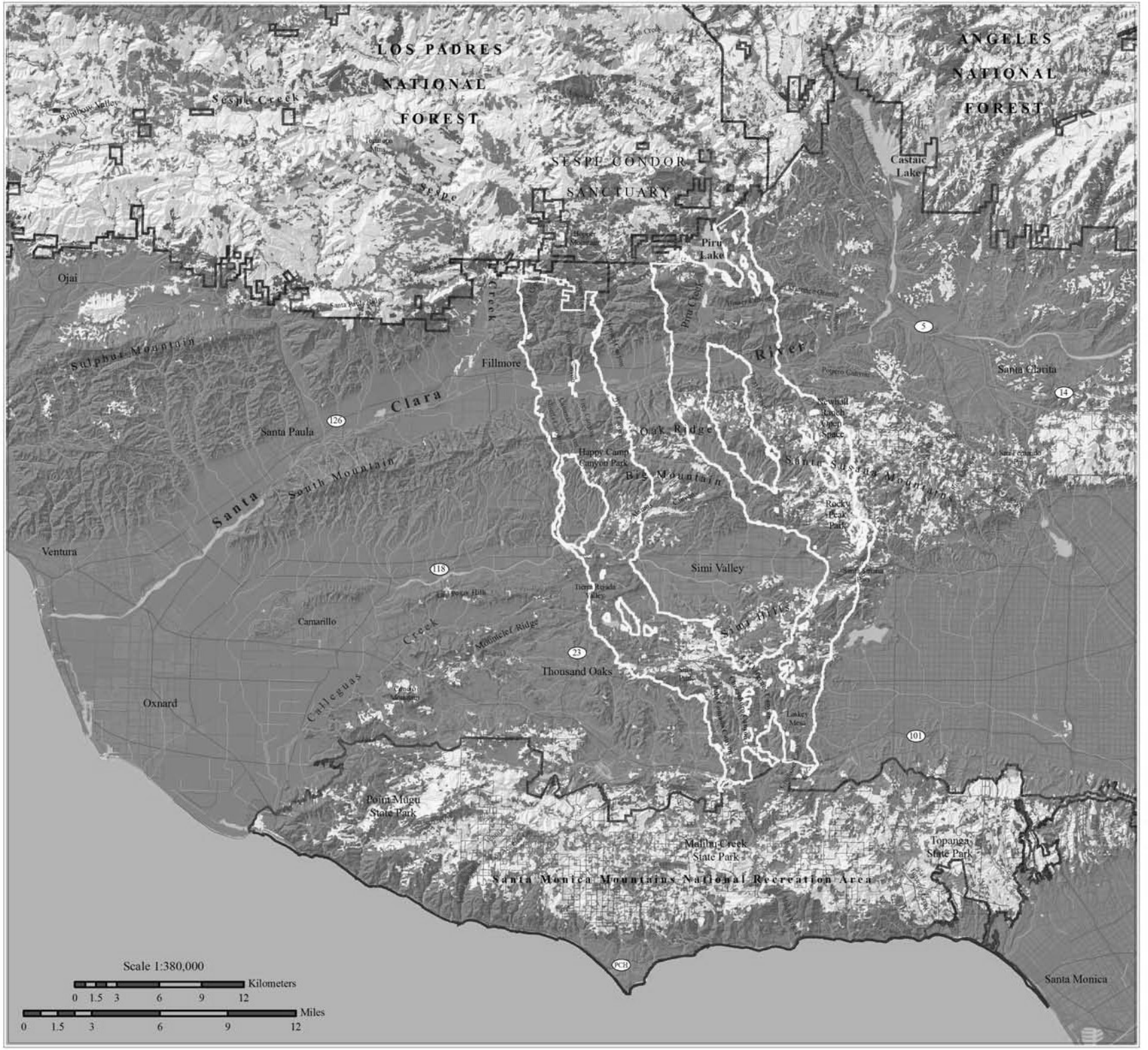

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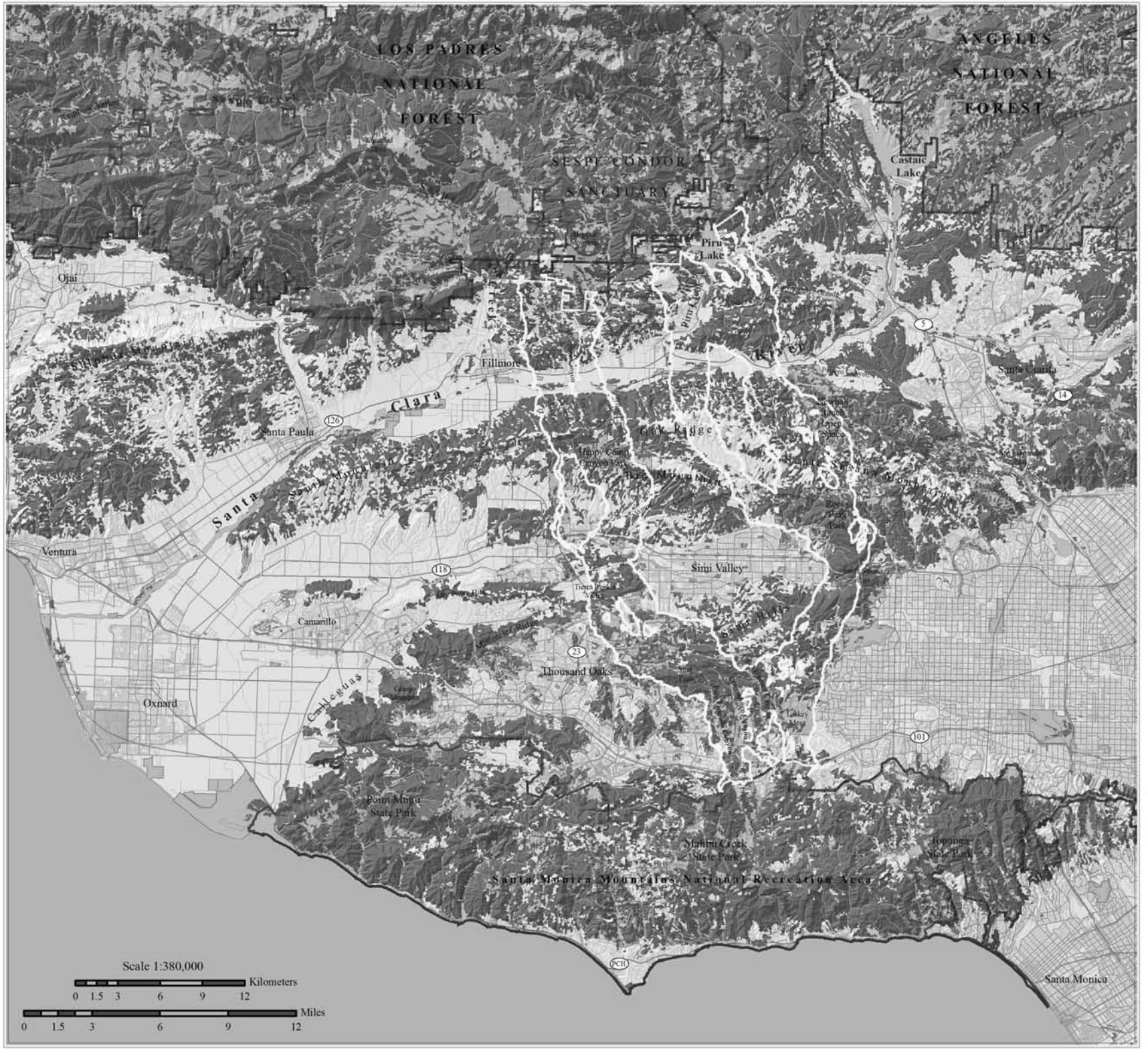
Figure 29.
Potential Cores & Patches
for
Cactus wren
(Campylorhynchus brunneicapillus)



Core
Patch
< Patch
Protected Lands
Least Cost Union
Target Areas
Lakes & Reservoirs
Hydrography
County Boundary
Roads

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Justification for Selection: The continued elimination of oaks is a threat to the existence of this species in California (Verner and Boss 1980, Zeiner et al. 1990). Overgrazing causes reduced regeneration of oaks. As a cavity nester, this species is also indicative of intact bird communities; they are highly susceptible to competition with invasive non-native birds such as feral parrots (Butler 2005) and European starlings, which are associated with degraded habitats.

Distribution & Status: Acorn woodpeckers occur from northwestern Oregon, California, the American Southwest, and western Mexico through the highlands of Central America, as far south as northern Columbia (Koenig and Haydock 1999). They are typically found below 2100 m (6,890 ft), though most good habitats are below 915 m (3,002 ft) in elevation (Zeiner et al. 1990). This species isn't considered sensitive by any government entities.

Habitat Associations: Acorn woodpeckers are residents of foothill and montane hardwood and hardwood-conifer habitats (Roberts 1979, Zeiner et al. 1990). The acorn woodpecker relies on large stands of old trees (Ligon and Stacey 1996). They excavate cavities in winter and spring in live trees or snags of oaks, sycamores, or conifers (Zeiner et al. 1990), though snags are preferred (Hooge et al. 1999). The acorn woodpecker is a highly specialized species that lives in close association with oaks, because they depend largely on acorns for their winter diet (Ritter 1938, MacRoberts 1970, Bock and Bock 1974; Hannon et al.1987, Koenig and Mumme 1987, Zeiner et al. 1990, Koenig and Haydock 1999).

Spatial Patterns: Acorn woodpeckers are cooperative breeders that live in social groups of 2 to 15 individuals (MacRoberts and MacRoberts 1976; Koenig et al. 1995, Hooge et al. 1999). Territory size is based on the key resource, the roost cavity and granary tree (Ligon and Stacey 1996). MacRoberts and MacRoberts (1976) found territory sizes from 3.5 to 9 ha (8.7 to 22.2 ac), while Swearingen (1977) found average territory size to be 4.7 ha (11.5 ac) in the Central Valley, with a range from 1.5 to 8.1 ha (3.8 to 20 ac). Smaller territory sizes have been recorded for the Coast Ranges (Zeiner et al. 1990).

On the western slope of the Sierras, upslope movement occurs in fall to mixed conifer habitat with black oak (Verner and Boss 1980, Zeiner et al. 1990). Dispersal distances of 0.22 $\pm$ 0.48 km (0.14 $\pm$ 0.3 mi) for males and 0.53 $\pm$ 0.52 km (0.32 $\pm$ 0.33 mi) for females have been recorded. The usual avian pattern of greater dispersal distance by females holds true for acorn woodpeckers (Koenig et al. 2000). The maximum-recorded dispersal distance for this species is 4.3 km (2.7 mi; Koenig et al. 2000).

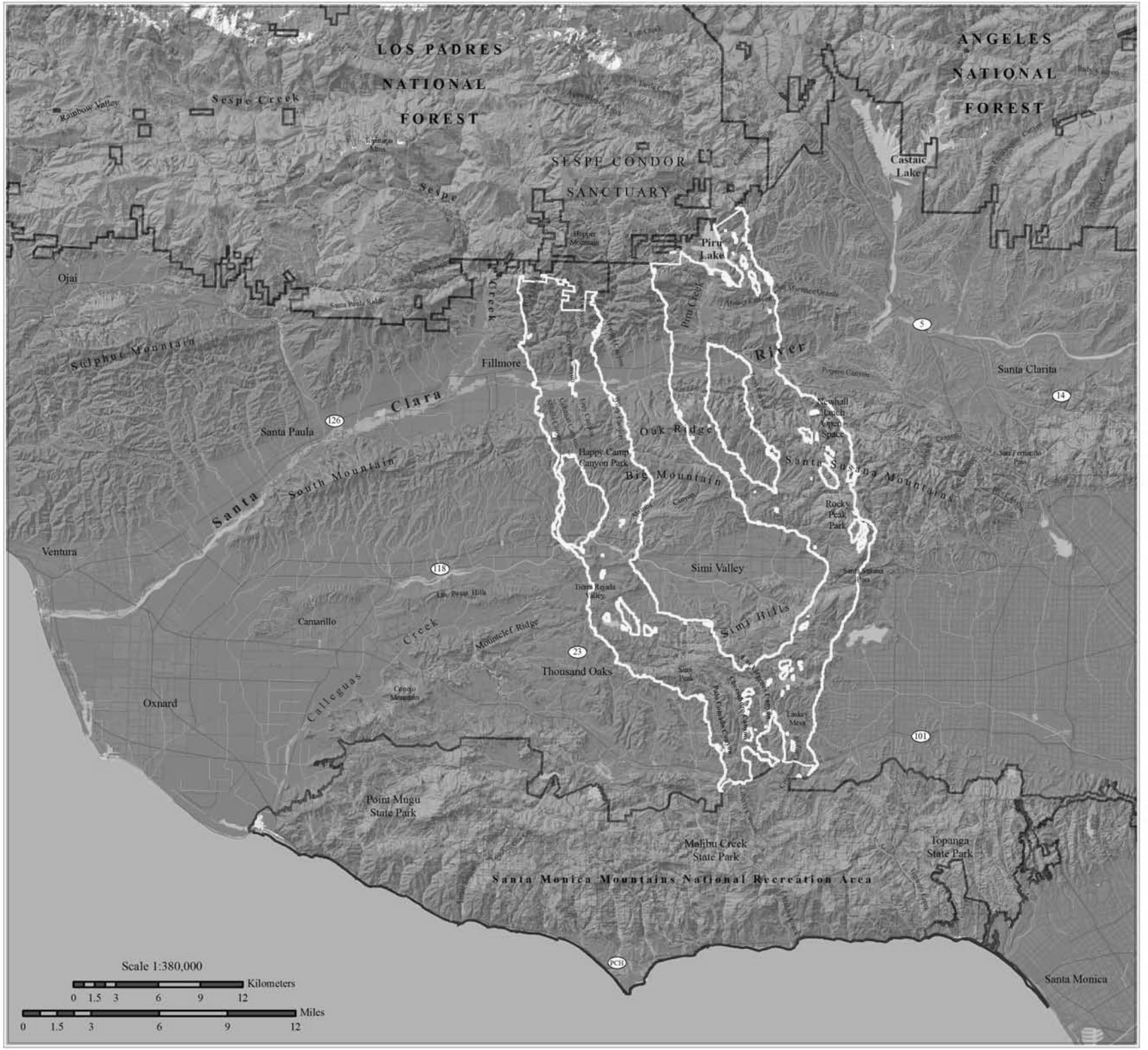
Conceptual Basis for Model Development: This species prefers mature oak woodlands and hardwood coniferous forest below 2100 m. Core areas potentially supporting 50 or more individuals were defined as ≥ 100 ha (247 ac). Patch size was classified as ≥ 3 ha (7.4 ac) but < 100 ha. Dispersal distance was defined as 8.6 km (5.3 mi), using twice the maximum reported distance of 4.3 km.

Results & Discussion: Oak woodlands and riparian habitats are fairly widespread in the planning area but are somewhat scattered in the Least Cost Union, limiting the amount of suitable habitat for acorn woodpecker (Figure 30). Several patches of highly suitable habitat were captured in the Union, with potential core areas limited to Happy Camp Canyon and the north facing slopes of Oak Ridge Mountain in the Santa Susana Mountains, and Pole and Toms canyons in the foothills of the Sierra Madre Range (Figure 31). All potential cores and patches of suitable habitat identified by the analysis are within the dispersal distance of this species (figure not shown). Acorn woodpecker movements will likely be accommodated by the Least Cost Union.

As cavity-nesting birds, acorn woodpeckers are susceptible to being extirpated by birds associated with urban areas, such as feral parrots and European starlings that can outcompete woodpeckers for nesting cavities. To protect and maintain habitat continuity between protected cores areas for acorn woodpecker, we recommend that:

- Suitable native vegetation is provided in the vicinity of potential crossing points to facilitate movement across barriers (e.g. roads, developments, etc.).
- Existing road density be maintained or reduced in the Linkage Design.
- Overgrazing is discouraged in oak woodlands to allow for regeneration.

Figure 30.
Habitat Suitability
for
Acorn woodpecker
(Melanerpes formicivorus)



Degree of Suitability

- High
- Medium to High
- Medium
- Low to Medium
- Low
- Protected Lands
- Least Cost Union
- Target Areas
- Lakes & Reservoirs
- Hydrography
- County Boundary
- Roads

N

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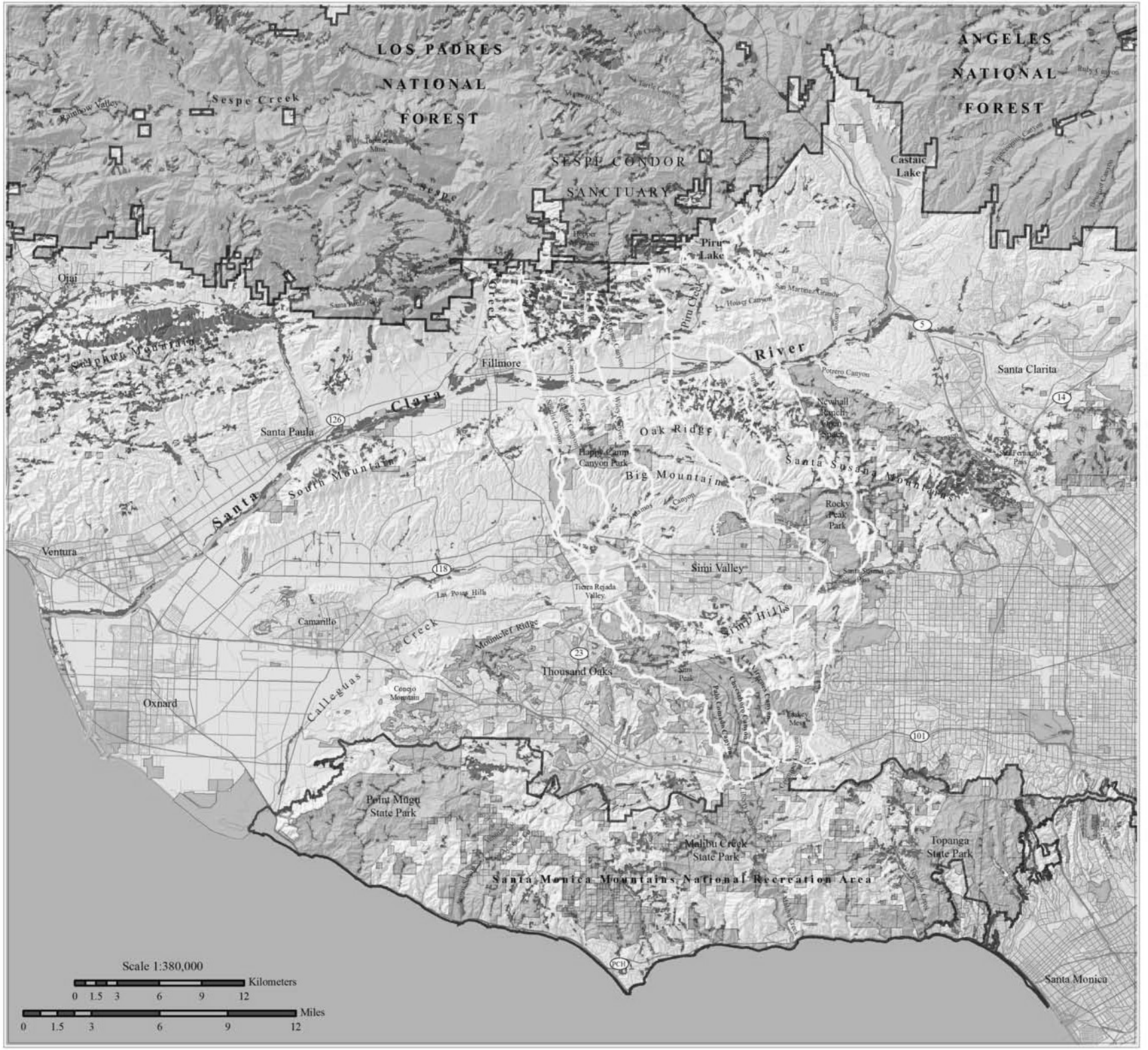
Figure 31.
Potential Cores & Patches
for
Acorn woodpecker
(Melanerpes formicivorus)



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Western toad (*Bufo boreas*)


Chris Brown

Justification for Selection: This species is an indicator of the quality of habitat connections needed between slow moving aquatic habitat (chiefly ponds and quiet backwaters) and upland habitat. Along with other native amphibians, this species is likely sensitive to the effects of urban development in southern California (Riley et al. 2005).

Distribution & Status: The western toad ranges from western British Columbia and southern Alaska south through Washington, Oregon, and Idaho to northern Baja California, and east to Montana, western and central Wyoming, Nevada, high elevation areas in Utah, and western Colorado (Stebbins 1985). The western toad is not considered a special status species.

Habitat Associations: In California, western toads occur up to 3,048 m (10,000 ft) elevation in most habitats except deserts (Zeiner et al. 1988, Sullivan 1994). Upland habitats in the planning area include grasslands, coastal scrub, chaparral, and oak and riparian woodlands. Aquatic habitats include lakes, ponds, vernal pools, roadside ditches, irrigation canals, permanent and intermittent streams, and rivers (Zeiner et al. 1988). Eggs are laid in water 6 to 12 inches (30 cm) in depth (Olson 1992, Stebbins 1954).

Spatial Patterns: While there is substantial variation in home range, individuals living in low elevation areas are occasionally encountered up to 1000 m (3,281 ft) from potential breeding sites, and some have been tracked through a wide range of habitats up to 5 km (3.1 mi) from their breeding areas (Zeiner et al. 1988, Corn et al. 2001).

Dispersal distances among breeding sites have not been measured. After breeding, adult toads may move from 1 km to 5 km (0.62 to 3.1 mi) through a wide range of potentially inhospitable habitats (Zeiner et al. 1988, Corn et al. 2001). Tadpole dispersal is probably not significant; breeding adults in a population tend to lay their eggs at the same location (Sullivan 1994) and their tadpoles clump in large masses until they metamorphose (Nussbaum et al. 1983).

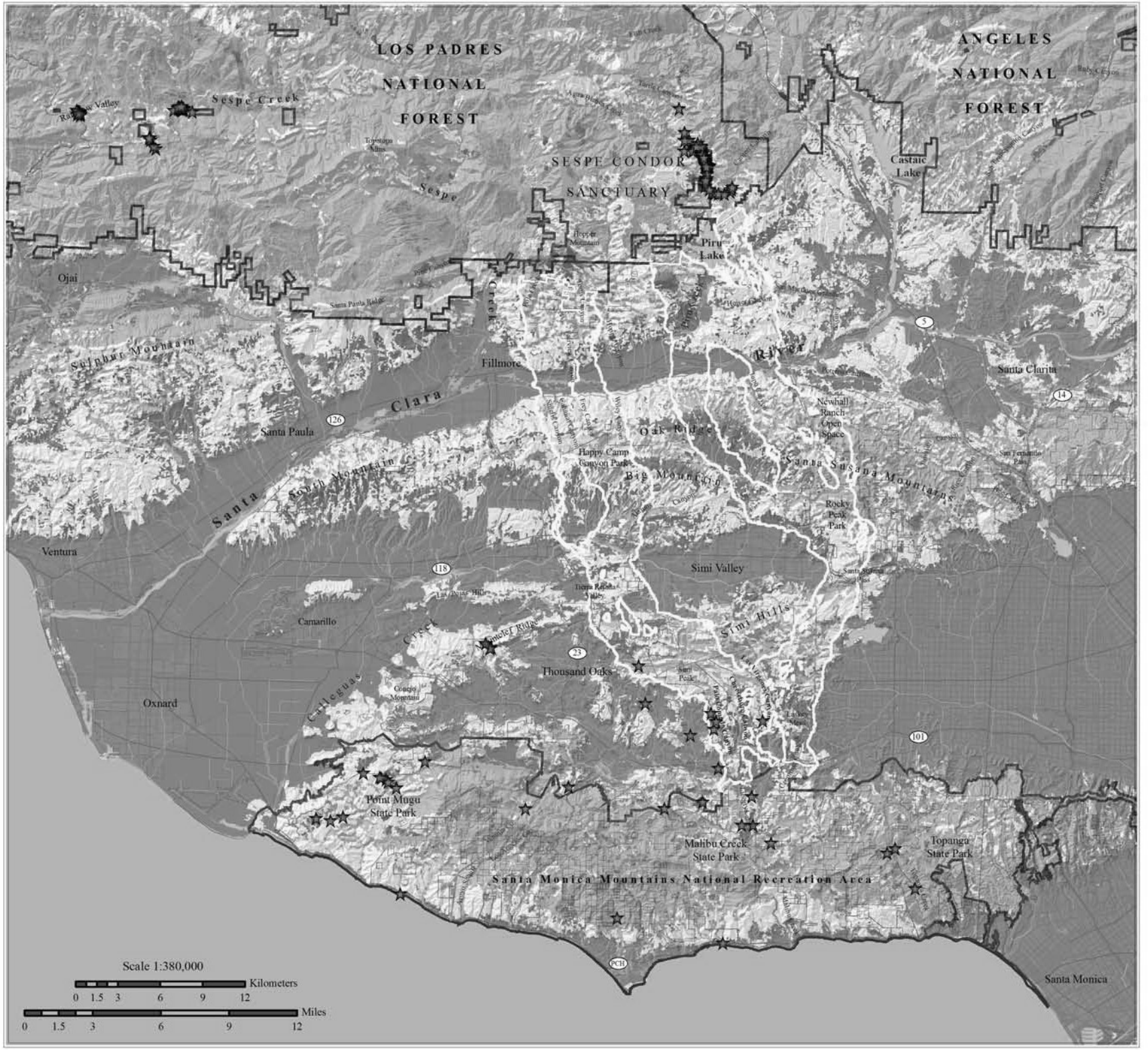
Conceptual Basis for Model Development: Western toads prefer grassland, coastal scrub, chaparral, and oak and riparian woodland habitats. Minimum patch size needed for 2 toads is less than the 30-m minimum mapping unit. Because habitat quantity is a poor predictor of population density in toads, we did not designate a minimum patch size but included all suitable habitat as potential core areas. Dispersal distance used is 10 km (6.2 mi; twice the maximum reported distance an individual moved from a breeding site).

Results & Discussion: All three branches of the Least Cost Union contain fairly contiguous suitable habitat for western toad, with the central branch containing the most highly suitable habitat (Figure 32). The western toad has been recorded in Liberty, Las Virgenes and Palo Comado canyons, and to the west of Simi Peak in the Union, and on Mount Clef Ridge. All suitable habitat identified in the planning area was delineated as potential core areas for this species (Figure 33). Distances among all cores and patches of suitable habitat are within the dispersal distance of this species (figure not shown), but barriers may exist between suitable habitat patches. We conclude that the Union will likely to serve the movement needs of western toad, though habitat added to the Union on Conejo Mountain and Mount Clef Ridge will also benefit this species.

To protect and restore habitat connectivity for the western toad, we recommend that:

- Riparian habitats needed for breeding and movement are restored.
- Invasive species be eradicated that destroy breeding habitat (e.g., giant reed) and prey on tadpoles (e.g., bullfrogs and fish).
- Road barriers be modified, where necessary, to allow amphibians to move along stream courses.
- Water quality that is compromised by agricultural, urban, and industrial runoff be restored.

Figure 32.
Habitat Suitability
for
Western toad
(Bufo boreas)



Degree of Suitability

- High
- Medium to High
- Medium
- Low to Medium
- Low
- Protected Lands
- ★ Recorded Occurrence*
- Least Cost Union
- Target Areas
- Lakes & Reservoirs
- Hydrography
- County Boundary
- Roads

*Data Source: USFS and National Park Service Ecological Monitoring Data

N

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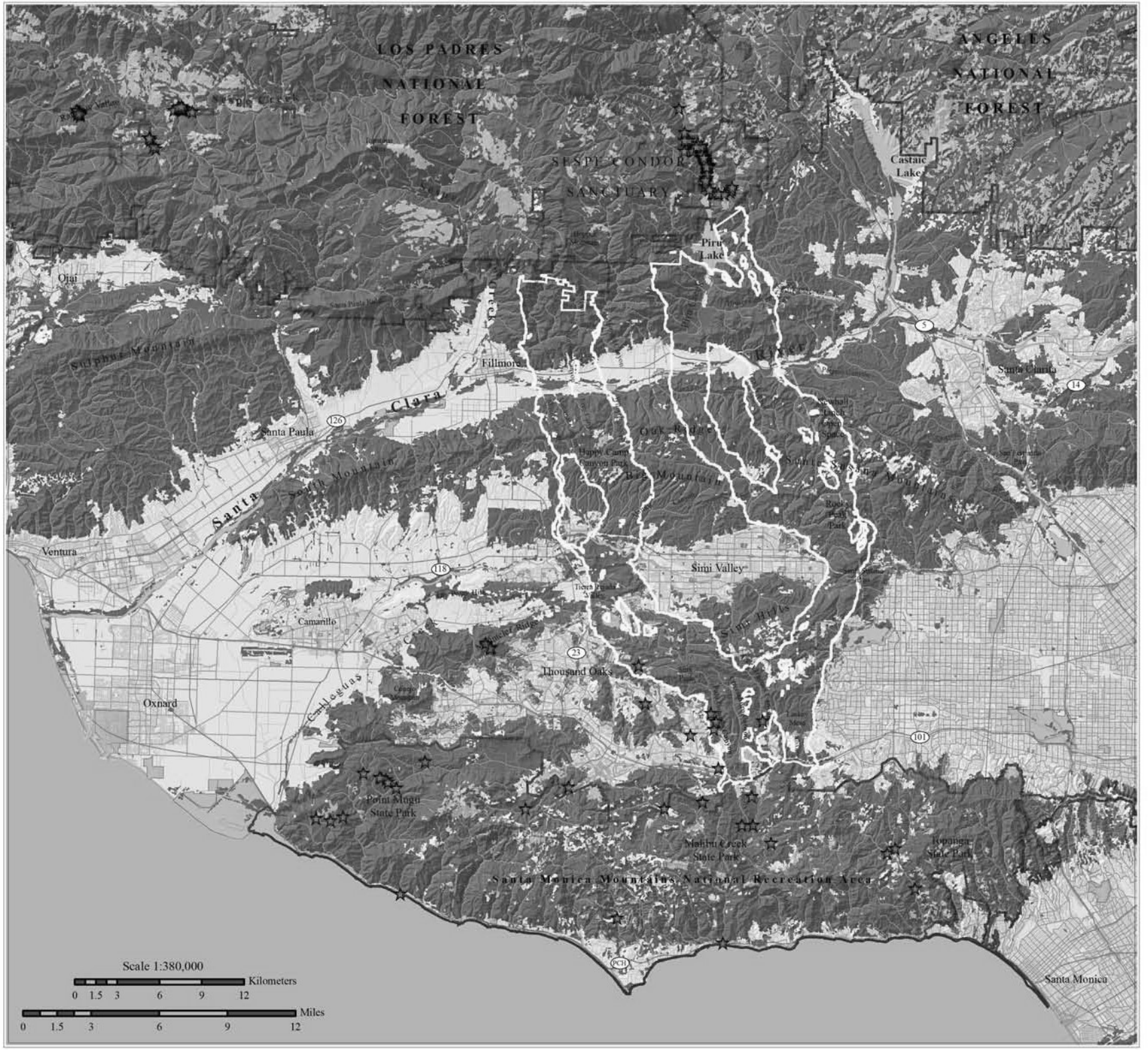
Figure 33.
Potential Cores & Patches for Western toad
(Bufo boreas)



Core
Recorded Occurrence*
Protected Lands
Least Cost Union
Target Areas
Lakes & Reservoirs
Hydrography
County Boundary
Roads

*Data Source: USFS and National Park Service Ecological Monitoring Data

N

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California kingsnake (*Lampropeltis getula*)



Justification for Selection: This species is attracted to warm roads in the evening in late spring and summer, making them particularly susceptible to roadkill (McGurty 1988). This species is also likely sensitive to urban-caused habitat fragmentation in the study area (Busteed 2003).

Distribution & Status: California kingsnake ranges throughout the western United States, from Baja California to Oregon and southern Utah to western Arizona. Elevation ranges from sea level to 2,100 m (7,000 ft; Stebbins 1985, Zeiner et al. 1988).

While this subspecies is not considered a special status species, kingsnakes are declining in the wild due to heavy collecting pressure, habitat loss and degradation (McGurty 1988). Regulatory agencies have instituted a law to ban the taking of this species from the wild, but kingsnakes, in all their striking variations, are still, unfortunately, a hot commodity.

Habitat Associations: California kingsnake may utilize meadows, grassland, oak woodland, open coniferous forest, chaparral, and coastal scrub habitats but they are most abundant in valley-foothill riparian and other habitats occurring in the vicinity of rivers and streams (Zeiner et al. 1988). When inactive, kingsnakes seek cover in rocky outcrops, rodent burrows and under surface objects such as flat rocks, logs, and boards. At montane localities with cold winters, individuals hibernate in rodent burrows and in deep fissures in rock accumulations (Zeiner et al. 1988).

Spatial Patterns: Research on home range size, density estimates and movement ecology for California kingsnake is lacking. Although, this species is presumed to seasonally migrate over relatively short distances to and from winter hibernacula, no distance estimates were found in the literature.

Conceptual Basis for Model Development: Movement between protected core areas in the linkage is multigenerational. Suitable habitat for the kingsnake was defined as valley-foothill riparian, riparian woodland, wet meadow, grassland, coastal sage, chaparral, oak woodland, and coniferous forests. Since no data are available on the home range size of this species, all suitable habitat patches were delineated as potential cores areas. Dispersal distance was not estimated for this species.

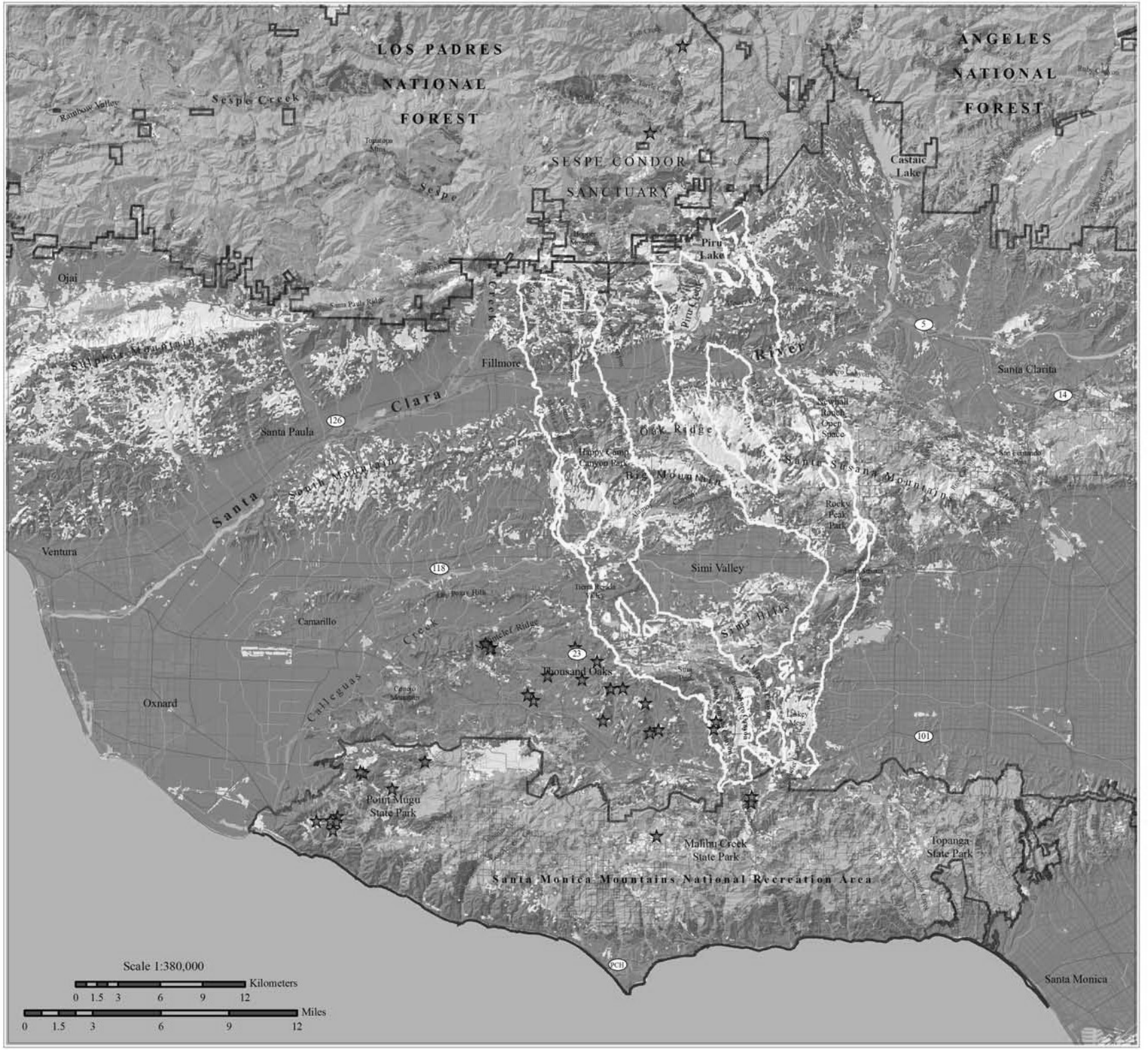
Results & Discussion: Highly suitable habitat for kingsnake is fairly widespread in both targeted protected areas and the Least Cost Union (Figure 34). All suitable habitat is considered potential core areas (Figure 35). The spatial configuration of suitable habitat

for kingsnake suggests that all branches of the Union will likely to serve the movement needs of this species.

Snakes are particularly vulnerable to roadkill, since they preferentially aggregate on or near warm roads to thermoregulate (Trombulak and Frissell 2000). To protect and restore habitat for California kingsnake, we recommend that:

- Riparian buffers of 1 km are added along each riparian route in the linkage.
- Road barriers are modified to allow kingsnakes to move along water courses and suitable upland habitats.
- Anti-poaching laws are enforced.

Figure 34.
Habitat Suitability
for
California kingsnake
(Lampropeltis getula)



- High
- Medium to High
- Medium
- Low to Medium
- Low
- Protected Lands
- ★ Recorded Occurrence*
- Least Cost Union
- Target Areas
- Lakes & Reservoirs
- Hydrography
- County Boundary
- Roads

*Data Source: USFS and National Park Service Ecological Monitoring Data

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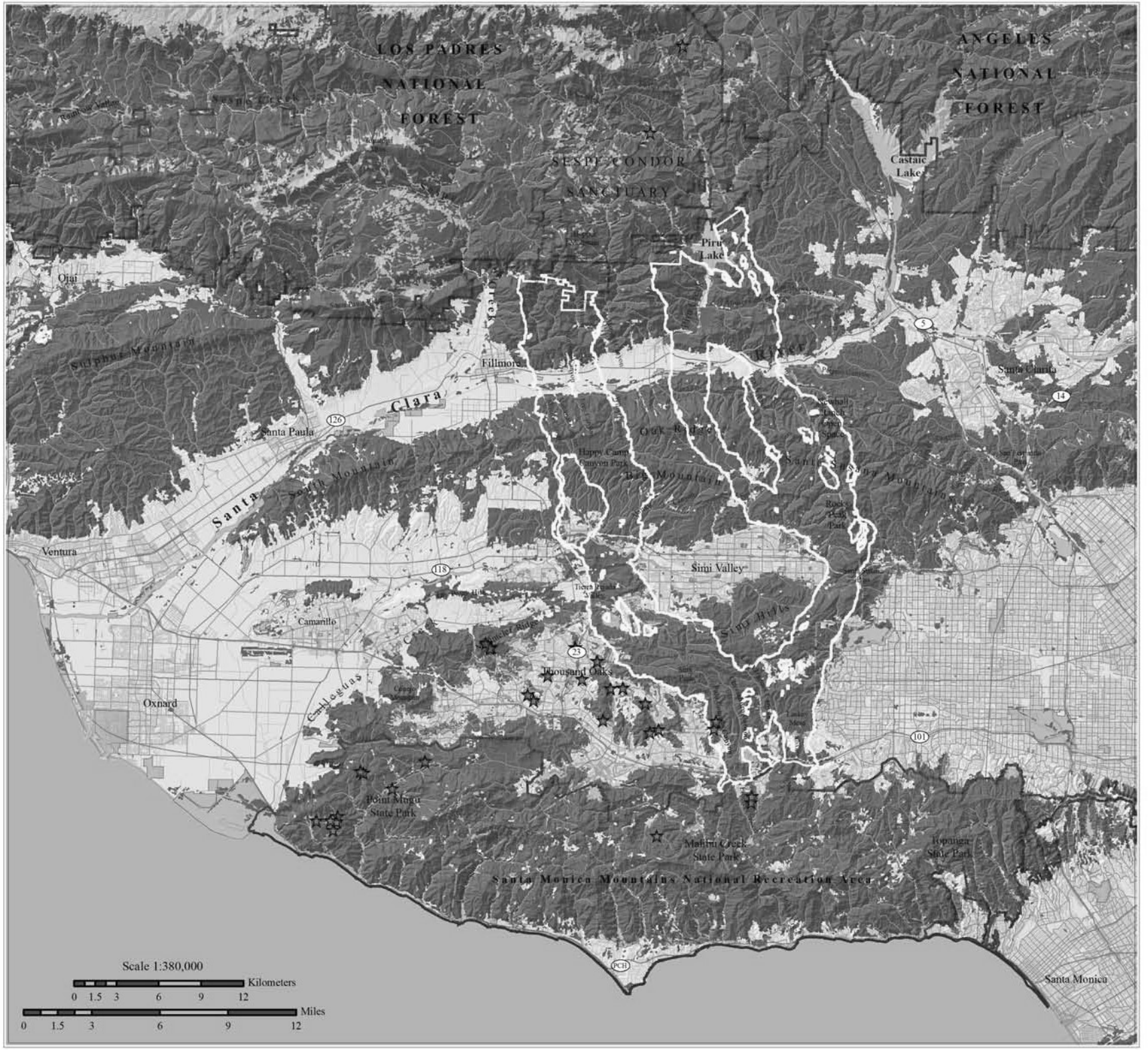
Figure 35.
Potential Cores
for
California kingsnake
(Lampropeltis getula)



Core
Recorded Occurrence*
Protected Lands
Least Cost Union
Target Areas
Lakes & Reservoirs
Hydrography
County Boundary
Roads

*Data Source: USFS and National Park Service Ecological Monitoring Data

N

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Coastal whiptail (*Aspidoscelis tigris stejnegeri*)



Justification for Selection: Whiptails utilize patches and need continuous open spaces for movement between core areas. Edge effects limit dispersal. They are habitat generalists, but susceptible to habitat fragmentation, roads, highways, and extremely impervious environments (R. Fisher, pers. comm.).

Distribution & Status: Coastal whiptails are widely distributed, but uncommon over much of their range in California, except in desert regions where they are abundant in suitable habitats (Zeiner et al. 1988). They are found throughout the state except in the humid northwest, along the humid outer Coast Ranges, and in mountainous regions above 2,290 m (7,500 ft).

Habitat Associations: Coastal whiptails occur in a variety of habitats including valley-foothill hardwood, valley-foothill hardwood-conifer, valley-foothill riparian, mixed conifer, pine-juniper, chamise-redshank chaparral, mixed chaparral, desert scrub, alkali scrub, and alluvial fans (Zeiner et al. 1988). Whiptails spend little time in open areas, but will cross barren spaces in order to reach the cover of dense shrubs in sparsely vegetated areas (Zeiner et al. 1988). They are often found associated with sandy areas along gravelly arroyos or washes (Stebbins 1954). Loose soil for foraging and nest construction may be an important habitat element (Zeiner et al. 1988). Vitt and Ohmart (1977) reported that the diet of whiptails may change seasonally to reflect the abundance of seasonally available prey items, which may include a wide variety of ground-dwelling invertebrates including grasshoppers, beetles, ants, termites, insect larvae and spiders (Stebbins 1954).

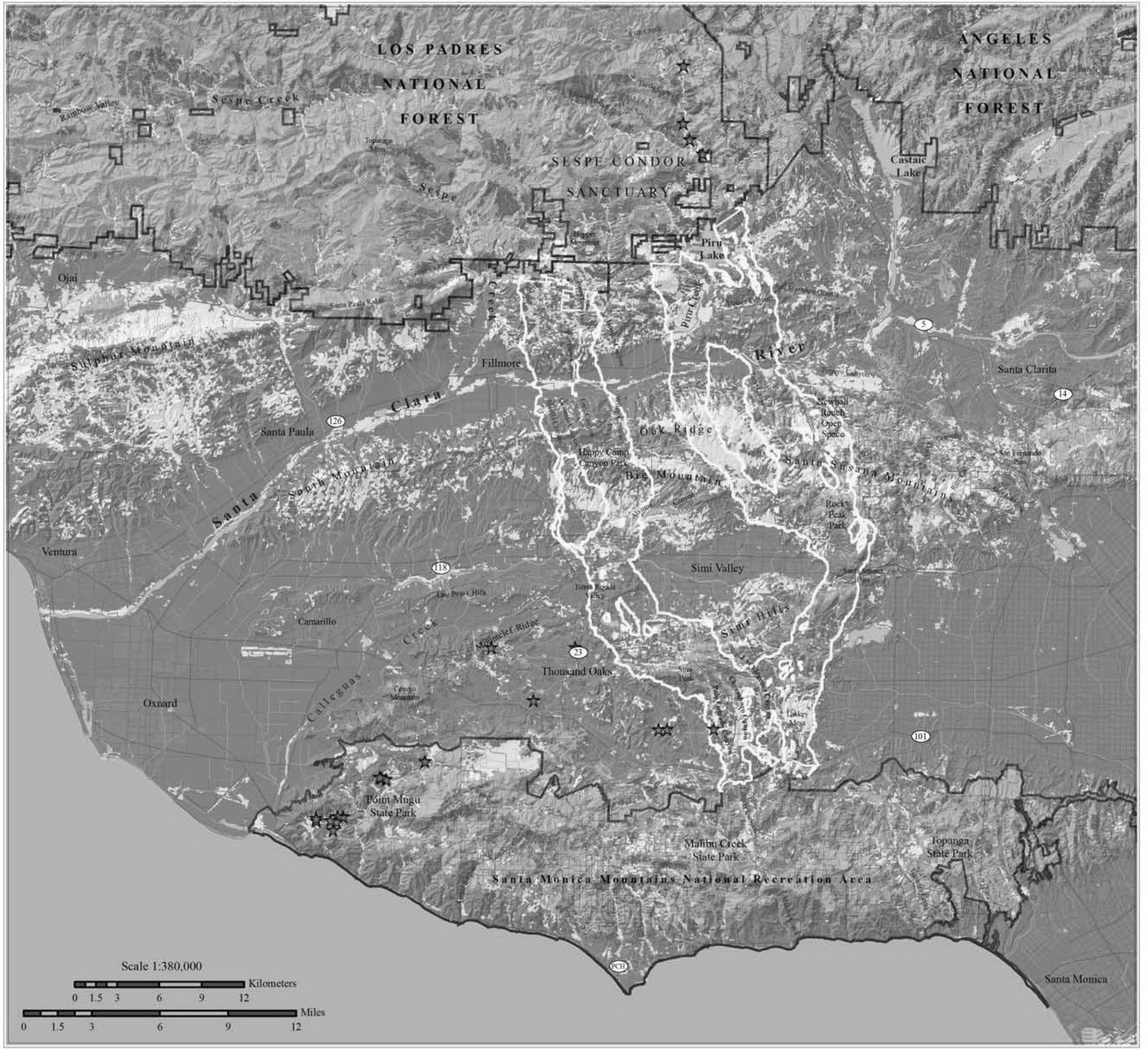
Spatial Patterns: Average home ranges for whiptails (excluding wandering individuals) have been calculated by Milstead (1957) to be about .1 ha (.26 ac). Jorgensen and Tanner (1963) have reported home range sizes of .7 ha (.18 ac) for males and .04 (.1 ac) for females. Observed overlaps in the home ranges of adult whiptails, and apparent lack of aggressive behavior between individuals suggest that there is a lack of male territoriality in this species (Milstead 1957).

Little is known about dispersal distances for this species but they are capable of making extensive movements, sometimes moving hundreds of meters from one location to another (Jorgensen and Tanner 1963, McCoy 1965, Anderson 1993). Most or all essential habitat requirements are apparently found within the normal area of activity (Zeiner et al. 1988). When long-distance movements do occur they are unpredictable and related to food availability.

Conceptual Basis for Model Development: Movement in the linkage is multi generational. Coastal whiptail prefers oak woodland, hardwood-conifer, valley-foothill riparian, mixed conifer, pine-juniper, chaparral, scrub, and alluvial fan habitats, below 2,290 m. Potential core areas were defined as greater than or equal to 2.5 ha (6.18 ac). Patch size was classified as $\geq$ 0.2 ha (0.49 ac) but less than 2.5 ha. Dispersal distance was defined as 400 m (1,312 ft).

Results & Discussion*:* All three branches of the Least Cost Union contain medium to high suitable habitat for the whiptail, with the central and eastern branches containing the most contiguous habitat (Figure 36). The whiptail has been recorded in Palo Comado Canyon in the Union, and on Mount Clef Ridge. Almost all suitable habitat identified in the planning area was delineated as potential core areas for this species (Figure 37). Distances among all cores and patches of suitable habitat are within the dispersal distance of this species (figure not shown), but barriers may exist between suitable habitat patches. We conclude that the linkage will likely serve the movement needs of the whiptail.

Figure 36.
Habitat Suitability
for
Coastal whiptail
(Cnemidophoris tigris stejnegeri)



Degree of Suitability

- High
- Medium to High
- Medium
- Low to Medium
- Low
- ★ Recorded Occurrence*
- Protected Lands
- Least Cost Union
- Target Areas
- Lakes & Reservoirs
- Hydrography
- County Boundary
- Roads

*Data Source: USFS and National Park Service Ecological Monitoring Data

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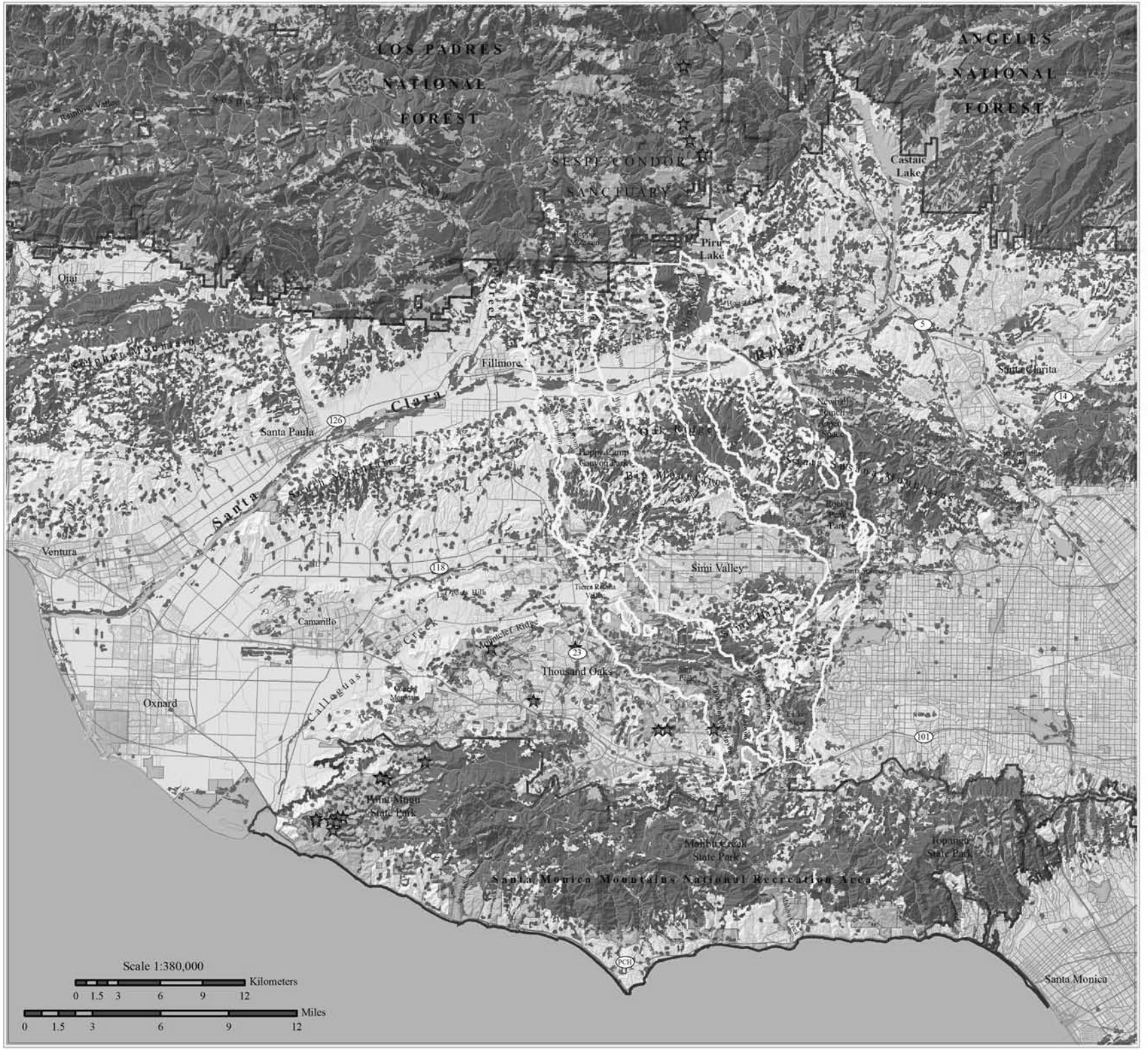
June 2006

www.scwildlands.org

Figure 37.
Potential Cores & Patches
for
Coastal whiptail
(Cnemidophoris tigris stejnegeri)



Core
Patch
< Patch
Recorded Occurrence*
Protected Lands
Least Cost Union
Target Areas
Lakes & Reservoirs
Hydrography
County Boundary
Roads

*Data Source: USFS and National Park Service Ecological Monitoring Data

N

Map Produced By:

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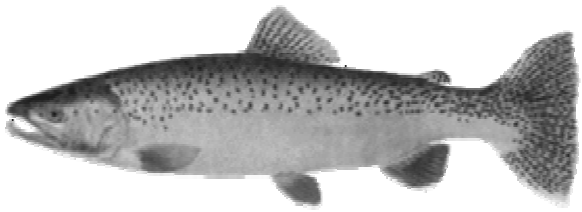
Southern steelhead trout (*Oncorhynchus mykiss mykiss*)


www.caltrout.org

Justification for Selection: Steelhead trout possess unique adaptations, represent an important part of the state's anadromous resources and, because the steelhead inhabits an entire river ecosystem, and requires clean, cool water year-round, it serves as a vital indicator of the overall health of the aquatic ecosystems of southern California coastal watersheds (Finney and Edmondson 2002, Titus et al. 1999).

In original population numbers, steelhead could have been considered a keystone species, and appear to be keystone food resources for vertebrate predators and scavengers in some regions (Willson and Halupka 1995). A growing body of evidence indicates that chemical nutrients delivered by spawned-out carcasses can play a critical role in sustaining the productivity of riparian and lacustrine ecosystems, perhaps including the next generations of juvenile salmon (Richey et al. 1975, Kline et al. 1990). Variation in anadromous fish populations can have major effects on the productivity, phenology and metapopulation dynamics of wildlife and hence on regional biodiversity (Willson and Halupka 1995). The loss of southern steelhead trout from many historically used streams in the planning area has certainly affected these ecosystems. However, increasing opportunities and interest exist to restore steelhead populations in streams throughout the region and waterway connectivity is a key requirement for success.

Distribution & Status: Historically, the steelhead trout was found in the North Pacific Ocean from the Kamchatka Peninsula in Asia to the northern Baja peninsula, and likely inhabited most coastal streams in Washington, Oregon and California as well as many inland streams in these states and Idaho (McPhail and Lindsey 1970). During the twentieth century, over 23 indigenous and naturally reproducing stocks of steelhead are believed to have been extirpated, and many more are thought to be in decline (NMFS 2000a). Presently, the species distribution extends from the Kamchatka Peninsula, east and south along the Pacific coast of North America, to at least Malibu Creek in southern California. A recent discovery of steelhead in San Mateo Creek on the border of Orange and San Diego Counties has confirmed the ability of the steelhead to repopulate areas of its historic range significantly south of Malibu Creek (CDFG 2000, Finney and Edmondson 2002).

The Southern California steelhead population has declined by 99% since the turn of the century (Titus et al. 1999). All naturally spawned populations and their progeny in rivers from the Santa Maria River, San Luis Obispo, to Malibu Creek, Los Angeles County are considered endangered. On August 18th, 1997, the National Marine Fisheries Service issued a Final Rule listing two Evolutionarily Significant Units (ESUs) (Southern California and Upper Columbia River) as endangered and three ESUs (Central California Coast, South-Central California Coast, and Snake River Basin) as threatened.

The major cause of decline of steelhead in California is freshwater habitat loss and degradation, from inadequate stream flows, blocked access to historic spawning and rearing areas by dams, and human activities like land development, logging, mining and agriculture that discharge sediment and debris into watercourses (Jantz et al. 1990, CalTrout 1999). In particular, habitat degradation from urbanization and urban runoff pollution has resulted in sediment in streams clogging spawning gravel, harming the natural reproduction and productivity of the steelhead (Jantz et al. 1990, CalTrout 1999).

Habitat Associations: Unlike juvenile salmon that typically migrate to the ocean after just a few months of freshwater rearing, juvenile steelhead trout reside in coastal streams from one to three years (Finney and Edmondson 2002). Steelhead use all segments of a river or stream system to complete the freshwater phase of their life-history: estuaries to acclimate to salinity changes, the middle reaches of the main stem to reach tributaries, and headwaters tributaries to spawn and rear (Finney and Edmondson 2002). Steelhead require cool, clean water year-round to sustain themselves and need cool, clean, well-oxygenated water flowing over clean gravel to breed and develop (McEwan and Jackson 1996).

Major streams in southern California originate in the coastal mountains and often cross broad low-elevation alluvial flats which present inhospitably warm and fluctuating temperatures and the streams themselves may be intermittent. The higher-elevation headwaters or well-shaded reaches, therefore, are the primary spawning and rearing areas for steelhead today. The optimum water depth for steelhead spawning is approximately 36 cm (14 in) and ranges from about 15 to 91 cm (6 to 36 in; Bovee 1978). Fry typically use water approximately 20 cm (8 in) in depth and can use water 5 to 81 cm (2 to 32 in) deep, while older juveniles typically use a water depth of about 38 cm (15 in) but can use water 5 to 152 cm (2 to 60 in) deep (Bovee 1978).

The ability of some southern steelhead to survive in warm (>70° F [21° C]) isolated pools (Higgins 1991) possibly is due to greater physiological tolerances to higher temperatures and lower oxygen levels than are shown by other steelhead stocks. It has been surmised that steelhead in southern California also rely heavily on estuaries, because many of their streams seasonally had very low flows or dried completely in the alluvial fan areas (Higgins 1991). Evidently large numbers of juvenile southern steelhead often could be caught in coastal lagoons in the 1930s and earlier (Swift et al. 1993). Most of the estuaries today are much shallower and warmer than they were originally.

Spatial Patterns: Steelhead trout typically migrate to marine waters after spending 2 years in fresh water. Then they reside in marine waters for typically 2 or 3 years prior to returning to their natal stream as 4 or 5-year olds. In California, most steelhead spawn from December through April, often making their way past normally dry sections of rivers, small streams, and tributaries during the winter rainstorms that increase in-stream flows (Finney and Edmondson 2002). This ability to migrate, spawn, hatch, rear, and mature in subsequently hydrologically isolated and marginal aquatic environments until the next storm event re-establishes a migration corridor between the inland and marine environment makes the steelhead uniquely able to exist in the southern extent of their range (Finney and Edmondson 2002).

Migration and life-history patterns of southern California steelhead depend more strongly on rainfall and streamflow than is the case for steelhead populations farther north (Titus

et al 1999). River entry ranges from early November through June with peaks in January and February. Average rainfall is substantially lower and more variable in this ESU than in regions to the north, resulting in increased duration of sand berms across the mouths of streams and rivers and, in some cases; complete dewatering of the marginal habitats (NOAA 1996). Environmental conditions in marginal habitats may be extreme (e.g., elevated water temperatures, droughts, floods, and fires) and presumably impose selective pressures on steelhead populations.

Steelhead in general are known to have well-developed homing abilities (Moyle 1976), although it has been suggested that southern steelhead commonly stray from their natal streams (Higgins 1991). Straying, if it actually occurs at significant levels in southern steelhead, may be selectively advantageous because it would allow spawners to opportunistically utilize more favorable streams when their natal streams dried up or were blocked by sand berms (Higgins 1991).

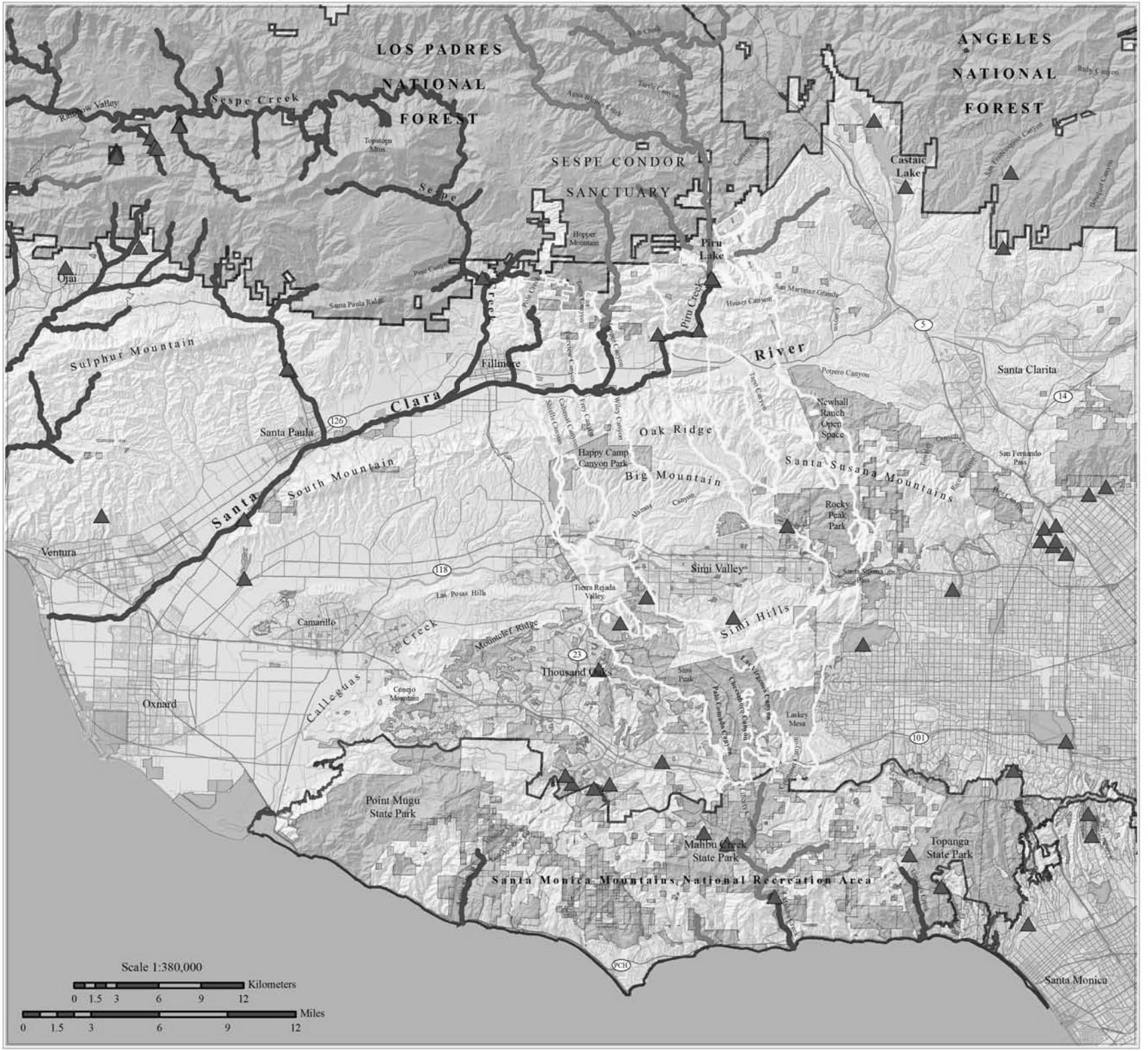
Conceptual Basis for Model Development: Steelhead trout can move 40 km (25 mi) from the ocean to the upper reaches of the watershed when surface waters are sufficient. Dams, diversions and road crossings are significant barriers to movement.

Results & Discussion: The current known extent of southern steelhead trout in the planning area includes the Ventura River and San Antonio Creek in the Ventura Watershed, Santa Clara River, Santa Paula Creek, and Sespe Creek in the Santa Clara River Watershed, and Malibu Creek, Arroyo Sequit, and Topanga Creek in the Santa Monica Bay Watershed (Figure 38). Historically, steelhead moved further up the Santa Clara River to spawning and rearing areas in upper Piru Creek, prior to the reservoir being built for Piru Lake (McEwan and Jackson 1996). The Least Cost Union would promote steelhead movement up Santa Paula, Sespe, and Piru creeks in the Santa Clara River Watershed if habitat is added to the Union along these drainages, barriers are removed, and habitat restoration efforts are undertaken (Figure 38). Habitat was also added to the Union along the mainstem of the Santa Clara River to maintain connections from the coast to the inland drainages. Steelhead trout were also historically present further up Malibu Creek before Rindge Dam was erected (McEwan and Jackson 1996). If barriers are removed and habitat restoration efforts undertaken, the linkage would promote steelhead movement from the coast to the confluence of Malibu and Las Virgenes creeks in the Malibu Creek Watershed (Figure 38).

Restoration of steelhead trout populations will require removal of or modifications to dams, diversions and other barriers; sustaining winter/spring flows to allow for migration; and improving water quality. Fish ladders have been installed on the Vern Freeman Dam on the Santa Clara River and on the Harvey Dam on Santa Paula Creek to assist steelhead trout making the journey upstream. Both need some modification since they were constructed based on a design used for salmon in northern parts of their range. Comprehensive data has recently been collected (Stoecker and Kelley 2005) on impediments to southern steelhead trout in the Santa Clara River Watershed and the feasibility of restoring healthy steelhead runs in historically occupied habitat.

In the Santa Monica Bay Watershed, plans are underway to remove the now defunct Rindge Dam on Malibu Creek, which will increase steelhead habitat from 4.0 stream km to at least 12 km (2.5 to 7.5 mi), allowing them to reach their historical spawning grounds (McEwan and Jackson 1996). Comprehensive data has also recently been collected in

Figure 38.
Potential habitat
for
Southern steelhead trout
(Oncorhynchus mykiss)



Occupied Habitat*
Potential Spawning & Rearing Habitat*
Protected Lands
Least Cost Union
Target Areas
Dams
Lakes & Reservoirs
Hydrography
County Boundary
Roads

*Data Source: National Marine Fisheries Service (NOAA Fisheries)

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the Santa Monica Mountains on barriers to movement for steelhead trout and potential spawning and rearing habitat was also identified (Caltrout 2006).

The single greatest limiting factor in the recovery of southern steelhead is the network of regional dams and other fish passage barriers (McEwan and Jackson 1996). Steelhead trout are no longer able to reach important upstream reproduction and nursery areas in most of the major coastal drainages south of San Francisco Bay (Titus et al. 1999). To restore the full range of fish fauna to southern California aquatic systems and their watersheds, the priorities should be to focus on restoring fish passage to historic spawning and rearing areas, address watershed-wide degradation of aquatic ecosystems, and ensure adequate representation of southern California interests in all state and federal programs designed to address the recovery of steelhead in California (Finney and Edmondson 2002).

The National Marine Fisheries Service, charged with the conservation and recovery of anadromous fish, has developed guidelines for the design of stream crossings to aid upstream and downstream passage of migrating salmonids (2000b). Preferred crossings in order of preference are 1) bridge (with no encroachment into the channel 100-year flood plain); 2) streambed simulation strategies: bottomless arch, embedded culvert design, or ford; embedded round metal culvert, concrete box culvert, or compound culvert designs. Substrate and flow conditions within the crossing mimic that natural streambed above and below the structure; 3) non-embedded culvert: less than 0.5%slope; and 4) baffled culvert, or structure designed with a fishway: slopes greater than 0.5% (NMFS 2000b).

To maintain and restore steelhead runs in the planning area, we recommend that:

- Barriers are removed or fish passages constructed across barriers to allow steelhead access to additional spawning and rearing habitat (Higgins 1991, McEwan and Jackson 1996, Stoecker and Kelley 2005, Caltrout 2006).

- A centralized information sharing system is created that can be utilized by all agencies, land managers, academic institutions, and other researchers working on the conservation and recovery of southern steelhead trout (Finney and Edmondson 2002).

- Overgrazing is discouraged. Unrestricted or mismanaged grazing strategies can destroy habitat, erode banks and pollute the water (Caltrout 1999).

- Water removal (groundwater pumping, impoundments, diversions) is prohibited from occupied or potentially restorable steelhead streams to leave minimum flows for fish in both streams and lagoons (McEwan and Jackson 1996).

- Estuaries are rehabilitated through better watershed management practices to reduce the input of sediments and to increase freshwater inflows (McEwan and Jackson 1996).

- All suggestions by Stoecker and Kelley (2005) and Caltrout (2006) to restore habitat connectivity and integrity for steelhead trout be implemented.

Chalcedon checkerspot butterfly (*Euphydryas chalcedona*)



Justification for Selection: Chalcedon checkerspot is considered an indicator species for undisturbed coastal sage scrub (Hogue 1993). It is also a primary pollinator for many plant species, and may functionally increase the size of a plant's available gene pool in proportion to the flight range of the pollinator and enhance the speed of dissemination of novel genes (Ballmer unpub).

Distribution & Status: Chalcedon checkerspot have enormous geographic variation, with 38 subspecies named (Scott 1986). They are treated by some as three separate species: *Euphydryas anicia*, *E. chalcedona*, and *E. colon. E chalcedona* is found from Alaska south along the Pacific coast through California and Arizona to Baja California and Mexico, east to Montana, the Dakotas, Wyoming, Colorado, and New Mexico. The species is primarily associated with the coastal foothills (Orsak 978)

Habitat Associations: Chalcedon checkerspots can be found in desert hills, chaparral, coastal sage scrub, oak woodlands, grasslands, open forest and alpine tundra from the Upper Sonoran Zone to the Alpine Zone (Scott 1986, Hogue 1993, Heath 2004).

Food plants for the chalcedon checkerspot includes many members of the figwort family (*Scrophulariaceae*), especially bush monkeyflower (*Mimulus aurantiacus*) and coast figwort (*Scrophularia californica*), as well as paintbrushes (*Castilleja* spp.), and Penstemon (*Penstemon antirrhinoides, P. cordifolia*) (Orsak 1978). Caterpillar hosts include penstemon and paintbrush, and species from several other plant families including Caprifoliaceae, Boraginacea and Rosaceae (Orsak 1978). Adults are readily attracted to moisture and also to flowers of buckwheats (*Eriogonum* spp.) and yerba santa (*Eriodictyon crassifolium*) in many areas of southern California (Orsak 1978).

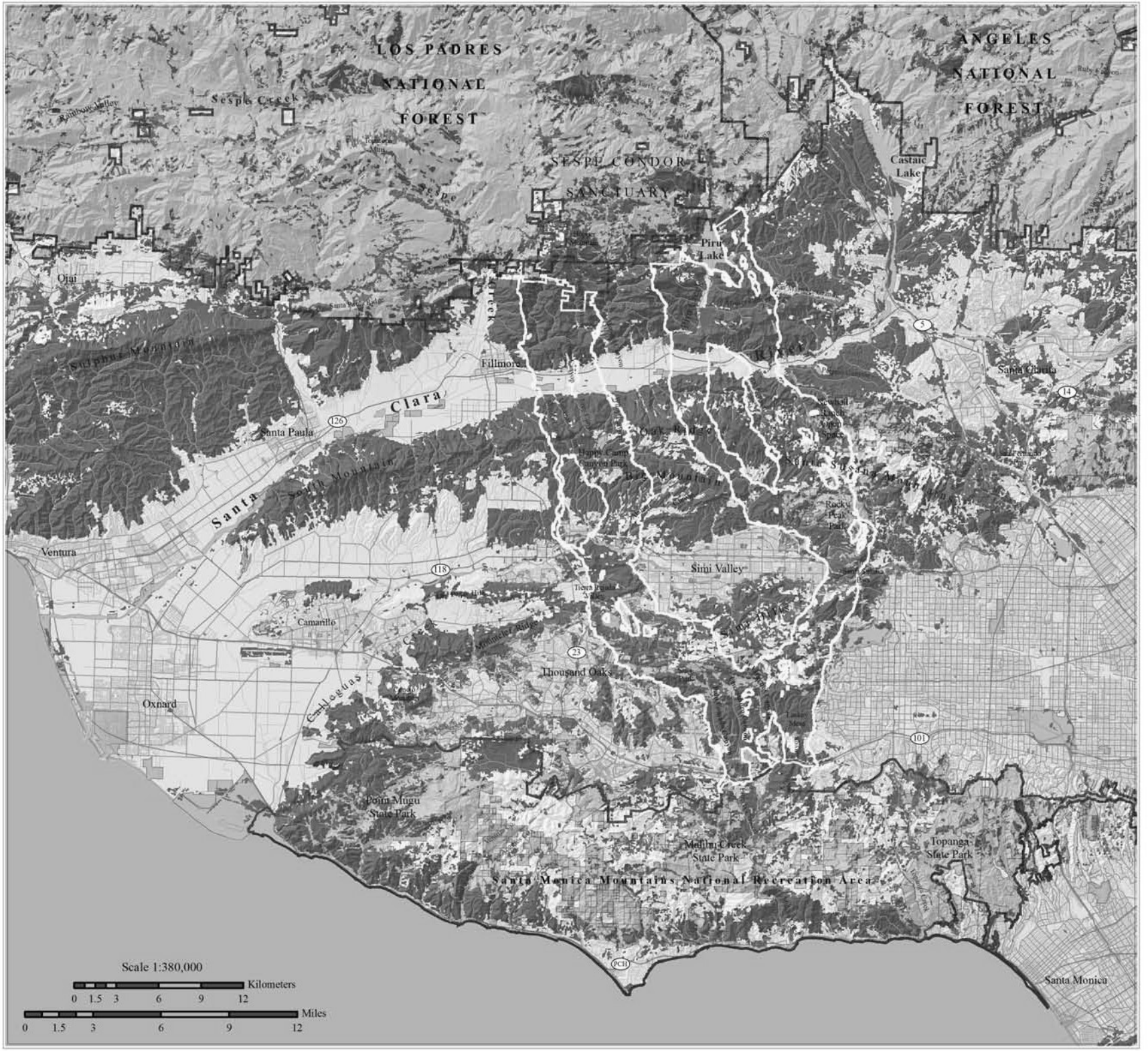
Spatial Patterns: Flight time is from March through June, and September through November. Flight distances between recaptures averaged 65 m (213 ft) at one site, 146 m (479 ft) at another, for males, but only 18 m (59 ft) for females (Scott 1986).

The average life span for males is 9-10 days in nature. Males seek females all day, by patrolling all over the habitat or by perching (especially on hilltops, but often on exposed vegetation in clearings), depending on the locality.

Conceptual Basis for Model Development: Movement through the linkage is multi-generational. Potential habitat for the chalcedon checkerspot butterfly include chaparral, coastal sage scrub, oak woodlands, grasslands, and open forest.

Results & Discussion: Potential habitat for the chalcedon checkerspot butterfly is widespread in the planning area, with all branches of the Least Cost Union containing suitable habitat (Figure 39). Habitats in the Union are expected to support intergenerational movements of this species between targeted core areas. The checkerspot butterfly would also benefit from a connection across Conejo Mountain to Mount Clef Ridge and the Tierra Rejada Valley. To ensure the long-term survival of the chalcedon checkerspot butterfly in the planning area, habitat integrity, host plant colonies and nectar sources need to be maintained and restored.

Figure 39.
Potential habitat
for
Chalcedon checkerspot butterfly
(Euphydryas chalcedona)



Potential Habitat
Protected Lands
Least Cost Union
Target Areas
Lakes & Reservoirs
Hydrography
County Boundary
Roads

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Damselflies (*Odonata - Zygoptera* spp.)

Justification for Selection: A mature ecosystem often contains a diversity of invertebrates with overlapping functions, which contribute to community stability and resilience. Damselflies serve as food for fish, birds and frogs (Smith and Pritchard 1956). Adults feed on mosquitoes and gnats (Powell and Hogue 1979). Invertebrates are integral components of communities, without their functional presence, the structure and productivity of most, if not all, habitats would collapse (Ballmer unpub).


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Distribution & Status: Damselflies are widespread wherever there is permanent, clean freshwater. About 40 species of the *Zygoptera* are found in California (Manolis 2003). The most common damselflies are the bluets of the Coenagrionidae Family.

Habitat Associations: Damselflies are aquatic in the nymphal or larval state and as adults are terrestrial or aerial. Adults stay close to the water in which they will lay their eggs. Nymphs (a.k.a. naiads) are predaceous water dwellers, eating immature insects, crustaceans, tadpoles, fish and young salamanders (Essig 1926).

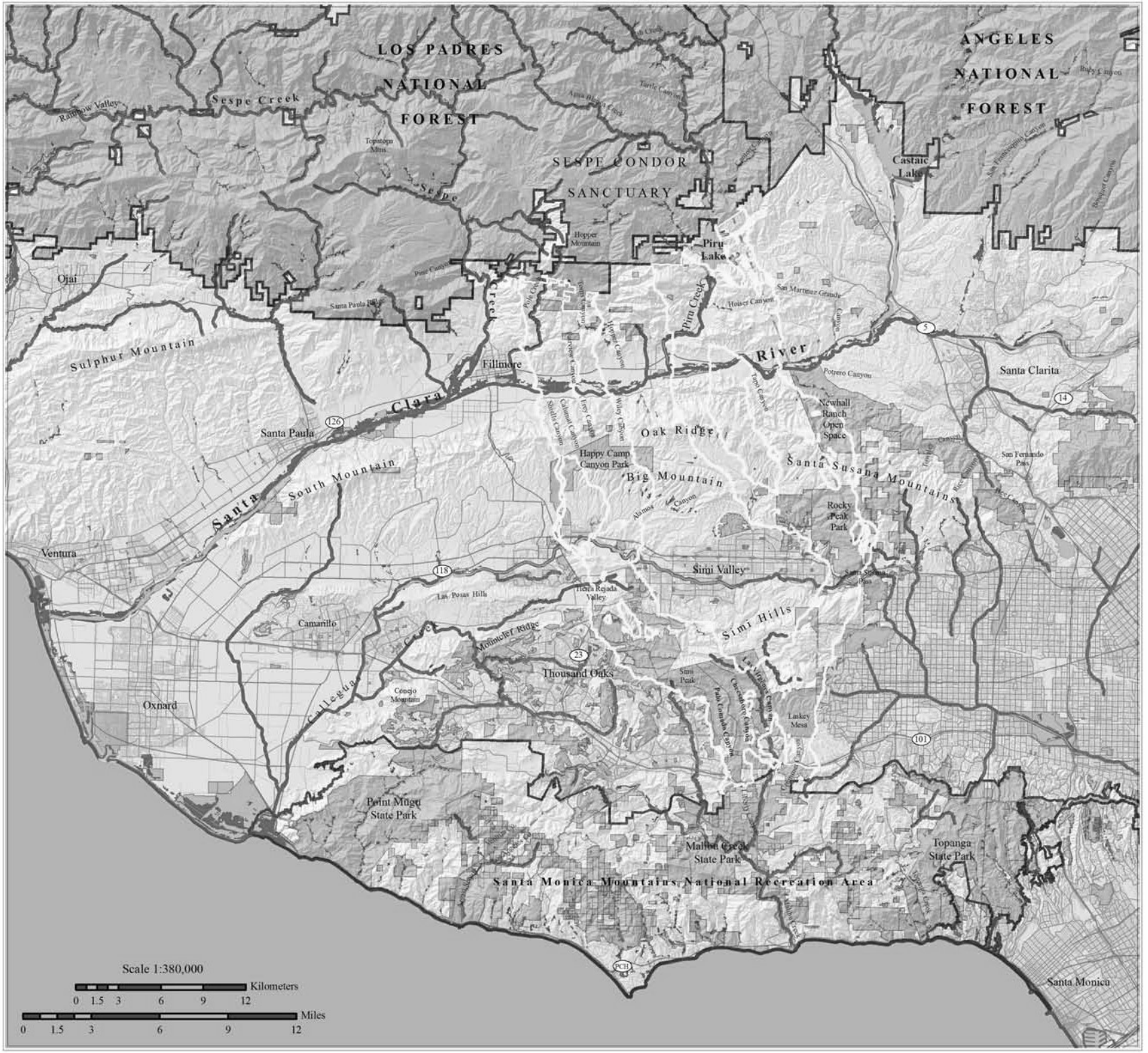
Broad-winged damselflies (Family Calopterygidae), such as the common Ruby Spot *(Hetaerina americana*) are likely to be seen only near rapidly flowing streams in the mountain canyons surrounding the Los Angeles Basin. Dancers (Family Coenagrionidae) are normally seen around small streams in the mountains, most commonly in the San Gabriel and Santa Monica Mountains (Hogue 1993).

Spatial Patterns: Adult damselflies are not strong fliers and are usually found near the bodies of water in which they breed (Hogue 1993).

Conceptual Basis for Model Development: Movement in the linkage is multi generational. All perennial streams were identified as potential habitat for damselflies.

Results & Discussion: Habitat for damselflies is limited to clean perennial freshwater streams, which are limited in the planning area. Streams identified as potential habitat (Figure 40) are perennial but water quality is impaired in several of these drainages, which are listed under Section 303(d) of the Clean Water Act. Habitats in the Union are not sufficient to accommodate this species. We added habitat to the Union along the Santa Clara River, Santa Paula Creek, Sespe Creek, and Piru Creek to support the needs of damselflies. Please see the Impediments to Streams section for recommendations to protect and restore habitat for damselflies and other riparian dependent species.

Figure 40.
Potential habitat for Damselflies
(Odonata - Zygoptera spp.)



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Harvester ant (*Pogonomyrmex rugosus*)



Justification for Selection: Harvester ants exert dominant influences on the landscape in pinyon-juniper, grassland coastal sage, and desert habitats, where these species extensively rework the soil, contribute to soil nutrient heterogeneity, and alter herb and shrub cover (MacMahon et al. 2000).

The soil excavations of ant colonies, and numerous other soil-dwelling arthropods, help to aerate the soil and to move organic particulates from the soil surface to greater depths (Ballmer unpub). Some ants also sequester quantities of seeds under ground, providing a seed bank for some plant species. Harvester ants aid in seed dispersal for some plants (Ballmer unpub). Harvester ant seed predation continuously alters the distribution and relative abundance of flower types in California grasslands (Moldenke 1976). This, along with varying rainfall, causes great variation from year to year of floral productivity.

Distribution & Status: Harvester ants are found in western Oklahoma, western Texas, southeastern and southwestern Colorado, New Mexico, southern Utah, Arizona, southern and central Nevada, southern California and Mexico. Western harvester ants are more common at higher elevations. They are known up to 2,743 m (9,000 ft).

Harvester ants, like all native ants, are threatened by the invasion of Argentine Ants (*Linepithema humile*). Agriculture, flood control, and urbanization promote biological invasions by Argentine ants that eliminate native ant colonies. The coast horned lizard, a sensitive species that is declining, is highly dependent on native ants for sustenance (Pianka and Parker 1975, Montanucci 1989, Suarez et al. 2000, Suarez and Case 2002, Fisher et al. 2002).

Habitat Associations: Harvester ants are characteristic or indicator species of dry river beds: washes, arroyos, and basins below mountains where water is seldom present, vegetation is partly riparian, partly coastal sage scrub, but very sparse (Hogue 1993). During long dry periods, coastal sage may infringe and isolated chaparral species may occur (Hogue 1993).

Founding queens of *P. rugosus* have a higher tolerance for dessication and hence this species dominates in drier soil microhabitats consisting of coarser soils (Johnson 2000).

Spatial Patterns: Harvester ants form colonies composed of 1,000-22,000+ individuals and typically collect vast quantities of seeds and dead insects during the warmer seasons of the year (MacKay 1981). In most habitats harvester ant colonies are fairly regularly spaced, a common sign of territorial behavior in other groups of animals. In southern Arizona, *P. rugosus* colonies were found to be spaced at an average of 17 m

(56 ft) apart (Holldobler 1974). Harvester ant colonies can occupy the same nest for 20 years (Gordon 1991, 1992).

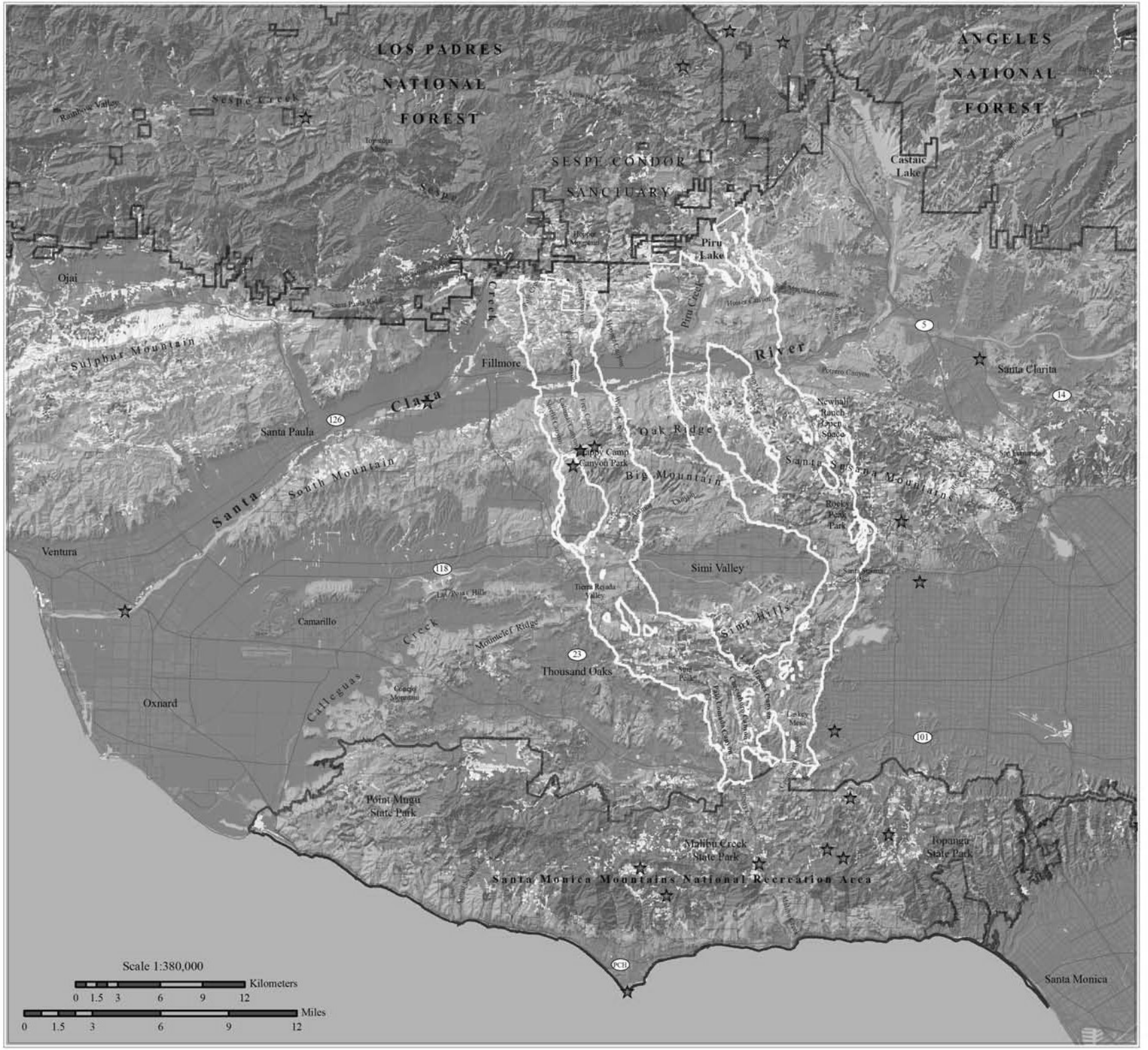
P. rugosus had random dispersion patterns in the Chihuahuan Desert, where intra- and interspecific encounters were infrequent (Whitford et al. 1976). Neighborhood interactions affect establishment, survivorship, and colony spacing within habitats where colony densities are high, whereas at broader scales, variability in soils, vegetation, or land-use practices affects the density and distribution of *Pogonomyrmex* spp. (MacMahon et al. 2000).

Conceptual Basis for Model Development: We modeled potential habitat for coast horned lizard as a surrogate for harvester ant. Horned lizards may use alluvial fans, alkali flats, alkali desert scrub, dunes, open coastal scrub and chaparral, grassland, and clearings in coniferous forests, broadleaf woodlands, and riparian woodlands. They avoid urban and agricultural developments and areas of high road density.

Results & Discussion*:* Potential habitat for the harvester ant is widespread in the linkage planning area. All branches of the Least Cost Union contain suitable habitat for this species (Figure 41), with documented occurrences of coast horned lizard in the western branch of the Union in the Santa Susana Mountains. With habitat restoration, we believe that the Least Cost Union will serve this species. The harvester ant would also benefit from the Conejo Mountain and Mount Clef Ridge additions to the Union.

To maintain connectivity for harvester ants, we recommend that no additional agriculture, flood control, or urbanization be permitted in the Linkage Design. Irrigation of landscapes encourages the spread of Argentine ant populations into natural areas, where they cause a halo of local extinctions of native ant populations extending 200 m (656 ft) into native vegetation (Suarez et al. 1998, Bolger et al. 2000). We suggest protection and restoration of contiguous swaths of natural habitats with buffers of at least 1 km (0.62 mi) to maintain the integrity of the linkage.

Figure 41.
Habitat Suitability
for
Harvester ant
(Pogonomyrmex rugosus)



Degree of Suitability

- High
- Medium to High
- Medium
- Low to Medium
- Low
- ★ Coast horned lizard occurrences*
- Protected Lands
- Least Cost Union
- Target Areas
- Lakes & Reservoirs
- Hydrography
- County Boundary
- Roads

*Data Source: CNDDB, USFS

N

Scale 1:380,000

Kilometers
0 1.5 3 6 9 12

Miles
0 1.5 3 6 9 12

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Burrowing scorpion (*Anuroctonus phaiodactylus*)

Justification for Selection: Predatory species like the burrowing scorpion are considered the charismatic megafauna of the arthropod world (T. Longcore, pers. comm.), exerting important influence over the invertebrate community.



Distribution & Status: The burrowing scorpion is found in Nevada, California, western Utah, and Baja California, Mexico. The burrowing scorpion has no special status.

For these organisms, roads, concrete-lined ditches, irrigation canals, expanses of irrigated land (e.g. agriculture, golf course), and other non-habitats can be effective barriers to movement and/or direct causes of mortality (Ballmer unpub).

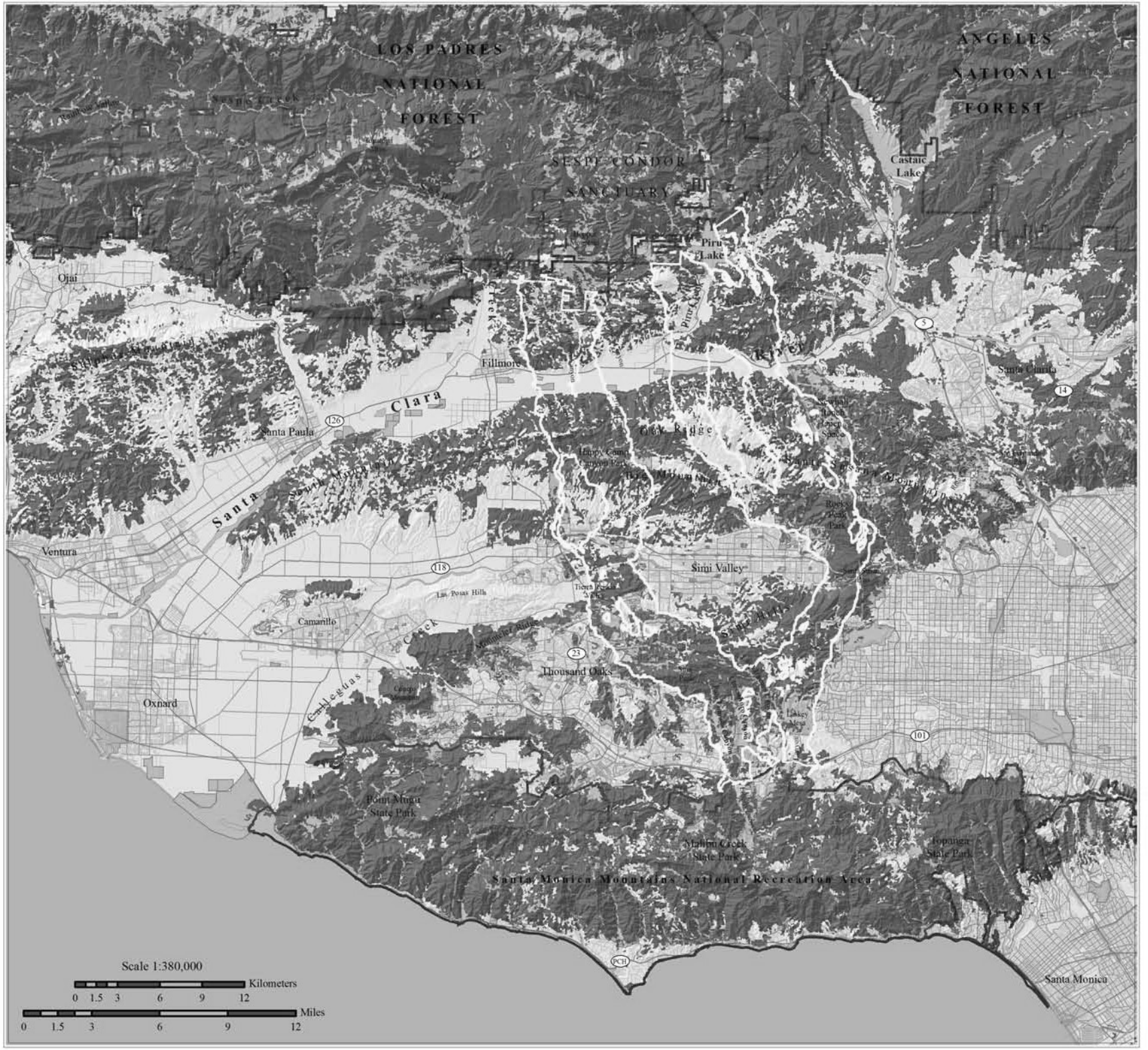
Habitat Associations: The burrowing scorpion needs contiguous coastal sage and or chaparral habitats with undisturbed soil (T. Longcore, pers. comm.). This species is generally nocturnal, moving about at night in search of soft-bodied insects for food. They usually feed on beetles, cockroaches, crickets, centipedes, spiders, sun spiders, and other ground dwellers (Hogue 1993).

Spatial Patterns: The burrowing scorpion is a ground-dwelling species that may occur in low densities and wander relatively great distances in search of mates. Burrowing scorpions dig burrows, often in colonial aggregations and ambush prey from the mount of its burrow during the night, retreating into its shelter during the day or when startled or threatened (Hogue 1993).

Conceptual Basis for Model Development: Movement in the linkage is multi generational. We modeled potential habitat for this species as coastal sage scrub and chaparral habitats.

Results & Discussion: Potential habitat for the burrowing scorpion is widespread in the planning area, with all branches of the Least Cost Union providing suitable habitat (Figure 42). The western and eastern branches of the Union provide the most contiguous habitat for this species. However, since one of the few natural communities this species utilizes is coastal sage scrub, the burrowing scorpion would certainly benefit from adding the coastal sage connection from Conejo Mountain to Mount Clef Ridge and the Tierra Rejada Valley. We conclude that, with the suggested additions, the linkage will likely serve this species. We suggest habitat restoration in areas of the Linkage Design historically occupied by coastal sage scrub. Lighting should be directed away from the linkage and crossing structures for this nocturnally active species (Rich and Longcore 2006).

Figure 42.
Potential habitat for Scorpion
(Anuroctonus phaiodactylus)



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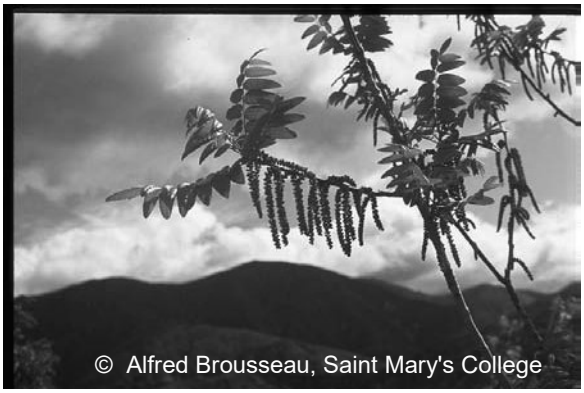
California black walnut (*Juglans californica*)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Justification for Selection: California black walnut is considered one of California's rare and imperiled natural communities, severely threatened by habitat fragmentation and degradation (CNPS 2001). Walnut trees provide habitat and a highly nutritious food source for wildlife (Anderson 2002).

Distribution & Status: California black walnut is endemic to the state and is restricted to a narrow band within the southern California coastal foothills, from the Transverse Range in Santa Barbara County south to the Peninsular Ranges of San Diego County (Hickman 1993, CNPS 2001, Anderson 2002). The elevational range extends from near sea level in the Santa Monica Mountains to 1,067 m (3,500 ft) in the San Bernardino Mountains (Anderson 2002).

In the linkage planning area, California black walnut occurs extensively in the Santa Clarita River drainage near Sulphur Mountain, in the Simi Hills and Santa Susana Mountains, and on the northern slope of the Santa Monica Mountains (Quinn 1989). A unique forest association of bigcone Douglas-fir (*Pseudotsuga macrocarpa*), oaks, and walnut occurs on the northeast side of the Santa Susana Mountains and a magnificent oak–walnut forest, dominated by coast live oak (*Quercus agrifolia*), covers more than 5 square miles on the north face of Sulphur Mountain (Anderson 2002).

The California black walnut forest community is a much fragmented, declining natural community that is rare in southern California due to habitat loss and degradation caused by urbanization and grazing (CNPS 2001). California walnut woodlands appear to have low regeneration, which is likely caused by a combination of livestock grazing, invasion of nonnative annual grasses, seedling predation, and disease. California walnut woodlands are designated as a sensitive natural community (CDFG 2005) and are not well-represented on public lands (Stephenson and Calcarone 1999).

Habitat Associations: California black walnut occurs along slopes and in canyons within chaparral, coastal sage scrub, grassland, and cismontane woodlands (CNPS 2001, Anderson 2002). It usually occupies mesic areas (riparian corridors, floodplains, and north-facing slopes) and prefers soils with high clay content (Quinn 1990, Hickman 1993, Stephenson and Calcarone 1999, CNPS 2001), but it may also be found in dry situations where it is sustained by ground-water supplies (Faber et al. 1989). It can be the dominant tree in the canopy or can occur in mixed stands with other hardwoods.

Spatial Patterns: California black walnuts are wind pollinated from male catkins found on the same tree. They flower from March to May and their fruits reach full maturity in the fall (Quinn 1989). Seedlings appear in the spring and mature rapidly in moist sunny locations (Swanson 1976). California black walnut prefers north- and east-facing slopes (Anderson 2002).

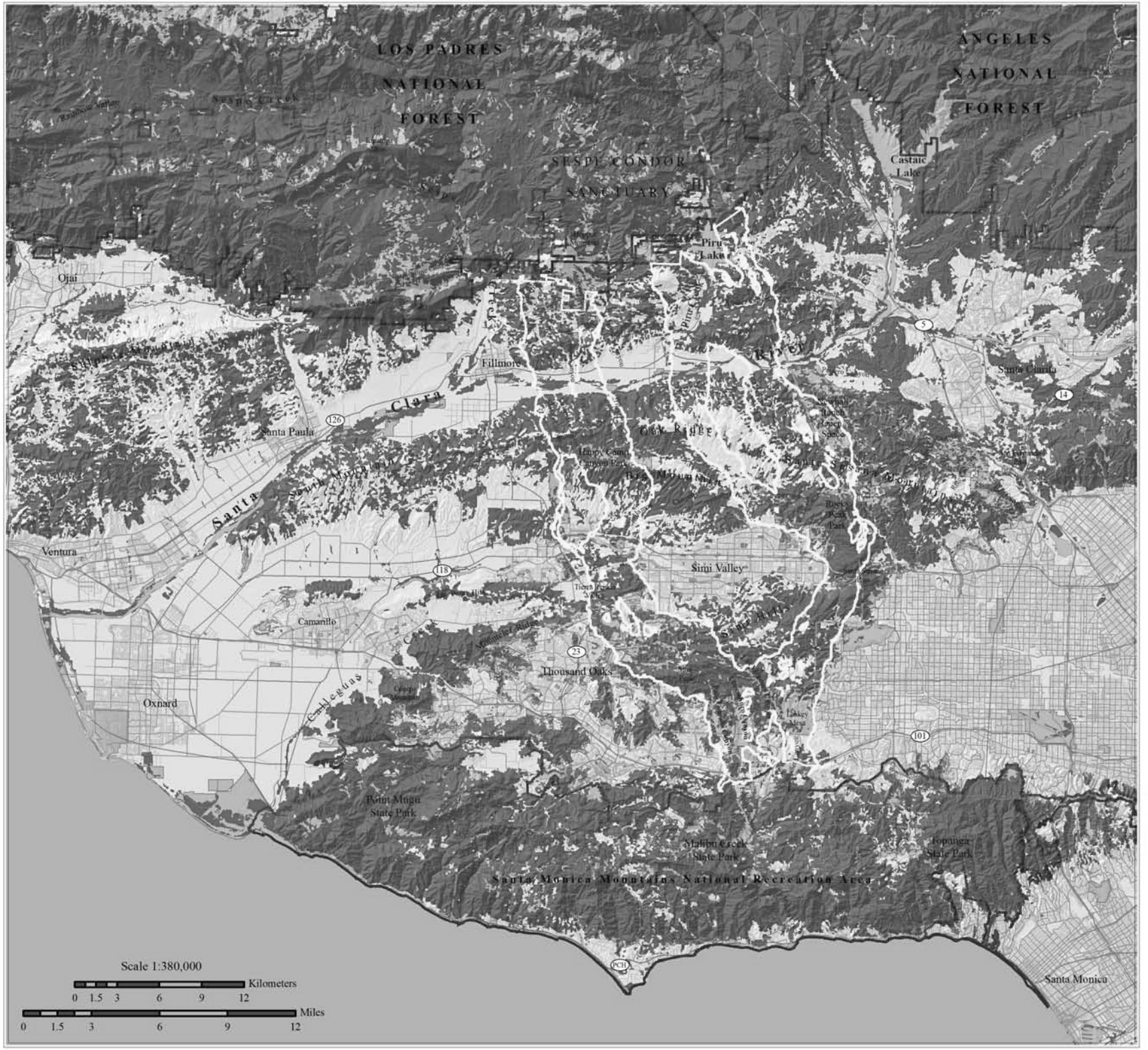
Streams may provide for direct transport of seeds and movement of wildlife that act as seed dispersal agents. The fruit of the walnut is stored, buried or eaten by both California ground squirrels (*Spermophilus beecheyi*) and western gray squirrels (*Sciurus griseus*) (Quinn 1989). Seeds may also be transported by coyotes up to 16 km (10 mi) (S. Riley pers. comm.) and by crows or ravens up to 1.6 km (1 mi; K. Garrett, pers. comm.).

Conceptual Basis for Model Development: California black walnut may be found in chaparral, coastal sage scrub, grassland, and cismontane woodlands below 1,067 m.

Results & Discussion: Potential habitat for walnut is widespread in the planning area, with both the western and eastern branches of the Least Cost Union providing fairly contiguous patches of suitable habitat for germination and establishment of black walnut, as well as live-in and move-through habitat for potential seed dispersers (Figure 43). We conclude that the Union will likely serve the needs of this species.

Development on private lands and loss of suitable habitat for establishment (south slope drainages, north-slope hillsides) appears to be the primary threat to this community, so protection is needed on private lands, as well as a concerted effort to bring some of the best examples of remaining stands under permanent protection. Research needs to be conducted to better determine current distribution, and the effect of fire regimes and nonnative grasses on regeneration of California walnut (Stephenson and Calcarone 1999).

Figure 43.
Potential habitat
for
California black walnut
(Juglans californica)



Potential Habitat
Protected Lands
Least Cost Union
Target Areas
Lakes & Reservoirs
Hydrography
County Boundary
Roads

N

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Justification for Selection: Valley oak riparian forests and woodlands are intensively used by wildlife. Valley oak riparian forest has the most complex structure of any vegetation type in California, and as a result, is among the most diverse in terms of the animal life it supports (Pavlik et al. 2000). Collectively, valley oak riparian forests support 67 nesting bird species (Gaines 1980, Schlorff and Bloom 1984). Valley oak woodlands are used by 21 species of amphibian (8 of special status in California), 31 reptiles (12 of special status in CA), 142 bird species (28 of special status in CA), and 74 mammals (24 of special status in CA) (CDFG 2005). To date, valley oak has not shown symptoms of Sudden Oak Death, which may make them even more critical to the long term viability of oak woodland-dependent wildlife (California Partners in Flight 2002).

Distribution & Status: Valley oak is endemic to California, occurring below 1,700 m (5,600 ft) in the Coast Ranges, Sierra Nevada foothills, and Central Valley from Tehama County south, and reaching its southern limit in the San Fernando and Santa Clarita Valleys and the Santa Monica Mountains in Los Angeles County (Griffin and Critchfield 1972, Thomas 1987, Pavlick et al. 2000). Valley oak forms extensive woodlands, particularly in the Central Valley, but in the South Coast Ranges, valley oak is a minor component of several plant communities (Griffin and Critchfield 1972).

Historically, valley oak forests and woodlands were much more extensive (Bartolome 1987). In 1998, the California GAP Analysis Project estimated valley oak to cover a total of 287,323 ha (709,991 ac) in the state (Davis et al. 1998). In the central and south coast bioregions, an estimated 275 ha (680 ac) of valley oak woodland occur on public lands, representing only 8% of the total extent of this community in the southern part of the state (Stephenson and Calcarone 1999). Rapid expansion of agriculture, vineyards, and urban development, in addition to restricted recruitment within remnant stands, has seriously reduced the amount of valley oak woodlands (Griffin 1971, Bolsinger 1988, Adams et al. 1992, Stephenson and Calcarone 1999). Valley oak woodlands and forests are designated as sensitive natural communities by the state (CDFG 2005).

Seedling regeneration is low and may jeopardize the long-term viability of valley oak woodlands; many stands are reported to lack trees younger than 75-125 years (Pavlick et al. 2000). Factors limiting the recruitment and regeneration of valley oaks include drought stress, predation by deer, ground squirrels, gophers, insects and livestock, soil cultivation around mature trees, lowering of the water table caused by groundwater pumping, and competition from annual herbaceous species and nonnative grasses (Griffin 1976, Griggs 1990, Danielsen and Halvorson 1991, Stephenson and Calcarone 1999). Mature trees are sensitive to over watering, saline irrigation runoff, lowered water tables, pruning, grade changes, and blankets of asphalt covering the root system (Griffin 1973, Rossi 1980).

Habitat Associations: Valley oaks may occur on valley floors and moderate slopes, in open grasslands, savannah and woodlands, and in riparian areas in chaparral (Stephenson and Calcarone 1999). Valley oak grows on intermittently flooded or seasonally saturated soils in valley floors and on alluvial or residual soils in lower foothill communities, with slopes less than 35 percent (Allen et al. 1991, Sawyer and Keeler-Wolf 1995).

Spatial Patterns: Valley oak is wind pollinated and animal dispersed. Male flowers are arranged in long catkins that produce wind-borne pollen, usually March-April (Roberts 1995). Acorns mature and drop to the ground in the fall, and germination usually occurs soon afterwards (Roberts 1995). Seed-caching animals, such as scrub jay, Stellar's jays, yellow-billed magpies and California ground squirrel, are important because acorns buried by these animals have a greater chance of germination and successful establishment (Griffin 1976, Carmen et al. 1987). Acorns can be moved 0.62 to 1.2 km (1-2 mi) by birds, but germination and establishment may be restricted to nodes beneath existing oaks.

Conceptual Basis for Model Development: Valley oaks may occur in open grasslands, savannah and woodlands, and in riparian areas in chaparral below 1,700 m. Dispersal distance was defined as 1.2 km.

Results & Discussion: Potential habitat for Valley oak is somewhat restricted in the planning area, though it is well distributed in the Least Cost Union (Figure 44). We conclude that the Union is likely to serve this species, as sufficient suitable habitat exists for germination and establishment of Valley oak, and for birds and small mammals that disperse acorns (e.g., scrub jay, ground squirrel) to move through habitats in the Union.

Oak woodlands should be managed at the landscape level to accommodate species interactions at multiple scales and prevent the invasion of protected habitat patches by exotic plants and animals (Sisk et al. 1997). Linking and buffering large contiguous areas of oak woodland and associated habitats are priorities for protection and restoration because fragmentation alters bird species composition, favoring nest predators and exotic competitors (Merelender et al. 1998, Purcell and Verner 1999). To protect and restore habitat for Valley oak, we recommend that:

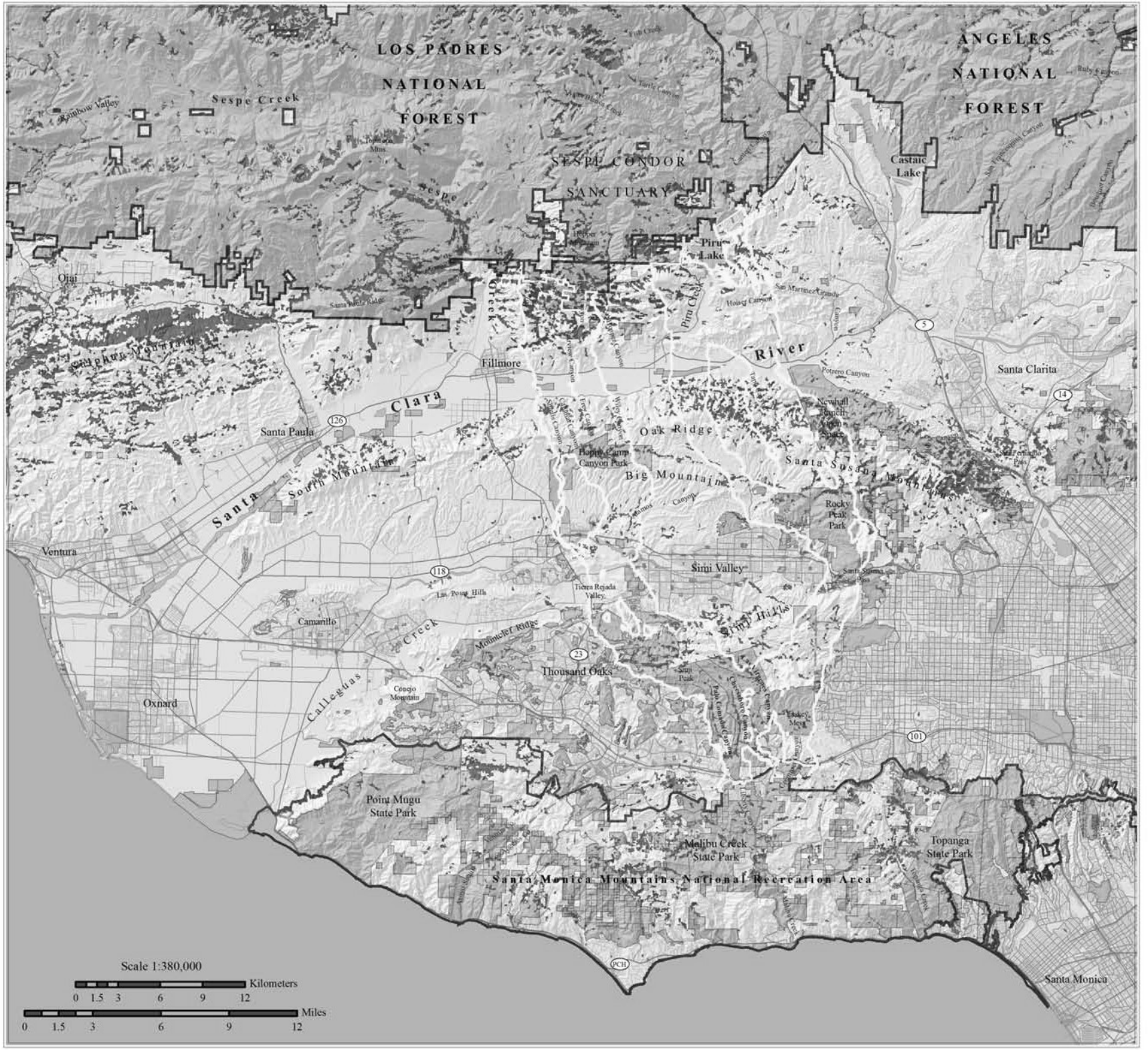
- Sites with intact oak regeneration and decay processes and diverse age class structures should be preserved to insure viable future habitat (California Partners in Flight 2002).

- Seedlings and saplings be protected from overgrazing (California Partners in Flight 2002).

- Ecologically sensitive fire management activities, including carefully planned low-intensity prescribed burns may also contribute to improved oak recruitment and may prevent large, higher intensity fires that destroy oak woodlands (Standiford and Tinnin 1996).

- Light and Pedroni (2001) recommended creation of policies on oak woodland conservation that regard the oak woodland as the functional unit.

Figure 44.
Potential habitat for Valley oak
(Quercus lobata)



Potential Habitat
Least Cost Union
Target Areas
Lakes & Reservoirs
Hydrography
County Boundary
Roads

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Bigberry manzanita (*Arctostaphylos glauca*)


Charles Webber © California Academy of Sciences

Justification for Selection: Bigberry manzanita may be impacted by disruption of ecological processes in linkage areas, particularly changes in fire frequency associated with urban development adjacent to linkages.

Distribution & Status: Bigberry manzanita is distributed from Mount Diablo in Contra Costa County, California south through the South Coast, Transverse, and Peninsular ranges and interior regions of the Sierra Juarez and Sierra San Pedro Martir to central Baja California (Eastwood 1934, Minnich and Howard 1984, Vasek and Clovis 1976). Bigberry manzanita is typically found on dry slopes below 1500 m (4500 ft; Munz 1959) but has been recorded at elevations up to 1890 m (6200 ft; Hickman 1993).

Habitat Associations: Bigberry manzanita is associated with intact chaparral, Joshua tree woodland, and pinyon-juniper woodland (CNPS 2001). It is usually not a dominant chaparral species except in mixed chaparral of the San Gabriel and San Bernardino mountains (Minnich and Howard 1984). It occasionally forms dense, pure stands or codominates with Eastwood manzanita in manzanita chaparral (Hanes 1977). Bigberry manzanita also occurs in singleleaf pinyon (*Pinus monophylla*)-Utah juniper (*Juniperus osteosperma*) communities bordering the Sonoran and Mojave deserts (Vasek and Clovis 1976).

Bigberry manzanita has no statistically significant association with aspect or degree of slope (Hanes 1971). Bigberry manzanita grows in soils derived from granite, limestone, quartz diorite, or serpentine and that range in texture from sandy loam with considerable coarse fragment to loam (Hellmers et al. 1955, Horton and Kraebel 1955, Hanes and Jones 1967).

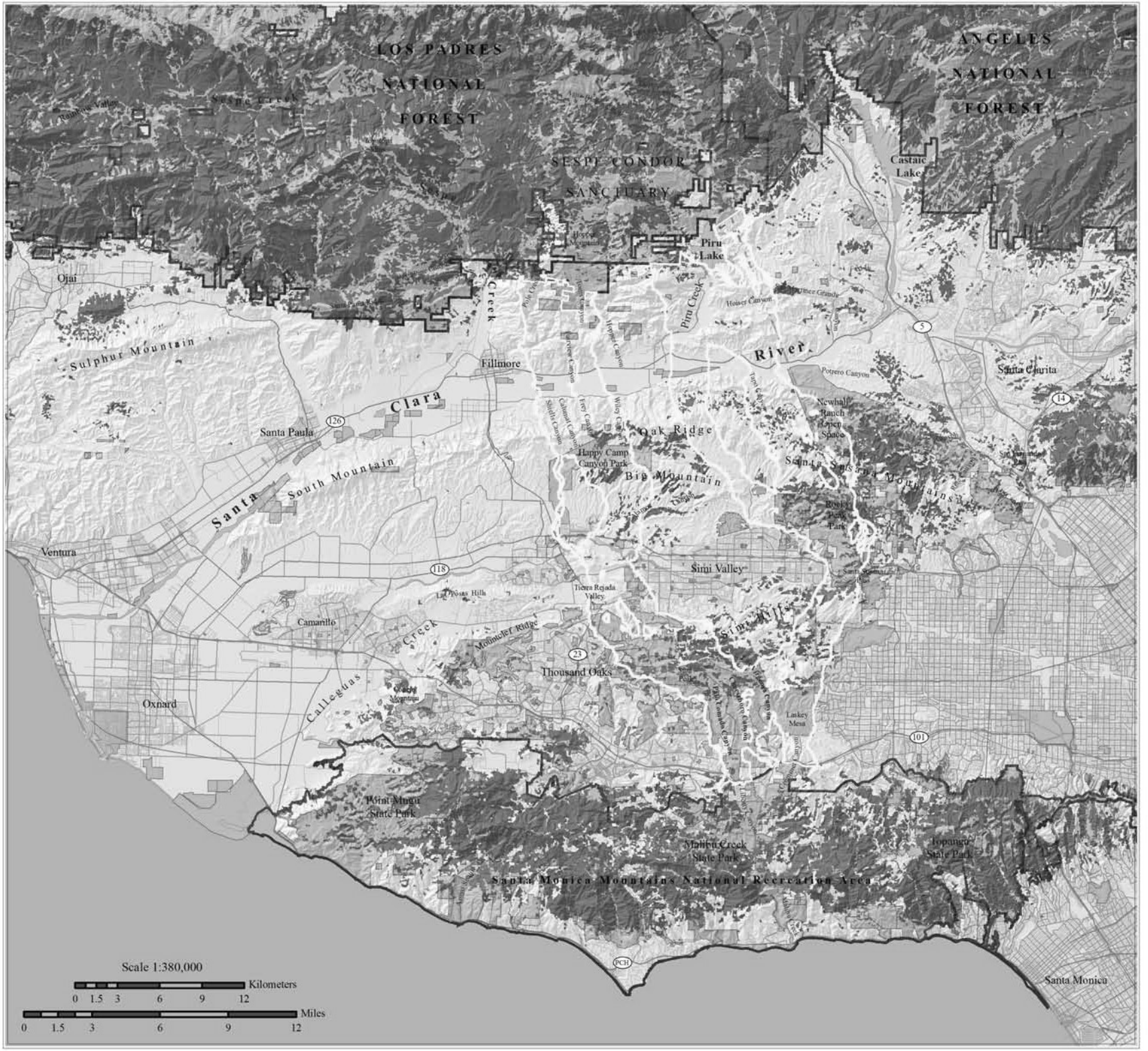
Spatial Patterns: Bigberry manzanita have limited localized dispersal. Birds, rodents, and coyotes eat the fruits and various seed-eating rodents consume the seeds (Horton and Wright 1944, Keeley 1977). Seeds are transported by coyotes, as well as cedar waxwing and related chaparral birds (Wishner pers comm., Sauvajot pers comm.)

Bigberry manzanita is an obligate post fire seeder, with germination after fire scarification of the stone (Wright and Bailey 1982, Minnich and Howard 1984). It is best adapted to high-intensity, long-interval (100+ years) fires (Keeley and Hays 1976, Keeley and Keeley 1977), but can be destroyed by repeated short-interval fires (Dunn et al. 1988).

Conceptual Basis for Model Development: Bigberry manzanita may be found in chaparral and pinyon-juniper woodlands below 1,890 m. Coyotes and chaparral birds may disperse the fruit up to a few miles.

Results & Discussion: Potential habitat for Bigberry manzanita in the planning area closely follows the distribution of chaparral habitats (Figure 45). While potential germination habitat for the manzanita is not widespread in the Least Cost Union, the linkage is still likely to serve the needs of this species by facilitating movements of the primary seed dispersers (e.g., coyote).

Figure 45.
Potential habitat
for
Bigberry manzanita
(Arctostaphylos glauca)



Potential Habitat
Protected Lands
Least Cost Union
Target Areas
Lakes & Reservoirs
Hydrography
County Boundary
Roads

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This chapter is the heart of the report. It summarizes the goals of the Linkage Design and presents a map and description of the land within it. However, assessing and maintaining linkage function requires us to also identify barriers to movement, including land uses that may hinder or prevent species from moving through the linkage. Much of this chapter therefore describes existing barriers within the linkage and recommends actions to improve linkage function.

Goals of the Linkage Design

To accommodate the full range of target species and ecosystem functions, the Linkage Design (Figure 46) should 1) provide live-in and move-through habitat for multiple species, 2) support metapopulations of smaller species, 3) ensure availability of key resources, 4) buffer against edge effects, 5) reduce contaminants in streams, 6) allow natural processes to operate, and 7) allow species and natural communities to respond to climatic changes. We elaborate on these goals below.

The Linkage Design must be wide enough to provide live-in habitat for species with dispersal distances shorter than the linkage. Harrison (1992) proposed a minimum corridor width for a species living in a linkage as the width of one individual's territory (assuming territory width is half its length). Thus, our minimum corridor width of 2 km should accommodate species with home ranges of up to about 8 km^2 (3 mi^2). This would accommodate all focal species except the largest, such as mountain lion, mule deer and badger.

The Linkage Design must support metapopulations of less vagile species. Many small animals, such as western toad, whiptail, kingsnake, desert woodrat, and many invertebrates, may require dozens of generations to move between core areas. These species need a linkage wide enough to support a constellation of populations, with movements among populations occurring over decades. We believe 2 km is adequate to accommodate most target species living as metapopulations within the linkage area.

The Linkage Design was planned to provide resources for all target species, such as host plants for butterflies and pollinators for plants. For example, many species commonly found in riparian areas depend on upland habitats during some portion of their life cycle, such as some butterflies that use larval host plants in upland areas and drink from water sources as adults.

The Linkage was also designed to buffer against "edge effects" even if adjacent land becomes developed. Edge effects are adverse ecological changes that enter open space from nearby developed areas, such as weed invasion, artificial night lighting, predation by house pets, increases in human-associated or opportunistic species like house mice (*Mus musculus*), elevated soil moisture from irrigation, pesticides and pollutants, noise, trampling, and domesticated animals that attract native predators. Edge effects have been best-studied at the edge between forests and adjacent agricultural landscapes, where negative effects extend 300 m (980 ft) or more into the forest (Debinski and Holt 2000, Murcia 1995) depending on forest type, years since the

edge was created, and other factors (Norton 2002). The best available data on edge effects for southern California habitats include reduction in leaf-litter and declines in populations of some species of birds and mammals up to 250 m (800 ft) in coastal scrub (Kristan et al. 2003), collapse of native plant and animals communities due the invasion of argentine ants up to 200 m (650 ft) from irrigated areas (Suarez et al. 1998), and predation by house cats which reduce small vertebrate populations 100 m (300 ft) from the edge (K. Crooks, unpublished data). Domestic cats may affect wildlife up to 300 m (980 ft) from the edge based on home range sizes reported by Hall et al. (2000). The proximity of human activities near natural areas can also result in indirect impacts and habitat alteration from trail proliferation, higher fire frequencies, etc., and these changes in turn may impact native species (Buechner and Sauvajot 1996). These impacts can be partially mitigated by maintaining high quality habitat in conservation areas, particularly adjacent to human-developed areas (Sauvajot et al. 1998).

Upland buffers are needed adjacent to riparian vegetation or other wetlands to prevent aquatic habitat degradation. Contaminants, sediments, and nutrients can reach streams from distances greater than 1 km (0.6 mi) (Naicker et al. 2001, Maret and MacCoy 2002, Scott 2002), and fish, amphibians, and aquatic invertebrates often are more sensitive to land use at watershed scales than at the scale of narrow riparian buffers (Goforth 2000, Fitzpatrick et al. 2001, Stewart et al. 2001, Wang et al. 2001, Scott 2002, Willson and Dorcas 2003, Riley et al. 2005).

The Linkage Design must also allow natural processes of disturbance and recruitment to operate with minimal constraints from adjacent urban areas. The Linkage should be wide enough that temporary habitat impacts due to fires, floods, and other natural processes do not affect the entire linkage simultaneously. Wider linkages may be more robust to changes in disturbance frequencies that are caused by human actions. Before human occupation, naturally occurring fires (due to lightning strikes) were rare in southern California (Radtke 1983). As human populations in the region soared, fire frequency has also increased dramatically (Keeley and Fotheringham 2000). Although fire can reduce the occurrence of exotic species in native grasslands (Teresa and Pace 1998), it can have the opposite effect in some shrubland habitats (Giessow and Zedler 1996), encouraging the invasion of non-native plants, especially when fires are too frequent. While effects of altered fire regimes in this region are somewhat unpredictable, wider linkages with broader natural communities should be more robust to these disturbances than narrow linkages.

The Linkage Design must also allow species to respond to climate change. Plant and animal distributions are predicted to shift (generally northwards or upwards in elevation in California) due to global warming (Field et al. 1999). The linkage must therefore accommodate elevational shifts by being broad enough to cover an ecologically meaningful range of elevations as well as a diversity of microhabitats that allow species to colonize new areas.

Description of the Linkage Design

For most species, U.S. Route 101 and State Routes (SR) 23, 118, and 126 are the most obvious barriers between core reserves in the Santa Monica and Sierra Madre mountains, while Interstate 5 (I-5) and SR-14 impede movement between the Santa

Figure 46.
Linkage Design



Linkage Design
Protected Lands
Riparian Buffer
Important Habitat Areas
Hydrography
Lakes & Reservoirs
County Boundary
Roads

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Susana and San Gabriel Mountains. The Linkage Design has several major swaths or branches of habitat to accommodate the diverse species and ecosystem functions it is intended to serve (Figure 46).

Liberty Canyon (Figure 47) was delineated by the landscape permeability analysis for mule deer, but also provides connectivity and suitable habitat for mountain lion, badger, brush rabbit, desert woodrat, loggerhead shrike, California thrasher, western toad, California kingsnake, western whiptail, and harvester ant. This branch of the linkage is dominated by coastal sage, oak woodland, and grassland habitats, with riparian forests along drainages. Liberty Canyon has been a major focus of conservation efforts to maintain connectivity between the Santa Monica Mountains and the Simi Hills, and much research has been done to document the importance of this connection to wildlife movement (Soulé 1989, Kohn et al. 1999, Edelman 1991, Sauvajot et al. 2000, Allen 2001, Riley et al. 2003, Ng et al. 2004, Riley et al. 2006a). The National Park Service is engaged in ongoing carnivore research in this region and continues to monitor wildlife movement, particularly that of mountain lions, including 4 juveniles that have been collared with GPS tracking devices. Biologists at the National Park Service are currently working with Caltrans to assess options for possible enhancement of a wildlife crossing at Liberty Canyon along the 101 Freeway. Liberty Canyon was also featured in a documentary in 2003 by National Geographic News Today, entitled *Struggling to Link Land for Cougars in California*.



Figure 47. Looking southwest at Liberty Canyon, with the existing bridge the 101 Freeway visible on the left side of the photo. Most natural habitats in this photo are already protected from habitat conversion.

East of Liberty Canyon, Las Virgenes Creek flows from the Simi Hills under the 101 Freeway (Figure 48). Although restricted by development for a stretch south of the freeway, this is the best riparian connection between the Simi Hills and the Santa Monica Mountains. Las Virgenes Creek has a well-developed riparian forest with cottonwood, sycamores, and various willows in the canopy with a dense understory of mulefat, blackberry, and other herbaceous species. The majority of upper Las Virgenes Creek, north of the freeway is included as part of the Santa Monica Mountains National Recreation Area and is protected from habitat conversion, though a section of the creek has been channelized for flood control purposes. South of the freeway, the creek flows through some commercial and residential development in the city of Calabasas for a few kilometers (1.2 mi). The creek banks have been stabilized through this area for flood control purposes but the creek bottom remains natural. Although somewhat degraded through this stretch, the creek is still dominated by native plant species in large part because the Resource Conservation District (RCD) of the Santa Monica Mountains helped coordinate a riparian restoration project here a few years ago. Malibu Creek State Park begins just south of this area, protecting the rest of the creek from habitat conversion. The Las Virgenes Creek connection is especially critical for species that are dependent on riparian habitats for breeding and movement, such as southern steelhead trout, western toad, and damselflies, but other species that use riparian corridors as travel routes (e.g., desert woodrat, brush rabbit, bobcat) will also benefit from maintaining and restoring connectivity here.

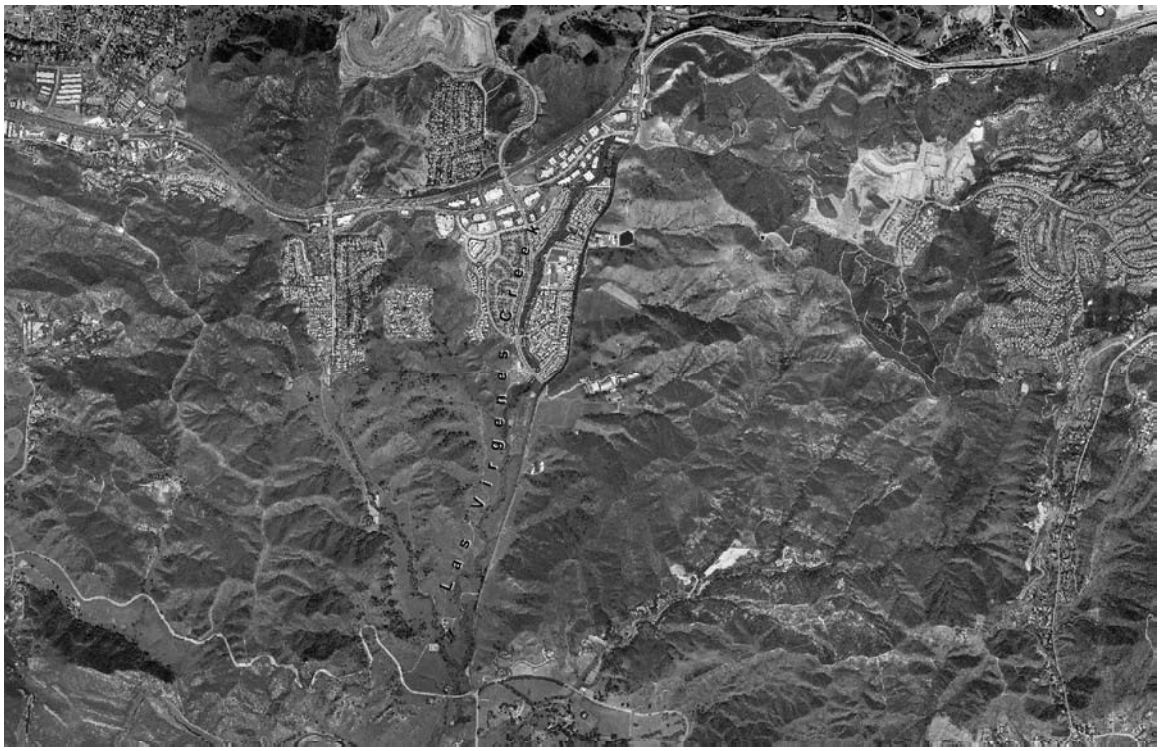


Figure 48. Las Virgenes Creek flowing south from the Simi Hills, under the 101 Freeway, through a stretch of development, and then flowing wild to its confluence with Malibu Creek.

Crummer Canyon (Figure 49) is in the eastern branch of the linkage, extending from the Santa Monica Mountains to the Simi Hills. This branch of the linkage was delineated by the landscape permeability analyses for mountain lion, badger and mule deer, and suitable habitat also occurs for brush rabbit, acorn woodpecker, loggerhead shrike, western toad, western whiptail, chalcedon checkerspot butterfly, valley oak, and California black walnut. There is a well-developed riparian forest in Crummer Canyon, surrounded by oak savanna, coastal sage, and grassland habitats in the uplands. Crummer Canyon flows off of Laskey Mesa in the Simi Hills. The mesa is part of Ahmanson Ranch, a recent conservation investment by the state that protects 1,138 ha (2,811 ac); it is managed by the Santa Monica Mountains Conservancy and is now called the Upper Las Virgenes Open Space Preserve. Immediately south of the freeway, contiguous dedicated open space occurs all the way to Malibu Creek State Park.

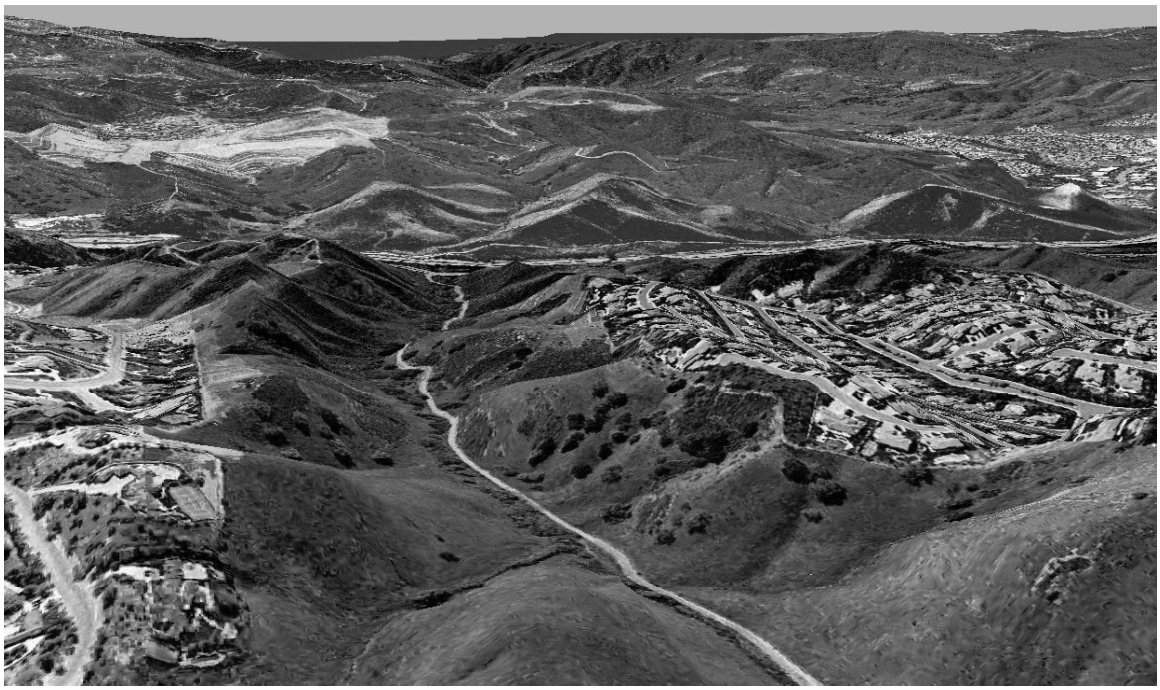


Figure 49. Looking south down Crummer Canyon from Laskey Mesa in the Simi Hills, across the 101 Freeway to the Santa Monica Mountains.

The next branch of the Linkage Design encompasses Conejo Mountain and Mount Clef Ridge (Figure 50). This branch extends from Pt. Mugu State Park in the western Santa Monica Mountains, following Conejo Creek across the 101 freeway, then through Wildwood Park and over Mount Clef Ridge, and across SR-23 to the Tierra Rejada Valley. This branch of the Linkage Design is dominated by coastal sage scrub, which is designated by the State as a sensitive natural community, providing the most contiguous connection for species associated with this rare plant community. This branch of the linkage was added primarily to serve the needs of the cactus wren, which as its name implies, is highly dependent on stands of cactus for breeding and foraging habitat. There are large stands of prickly pear cactus (*Opuntia* spp) on both sides of the 101 Freeway in this area. In addition to the cactus wren, this branch of the linkage is expected to serve almost all other focal species identified by regional ecologists,

including mountain lion, badger, mule deer, brush rabbit, desert woodrat, California thrasher, loggerhead shrike, western toad, California kingsnake, chalcedon checkerspot butterfly, scorpion, and California black walnut. A number of stepping stones of protected land have already been secured in this area as part of the Rim of the Valley Corridor and Conejo Open Space Conservation Agency parklands, including Wildwood Park, and a number of other parcels of dedicated open space. There are also current efforts within the city of Thousand Oaks to protect habitat on Mount Clef Ridge. The minimum width of 2 km was imposed here to ensure that the functional processes of the linkage are protected. Agricultural lands in the Las Posas Hills and Tierra Rejada Valley border the northern boundary of this branch of the linkage, and some agricultural lands were included in the Linkage Design to maintain the minimum corridor width in this area.

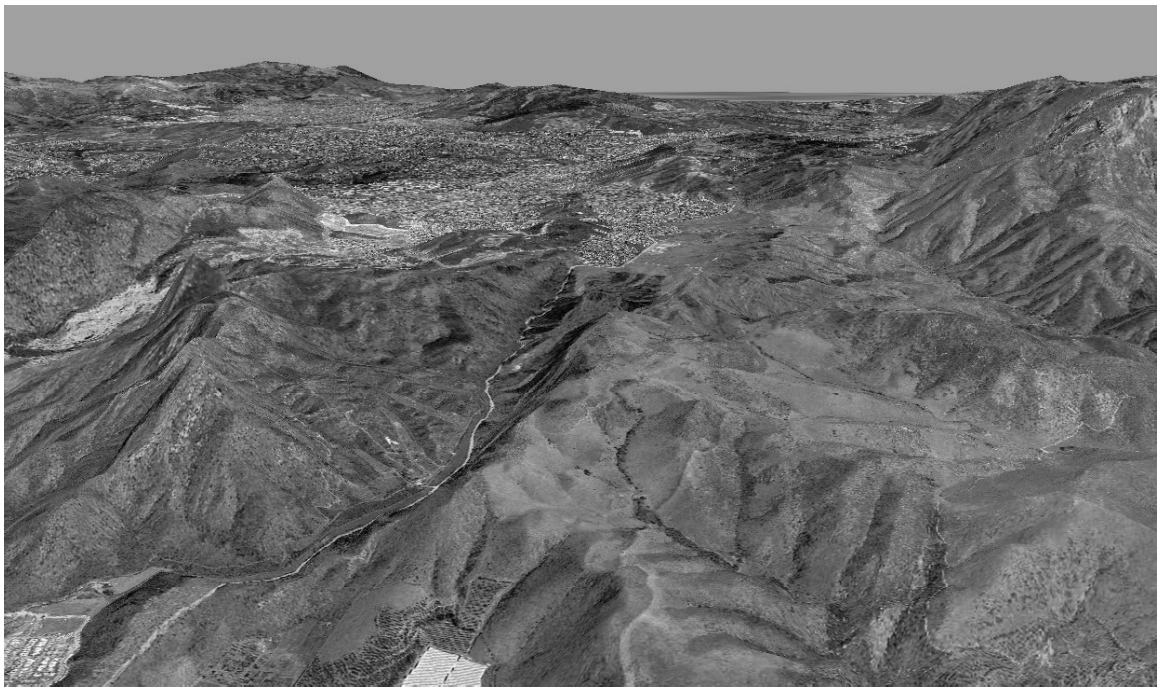


Figure 50. Looking east towards Thousand Oaks, with Conejo Mountain at the right of the photo, the 101 Freeway visible toward the center, and Wildwood Park and Mount Clef Ridge to the left.

The Alamos Canyon area of the Linkage Design is in the western branch of the linkage, and extends from Happy Camp Canyon Park near Big Mountain and Oak Ridge in the Santa Susana Mountains to protected lands south of SR-118 in the western Simi Hills near the Tierra Rejada Valley. From here, there is a contiguous connection of protected habitat all the way to Malibu Creek State Park in the Santa Monica Mountains. This branch of the linkage was delineated by the landscape permeability analysis for mule deer. It follows Alamos Canyon, which flows out of the Santa Susana Mountains through large areas of riparian forests dominated by coast live oak, sycamore, cottonwood, and willows before emptying into the broad bajada of the Arroyo Simi (Figure 51). From the Arroyo Simi, an animal traveling southbound would encounter the grassland and coastal sage habitats of the Tierra Rejada Valley and to the west of the Wood Ranch Reservoir to reach the Simi Hills (Figure 51). This branch of the Linkage Design includes both riparian and upland habitats that serve the movement needs of

diverse species including mountain lion, badger, mule deer, brush rabbit, desert woodrat, loggerhead shrike, acorn woodpecker, western toad, western whiptail, harvester ant, valley oak, black walnut and Bigberry manzanita. LSA Associates, Inc. (2004) was recently contracted by Caltrans to monitor wildlife movement along SR-118 to identify opportunities to enhance habitat connectivity in support of an approved transportation project along this route. In their study, several species, including bobcat, mule deer, and mountain lion were documented moving through this area (LSA 2004). Some habitats immediately south of SR-118 in Alamos Canyon have been protected as open space, but additional habitat must be secured to ensure the viability of this connection. The Nature Conservancy and the Santa Monica Mountains Conservancy have been working with local agencies, including the cities of Simi Valley and Moorpark, and landowners in the area to maintain the Alamos Canyon connection.



Figure 51. Looking north toward the Santa Susana Mountains, with Wood Ranch Reservoir in the foreground, agriculture and open space in the Tierra Rejada Valley, and Happy Camp, Faulkner, and Alamos Canyons flowing from the Santa Susanas.

The Rocky Peak area of the Linkage Design (Figure 52) is in the eastern branch of the linkage and was delineated by the least cost corridor analyses for mountain lion, badger, and mule deer, but it also provides live-in and or move-through habitat for virtually every other focal species modeled, with the exception of steelhead trout. The landscape in this area of the linkage is quite remarkable, with striking rocky outcrops surrounded by coastal sage and chaparral, with oak woodlands and riparian forests along canyon bottoms. Much research has been conducted to document wildlife movement in this area, including two of our focal species, mountain lion and mule deer that have been confirmed using various passageways across or under SR-118 (Edelman 1991, Ng

2000, LSA 2004, Riley et al. 2006). A proposed and already approved project for the Rocky Peak Interchange is what prompted the wildlife movement studies undertaken by Caltrans (LSA 2004). Alternatives are being considered, including moving the interchange to outside of the Linkage Design and maintaining and enhancing existing structures within the linkage to maintain existing conservation investments. Conservation planning efforts in this area of the Linkage Design have been very successful. Several existing protected areas occur here, including Rocky Peak Park north of SR-118, which is overseen by the Santa Monica Mountains Conservancy, Santa Susana State Historic Park administered by California State Parks, and Corriganville Park managed by the Simi Valley Open Space District.



Figure 52. Looking southwest from Rocky Peak Park in the Santa Susana Mountains north of SR-118, toward Corriganville Park and the Santa Susana State Historic Park south of the freeway.

Three separate branches were identified between the Santa Susana Mountains and the Sierra Madre Ranges of Los Padres National Forest (Figure 53). The western branch extends from the Santa Susana Mountains near Alamos Canyon and encompasses habitats between Sheils and Wiley Canyon down to the Santa Clara River, and then takes in habitat from Pole Creek to Tom's Canyon north of SR-126. As described previously, this branch of the linkage was delineated by landscape permeability analysis for mule deer but several focal species that utilize coastal sage and oak woodland habitat will benefit from maintaining connectivity here. The central branch was delineated by the analysis for badger, a grassland specialist. It stretches from the extensive grasslands on Oak Ridge in the Santa Susana Mountains down several canyons lined with dense oak woodlands, to coastal sage and agriculture bordering the Santa Clara River, to grassland and riparian habitats in Piru Creek. The eastern branch

of the linkage was delineated by the landscape permeability analysis for mountain lion, as well the two other modeled species. This branch of the linkage extends from Hoiser Canyon in the Sierra Madre Ranges, crosses the Santa Clara River, and encompasses habitat in Tapo, Salt, and Potrero Canyons in the Santa Susana Mountains. All three branches of the linkage include agricultural lands that line the Santa Clara River in this area. The eastern branch has the least amount of agriculture and is dominated by coastal sage scrub and grassland habitats with oak woodlands and riparian foresters interspersed.



Figure 53. Looking south from the Sierra Madre Ranges to the Santa Susana Mountains and on to the Simi Hills. On the left is the eastern branch that extends from Hoiser to Tapo Canyons. The central branch extends from Piru Creek to Smith Canyon. Both the eastern and central branches converge at Rocky Peak. The western branch extends from Hopper Mountain to the Alamos Canyon area.

Three riparian connections were added to the Linkage Design, primarily to accommodate steelhead trout movement and promote the recovery of this species (Figure 54). Of course, other focal species that require riparian and aquatic habitats for breeding or foraging, or use riparian corridors as travel routes will also benefit from protecting and restoring these riparian corridors and adjacent upland habitats, as will several other species not addressed by our analyses, including listed and sensitive species such as arroyo toad, two-striped garter snake, and western pond turtle. The Santa Clara River addition extends from the estuary at the ocean all the way through the Linkage Design to its eastern boundary, serving primarily as a migration corridor for steelhead trout to reach their spawning and rearing grounds in Piru, Sespe, and Santa

Paula Creeks. Most of Piru Creek was included in the central branch of the linkage, but we added lower Piru to its confluence with the Santa Clara River, and all of Sespe and Santa Paula Creeks from the River to protected habitats in the Sierra Madre Ranges of Los Padres National Forest. These additions include a 2-km (1.2-mi) riparian buffer (1 km to either side of the stream or river; see Figure 46) to support species habitat requirements and protect water quality within the linkage and downstream. These riparian connections provide live-in and move-through habitat for several species and help maintain natural hydrological and fluvial processes important to sustaining habitat quality.



Figure 54. Looking south from the Sierra Madre Mountains toward the Santa Susana Mountains. The Santa Clara River is at the center of the photo, with the confluence of Sespe Creek and the River visible at the lower left, and the confluence of Santa Paula and the River on the right.

Given the marked gradient between the Santa Monica Mountains at the coast and the higher elevations in the Sierra Madre Ranges, the Linkage Design encompasses a diversity of natural communities, including 14 different major vegetation types (Table 3). Although natural vegetation comprises most of the Linkage Design, urban development covers roughly 2% of its area, mostly around the choke-point in the Tierra Rejada Valley where natural habitats are constricted by development in Thousand Oaks and Simi Hills, and between Liberty and Crummer Canyons in Calabasas. Agriculture covers 5% of the linkage, primarily along the Santa Clara River and near the Los Posas Hills and the Tierra Rejada Valley. Habitats in the linkage intergrade between those found in the two targeted core areas, with coastal scrub, chaparral, oak woodland, and grassland representing the primary habitat types. Coastal sage scrub is by far the most common vegetation community, covering 47% of land in the Linkage Design. As the name of this

rare plant community implies, it occupies coastal facing slopes throughout the linkage planning area.

A diversity of wetland habitats occur throughout the linkage and core areas, including riparian forests, woodlands, and scrubs, alluvial fans, washes, springs, and seeps. Santa Paula, Sespe, Piru, Pole, Tom's, and Hoiser creeks all emanate from the Sierra Madre Ranges and empty into the Santa Clara River. Sheils, Calumat, Frey, Wiley, Smith, Tapo, Salt, and Potrero creeks flow from the Santa Susana Mountains into the Santa Clara River. Other significant riparian habitat in the Linkage Design occurs along Alamos Canyon and Hummingbird Creek which originate in the Santa Susana Mountains and empty into the Arroyo Simi, and along Liberty, Las Virgenes, and Crummer canyons which begin in the Simi Hills and flow toward the Santa Monica Mountains. In this xeric region, riparian habitats support a disproportionately large number of both aquatic and terrestrial species and are key to movement through the Linkage Design for numerous focal species.

Table 3. Approximate Vegetation and Land Cover in the Linkage Design

	Total Area Linkage Design		**Area Protected in Linkage Design**		**% Protected**	**% of Total Area**
Land Cover Types	***Acres***	***Hectares***	***Acres***	***Hectares***		
Agriculture	5693	2304	740	299	13%	5%
Annual Grassland	17954	7266	5579	2258	31%	14%
Barren	3898	1578	805	326	21%	3%
Chamise-Redshank Chaparral	1637	663	691	280	42%	1%
Coastal Oak Woodland	12325	4988	4662	1887	38%	10%
Coastal Scrub	58763	23781	20492	8293	35%	47%
Desert Wash	296	120	0	0	0%	0.002%
Mixed Chaparral	15614	6319	7581	3068	49%	12%
Montane Hardwood	7	3	0	0	0%	0.00006 %
Montane Hardwood-Conifer	206	83	174	71	84%	0.2%
Montane Riparian	3818	1545	910	368	24%	3%
Saline Emergent Wetland	17	7	17	7	100%	0.01%
Urban	2863	1159	191	77	7%	2%
Valley Foothill Riparian	1250	506	509	206	41%	1%
Valley Oak Woodland	1007	407	727	294	72%	1%
Water	263	107	171	69	65%	0.2%
TOTAL	***125613***	***50834***	***43249***	***17502***	***34%***	***100%***

All branches of the Linkage Design include substantial public ownerships that protect natural habitats from development. However, other uses may still threaten the integrity of these habitats, and should be carefully managed on these lands. For example, use of off-road vehicles, mining, and livestock grazing can impact these habitats, especially riparian habitats and fluvial processes. The final Linkage Design encompasses 50,834 ha (125,613 ac), of which approximately 34% (17,502 ha or 43,249 ac) currently enjoys

some level of conservation protection, mostly in land overseen by the Santa Monica Mountains Conservancy, National Park Service, California State Parks, The Nature Conservancy, Mountain Recreation and Conservation Authority, Conejo Open Space Conservation Agency, Eastern Ventura County Conservation Authority, and the Rancho Simi Recreation and Park District.

Removing and Mitigating Barriers to Movement

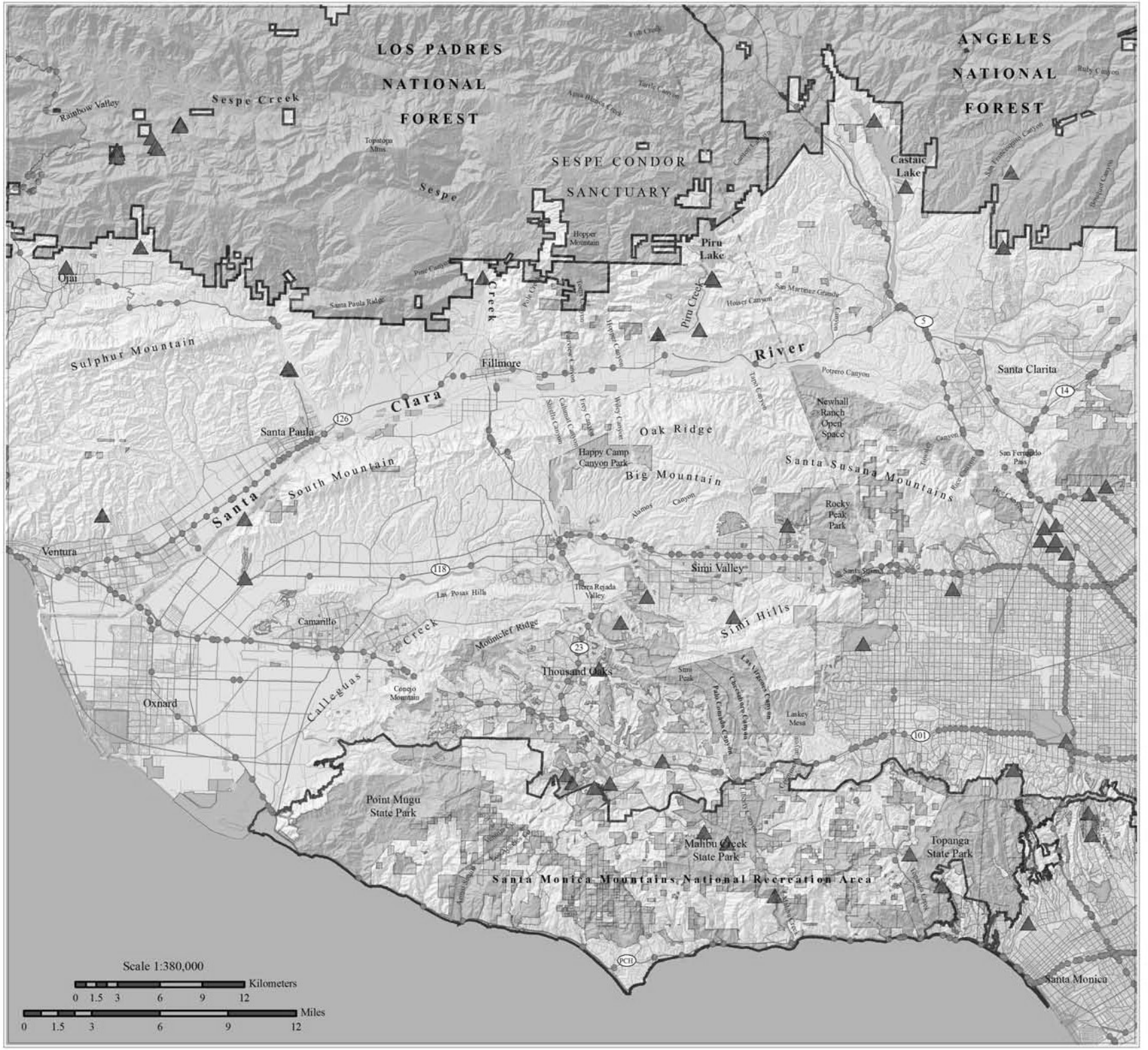
Five types of features impede species movements through the Linkage: roads, railroads, and impediments to stream flow, urban and agricultural development, and recreational activities. This section describes these impediments and suggests where and how their effects may be minimized to improve linkage function.

This discussion focuses on methods to facilitate movement of terrestrial species across roads, and on structures to facilitate stream flow under roads. Although some documents refer to such structures as "corridors" or even "linkages," we use these terms in their original sense to describe the entire area required to link the landscape and facilitate movement between large protected core areas. Crossing structures represent only small portions, or choke points, within an overall habitat linkage or movement corridor. Investing in specific crossing structures may be meaningless if other essential components of the linkage are left unprotected. Thus it is essential to keep the larger landscape context in mind when discussing existing or proposed structures to cross movement barriers. This broader context also allows awareness of a wider variety of restoration options for maintaining functional linkages. Despite the necessary emphasis on crossing structures in this section, we urge the reader to keep sight of the primary goal of conserving landscape linkages to promote movement between core areas over broad spatial and temporal scales.

Roads as Barriers to Upland Movement: Wildland fragmentation by roads is increasingly recognized as one of the greatest threats to biodiversity (Noss 1983, Harris 1984, Wilcox and Murphy 1985, Wilcove et al. 1986, Noss 1987, Reijnen et al. 1997, Trombulak and Frissell 2000, Forman and Deblinger 2000, Jones et al. 2000, Forman et al. 2003). Roads kill animals in vehicle collisions, create discontinuities in natural vegetation (the road itself and induced urbanization), alter animal behavior (due to noise, artificial light, human activity), promote invasion of exotic species, and pollute the environment (Lyon 1983, Noss and Cooperrider 1994, Forman and Alexander 1998). Roads also fragment populations by acting as semi-permeable to impermeable barriers for non-flying animals (e.g., insects, fish, amphibians, reptiles, and mammals) and even some flying species (e.g., butterflies and low-flying birds). The resulting demographic and genetic isolation increases extinction risks for populations (Gilpin and Soulé 1986). For example Ernest et al. (2003) has documented little flow of mountain lion genes between the Santa Ana and Palomar ranges (where I-15 is the most obvious barrier), and between the Sierra Madre and Sierra Nevada (where I-5, and urbanization along SR-58, are the most obvious barriers). Within this planning area, Riley et al. (2006a) have documented genetic isolation of bobcats and coyotes in subpopulations separated by the 101 Freeway. Fragmentation also results in smaller populations, which are more susceptible to extinction due to demographic and environmental stochasticity.

The impact of a road on animal movement varies with species, context (vegetation and topography near the road), road type, and level of traffic (Clevenger et al. 2001). For

Figure 55. Infrastructure in the Planning Area



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example, a road on a stream terrace can cause significant population declines in amphibians that move between uplands and breeding ponds (Stephenson and Calcarone 1999), but a similar road on a ridgeline may have negligible impact. Most documented impacts on animal movement concern paved roads. Dirt roads may actually facilitate movement of some species, such as mountain lions (Dickson et al. 2004), while adversely impacting other species, such as snakes that sun on them and may be crushed even by infrequent traffic.

Roads in the Linkage Design: At the time of this report, there are 339.93 km (211.22 mi) of paved roads in the Linkage Design (Table 4). There are several major transportation routes (i.e., I-5, US Route 101, and SR-14, 23, 118, and 126) that pose substantial barriers to movement (Figure 55). A survey of these roads found a variety of existing structures (i.e., bridges, pipes, and culverts) that might be useful for implementing road mitigation projects (Figure 55).

Table 4. Major transportation routes in the Linkage Design.

Road Name	Length (km)	Length (mi)
U.S. Route 101	5.62	3.49
Interstate 5	3.44	2.14
State Route 126	12.07	7.50
State Route 23	6.58	4.09
State Route 118	7.37	4.58
State Route 14	2.35	1.46
All Other Paved Roads	302.51	187.97
Total Length of Paved Roads	**339.93**	**211.22**

Types of Mitigation for Roads: Forman et al. (2003) suggest several ways to minimize the impact of roads on linkages by creating wildlife crossing structures and reducing traffic noise and light, especially at entrances to crossing structures. Wildlife crossing structures have been successful both in the United States and in other countries, and include underpasses, culverts, bridges, and vegetated land bridges. Most structures were initially built to accommodate streamflow, but research and monitoring have also confirmed the value of these structures in facilitating wildlife movement. The main types of structures, from most to least effective, are vegetated land-bridges, bridges, underpasses, and culverts.

There are approximately 50 vegetated wildlife overpasses (Figure 56) in Europe, Canada, and the U.S. (Evink 2002, Forman et al. 2003). They range from 50 m (164 ft) to more than 200 m (656 ft) in width (Forman et al. 2003).

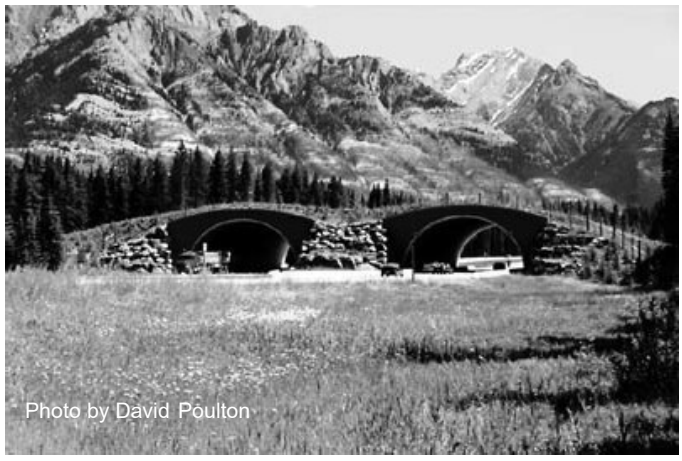

Figure 56. An example of a vegetated land bridge built to enhance movement of wildlife populations.

Soil depths on overpasses range from 0.5 to 2 m, allowing growth of herbaceous, shrub, and tree cover (Jackson and Griffin 2000). Wildlife overpasses can maintain ambient conditions of rainfall, temperature, light, vegetation, and cover, and are quieter than underpasses (Jackson and Griffin 2000). In Banff National Park, Canada, some large mammal species preferred overpasses to other crossing structures (Forman et al. 2003) although in some cases, underpasses were used equally or preferred (Clevenger and Waltho 2006). Similarly, woodland birds used overpasses significantly more than they did open areas without an overpass. Other research indicates overpasses may encourage birds and butterflies to cross roads (Forman et al. 2003). Overpass value can be increased for small, ground-dwelling animals by supplementing vegetative cover with branches, logs, and other cover (Forman et al. 2003).

Bridges over waterways are also effective crossing structures, especially if wide enough to permit growth of both riparian and upland vegetation along both stream banks (Jackson and Griffin 2000, Evink 2002, Forman et al. 2003). Bridges with greater openness ratios are generally more successful than low bridges and culverts (Veenbaas and Brandjes 1999, Jackson and Griffin 2000). The best bridges, termed *viaducts* (Figure 57), are elevated roadways that span entire wetlands, valleys, or gorges, but are cost-effective only where topographic relief is sufficient to accommodate the structure (Evink 2002).



Figure 57. A viaduct in Slovenia built to accommodate wildlife, hydrology, and human connectivity.



Figure 58. Culvert on German highway, with rail for amphibians and fence for larger animals.

Although inferior to bridges, culverts can be effective crossing structures for some species (Jackson and Griffin 2000). Only very large culverts are effective for carnivores and other large mammals (Figure 58). Gloyne and Clevenger (2001) suggest that underpasses for ungulates should be at least 4.3 m (14 ft) high and 8 m (26 ft) wide, with an openness ratio of 0.9 (where the openness ratio = height x width/length). Earthen flooring is preferable to concrete or metal (Evink 2002).

For rodents, pipe culverts (Figure 59), about 1 ft in diameter without standing water are superior to large, hard-bottomed culverts, apparently because the overhead cover makes them feel secure against predators (Clevenger et al. 2001, Forman et al. 2003).

In places where a bridged undercrossing or vegetated overcrossing is not feasible, placing pipe culverts alongside box culverts can help serve movement needs of both small and large animals. Special crossing structures that allow light and water to enter have been designed to accommodate amphibians (Figure 60). Retaining walls should be installed, where necessary, along paved roads to deter small mammals, amphibians, and reptiles from accessing roadways (Jackson and Griffin 2000). Concrete retaining walls are relatively maintenance free, and better than wire mesh, which must be buried and regularly maintained.



Figure 59. Pipe culvert designed to accommodate small mammals.



Figure 60. Amphibian tunnels allow light and moisture into the structure.

Noise, artificial night lighting, and other human activity can deter animal use of a crossing structure (Yanes et al. 1995, Pfister et al. 1997, Clevenger and Waltho 1999, Forman et al. 2003, Clevenger and Waltho 2006), and noise can deter animal passage (Forman et al. 2003). Shrub or tree cover should occur near the entrance to the structure (Evink 2002). Existing structures can be substantially improved with little investment by installing wildlife fencing, earthen berms, and vegetation to direct animals to passageways (Forman et al. 2003). Regardless of crossing type, wildlife fencing is necessary to funnel animals towards road crossing structures and keep them off the road surface (Falk et al. 1978, Ludwig and Bremicker 1983, Feldhammer et al. 1986, Forman et al. 2003). Earthen one-way ramps can allow animals that wander into the right of way to escape over the fence (Bekker et al. 1995, Rosell Papes and Velasco Rivas 1999, Forman et al. 2003).

Recommendations to Mitigate the Effects of Road Barriers in the Linkage Design: Following standard practice (Clevenger and Wierzchowski 2005) where a road bisects a major wildland, we recommend crossing structures at intervals of 1.5 to 2 km (0.9 to 1.3 miles), or at least one major structure (either bridged undercrossings or wildlife overpasses) per branch of the Linkage Design. The precise timing and location for constructing new or improved crossing structures may not be critical, and can consider cost, feasibility, and other factors. For cost efficiency, crossing improvements need not be made immediately, but can be incorporated into future road upgrade projects, such as lane additions or ramp remodeling in the vicinity of the Linkage Design. Vegetated overpasses or open bridges, supplemented by culverts for smaller species, should be sited along natural travel routes and spaced less than 2 km (1.3 mi) apart on average, with a maximum spacing between adjacent structures not to exceed 2.8 km (1.8 mi). Excellent examples of roads retrofitted with large crossing structures at similar intervals

include SR-260 between Payson and Forest Lakes, Arizona; the Trans-Canada Highway in Banff National Park, Canada; I-75 through the Everglades in Florida; and I-4 near Daytona Beach, Florida. It is also important that the entire road be fenced to funnel animals toward crossing structures. The Ventura County Planning Division recently completed a report entitled, Roads and Biodiversity Project: Guidelines for Safe Wildlife Passage (2005) that provides excellent suggestions for improving connectivity across transportation barriers.

Recommended Crossing Structures on U.S. Route 101: Although a number of freeways pass through the Linkage Design, the 101 Freeway is likely the most substantial impediment to movement. A few crossing structures that may be adequate to accommodate some wildlife movement currently exist, while others need to be improved or built.

Liberty Canyon: The most permeable route of the least cost corridor for mule deer crossed the 101 Freeway here and suitable habitat exists in this area for the majority of the selected focal species. Liberty Canyon is one of the few remaining areas along the 101 Freeway where habitat is still contiguous on both sides of the freeway. There is an existing bridge (Figure 61), measuring 4.9 m (16.1 ft) high, 46.7 m (153.2 ft) wide, and 44.3 m (145.3 ft) long. Deer utilize this structure regularly to cross between ranges, as do coyotes, and raccoons (Ng et al. 2004). Although none of the mountain lions radio-collared by the National Park Service in the Santa Monica Mountains have yet crossed the freeway to reach the Simi Hills, one lion moved to within 500 meters of this structure (Riley et al. 2006b). The National Park Service, California State Parks, Santa Monica Mountains Conservancy, and other local open space agencies have been working to preserve and restore the connection between Liberty Canyon and other protected areas. The National Park Service is also working with Caltrans to assess options for improving habitat connectivity at Liberty Canyon. We recommend providing a wildlife-specific crossing structure at this location to prevent co-location of vehicle traffic and animal movement options (the current situation). This could be accomplished with a wildlife underpass or overpass, and could take advantage of existing topography and infrastructure already in place (e.g. existing drainage culvert, see below). Habitat restoration in the immediate vicinity of a wildlife crossing structure is also recommended, as well as fencing to direct animals away from the freeway and towards the crossing structure.



Figure 61. Looking toward the Simi Hills through the Liberty Canyon underpass.

Immediately west of the bridge is a drainage culvert (Figure 62) for the intermittent creek that flows through Liberty Canyon. The structure is roughly 1 m in diameter and about 190 m long. Ng et al. (2004) recorded raccoon, opossum, spotted skunk, and striped skunk using this passage to cross the freeway. Various willows, mule fat, and poison

oak occur along the drainage with coastal sage scrub, and oak woodland and savannas in the surrounding uplands. The Santa Monica Mountains Conservancy has already initiated habitat restoration efforts along the creek. There is currently a fence obstructing the path from the riparian zone to the structure. We recommend removing this fence and upgrading this structure to a larger, more wildlife-friendly crossing with natural flooring, possibly as part of a future transportation improvement project or linked to the crossing structure recommended above.



Figure 62. Drainage culvert at Liberty Canyon.

Las Virgenes Creek: Las Virgenes Creek offers the best connection for riparian dependent species traveling between the Simi Hills and the Santa Monica Mountains. The creek flows from the Simi Hills under the 101 Freeway through a multi-chambered concrete tunnel (Figure 63), measuring 98.9 m (324.5 ft) long, 4.8 m (15.8) wide, and 4.0 m (13.1 ft) high. The structure runs diagonally under the freeway, limiting visibility to the other side. Immediately south of the freeway, the creek is directed through a concrete channel for a distance of roughly 76 m (250 ft). This is flood control for the office complex and shopping center that abut the creek in this area. After flowing through a bridge under Agoura Road (Figure 64), the creek bottom is again natural, though degraded and constricted for about 1 km (0.6 mi) before reaching Malibu Creek State Park and eventually emptying into Malibu Creek bound for the ocean. For much of its length, the creek is dominated by a well-developed riparian forest, with mature cottonwood, sycamore, and willows in the canopy and a dense understory of herbaceous plant



Figure 63. Las Virgenes Creek flowing through a concrete tunnel under the 101 freeway.



Figure 64. A channelized portion of Las Virgenes Creek flowing under a bridge for Agoura Road.

species. Ng et al. (2004) documented movement of bobcat and raccoon through this structure. We recommend upgrading the concrete tunnel under the freeway to a large bridged underpass that provides visibility to the other side and natural flooring during the next transportation improvement project in this area. We also suggest precluding any further development in the uplands along the creek, removing the concrete from the creek bottom between the freeway and Agoura Road, and continuing and expanding riparian restoration to improve habitat conditions in degraded sections of Las Virgenes Creek (See Impediments to Streams Section). The RCD of the Santa Monica Mountains implemented a stream restoration project in this area previously and this work has resulted in significant improvements immediately between Lost Hills Road and existing residential developments.

Crummer Canyon: The least cost corridors for mule deer, badger and mountain lion all traversed the 101 Freeway at Crummer Canyon, though no useable infrastructure to accommodate wildlife movement currently exists. The trash guard at the entrance of an existing culvert precluded a full evaluation of this structure (Figure 65); the trash guard itself prevents use by most medium-sized and large wildlife species. At its entrance, the concrete structure appears to be a box culvert, which measures 1.8 m (6 ft) in height and width, but about 0.9 m (3 ft) in it becomes a circular pipe approximately 1.5 m (5 ft) in diameter that immediately heads to the west, so there is no visibility to the other side. The creek runs below both Mureau Road and the 101 Freeway and likely passes through an elaborate pipe system to reach contiguous protected lands immediately south of the freeway that stretch all the way to Malibu Creek State Park. With the tremendous investments in conserving land on both sides of the freeway here, including the Ahmanson Ranch acquisition, we strongly recommend installing a wildlife-friendly undercrossing here that is tall enough and sufficiently wide to provide a view to the other side, with earthen substrate flooring. Installing ecological infrastructure here would benefit a number of other focal species, in addition to those mentioned above, including brush rabbit, California kingsnake, western whiptail, and western toad.



Figure 65. Concrete culvert with trash guard draining Crummer Canyon.

Conejo Grade: In the western branch of the linkage, there is a concrete box culvert (Figure 66) that measures 2.2 m (7.2 ft) wide, 2.6 m (8.5 ft) high, and 45 m (148 ft) long. The structure was built in 1936, likely to facilitate movement of cattle. This structure ultimately links Point Mugu State Park and Conejo Mountain in the western Santa Monica Mountains to Wildwood Park and other protected open space on Mount Clef Ridge. Ng et al. (2004) recorded raccoon and opossum using this structure but all species that utilize coastal sage scrub will benefit from maintaining connectivity here. Fencing in the immediate vicinity of the structure may preclude current use by other wildlife species (Ng 2000, Ng et al. 2004). We suggest enlarging this structure to

provide better visibility to the other side and removing fencing that may impede wildlife use. Directional fencing should also be used to help animals find and utilize the structure. In addition or as an alternative, another wildlife-friendly crossing structure is recommended along the 101 Freeway at the Conejo Grade. The existing topography could be utilized to install an excellent crossing structure that would connect very high quality habitat on either side of the freeway in an area known to be utilized by target species. Indeed, a dispersing male mountain lion was recently recorded in the area, immediately adjacent to the 101 Freeway, but he did not actually cross the road (Riley et al. 2006b). Recommended dimensions for undercrossing(s) along the Conejo Grade are at least 4.3 m (14 ft) high and 8 m (26.ft) wide to encourage use by mule deer (Gloyne and Clevenger 2001) and other species, and the flooring should be a natural substrate.



Figure 66. Large concrete box culvert at Conejo Grade.

Recommended Crossing Structures on State Route 23: Caltrans is working in cooperation with the National Park Service to monitor wildlife movement at several culverts under SR-23 as part of an effort to improve habitat connectivity along this stretch of highway. Proposed improvements will include clearing tunnels and culverts and installing wildlife-proof fencing with escape gates to direct animals off of the road and through underpasses. Implementation is slated to occur in the next several months as mitigation for a lane addition along SR-23. The pipe culvert to the right (Figure 67) is located north of the Tierra Rejada Valley; it measures 2.6 m (8.5 ft) high, 2.2 m (7.2 ft) wide, and 133.4 m (437.7 ft) long. Ng et al. (2004) recorded bobcat, coyote, raccoon, and opossum utilizing this structure to travel between habitats on either side of SR-23. Rural residential and agricultural lands are interspersed with dedicated parks and open space in this part of the linkage but opportunities remain to protect habitat and enhance wildlife movement between Los Angeles Avenue and Olsen Road. We strongly encourage



Figure 67. Pipe culvert north of Tierra Rejada, typical of most crossing structures on SR-23.

protection of remaining natural habitats and applying conservation measures to maintain the rural character of the Tierra Rejada Valley.

Recommended Crossing Structures on State Route 118: As part of a transportation improvement project on SR-118, Caltrans contracted with LSA Associates Inc. (2004) to monitor wildlife movement at several existing structures between the cities of Moorpark and Chatsworth to identify recommendations to improve habitat connectivity as mitigation for the transportation project. These and other recommendations are now being discussed as part of an informal working group of land management and other agencies (the Ventura County State Route 118 Wildlife Corridor Multi-Agency Working Group). Below we describe conditions and suggestions for improving wildlife movement along SR-118 consistent with the Linkage Design.

Alamos Canyon West: This potential passageway is located along an unnamed drainage that empties into the Arroyo Simi. The structure consists of double pipe culverts, each measuring 3.1 m (10 ft) in diameter and approximately 243.8 m (800 ft) in length (Figure 68). There is no visibility to the other side because the culvert drops at about a 45 degree angle at the northern entrance. In addition to no visibility due to the slope of the culvert, vegetative debris collects on the southern side of SR-118 following storm events. In preparation of post-fire storms, Caltrans cleared the culvert and removed riparian vegetation approximately 61 m (200 ft) downstream (Amy Pettler, Caltrans, pers. comm. *in* LSA 2004). Upland vegetation north and south of the culvert is dominated by California buckwheat (*Eriogonum fasciculatum*), sagebrush (*Artemisia californica*), and chaparral yucca (*Yucca whipplei*), while Freemont cottonwood (*Populus fremontii* ssp. *fremontii*), various willows (*Salix* sp.), and rushes (*Juncus* sp.) occur along the drainage. LSA (2004) recommended that either the twin culverts be replaced with an open bridged structure or the pitch at the northern entrance of the culvert be regraded to allow visibility to the other side. We concur with these recommendations. We also suggest maintaining riparian vegetation to facilitate movement of species associated with riparian and aquatic habitats, such as damselflies, desert woodrat, and western toad. LSA documented a variety of mammals in the general vicinity north and south of this crossing, but did not document movement of these target species through the passageway.



Figure 68. Double pipe culverts at Alamos Canyon West convey flow to the Arroyo Simi.

Alamos Canyon: The least cost corridor for mule deer crosses SR-118 using Alamos Canyon. This excellent bridged underpass provides a clear view to the other side and measures roughly 4.9 m (16 ft) high, 41.8 m (137 ft) wide, and 48.9 m (160 ft) long (Figure 69). There is an asphalt road on one side of the structure that is not in use. The openness of this structure and the gap between the north and southbound lanes allows natural light and moisture to enter the passageway supporting well-developed coastal sage vegetation on natural substrate to one side of the structure. Dominant vegetation in the vicinity of the structure consists of California buckwheat, sagebrush, chaparral coyote brush (*Baccharis pilularis*), and yucca, while oak (*Quercus* spp.), mule fat (*Baccharis salicifolia*), elderberry (*Sambucus* spp.), and laurel sumac (*Malosma laurina*) occur along the drainages.



Figure 69. Looking north toward the Santa Susana Mountains through the first-rate bridged crossing at Alamos Canyon.

In addition to being the most permeable route for mule deer, Alamos Canyon provides suitable habitat for a number of focal species, including mountain lion, badger, brush rabbit, loggerhead shrike, California thrasher, chalcedon checkerspot butterfly, and scorpion. A variety of wildlife have been documented using this well-designed structure, including mountain lion (Psomas 2002), bobcat (Psomas 2002, LSA 2004), coyote (Ng 2000, LSA 2004),) mule deer, striped skunk, raccoon (Ng 2000), small mammals and birds (LSA 2004).

LSA (2004) recommended removing the paved road surface and replacing it with decomposed granite. If this road is used for maintenance activities then we agree with this suggestion. If the road is not needed for vehicular access, complete removal of the pavement and restoration of natural vegetation is recommended. LSA also recommended installing gates to reduce human traffic (e.g., illegal dumping, homeless camps) in the area (2004). This recommendation has been implemented successfully as gates have been installed and these activities weren't noted during recent fieldwork.

It is critical that this structure be maintained and that lands near it are protected for use by wildlife. We advise acquisition of open space or conservation easements of contiguous natural habitats between Happy Camp Canyon Park and protected areas in the Simi Hills and Tierra Rejada Valley to enhance the ecological integrity of this linkage.

Alamos Canyon East: This potential passageway consists of a 1.83 m (6 ft) diameter pipe culvert, extending approximately 183 m (600 ft) under SR-118 (Figure 70). This structure is located roughly 150 m (492 ft) east of the bridged structure described above. LSA (2004) documented use of this structure by bobcat, skunk, opossum, and raccoon, and recorded a variety of medium and large-sized mammals in the vicinity of this structure, both north and south of SR-118. Natural habitats occur on either side of the freeway, though no vegetation occurs in the structure itself. We suggest increasing vegetative cover near the entryways of the passage to provide cover for wildlife. LSA (2004) recommended enlarging this culvert to at least a 2.4 m by 2.4 m (8 ft by 8 ft) concrete box culvert or arch with natural substrate flooring by "tunnel jacking" (NRCC 2002) during the next transportation improvement project in this area. If this recommendation is implemented, we also suggest installing smaller pipe culverts along side the enlarged structure to encourage movement of small mammals, amphibians and reptiles.

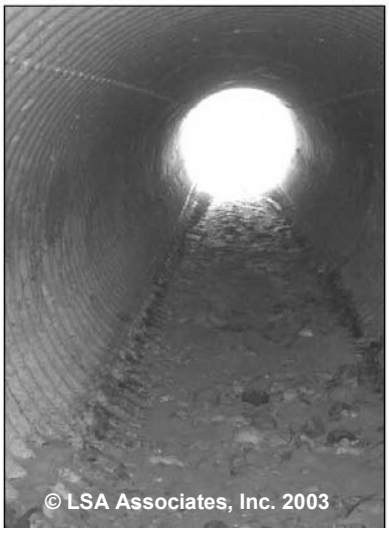

Figure 70. Pipe culvert at Alamos Canyon east.

Hummingbird Creek: Hummingbird Creek is dominated by Fremont cottonwood (*Populus fremontii*), various willows, and mule fat, with oak savanna and chaparral in the uplands. It flows under SR-118 through a concrete-lined channel that measures 3.8 m (12.5 ft) in height, 3.9 m (12.8 ft) in width and 144.9 m (475.4 ft) in length (Figure 71). The functionality of this linkage is already compromised due to the dense residential and commercial development along Kuehner Drive on the south side of SR-118. However, natural habitats are still contiguous on either side of the structure. Although constrained, this is one of the few riparian connections along this stretch of the freeway and it should be maintained and enhanced to facilitate movements of riparian dependent species. In addition, bobcat, raccoon, and striped skunk have been documented using this structure (Ng 2002) and other target species have been recorded via scent stations and diagnostic sign (LSA 2004).


Figure 71. Looking south through the arched culvert at Hummingbird Creek.

The westernmost boundary of Rocky Peak Park is along North Kuehner Drive and the Hummingbird Creek connector trail begins at the Kuehner Drive/SR-118 intersection. White Oak Park and Hummingbird Creek Trail areas are located north of and parallel to SR-118 and are contiguous with Corriganville and Rocky Peak Parks to the east. We recommend maintaining and enhancing the remaining natural habitats in this area with appropriate measures to confine light and noise pollution to home sites. We agree with LSA (2004) that the highway fence south of the freeway should be relocated to direct animals toward Corriganville Park to the east. Riparian and upland habitats, particularly south of the freeway, should be restored and allowed to persist to provide habitat and cover for wildlife. Recreational activity is high in this area, including hiking, mountain biking, and off-road vehicle use. Recreation should be limited to the currently permitted passive activities, such as hiking and birding.

Corriganville: The least cost corridors for mountain lion, badger, and mule deer all cross SR-118 at Corriganville Park. At this location, there is a large concrete box culvert that measures 58.3 m (191.3 ft) in length, 4.6 m (15.1 ft) wide, and 4.7 m (15.4 ft) high, linking Corriganville Park south of SR-118 with Rocky Peak Park north of SR-118 (Figure 72). Coastal sage scrub is the dominant plant community on both sides of the structure. Several researchers have confirmed use of this passage by wildlife. Mountain lion have been documented using the Corriganville Tunnel on several occasions (Edelman 1991, Ng 2000, LSA 2004, Riley et al. 2006b). Ng also recorded mule deer, coyote, bobcat, raccoon, and striped skunk using this structure. LSA (2004) captured a mountain lion on film that had been radio-collared as part of a National Park Service study. This young male appears to have used this structure to cross SR-118 at least 18 times over the course of the study (Riley et al. 2006b).



Figure 72. Several target species have been documented using this box culvert to travel between habitats north and south of SR-118.

In addition to providing habitat for wildlife, both Corriganville and Rocky Peak Parks are used recreationally by hikers, bicyclists, equestrians, and youth groups that also use this structure to go between the two parks. To maintain the integrity of this passageway, we recommend that the park facilities remain rustic (e.g., dirt parking lots) without night lighting or fencing that could deter or block wildlife movement; ideally, park use in the vicinity of the crossing structure would be limited to daytime use. To restrict human activities near the crossing structure, especially from dusk to dawn, LSA (2004) proposed installing a locking security fence at the parking lot entrance to Corriganville Park and at Foothill Park to regulate access.

Rocky Peak: The least cost corridor for mule deer crossed SR-118 at Rocky Peak Road, which is located approximately 0.80 km (0.5 mi) east of the Corriganville structure described above. This roadway overpass connects Santa Susana State Historic Park

south of SR-118, with Rocky Peak Park to the north. The paved road crosses over SR-118 as a bridge structure, measuring 18.3 m (60 ft) in width and approximately 39.6 m (130 ft) in length (Figure 73). Dominant plant communities in the vicinity of the structure include coastal sage scrub and chamise chaparral. LSA (2004) documented coyote, bobcat, raccoon, and skunk utilizing this structure, in addition to vehicles, equestrians, hikers, and cyclists. Caltrans biologists documented mule deer at Rocky Peak Road over three field seasons (pers. comm. Amy Pettler, Caltrans, April 9, 2004 *in* LSA 2004).



Figure 73. Looking south from Rocky Peak Park toward Santa Susana State Historic Park at the bridge for Rocky Peak Road over SR-118.

A transportation improvement project for the Rocky Peak Road interchange is currently being evaluated. Under existing conditions, Rocky Peak Road can only be accessed from SR-118 via the westbound off-ramp, while access to SR-118 from Rocky Peak Road is limited to the eastbound on-ramp from Santa Susana Pass Road. The proposed project would include installation of an eastbound off-ramp and a westbound on-ramp. The earthen fill for this improvement project is in place (Figure 73), but no other infrastructure has been built. LSA (2004) proposed an alternative to completing this project that Caltrans is taking into consideration. They suggested constructing on-off ramps at Iverson Road or Movie Lane instead of at Rocky Peak Road to meet project goals of an additional interchange for emergency vehicles turn-around and to accommodate traffic projections. This alternative would enhance the existing site for use by wildlife, particularly if it included closing the existing on-off ramps at Rocky Peak Road. The existing bridge could be converted to a vegetated land bridge, with native shrubs and trees tall enough to block lighting and reduce noise from traffic. As LSA suggested, if necessary, one lane could be converted to decomposed granite for emergency vehicle access (2004).

Santa Susana Arch: This structure is located approximately 1.61 km (1 mi) east of Rocky Peak Road, linking Santa Susana State Historic Park south of SR-118 with Joughin Dedicated Open Space and Rocky Peak Park north of the freeway. The passageway is a concrete arch shaped culvert with a flat bottom, measuring 1.5 m (5 ft) high, 1.8 m (6 ft) wide, and approximately 152.4 m (500 ft) long (Figure 74). LSA (2004) captured this family of raccoons on film on several occasions during their study, as they frequently utilized this structure to cross under the freeway. Several rodents were also recorded but were not identified to species. Residential development occurs on the eastern bluff above the canyon north of SR-118, while the canyon itself and habitats to the west are protected as part of Rocky Peak Park and Joughin Open Space. Coast live oak, poison oak (*Toxicodendron diversilobum*), sycamore (*Platanus racemosa*), and cottonwood line the drainage with laurel sumac and other coastal scrub species in the uplands. We concur with LSA (2004) that enhancing vegetative cover at the culvert entrances would encourage additional wildlife to use this passage.

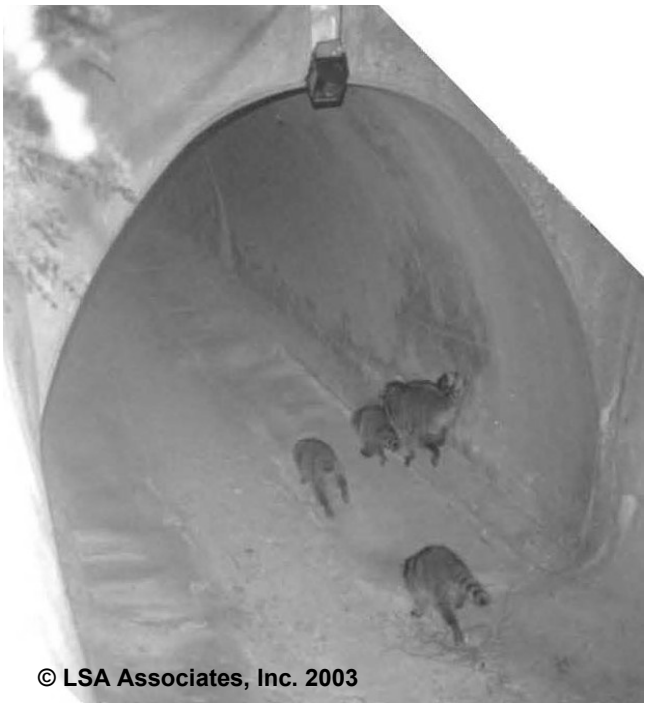

Figure 74. A family of raccoons utilizing the Santa Susana Arch passage under SR-118.

Recommended Crossing Structures on State Route 126: A great majority of the Santa Clara River Valley has been in agriculture since the late 1800's but opportunities remain to restore functional connectivity here. Although most of SR-126 was built at grade, several existing structures facilitate various levels of animal movement across this transportation barrier.



Figure 75. Looking south toward the Santa Susana Mountains under the bridge for Santa Paula Creek on SR-126.

Santa Paula Creek: Santa Paula Creek flows under SR-126 through a bridge structure (Figure 75), measuring roughly 53 m (173.9 ft) wide, 6 m (19.7 ft) high, and 11 m (36.1 ft) in length. The lower stretch of the creek is channelized for flood control for a distance of approximately 1.5 km through the community of Santa Paula. This creek is included in the Linkage Design to support the

movement needs of southern steelhead trout, though several other focal species will benefit from restoring this connection. In a recent survey of steelhead trout habitat in the Santa Clara River Watershed, upper Santa Paula Creek and its tributaries (Sisar and Bear creeks) received the highest habitat quality score, but other stream barriers must be addressed to access the 18.5 miles of historic steelhead habitat in this subwatershed (Stoecker and Kelley 2005). We strongly support implementation of all recommendations identified in this report. Please see the section on stream barriers for additional suggestions to improve habitat conditions in riparian zones.

Sespe Creek: A portion of Sespe Creek is designated as a Wild and Scenic River and much of the upper watershed is designated as Wilderness. Multi-chambered concrete bridges span both Sespe Creek and the Sespe Creek Overflow (Figure 76) on SR-126, with each bridge measuring roughly 4.6 m (15 ft) high, 220 m (721.8 ft) wide, and 24 m (78.7 ft) long. In lower Sespe Creek, bank stabilization borders the community of Fillmore and upland habitats have long been converted to agriculture but overall the creek remains wild. Sespe Creek is the most productive of all the steelhead trout streams in southern California. Stoecker and Kelley (2005) identified 123 miles of



Figure 76. Looking down Sespe Creek toward its confluence with the Santa Clara River (left). Looking south toward Santa Susana Mountains through overflow bridge (right).

habitat historically accessible to steelhead trout in this subwatershed. However, to reach this habitat, migration barriers on the mainstem of the Santa Clara River must be addressed. Please see the Impediments to Streams section for recommendations to restore functional connectivity in riparian zones. In addition to supporting steelhead trout, Sespe Creek provides habitat for many other special status species (e.g., red-legged frog, arroyo toad, and western pond turtle) and provides for the movement needs of several riparian and terrestrial focal species.

Hopper Mountain to Oak Ridge: This branch of the linkage was delineated by the landscape permeability analysis for mule deer. It is dominated by coastal sage scrub, with valley oak and coast live oak woodlands lining the canyons and grasslands interspersed. These natural habitats are separated by agricultural crops that line the Santa Clara River. From the foothills north of SR-126 to the Santa Clara River south of the freeway, there is a distance ranging from 0.45 to 2.2 km (0.3 to 1.4 mi) that is occupied by agriculture, and south of the river for another 0.25 to 0.6 km (0.16 to 0.35 mi). There are a number of small drainage culverts in this stretch of the highway, sited every 300 to 500 m (0.19-0.31 mi), with average dimensions of 0.76 m (2.5 ft) high and 0.91 m (3 ft) wide, similar to the one depicted in Figure 77. We recommend maintaining

these structures, acquisition or conservation easements of any large parcels, and restoration of natural habitats that have been converted to agriculture.



Figure 77. An example of a drainage culvert on State Route 126.

Piru Creek: The least cost corridors for badger, mountain lion, and mule deer crossed SR-126 using Piru Creek and upland habitats to the east. Piru Creek flows under SR-126 through a multi-chamber concrete bridge (Figure 78), measuring roughly 4.6 m high (15 ft), 126 m (413.4 ft) wide, and 11 m (36.1 ft) long. South of the freeway, the creek and the immediate uplands on the eastern bank are dominated by alluvial fan sage scrub with willow, mule fat, and other riparian plant species in wetter sites, while north of the freeway there is very little vegetative cover until above Piru Creek Road where there is a well-developed riparian forest stretching to the Santa Felicia Dam (see Impediments to Streams section). Piru Creek, although altered and degraded by dams and diversions, still provides habitat for several special status aquatic and semi-aquatic species, including steelhead trout, and should be a focus of riparian restoration efforts. Piru Creek also provides habitat connectivity for mountain lion, badger, brush rabbit, desert woodrat, kingsnake, and western toad.



Figure 78. Looking up Piru Creek toward the Sierra Madre Ranges.

East of Piru Creek, agriculture is the dominant land cover along SR-126 and the Santa Clara River in this branch of the linkage. From the foothills north of SR-126 to the Santa Clara River south of the freeway, there is a distance ranging from 0.45 to 1.4 km (0.27 to 0.83 mi) that is occupied by agriculture, and south of river for another 0.1 to 0.49 km (0.06 to 0.30 mi) before reaching natural habitats. About 1 km (0.62 mi) east of Piru Creek, there is a 2-lane dirt road that passes beneath SR-126 via an arched culvert built for agricultural operations at Camulos Ranch (Figure 79). Small drainage culverts also occur every 300 to 500 m (0.19-0.31 mi) under SR-126, comparable to the one portrayed in Figure 80, where bobcat and raccoon tracks were noted during field surveys. This is the best connection for grassland specialists, such as badger, between the Santa Susana Mountains and the Sierra Madre Ranges. We recommend

maintaining these structures, acquisition or conservation easements of any large parcels in this area, and habitat restoration of areas that have been converted to agriculture.



Figure 79. 2-lane arched culvert at Camulos Ranch.



Figure 80. Example of concrete drainage culverts.

Tapo Canyon: The eastern branch of the linkage between Tapo and Potrero Canyons is dominated by fairly contiguous natural habitats, including coastal sage scrub, chaparral, grassland, oak woodlands and riparian forests, with just a patch of agriculture both above and below SR-126 for about a 0.67 km (0.41 mi) stretch along the highway. There is a one-lane dirt road that goes under the highway through an arched culvert for agricultural operations on Newhall Ranch (Figure 81), along with several small drainage culverts (Figure 82). These structures should be maintained and enhanced during the next transportation improvement project. We strongly recommend maintaining the wild character of this branch of the linkage, one of the last remaining areas where natural habitats are still contiguous between the Santa Susana Mountains and the Sierra Madre Ranges. We suggest acquisition of open space or conservation easements, and habitat restoration where necessary to enhance the ecological integrity of the linkage.



Figure 81. 2-lane arched culvert at Newhall Ranch.



Figure 82. Typical example of concrete drainage culverts.

Recommended Crossing Structures on Interstate 5: The San Fernando Pass is dominated by oak woodlands, interspersed with coastal sage scrub and chaparral, providing contiguous habitat for the majority of focal species. The 4-lane bridged underpass for The Old Road (Figure 83), likely facilitates some degree of animal movement due to the proximity of natural habitats on either side of the structure. There is a trailer park to the right of the photo that impedes access to the underpass and connectivity is reduced in this area due to traffic speed and volumes. The bridge measures roughly 20 m (66 ft) high, 23 m (75 ft) wide, and 11 m (36 ft) long. The Weldon Road overpass (Figure 84), lies roughly 1.5 km to the north, with dimensions measuring 13 m (43 ft) wide and 67 m (220 ft) long. This structure appears only to serve a fairly active paintball facility. The connectivity value of this structure could be improved by converting this structure to a vegetated land bridge, with native shrubs and trees tall enough to block lighting and reduce noise from the traffic below. One lane could be reserved for access to the paintball facility. Open space acquisition or protection of conservation easements in this area would also enhance its ecological linkage value.



Figure 83. Interstate 5 bridged underpass for The Old Road.



Figure 84. The bridged overpass for Weldon Road over Interstate 5.

Recommended Crossing Structures on State Route 14: There is a 2-lane bridged underpass for the Sierra Highway (Figure 85) that measures roughly 10 m (33 ft) high, 38 m (125 ft) wide, and 9 m (30 ft) long. Sierra Highway is a quiet road at this point, especially at night, and we expect this structure accommodates some level of wildlife movement. Open space acquisition or protection of conservation easements, and measures to confine light and noise to developed areas in this area would enhance its ecological linkage value.

There is also an excellent bridged underpass for Los Pinetos Canyon that connects contiguous natural habitats on either side of the freeway (Figures 86, 87). This structure measure approximately 7 m (23 ft) high, 42 m (138 ft) wide, and 24 m (79 ft) long. The property in the area of Los Pinetos Canyon is owned by the City of Santa Clarita. To the east of SR-14, there is a partially paved abandoned road up the canyon, slightly visible in Figure 86, though it doesn't pass beneath the bridge. To the west of the freeway and just south of the structure there is an abandoned industrial park, though an animal traveling through the structure would encounter dense oak woodlands and coastal sage habitats, not the industrial park. Open space acquisition or protection of conservation easements in this area would significantly enhance its ecological linkage value. We suggest habitat restoration of vegetation leading up to the structure and placement of some boulders, logs, and other cover through the structure to provide safe passage for smaller species.



Figure 85. The SR-14 bridged underpass for Sierra Highway.



Figure 86. Looking toward the San Gabriel Mountains at the Los Pinetos Bridge on SR-14.

Other Recommendations Regarding Paved Roads within the Linkage Design:

Transportation agencies have the opportunity to use road improvement projects as opportunities to replace culverts with bridges (expansive enough to allow vegetation to grow) and use earthen substrate flooring. In locations where a bridge is not feasible and only a culvert can be provided, connectivity for small species (e.g. small mammals,



Figure 87. Looking west to the San Fernando Pass at the Los Pinetos Bridge on SR-14.

amphibians, and reptiles) may be enhanced by installing smaller culverts (designed to remain free of water) parallel to the main culvert.

- The ecological value of crossing structures can be improved by encouraging the growth or restoring woody vegetation leading up to both sides of crossing structures to provide cover for wildlife and to direct their movement toward the crossing structure. Work with the USFS, CNPS, local RCDs, or other agencies and organizations for guidance on how to restore riparian communities and vegetative cover at passageways.

- Installation of appropriate wildlife fencing along major roads and freeways is critical to guide animals to crossing structures and keep them off road surfaces. Install escape structures, such as earthen ramps or one-way gates, to allow animals to escape if they get trapped within roadway rights-of-way.

- Smaller retaining walls or fine mesh fencing can be used to guide amphibians and reptiles to crossing structures.

- On freeways and other paved roads, minimizing artificial night lighting, and directing the light onto the roadway and away from adjacent wildlands can help increase wildlife use of crossing structures.

- Where wildlife is expected, reduce traffic speeds and install signage to alert drivers to watch for wildlife.

Roads as Ephemeral Barriers: Structures designed for wildlife movement are increasingly common. In southern California, 26 wildlife crossing structures were installed along 22-miles of SR-58 in the Mojave Desert specifically for desert tortoise movement (Evink 2002). In the South Coast Ecoregion, the Coal Canyon interchange on SR-91 is now being converted, through a partnership with Caltrans, California State Parks, and Hills for Everyone, from a vehicle interchange into a wildlife underpass to facilitate movement between the Chino Hills and the Santa Ana Mountains. About eight wildlife underpass bridges and viaducts were installed along SR-241 in Orange County, although urbanization near this toll road has compromised their utility (Evink 2002). Elsewhere, several crossing structures, including three vegetated overpasses, have been built to accommodate movement across the Trans-Canada Highway in Banff National Park (Clevenger et al. 2001). In south Florida, 24 underpasses specifically designed for wildlife were constructed along 64km (38 mi) of Interstate 75 in south Florida. The structures are readily used by endangered Florida panthers and bears, and have reduced panther and bear roadkill to zero on that route (Lotz et al. 1996, Land et al. 2001). Almost all of these structures were retrofitted to existing highways rather than part of the original road design. This demonstrates that barrier or filter effects of existing roads are at least partially reversible with well-designed improvements.

Representatives from Caltrans have attended each of the workshops of the South Coast Missing Linkages effort, and the agency is incorporating wildlife crossing improvements into its projects with a focus in important linkage areas. For example, in February 2003 Caltrans started removing pavement from the Coal Canyon interchange in Orange

County and transferred the property to California State Parks expressly to allow wildlife movement between Cleveland National Forest and Chino Hills State Park.

Implementing these recommendations will take cooperation among land managers, planners, land conservancies and other non-profits, and transportation agencies. We urge them to work together to develop a long-term coordinated plan to ensure that wildlife-crossing structures are aligned in a way that maximizes their utility to animals. We recognize that it is unrealistic to expect the crossing structures to be built at the same time. However, an overall plan will ensure that, for instance, a planned crossing structure adjoins protected lands or land targeted for conservation.

Rail Line Barriers to Movement

Like highways, railroads can also impede plant and animal movement (Messenger 1968, Niemi 1969, Klein 1971, Stapleton and Kiviat 1979, Muehlenbach 1979, Lienenbecker and Raabe 1981, Forman 1995), though there are some differences. Railroads tend to follow straighter lines than roads and scatter deleterious particles widely over the land bordering the rail line (Forman and Boerner 1981, Forman et al. 2003). Mortality rates are likely a great deal lower per train than per vehicle on roads, though trains have been derailed from collisions with large mammals. Grain spilled from trains can attract deer and bears to feed on the rail line; such events have caused significant mortality to grizzly bears in Montana (Federal Register Feb 11 2004. 69: 6683-6685; C. Servheen, University of Montana, personal communication). Freight trains transporting cargo can also disperse non-native seeds, insects, and perhaps small mammals along railroad networks (Thomson 1940, Stapleton and Kiviat 1979, Forman et al. 2003).

Existing Rail Lines in the Linkage Design Area: Currently there are 2 railroads in the vicinity of the Linkage Design. Railroad construction began in 1887 in the Santa Clara River Valley, with a line extending from Saugus to Santa Paula, Ventura, and Santa Barbara, and new agricultural towns of Piru, Fillmore and Sespe sprang up as rail construction progressed. By the 1960's, much of the agricultural products were being transported by truck. In 1979, floods washed out sections of the line between Piru and Saugus and in 1984 the line was abandoned east of Piru. Newhall Land & Farming Company purchased the right of way between Rancho Camulos and Saugus and most of the tracks were removed. The Ventura County Transportation Commission plans to eventually rebuild the railroad through to Santa Clarita for use by MetroLink (Sperry, undated material).

In 1901, Southern Pacific built another line to the south of the original route, extending from Camarillo, through Moorpark and Simi Valley, then through the Santa Susana tunnel (7,369 ft) completed in 1904, to the San Fernando Valley (Sperry undated material). The tracks run parallel to SR-118 and are utilized by Simi Union Pacific Railroad for freight service, and Amtrak and Metrolink for passenger service. In the western branch of the linkage, at Alamos Canyon, the tracks run between the freeway and Los Angeles Avenue forming a band of parallel impediments to animal movement in this stretch of the linkage. Currently, there is bridge for the railroad (Figure 88) that conveys the flow of the unnamed tributary that runs through the Alamos Canyon West double culverts. There is also a concrete box culvert under Los Angeles Avenue that directs this flow to the Arroyo Simi. In the eastern branch, the tracks run south of the

freeway at grade for approximately 0.5 km before entering the Santa Susana Pass railroad tunnel for the rest of the linkage.



Figure 88. Railroad bridge across unnamed drainage in Alamos Canyon.

Recommendations to Mitigate the Effects of Rail Lines in the Linkage Design: Although the railroad is probably not a complete barrier, in concert with nearby SR-118 and Los Angeles Avenue, the railroad contributes to reduced connectivity in this area. We recommend a policy of using any railroad realignment as an opportunity not simply to mitigate loss of wildland connectivity, but to improve it. Ameliorating the adverse affects of railroads is similar to that for roads, providing viaducts, bridged underpasses, and tunnels (Reed and Schwarzmeier 1978, Borowske and Heitlinger 1981, Forman 1995). We suggest that crossing structures should be (a) aligned with crossing structures on SR-118 and SR-126, (b) integrated with sound walls to reduce noise, and (c) integrated with fences where beneficial to guide animals toward crossing structures.

Implementing these recommendations will take cooperation among the rail line operators and transportation agencies. We urge them to work together to develop a long-term coordinated plan to ensure that wildlife-crossing structures are aligned in a way that maximizes their utility to animals. A coordinated plan will ensure that, for instance, a planned crossing structure on SR-118 does not abut an impermeable section of the railroad for which no crossing structure is planned.

Impediments to Streams

Organisms moving through rugged landscapes often use riparian areas as travel routes. For example, many butterflies and frogs preferentially move along stream corridors (Orsack 1977, Kay 1989, USGS 2002). Although western pond turtles are capable of overland movements of up to 0.5 km (0.3 mi) (Holland 1991), they preferentially move along stream courses (Bury 1988). Even large, mobile vertebrates, such as mountain lions, have shown preferences for moving along riparian corridors (Beier 1995, Dickson et al. 2004).

For plants and animals associated with streams or riparian areas, impediments are presented by water diversions and extractions, road crossings, exotic species, water recharge basins, farming in streambeds, gravel mining, and concrete structures that stabilize stream banks and streambeds. Increased runoff can also create permanent streams in areas that were formerly ephemeral; permanent waters can support aggressive invasive species, such as bullfrogs and exotic fish that prey on native aquatic species, and giant reed or arundo (*Arundo donax*) that supplants native plant communities (Fisher and Crooks 2001, Riley et al. 2003).

Impediments to Streams in the Linkage Design: The Linkage Design encompasses several connections for species associated with riparian systems. The Santa Clara River is a prominent feature of the Linkage Design, providing connectivity between streams flowing from the Sierra Madre and Santa Susana Mountains. Piru, Tom's, Fairview, Sespe, and Santa Paula Creeks all originate from the Sierra Madre Ranges and empty into the Santa Clara River, while Sheils, Calumat, Frey, Wiley, Tapo, Salt, and Potrero Creeks all emanate from the Santa Susana Mountains and also flow into the Santa Clara River. From the Santa Susana Mountains to the Simi Hills, Alamos Canyon empties into the Arroyo Simi, which also drains the north slope of the Simi Hills. Hummingbird Creek also flows from the Santa Susana Mountains under SR-118 but terminates in Corriganville Park. Liberty, Las Virgenes, and Crummer Creeks all originate in the Simi Hills and flow into the Santa Monica Mountains, eventually emptying into Malibu Creek bound for the ocean. In times of high surface flows, these tributaries may provide avenues along which aquatic and semi aquatic species journey between the Santa Monica Mountains, Simi Hills, Santa Susan Mountains and the Sierra Madre Ranges. Today, riparian habitats are significantly reduced and or degraded in some places due to a combination of factors, including flood control, water diversions, ground and surface water extraction, water quality contamination, and exotic species invasions.

Several dams and diversions occur in the linkage planning area. The Vern Freeman Dam on the Santa Clara River near Saticoy was built in 1928 (Figure 89). It is a 6 m (20 ft) high concrete sill. A fish ladder was built in 1991 but is not functioning properly and needs to be addressed (Stoecker and Kelley 2005). On Santa Paula Creek, the lower reaches have been channelized for flood control by the Army Corps of Engineers (Figure 90). The Harvey Dam on Santa Paula Creek (Figure 91) occurs about 6.4 km (3.98 mi) upstream of the confluence with the Santa Clara River. Built in 1923, the Harvey Dam is 7 m (23 ft) high. The dam failed (Figure 92) in the winter floods of 2005 (Stoecker and Kelley 2005). The Santa Felicia Dam on Piru Creek was built in 1955; it is 64.92 m (213 ft) high (Figure 93). The Rindge Dam on Malibu Creek (Figure 94) was built in 1924, 4.18 km (2.6 mi) upstream of the estuary. A feasibility study is currently underway to remove Rindge Dam. Several other streams barriers occur in the planning area,

including several Arizona crossings (low-water crossings) and ineffective road crossings. Comprehensive data have recently been collected on impediments to southern steelhead trout in the Santa Clara River Watershed (Stoecker and Kelley 2005) and in the Santa Monica Mountains (Caltrout 2006) to aid in recovery efforts of this critically endangered species. For more detailed information on stream barriers and recommended actions to improve riparian connectivity please refer to these studies. Due to limited groundwater and surface water supplies, diversions and extractions are a concern for the long-term viability of riparian and aquatic habitats in the Linkage Design.

In addition to loss of surface and groundwater, water quality is also a concern. The Linkage Design encompasses portions of 4 different watersheds (Santa Clara River, Calleguas Creek, Malibu Creek, and Los Angeles River) and each has several drainages that are listed as impaired under Section 303(d) of the Clean Water Act (http://www.waterboards.ca.gov/losangeles/html/programs/regional_programs.html#Watershed). Water quality in the Santa Clara River Watershed is impaired due to agricultural practices that notably increase salts and nitrogen in streams. Other impairments include ammonia, coliform, chloride, DDT, eutrophication, trash, DO, pH problems, and crude oil spills. The Calleguas Creek Watershed is extremely impaired. DDT, PCBs, other pesticides, and some metals have been detected in both sediment and biota collected from this watershed. Agricultural activities appear to be the main source of many of these pollutants, although the naval facility, residential and urban activities have also contributed. The Mugu Lagoon and the Calleguas Creek Estuary are both considered toxic hot spots. In the Malibu Creek Watershed, water quality is impaired by excess nutrients, coliform, trash, and metals. Nonpoint source pollution from human activities is strongly implicated including ill-placed or malfunctioning septic systems, runoff from horse corrals, and urban runoff. The portion of the Los Angeles River Watershed in the Linkage Design is in the undeveloped headwaters, while the middle and lower watershed are highly developed and impaired (LARWQCB 2004). These impaired riparian stretches are eligible for the development of intensive management plans called Total Maximum Daily Load (TMDL) plans. TMDL plans are enacted by the Los Angeles Regional Water Quality Control Board to determine the cause of water quality deterioration and then an implementation plan is developed to return water quality to targeted values.

Invasive species also need to be addressed in the Linkage Design. Although most riparian areas in the Linkage Design are dominated by cottonwood, sycamore and various willows (*Salix* spp.), or coast live oak (*Quercus* agrifolia), aggressive invasive species have invaded several of these systems. For instance, Arundo, an introduced plant species that escaped cultivation, has invaded stream courses in the arid southwest, out-competing native plant species and forming monocultures that provide little habitat value to wildlife. Several exotic species have invaded or been introduced to streams and rivers in the linkage, including bullhead catfish, green sunfish, African clawed frog, bullfrog, crayfish, and others. These predatory species can decimate native amphibian, reptile, and fish populations and eradication or control through ongoing management actions is crucial to the survival of many aquatic and semi aquatic species.



Figure 89. Vern Freeman Dam on the mainstem of the Santa Clara River.



Figure 90. Channelization of lower Santa Paula Creek for flood control.



Figure 91. Harvey Dam on Santa Paula Creek before 2005 floods.



Figure 92. Harvey Dam on Santa Paula Creek failed during the 2005 floods.



Figure 93. Santa Felicia Dam on lower Piru Creek.

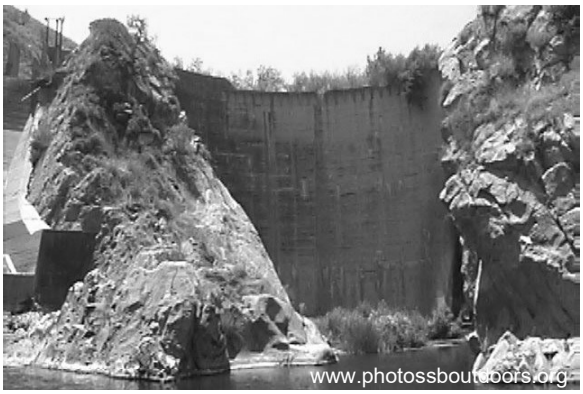

Figure 94. Rindge Dam on Malibu Creek, currently being evaluated for removal.

Examples of Mitigation for Stream Barriers: Few restoration projects have focused on restoring the natural dynamics of riparian systems (Bell 1997), where annual floods are a major component of ecosystem function. Many riparian plants are pioneer species that establish quickly following soil disturbance by floods (Ohmart 1994), as long as

threats like invasive species are controlled and physical processes restored (e.g., by removing dams and diversions or by mimicking natural flow regimes).

Continuity between upland and riparian vegetation is also important to maintaining healthy riparian communities. Many species commonly found in riparian areas depend on upland habitats during some portion of their lifecycle. Examples include butterflies that use larval host plants in upland habitat and drink water as adults and toads that summer in upland burrows. While the width of upland habitats needed beyond the stream's edge is unknown for many species, information on the western pond turtle suggests that a 1-km (0.6-mi) upland buffer (i.e., 0.5 km to either side of the stream) (Holland 1994) is needed to sustain populations of this species.

Measures to minimize development impacts on aquatic habitats often focus on establishing riparian buffer zones (Barton et al. 1985, Allan 1995, Wilson and Dorcas 2003). However, although these buffers are intended to prevent erosion and filter runoff of contaminants (U.S. Environmental Protection Agency), research suggests that current regulations are inadequate to protect populations of semiaquatic reptiles and amphibians (Wilson and Dorcas 2003). Buffers must contain enough upland habitat to maintain water-quality and habitat characteristics essential to the survival of many aquatic and semiaquatic organisms (Brosofske et al.1997, Wilson and Dorcas 2003). However, maintaining riparian buffers will not suffice for some species. For example, to preserve salamander populations in headwater streams, land use must be considered at the watershed level (Wilson and Dorcas 2003).

Recommendations to Mitigate the Effects of Streams Barriers in the Linkage Design: Several projects are already underway in the Linkage Design and core habitat areas to restore riparian connections. The goal of recovering steelhead trout populations has prompted discussions of removing obsolete dams, such as the Rindge Dam on Malibu Creek. Surveys have been conducted of impediments to southern steelhead trout and recommended actions identified in the Santa Clara River Watershed (Stoecker and Kelley 2005) and in the Santa Monica Mountains (Caltrout 2006). National Park Service, RCD of the Santa Monica Mountains, City of Malibu, and Caltrans have been working to restore connectivity for steelhead in Solstice Creek, removing check dams, replacing Arizona crossings with bridges, and modifying the two lowest culverts to optimize fish passage. Several other riparian restoration efforts have been carried out or are currently underway, including a highly successful project by the Mountains Restoration Trust to remove Arundo from Malibu Creek, and an Arundo removal project by the Ventura RCD in the Santa Clara River Watershed. The RCD in the Santa Monica Mountains has been leading an all volunteer effort to eradicate crayfish, invasive exotic predators from reaches of Topanga Creek. To enhance species use of riparian habitat and restore riparian connections through the Linkage Design area, we recommend:

- Wherever possible restore the natural historic flow regime or create a regime that provides maximum benefit for native biodiversity. Work with the NPS, USFS, NMFS, CDFG, BLM, departments of public works, water districts, watershed groups, and others to investigate the historic flow regimes and develop a surface and groundwater management program to restore and recover properly functioning aquatic and riparian conditions.

- Minimize the effects of road crossings in riparian zones. Coordinate with Caltrans, NPS, USFS, BLM, and CDFG, to further evaluate existing stream crossings and upgrade culverts, Arizona crossings (low-water crossings), bridges, and roads that impede wildlife movement. Use several strategies, including information on preferred crossings, designing new culverts, retrofitting or replacing culverts, general recommendations, post construction evaluation, maintenance, and long-term assessment (Carey and Wagner 1996, NFMS 2000, Evink 2002).

- Restore riparian vegetation in all drainages and upland vegetation within 1 km (0.6 mi) of streams and rivers. This may encourage plant and animal movement and increase water quality. Non-point sources of pollution should be identified and minimized.

- Discourage the construction of concrete-banked streams and other channelization projects.

- Remove exotic plants (e.g., Arundo) and animals (e.g., bullfrogs, African clawed frogs, crayfish) from washes, streams and rivers. Work with the Biological Resources Division at USGS, USFS, NPS, BLM, CDFG, RCDs, and other relevant agencies and organizations to survey streams and drainages for invasive species and develop a comprehensive removal strategy.

- Enforce existing regulations protecting streams and stream vegetation from illegal diversion, alteration, manure dumping, and vegetation removal. Agencies and laws with applicable jurisdiction include CDFG (Streambed Alteration Agreements), Army Corps of Engineers (Clean Water Act), and the Native Plant Protection Act.

- Prevent off-road vehicles from driving in riparian areas and washes and enforce closures, or, where necessary, re-route trails away from these sensitive areas. Review existing regulations relative to linkage goals and develop additional restrictions or recommend closures in sensitive areas.

- Aggressively enforce regulations restricting farming, gravel mining, suction dredging, and building in streams and floodplains.

- Increase and maintain high water quality standards. Work with the RCDs to help establish use of Best Management Practices for agricultural and rural communities in the Linkage Design and surrounding communities.

- Develop incentives and educational programs to encourage organic farming practices in the Santa Clara River Valley and the Tierra Rejada Valley to improve water quality.

- Support efficient water use and education programs that promote water conservation.

- Discourage development in flood prone areas.

- Support the protection of riparian and adjacent upland habitats on private lands. Pursue cooperative programs with landowners to improve conditions in riparian and upland habitats on private land in the Linkage Design.

- Distribute the brochure on Best Management Practices for Horse Owners, produced by the Santa Monica Mountains RCD, to all equestrian communities in the Linkage Design to improve water quality.

Other Land Uses that Impede Utility of the Linkage

Land management policies in the protected areas and the linkage can have substantial impact on habitat and movements of species through the Linkage Design area. It is essential that major land-management and planning entities (e.g., USFS, NPS, CSP, Los Angeles County, Ventura County, Cities, TNC, and SMMC) integrate the linkage plan into their policies and regulations.

Urban Barriers to Movement

Urban development, unlike roads or aqueducts, creates barriers that cannot be corrected by building crossing structures. Urban and suburban areas make particularly inappropriate landscapes for movements of most plants and animals (Marzluff and Ewing 2001). In addition to direct habitat removal, urban development creates edge effects that reach well beyond the development footprint. Most terrestrial mammals that move at night will avoid areas with artificial night lighting (Rich and Longcore 2006). Pet cats can significantly depress populations of small vertebrates near housing (Churcher and Lawton 1987, Crooks 1999, Hall et al. 2000). Irrigation of landscapes surrounding homes encourages the spread of Argentine ant populations into natural areas, where they cause a halo of local extinctions of native ant populations extending 200 m (656 ft) into native vegetation (Suarez et al. 1998, Bolger et al. 2000). Similar affects have been documented for amphibians (Demaynadier and Hunter 1998). Habitat disturbance caused by intense human activity (e.g., off-road vehicle use, dumping, camping and gathering sites) also tends to rise in areas surrounding urban developments (Buechner and Sauvajot 1996). Areas disturbed by human use show decreases in bird and small mammal populations (Sauvajot et al. 1998).

Urban Barriers in the Linkage Design Area: Urban developments comprise 2% of the Linkage Design area but several cities and communities occur just outside the boundary of the linkage, including Camarillo, Thousand Oaks, Westlake Village, Agoura Hills, Calabasas, and Hidden Hills along the 101 Freeway; Moorpark, Simi Valley, and Chatsworth along SR-118; mostly rural and large lot developments in the Tierra Rejada Valley along SR-23; Santa Paula and Fillmore along Highway 126; and Newhall and Sylmar bordering the I-5/SR-14 area. Most of these areas are largely impermeable to wildlife movement due to high-density development, high traffic volume, large numbers of pets, and light and noise pollution (e.g., some rural developments in the Tierra Rejada Valley may be an exception). The population in Ventura County is anticipated to grow by 31 percent by 2020 and Los Angeles is projected to increase by 25 percent (SCAG 1998). This projected growth should be appropriately distributed to accommodate wildlife movement through the Linkage Design if we hope to conserve biodiversity across the region.

There are several proposed developments in the vicinity of the linkage that are at various stages in the environmental review process. For example, in the vicinity of Alamos Canyon, The Canyons 2,880-acre residential development is proposed north of SR-118 and a business/industrial complex is proposed south of SR-118 (Psomas 2001, 2002, LSA 2004). The Simi Valley Landfill is just east of Alamos Canyon and is expected to expand (LSA 2004). The proposed development for Greenpark Village Runkle Canyon Specific Plan encompasses 1,600 acres with 1,150 acres of dedicated open space (Runkle Canyon Neighbors 2003, LSA 2004). Overall, these and other development projects have the potential to significantly impact the ecological integrity of the linkage unless they are properly designed to maintain habitat values and ecosystem functions in the linkage.

While topography, habitat, water supplies and other natural constraints limit opportunities for significant population growth in this region, the coastal area is a highly desirable place to live and there is no doubt that large-scale development projects will continue to be proposed. Fortunately, both Los Angeles and Ventura Counties have policies in place that limit development in sensitive habitat areas. The guiding principle of the Conservation and Open Space Element for the Santa Monica Mountains North Area Plan for managing the natural environment is "resource protection has priority over development". Critical to the maintenance of these resources are the habitat linkages present in the region (County of Los Angeles 2000). Virtually all habitat within the linkage and targeted protected areas in Los Angeles County are proposed as Significant Ecological Areas (i.e., Santa Monica Mountains SEA, Santa Susana Mountains/Simi Hills SEA, and Santa Clara River SEA) in the general plan update (PCR 2000 a,b,c). In Ventura County, the Save Open Space and Agricultural Resources (SOAR) ordinance restricts the conversion of open space and agricultural land to urban uses outside of the City Urban Restriction Boundary (CURB). Any developments proposed outside of the CURB must be approved by voters, giving residents an opportunity to influence future landscape patterns. Since increased urbanization of currently undeveloped areas in the linkage could impact wildland connectivity, we recommend that any development that is proposed in the Linkage Design be limited and very carefully evaluated and/or planned to maintain landscape connectivity.

Examples of Mitigation for Urban Barriers: Urban developments, unlike roads, create movement barriers that cannot be readily removed, restored, or mitigated. Mitigating impacts from potential urban developments in key areas through acquisition or conservation easements is therefore generally the most effective option. Mitigation for existing urban developments focuses on designing and managing buffers to reduce penetration of undesirable effects into natural areas (Marzluff and Ewing 2001). Management in buffers can include fencing in pets, reducing human traffic in sensitive areas or constriction points, limiting noise and lighting, reducing traffic speeds, minimizing use of irrigation, encouraging the planting of locally native vegetation, minimizing the use of pesticides, poisons and other harmful chemicals, and increasing enforcement of existing regulations.

Recommendations for Mitigating the Effects of Urban Barriers in the Linkage Design Area: We suggest the following actions as possible ways to reduce impacts of urban, suburban, and rural developments in the Linkage Design area.

- Encourage open space acquisition or protection of conservation easements with willing land owners in the Linkage Design.

- Encourage homes abutting the linkage area to have minimal outdoor lighting, directed toward the home and yard rather than into the linkage. Homeowners should use fences to keep dogs and domestic livestock from roaming into the linkage area. Residents should be encouraged to keep cats indoors at all times.

- Develop a public education campaign, such as the On the Edge program developed by the Mountain Lion Foundation (www.mountainlion.org) and other organizations, which encourages residents at the urban wildland interface to become active stewards of the land by reducing penetration of undesirable effects into natural areas. Topics addressed may include: living with wildlife, predator-safe enclosures for livestock and pets, landscaping, water conservation, noise and light pollution.

- Provide educational programs for landowners to increase their appreciation of natural communities, and to convey the importance of habitat protection and the need for connecting wild areas.

- Distribute the brochure on Best Management Practices for Horse Owners, produced by the Santa Monica Mountains RCD, to all equestrian communities in the Linkage Design.

- Work with Los Angeles and Ventura Counties and all cities to discourage major new residential or urban developments in key areas of the Linkage Design. Where development does occur:

    - Encourage clustering in any proposed development and other smart growth policies to maximize the amount of preserved open space and maintain contiguous blocks of habitat. Include buffers or other measures adequate to maintain linkage function.

    - Encourage preservation of sensitive natural communities (Holland 1986, County of Los Angeles 2000, CDFG 2005), such as riparian forests and woodlands, oak woodland and savanna, walnut woodland, and grassland within proposed development sites.

    - Promote the use of drought tolerant native plants in landscaping in areas adjacent to the linkage and prohibit the use of invasive, non-native plants that can supplant native plants and reduce habitat integrity in the linkage.

Recreation

Recreational use is not inherently incompatible with wildlife movement, although, intense recreational activities have been shown to cause significant impacts to wildlife and plants (Knight and Cole 1995). Areas with high levels of off-road vehicle use are more readily invaded by invasive plant species (Davidson and Fox 1974), accelerate erosion and reduce soil infiltration (Iverson 1980), and alter habitat use by vertebrates (Brattstrom and Bondello 1983, Nicolai and Lovich 2000). Even such relatively low-impact activities

as wildlife viewing, hiking, and horse back riding have been shown to displace wildlife from nutritionally important feeding areas and prime nesting sites (Anderson 1995, Knight and Cole 1995). The increased time and energy spent avoiding humans can decrease reproductive success and make species more susceptible to disease (Knight and Cole 1995). In addition, humans, horses, and pets can carry seeds of invasive species into natural areas (Benninger 1989, Benninger-Traux et al. 1992).

Recreation in the Linkage Design Area: There are several areas currently designated for recreation purposes in the Linkage Design, including Palo Comado, Cheeseboro, and Las Virgenes Canyons, Upper Las Virgenes Open Space Preserve, Wildwood Park, Tierra Rejada Park, Mt. McCoy Recreational Area, Rocky Peak Park, Corriganville Park, Santa Susana Historic State Park, Happy Camp Canyon Park, Towsley Canyon, and other dedicated parks and open space. The targeted core areas of the Santa Monica Mountains National Recreation Area and Los Padres National Forest provide a wide range of recreational opportunities, from nature-based dispersed recreational activities (e.g., hiking, bird watching) to high-density recreation in developed sites. The majority of recreational use is concentrated in areas with road access and is associated with developed facilities.

Examples of Mitigation for Recreation: If recreational activities are effectively planned, developed, managed, and monitored, most negative impacts can be avoided or minimized by limiting types of use, directing recreational activities away from particular locations, sometimes only for particular seasons, and with reasonable precautions.

Recommendations to Mitigate the Effects of Recreation in the Linkage Design Area: We provide the following initial recommendations that may help prevent or mitigate negative effects of recreation in the Linkage Design area:

- Monitor trail development and recreational use to provide a baseline and ongoing information for decisions regarding levels, types, and timing of recreational use.

- Consider recommendations from LSA (2004) to reposition some campsites and install fencing at Oak Park Campground to better facilitate wildlife movement under SR-118

- Work with regional monitoring programs, such as the California Resource Assessment Program, to collect information on special status species, species movements, and vegetation disturbance in areas of high recreational activity.

- Enforce existing regulations on recreational use.

- Work with the agencies and non-governmental organizations to develop and conduct on-the-ground, multi-lingual outreach programs to recreational users on how to lessen impacts in sensitive riparian areas.

- Prohibit off-road vehicles within the Linkage Design and limit off-trail activities to those that are consistent with maintaining functional habitat connectivity.

- Close, obliterate, and restore to natural habitat any unauthorized off-road vehicle routes and enforce closures.

- Enforce leash laws so that dogs are under restraint at all times.

- Work with park agencies and open space districts to develop recreational use plans that are consistent with Linkage Design objectives.

Land Protection & Stewardship Opportunities

A variety of land planning and resource conservation efforts are currently underway in the Linkage Design area. The South Coast Missing Linkages Project supports these efforts by providing information on linkages critical to achieving their conservation goals at a landscape scale. This section provides brief summaries of selected planning efforts, agencies, and organizations that may represent opportunities for collaborative conservation of Linkage Design objectives within the Santa Monica-Sierra Madre Connection. This list is not exhaustive, but provides a starting point for persons interested in becoming involved in preserving and restoring linkage function.

Arundo Task Force*:* The Ventura County and Los Angeles County task forces coordinate Arundo removal and control efforts. The Ventura RCD is spearheading the Santa Clara River Watershed Arundo Donax and Tamarisk Eradication Program funded through Proposition 13. This long-term project will map infested areas, monitor removal efforts, and conduct outreach to help restore watershed integrity, improve facultative filtration, remove large trash components in stream runoff, and improve groundwater recharge. For more information on the project go to: http://www.swrcb.ca.gov/rwqcb4/html/programs/nps/prop13_contract.html.

Bureau of Reclamation*:* Reclamation's Southern California Area Office (SCAO) is responsible for water conservation, reclamation and reuse projects to enhance water management practices throughout southern California. Reclamation is undertaking a collaborative effort with local entities to develop an effective water quality monitoring plan in the Santa Clara River Watershed that will identify impaired water bodies (pursuant to section 303(d) of the Clean Water Act), support the development of water quality recovery plans (Total Maximum Daily Load plans), and estimate the assimilative capacity for nutrients in the Santa Clara River Watershed. For more details, visit http://www.usbr.gov/lc/region/scao/sccwrrs2.htm.

California Coastal Coalition (CalCoast): is a non-profit advocacy group comprised of 35 coastal cities; five counties; AMBAG, BEACON, SANDAG and SCAG; along with business associations and allied groups committed to restoring California's coast through sand replenishment, increasing the flow of natural sediment, wetlands recovery and improved water quality. CalCoast was the co-sponsor, with the CA Shore and Beach Preservation Association, of the CA Public Beach Restoration Act (AB 64-Ducheny) which was signed into law in October of 1999. Visit http://www.calcoast.org to learn more about CalCoast.

California Department of Fish and Game: CDFG manages California's diverse fish, wildlife, and plant resources, and the habitats upon which they depend, for their ecological values and for their use and enjoyment by the public. Acquisition dollars for CDFG projects are authorized through the Wildlife Conservation Board as part of their

Concept Area Protection Plan (CAPP) process. For more information on the Department, visit their website at http://www.dfg.ca.gov.

California Department of Transportation: Caltrans strives to achieve the best safety record in the nation, reduce traveler delays due to roadwork and incidents, deliver record levels of transportation system improvements, make transit a more practical travel option, and improve the efficiency of the transportation system. Caltrans representatives have attended each of the South Coast Missing Linkages workshops and have shown leadership and a willingness to improve linkage function in the most important linkage areas. In February 2003, Caltrans started removing pavement from the Coal Canyon interchange on SR 91 in Orange County and transferred the property to California State Parks expressly to allow wildlife movement between the Santa Ana Mountains of the Cleveland National Forest and Chino Hills State Park. Caltrans is working to incorporate ecological infrastructure into a number of transportation improvement projects in the Linkage Design, including those planned for the 118, 101, and the 23 freeways. To find out more about the innovative plans being developed by Caltrans, visit their website at http://www.dot.ca.gov.

California Native Plant Society: The California Native Plant Society (CNPS) is a statewide non-profit organization of amateurs and professionals with a common interest in California's native plants. The Society seeks to increase understanding of California's native flora and to preserve this rich resource for future generations. Their members have diverse interests including natural history, botany, ecology, conservation, photography, drawing, hiking, and gardening. To learn more about native plants, go to www.lacnps.org .

California State Parks: California State Parks provides for the health, inspiration and education of the people of California by helping to preserve the state's extraordinary biological diversity, protecting its most valued natural and cultural resources, and creating opportunities for high-quality outdoor recreation. The Department is actively engaged in the preservation of the State's rich biological diversity through their acquisition and restoration programs. Ensuring connections between State Park System wildlands and other protected areas is one of their highest priorities. CSP is involved in the Coal Canyon habitat connection restoration project to preserve mountain lion movement under SR 91 at the north end of the Santa Ana Mountains. CSP administers critical lands in the linkage planning area, including Point Mugu State Park, Malibu Creek State Park, and Topanga State Park in the Santa Monica Mountains, and the Santa Susana State Historic Park. CSP co-sponsored the statewide Missing Linkages conference and is a key partner in the South Coast Missing Linkages effort. For more information, visit their website at http://www.parks.ca.gov.

California State Parks Foundation: The Foundation is the only statewide organization dedicated to preserving, advocating and protecting the legacy of California's State Parks. The Foundation supports environmental education, wildlife and habitat preservation, volunteerism, and sound park policy. Since its inception, the Foundation has provided over $110 million for projects and educational programs while building a statewide network of park supporters. These initiatives have helped the parks acquire more land, create more trails, restore wildlife habitat, build visitor centers, construct interpretive displays, and support family camping for underserved youth. CSPF is a partner in the

South Coast Missing Linkages. For more on their exciting programs, visit www.calparks.org.

California Wilderness Coalition: The California Wilderness Coalition builds support for threatened wild places on a statewide level by coordinating efforts with community leaders, businesspeople, decision-makers, local organizations, policy-makers, and activists. CWC was also a co-sponsor of the statewide Missing Linkages effort. For more information, visit them at http://www.calwild.org.

California Wild Heritage Campaign: The mission of the California Wild Heritage Campaign is to ensure the permanent protection of California's remaining wild public lands and rivers. Congresswoman Hilda Solis has introduced the Southern California Wild Heritage Act. The bill would significantly expand the National Wild and Scenic Rivers System and the National Wilderness Preservation System on federally managed public lands in Southern and Central California. A total of 13 new Wild and Scenic Rivers are included in the bill, totaling more than 312 miles, and 47 new Wilderness Areas and Wilderness Additions totaling 1,686,393 acres. The Campaign builds support for Wilderness and Wild and Scenic River protection by compiling a detailed citizen's inventory of California's remaining wild places; organizing local communities in support of those places; building a diverse, broad-based coalition; and educating the general public, government officials and the media about the importance of protecting California's wild heritage. For more information on the status of the Act, visit http://www.californiawild.org.

California Coastal Conservancy: The California Coastal Conservancy, established in 1976, is a state agency that uses entrepreneurial techniques to purchase, protect, restore, and enhance coastal resources, and to provide access to the shore. The Conservancy works in partnership with local governments, other public agencies, nonprofit organizations, and private landowners. To date, the Conservancy has undertaken more than 950 projects along the 1,100 mile California coastline and around San Francisco Bay. The Conservancy protects and improves coastal wetlands, streams, and watersheds; purchases and holds environmentally valuable coastal and bay lands; protects agricultural lands and supports coastal agriculture; and accepts donations and dedications of land and easements for public access, wildlife habitat, agriculture, and open space. Locally, the Conservancy has been very active in the Santa Clara River Watershed. For more information, visit http://www.coastalconservancy.ca.gov

California Trout, Inc. (CalTrout): CalTrout's mission is to protect and restore wild trout and steelhead and their waters throughout California. Improving fishing opportunities was and remains important, but it is a secondary goal. CalTrout was the nation's first statewide conservation group supported by trout fishermen with an altruistic goal: to protect and restore trout and the beautiful places where they live. CalTrout is very active in the restoration of southern steelhead trout runs in the planning area. To learn more about their activities, go to http://www.caltrout.org.

Cities of Simi Valley, Moorpark, Thousand Oaks, Calabasas, Agoura Hills, Fillmore, and Santa Paula: These cities have jurisdiction in the vicinity of the linkage, and many are already engaged in protecting open space and maintaining wildlife movement corridors. Land planning, land use, and open space policies in each city's General Plan can substantially influence implementation of the Linkage Design.

Cold Creek Docents: Since 1977, the Cold Creek Docents have been leading nature walks in the Cold Creek area of the Santa Monica Mountains. The Cold Creek Docents are dedicated: to educating the public, particularly school children, about the nature and cultural history of the Cold Creek watershed and its relationship to the Santa Monica Mountains and to worldwide ecological principles; to conducting hands-on programs that include geology, Chumash studies, ethnobotany, and chaparral ecology on Cold Creek area trails and at the Katherine Spensley Nature Education Center at UCLA Stunt Ranch Reserve; and to promoting appreciation, conservation, and stewardship of the Cold Creek watershed. For more information on their events or to become a docent, visit http://www.mountainstrust.org/docent.html.

Conejo Open Space Conservation Agency (COSCA): As the name implies, COSCA has been entrusted with the responsibility of preserving, protecting and managing open space resources in the Conejo Valley. COSCA was created in 1977 by a joint powers agreement between the City of Thousand Oaks (www.toaks.org) and the Conejo Recreation and Park District (www.crpd.org), enabling the two agencies to "jointly exercise their legal powers to create a jurisdictional framework for the conservation of natural open space lands, assure coordination of local land use and resource management decisions and establish an entity to focus community resources toward achievement of adopted General Plan goals." In this context, "open space" is defined as land which is in essentially a natural, undeveloped state, and does not include golf courses, developed park sites or landscaped greenbelts. For more information, visit http://www.conejo-openspace.org.

Conejo Open Space Foundation: The Foundation was formed in 1995 to promote and maintain the open space and trail system of the Conejo Valley and to educate residents as to their roles as custodians and protectors of the open space and the environment. To learn more, go to http://www.cosf.org.

County of Los Angeles: Los Angeles County is currently engaged in a 2025 General Plan update, which will likely include proposed revisions and expansions to existing Significant Ecological Areas (SEA). Three SEAs occur in the planning area: The Santa Monica Mountains SEA, which encompasses 99,431 acres and the Santa Susana Mountains/Simi Hills SEA, which covers 26,795 acres, and the Santa Clara River SEA (PCR 2000a,b,c); all three of these SEAs include several important wildlife movement areas. The General Plan update also provides an opportunity to ensure zoning in the Linkage Design is conducive to conserving linkage function. For more information on the General Plan update go to http://www.planning.co.la.ca.us.

County of Ventura: Ventura County uses growth management strategies, such as Save Open Space and Agricultural Resources (SOAR) to preserve farmland, open space and rural areas and limits growth to the City Urban Restriction Boundary (CURB) – SOAR requires countywide voter approval for any change to the County General Plan regarding agricultural, open space or rural land use designations. The County has several departments focused on the conservation of natural resources. Please visit http://www.countyofventura.org for more information.

Eastern Ventura County Conservation Authority: The Santa Monica Mountains Conservancy and the County of Ventura formed this joint powers authority (JPA) in 1990 to facilitate the opening and operation of Happy Camp Canyon Regional Park. Happy

Camp is a 3,000-acre wilderness area in the Rim of the Valley Trail Corridor between Moorpark and Simi Valley in the Santa Susana Mountains. Under an agreement with EVCCA, the Mountain Recreation Conservation Authority provides ranger services and volunteer trail assistance for the park. For more information on this JPA, go to http://smmc.ca.gov/EVCCA.html.

Environment Now: Environment Now is an active leader in creating measurably effective environmental programs to protect and restore California's environment. Since its inception, the organization has focused on the preservation of California's coasts and forests, and reduction of air pollution and urban sprawl. Environment Now uses an intelligent combination of enforcement of existing laws, and application of technology and process improvements to eliminate unsustainable practices. To find out more about their programs, visit their website at http://www.environmentnow.org

Farm Security & Rural Investment Act of 2002 (Farm Bill): This legislation responds to and provides funding for a broad range of emerging natural resource challenges faced by farmers and ranchers, including soil erosion, wetlands, wildlife habitat and farmland protection. Several programs have been developed through the Farm Bill including the Corridor Conservation Program, Farmland Protection Program, Wetlands Reserve Program, and Wildlife Habitat Incentives Program. To learn more about the Farm Bill, go to www.ers.usda.gov/features/farmbill/2002farmact.pdf

Friends of the Santa Clara River: The Friends have been actively engaged in watershed activities along the length of the river with a focus on the protection, enhancement, and management of the river's resources. The Friends are involved in several efforts including planning activities, habitat management, habitat restoration, and public education and outreach regarding the resource values of the river. The Friends own and manage a 230-acre river terrace property near the city of Santa Paula with over a mile of river frontage called the Hedrick Ranch Natural Area. Visit their website for more information at http://www.FSCR.org.

Los Angeles County Aquatic Resource In-Lieu Fee Mitigation Program: The purpose of this program is to provide a voluntary alternative compensatory mitigation option that results in better designed and managed aquatic resource restoration projects. Program funds may be used for activities directly related to aquatic habitat creation, restoration, or enhancement, to include exclusively the following activities: land acquisition; purchase of easements, purchase of water rights; development of mitigation and monitoring plans; permit fees; implementation of mitigation and monitoring plans; administrative costs; and long-term management of mitigation parcels. To find out more about this program, go to http://www.spl.usace.army.mil/regulatory/pn/200200035.pdf.

Malibu Creek Watershed Advisory Council: The Advisory Council is made up of a long list of representatives working to protect and preserve the health of the Malibu Creek Watershed and its adjoining watersheds. These representatives helped create the *1995 Natural Resources Plan*, which serves as a planning guide for overall watershed health. This Natural Resources Plan outlined 44 Action Items, later distilled to the Top Ten Watershed Restoration Priorities in the 2001 *Making Progress: Restoration of the Malibu Creek Watershed* report. Led by the RCD of the Santa Monica Mountains, the

Council meets every other month to discuss watershed-related issues pursuant to these priorities. Visit www.malibuwatershed.org to find out more.

Mountain Lion Foundation: The Mountain Lion Foundation works to ensure naturally sustaining populations of mountain lions. Using research, education, advocacy, legislation, and litigation, MLF works across the American West to stop unnecessary killing of mountain lions and to protect the ecosystems upon which they depend. MLF partners with groups whose mission directly impacts mountain lions and is proud to be a founding board member of South Coast Wildlands. MLF's Southern California office focuses on "Living with Lions" to reduce conflicts between people, pets and lions. MLF helps livestock owners build predator-safe enclosures, helps those suburban residents "On the Edge" understand how their personal choices may affect wildlife for miles around, as well as helps those working and playing "In the Wild" feel safer. For more information on the MLF's programs, visit their website at http://www.mountainlion.org.

Mountain Recreation and Conservation Authority (MRCA): The MRCA is a local partnership between the Santa Monica Mountains Conservancy, Conejo Recreation and Park District and the Rancho Simi Recreation and Park District. The MRCA is dedicated to the preservation and management of local open space and parkland, watershed lands, trails, and wildlife habitat. The MRCA manages and provides ranger services for almost 50,000 acres of public lands and parks that it owns and that are owned by the Santa Monica Mountains Conservancy or other agencies and provides comprehensive education and interpretation programs for the public. The MRCA works in cooperation with the Conservancy and other local government partners to acquire parkland, participate in vital planning processes, and complete major park improvement projects. The MRCA provides natural resources and scientific expertise, critical regional planning services, park construction services, park operations, fire prevention, ranger services, and educational and leadership programs for thousands of youth each year. To find out more, go to http://www.mrca.ca.gov/.

Mountains Restoration Trust (MRT): MRT is committed to preserving, protecting and enhancing the natural resources of the Santa Monica Mountains. MRT accomplishes this by working in several areas: land acquisition, cooperative planning, restoration, and offering education, and recreation programs. For nearly 20 years, MRT has offered a responsible approach to preservation and restoration based upon cooperative planning. MRT works with communities, land owners, and numerous governmental agencies to attain positive results in achieving preservation goals and public access. Visit http://www.mountainstrust.org to find out more.

National Parks Conservation Association: Their mission is to protect and enhance America's National Park System for present and future generations. NPCA plays a crucial role in ensuring that these special places are protected in perpetuity by advocating for the national parks and the National Park Service, educating decision-makers and the public about the importance of preserving the parks, helping to convince members of Congress to uphold the laws that protect the parks, supporting new legislation that addresses threats to the parks, fighting attempts to weaken these laws in the courts, and assessing the health of the parks and park management to better inform advocacy work. For more information, visit their website at http://www.npca.org.

National Park Service, Santa Monica Mountains National Recreation Area: The mission of the National Park Service (NPS) is "...to promote and regulate the use of the...national parks...which purpose is to conserve the scenery and the natural and historic objects and the wildlife therein and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations." Within this planning area, the NPS manages land within the Santa Monica Mountains National Recreation Area and is a key partner in the South Coast Missing Linkages Project. The Santa Monica Mountains are both ecologically and jurisdictionally fragmented so to achieve the NPS goals of resource protection, it is critical to understand and manage resources within the context of the surrounding landscape. Landscape linkages are critical to maintain ecological integrity in the Santa Monica Mountains and the Missing Linkages Project provides a scientific framework for assessing and identifying critical connections between the Santa Monica Mountains and surrounding ecosystems. In support of its resource protection mission and the objectives of the Missing Linkages Project, NPS scientists are engaged in numerous studies and monitoring programs related to habitat fragmentation, wildlife corridors, and landscape linkages. NPS rangers also provide educational and outreach programs about these issues to visitors and residents throughout the planning area. For more on NPS activities at Santa Monica Mountains National Recreation Area, see http://www.nps.gov/samo.

Rancho Simi Recreation and Park District: The District's mission is to provide a broad, well-rounded program of parks and recreation services for all District residents; to acquire land while available and at a reasonable price; to provide areas and facilities needed for indoor and outdoor recreation activities; to operate within an approved budget, offering recreation services at the most reasonable cost possible; to consistently strive to improve and expand recreation and park facilities through the use of property taxes, developers' fees, grants and major donations; to operate the District on a businesslike, economical basis in accordance with both accepted professional policy and taxpayer wishes; and to maintain facilities at a reasonable standard. The District covers 113 square miles which is bound by the Ventura County line on the east and south, west to the edge of the city limits of the City of Moorpark, and north to the Oak Ridge area of the Santa Susana Mountains. To find out more, go to http://www.rsrpd.org.

Regional Water Quality Control Board: The State WQCB strives to preserve, enhance and restore the quality of California's water resources, and ensure their proper allocation and efficient use for the benefit of present and future generations. The RWQCB oversees waters in the Linkage Design area. For more information, visit their website at http://www.swrcb.ca.gov.

Resource Conservation Districts (RCD): The federal district has 2 offices with responsibilities in this area: Ventura County RCD (www.vcrcd.org) and Santa Monica Mountains RCD (www.smmrcd.org). These non-profit agencies support conservation of natural ecosystems through programs that reduce the effects of on-going land-use practices on the environment. A major portion of their effort is to advise residents on the management of soil, water, soil amendments and other resources used for agriculture and home gardening. RCDs are supported by state and local grants. They provide leadership in partnership efforts to help people conserve, maintain, and improve our natural resources and environment. Programs include Emergency Watershed Protection, Environmental Quality Incentives, Resource Conservation and Development,

Soil Survey Programs, Soil and Water Conservation Assistance, Watershed Protection, River Basin, and Flood Operations, Wetlands Reserve and Wildlife Habitat Incentives. They do not enforce regulations but instead serve the interests of local residents and businesses. To find out more about California's RCDs visit http://www.carcd.org.

San Fernando Valley Audubon Society: Their mission is to preserve and enhance the natural habitat within the San Fernando Valley to increase the public's awareness and appreciation of bird life and the natural environment; and to create a social environment that encourages individual development and participation (http://www.sanfernandovalleyaudubon.org).

Santa Clara River Enhancement and Management Plan*:* The purpose of the SCREMP is to provide a guidance document that addresses the preservation, enhancement, and sustainability of resources for the entire length of the river, encompassing all land within the 500-year floodplain. The plan identifies land in the Linkage Design as having significant regional conservation value and calls for maintaining existing habitat values and river channel connectivity (AMEC 2004). The plan developed from a highly collaborative process that involved numerous stakeholders that is coordinated by the Ventura County Watershed Protection District and Los Angeles County Department of Public Works. The plan may provide opportunities for protecting land along the river in the Linkage Design area. The plan can be viewed at http://sdgis.amec.com/scremp/index.htm.

Santa Clara River Trustee Council*:* The Trustee Council, made up of representatives from the U.S. Fish and Wildlife Service and the California Department of Fish and Game, is administering $1.5 million to fund ecological restoration projects in the Santa Clara River watershed in Ventura and Los Angeles counties. Ecological restoration projects include habitat improvement, and ecological research, monitoring, and educational efforts associated with habitat restoration. The funds are from the settlement of claims for natural resource damages resulting from an ARCO pipeline oil spill into the Santa Clara River. Several projects have been proposed that would contribute to the protection and restoration of habitats in the Linkage Design. For more information on the Council, visit http://www.ventura.fws.gov/ SCRiverPlan/SCR.

Santa Monica Bay Restoration Commission: In recognition of the need to restore and protect the Santa Monica Bay and its resources, the State of California and the U.S. Environmental Protection Agency established the Santa Monica Bay Restoration Project (SMBRP) as a National Estuary Program in December 1988. The Project was formed to develop a plan that would ensure the long-term health of the 266 square mile Bay and its 400 square mile watershed, located in the second most populous region in the United States. That plan, known as the Santa Monica Bay Restoration Plan, won State and Federal approval in 1995. Since then the SMBRP's primary mission has been to facilitate and oversee the implementation of the Plan (http://www.santamonicabay.org).

Santa Monica Mountains Conservancy: This state agency was created by the Legislature in 1979 and is charged with the primary responsibility for acquiring land with statewide and regional significance. Through direct action, alliances, partnerships, and joint powers authorities, the Conservancy's mission is to strategically preserve, protect, restore, and enhance treasured pieces of Southern California's natural heritage to form an interlinking system of parks, open space, trails, and wildlife habitats that are easily

accessible to the general public. SMMC has been planning for habitat connectivity and acquiring land in the Linkage Design for the last few decades. The SMMC is a partner in the South Coast Missing Linkages effort. For more information on SMMC, visit them at http://www.smmc.ca.gov.

Santa Monica Mountains Natural History Association: The Association funds and supports walks, school programs and other interpretive activities at Leo Carrillo State Park and Point Mugu State Parks in the Santa Monica Mountains. These parks contain mountains, backcountry, beaches, canyons, woods, and ocean close to major urban centers. The association sponsors diverse programs that teach tidepooling and beach ecology. For more information about the Association and its many activities, go to http://www.parks.ca.gov/?page_id=22324.

Santa Monica Mountains Trails Council: The Santa Monica Mountains Trails Council is a volunteer, nonprofit organization dedicated to establishing and maintaining the public trail system throughout the Santa Monica Mountains, through advocacy and partnership with public and private sectors (http://www.smmtc.org).

Sierra Club's Santa Clara River Greenway Campaign*:* The stated goal of this effort is to bring the entire 500-year floodplain of the river from Fillmore to Acton into public ownership and protection. The campaign has identified a number of protection needs including water quality and quantity, plant and wildlife species habitats, movement corridors for wildlife, open space attributes and aesthetics, river fluvial dynamics, and agricultural resources (http://www.sierraclub.org).

Sierra Club's Southern California Forests Campaign: Sierra Club volunteers and staff have created the Southern California Forests Campaign to encourage public involvement in the 4 southern California Forest's Resource Management Plan revision process. The goals of the campaign are to reduce the threats to our forests and to enjoy, protect and restore them (http://www.sierraclub.org).

South Coast Wildlands: South Coast Wildlands is a non-profit group established to create a protected network of wildlands throughout the South Coast Ecoregion and is the key administrator and coordinator of the South Coast Missing Linkages Project. For all 15 priority linkages in the Ecoregion, South Coast Wildlands supports and enhances existing efforts by providing information on regional linkages critical to achieving the conservation goals of each planning effort (http://www.scwildlands.org).

South Coast Missing Linkages Project (SCML): SCML is an informal coalition of agencies, organizations and universities committed to conserving 15 priority landscape linkages in the South Coast Ecoregion. The project is administered and coordinated by South Coast Wildlands. Partners in the South Coast Missing Linkages Project include but are not limited to The Wildlands Conservancy, The Resources Agency California Legacy Project, California State Parks, California State Parks Foundation, United States Forest Service, National Park Service, Santa Monica Mountains Conservancy, Conservation Biology Institute, San Diego State University Field Station Programs, The Nature Conservancy, Environment Now, and the Zoological Society of San Diego's Conservation and Research for Endangered Species. For more information on this ambitious regional effort, go to http://www.scwildlands.org.

Southern California Wetlands Recovery Project*:* The Wetlands Recovery Project is a partnership of public agencies working cooperatively to acquire, restore, and enhance coastal wetlands and watersheds between Point Conception and the International border with Mexico. Using a non-regulatory approach and an ecosystem perspective, the Wetlands Recovery Project works to identify wetland acquisition and restoration priorities, prepare plans for these priority sites, pool funds to undertake these projects, implement priority plans, and oversee post-project maintenance and monitoring. The goal of the Southern California Wetlands Recovery Project is to accelerate the pace, extent, and the effectiveness of coastal wetland restoration in Southern California through developing and implementing a regional prioritization plan for the acquisition, restoration, and enhancement of Southern California's coastal wetlands and watersheds (http://www.coastalconservancy.ca.gov/scwrp).

The Nature Conservancy: TNC preserves the plants, animals and natural communities that represent the diversity of life on Earth by protecting the lands and waters they need to survive. The Conservancy has protected more than 117 million acres of land and 5,000 miles of river around the world. The Conservancy has undertaken significant conservation and planning efforts in the planning area, including critical lands in the Santa Susana Mountains and along the main stem of the Santa Clara River. TNC has protected a total of 4,600 acres in its LA-Ventura project area. TNC is actively acquiring land and conservation easements in the Santa Clara River floodplain, having conserved over 2,500 acres thus far representing 10.5 miles of the river. TNC is a partner in the South Coast Missing Linkage Project. For more information on their activities, go to http://www.tnc.org.

The Wildlands Conservancy: The Wildlands Conservancy is a non-profit, member-supported organization dedicated to land and river preservation, trail development and environmental stewardship through education. Their Save the Saints Program brings together multiple land trusts and conservancies to identify key lands for acquisition within National Forest boundaries and lands contiguous with the Forests in the Santa Ana, San Gabriel, San Jacinto, and San Bernardino Mountains. TWC is a vital partner in the South Coast Missing Linkages project. For more information, please visit their website at http://www.wildlandsconservancy.org.

Topanga Canyon Docents: The Topanga Canyon Docents was started in 1974 by a group of friends and activists who wanted to share their love of nature and the Santa Monica Mountains. They lead public nature walks and give programs for school children. They're committed environmentalists who've created an extremely popular and fun educational program (http://tc-docents.org).

Transportation Equity Act of the 21st Century (TEA-21): This Act was enacted June 9, 1998 as Public Law 105-178. TEA-21 authorizes Federal surface transportation programs for highways and highway safety The Critter Crossings Program was developed to address roadkill, habitat fragmentation, and habitat loss due to public roads. This Act provides funding for ecological infrastructure, water quality improvements, restoration of wetlands and habitat (http://www.fhwa.dot.gov/tea21).

Trust for Public Land (TPL): TPL conserves land for people to enjoy as parks, gardens and other natural places, ensuring livable communities for generations to come. TPL's Western Rivers Program works to reestablish and protect the natural function of river

systems. TPL has protected over 30,000 acres of river, wetland, and watershed lands in California (http://www.tpl.org).

US Army Corps of Engineers (ACOE): The mission of the ACOE is to provide quality, responsive engineering services for planning, designing, building and operating water resources and other civil works projects (Navigation, Flood Control, Environmental Protection, Disaster Response, etc.). The ACOE has conducted dam removal studies for the Rindge Dam on Malibu Creek and the Matilija Dam on Matilija Creek, a tributary of the Ventura River. They also are engaged in watershed planning efforts that may provide opportunities for restoration of natural water flow and riparian vegetation in the linkage. They recently completed a Reconnaissance Study of the Santa Clara River Watershed to determine federal interest in completing a Feasibility Study for a Santa Clara River Watershed Protection Plan that would cover the entire watershed (http://www.usace.army.mil).

US Fish and Wildlife Service (USFWS): The USFWS works to conserve, protect and enhance fish, wildlife, and plants and their habitats for the continuing benefit of the American people. The agency can provide support for prosecuting violations to the Endangered Species Act, law enforcement, permits, and funding for research on threatened and endangered species. The federal Endangered Species Act as amended (16 U.S.C. 1534) authorizes USFWS to acquire lands and waters for the conservation of fish, wildlife, or plants with the Land and Water Fund Act appropriations. The added protection provided by the Endangered Species Act may also be helpful for protecting habitat in the linkage from proposed development projects (http://www.fws.gov).

US Fish and Wildlife Service Partners for Fish and Wildlife Program This program supplies funds and technical assistance to landowners who want to restore and enhance wetlands, native grasslands, and other declining habitats, to benefit threatened and endangered species, migratory birds, and other wildlife. This program may be helpful in restoring habitat on private lands in the Linkage Design (http://partners.fws.gov).

US Forest Service: The mission of the USDA Forest Service is to sustain the health, diversity, and productivity of the Nation’s forests and grasslands to meet the needs of present and future generations. The four southern California Forests (Los Padres, Angeles, San Bernardino, and Cleveland) have recently finalized their Resource Management Plans. The Final Environmental Impact Statement and Forest Plans have identified connecting the four forests to the existing network of protected lands in the region as one of the key conservation strategies for protecting biodiversity on the forests. The USFS is allocated Land and Water Conservation Funds annually, which are designed to protect recreational open space, watershed integrity, and wildlife habitat and may be a source of funds for protecting land in the planning area. The Forest Service is taking a proactive role in habitat connectivity planning in the region as a key partner in the South Coast Missing Linkages Project. For more information, go to http://www.fs.fed.us/r5/scfpr.

US Geological Survey, Biological Resources Division: The Biological Resource Division (BRD) works with others to provide the scientific understanding and technologies needed to support the sound management and conservation of our Nation's biological resources. BRD develops scientific and statistically reliable methods and protocols to assess the status and trends of the Nation's biological resources. BRD

utilizes tools from the biological, physical, and social sciences to understand the causes of biological and ecological trends and to predict the ecological consequences of management practices. BRD enters into partnerships with scientific collaborators to produce high-quality scientific information and partnerships with the users of scientific information to ensure this information's relevance and application to real problems. For more information, go to http://www.biology.usgs.gov.

Ventura Coast Keepers/Wishtoyo Foundation*:* The Ventura Coastkeepers is affiliated with the National Waterkeeper Alliance, dedicated to protecting, preserving and restoring marine habitat, coastal waters, and watershed integrity. The Keeper organizations fill the gap between water pollution laws and the government's ability to enforce them. Wishtoyo is a Native American organization that utilizes traditional Chumash cultural values and practices to foster environmental awareness (http://www.wishtoyo.org).

Ventura County Watershed Protection District: The mission of the Watershed Protection District is to protect life, property, watercourses, watersheds, and public infrastructure from the dangers and damages associated with flood and stormwaters. They are currently working on the following projects in the planning area: Matilija Dam Ecosystem Restoration Project, Calleguas Watershed Management Plan Present Condition Model Results, and SCREMP (http://publicworks.countyofventura.org/fc/).

Ventura County Open Space District: In November 1998, voters decisively approved Advisory Measure A “authorizing legislation” (AB 1145) to develop an Open Space District (OSD); the County has received State authorization but hasn’t yet implemented their OSD. The purpose of the proposed OSD is to preserve, enhance and/or restore the agricultural resources and natural qualities of Ventura County (e.g., ridgelines, scenic viewsheds, agricultural lands, wildlife corridors, natural habitat, greenbelts between the cities, hillsides, wetlands, rivers and streams, and natural parksites) for the enjoyment and benefit of present and future residents of the County. OSDs are similar to non-profit land trusts and conservancies, protecting land using a combination of techniques including outright purchase or purchasing the “right” to develop the land (in voluntary transactions) (http://www.ventura.org/planning/studies_eirs/open_space.htm).

Ventura Hillsides Conservancy: The mission of the Conservancy is to "preserve the hillsides, canyons, and open space that contributes to the unique character and natural environment of the City of San Buenaventura and the surrounding region for the benefit of present and future generations." (http://www.venturahillsides.org).

Wildlife Conservation Board: The Wildlife Conservation Board administers capital outlay for wildlife conservation and related public recreation for the State of California. The Board, while a part of the California Department of Fish and Game, is a separate and independent Board with authority and funding to carry out an acquisition and development program for wildlife conservation (http://www.dfg.ca.gov/wcb).

A Scientifically Sound Plan for Conservation Action

In southern California, humans have become significant agents of biogeographic change, converting habitat to urban and agricultural uses and altering the movements of organisms, nutrients, and water through the ecosystem. The resulting fragmentation of natural landscapes threatens to impede the natural processes needed to support one of the world's greatest biological warehouses of species diversity.

This interaction between human development and unparalleled biodiversity is one of the great and potentially tragic experiments of our time. It creates a unique challenge for land managers and conservation planning efforts – to mitigate these major impacts to once intact ecosystems. The conservation plan for the Santa Monica-Sierra Madre Connection addresses these challenges by presenting a scientific framework and set of recommendations that can guide regional conservation planning and patterns of development in a manner that best preserves landscape level processes in the region.

The prioritization of this linkage for conservation and the demarcation of lands suggested for protection in the linkage are based on the best available conservation techniques and expertise of biologists working in the region. This project provides a strong biological foundation and quantifiable, repeatable conservation design approach that can be used as the basis for successful conservation action.

Next Steps

This Linkage Design plan acts as a scientifically sound starting point for conservation implementation and evaluation. The plan can be used as a resource for regional land managers to understand their critical role in sustaining biodiversity and ecosystem processes. Existing conservation investments in the vicinity are already extensive including lands managed by the US Forest Service, National Park Service, California State Parks, Santa Monica Mountains Conservancy, The Nature Conservancy, and other open space agencies. Each land parcel located within the targeted protected core areas or the linkage itself serves a unique role in preserving some aspect of the connection. Incorporating relevant aspects of this plan into individual land management plans provides an opportunity to jointly implement a regional conservation strategy.

Additional conservation action will also be needed to address transportation barriers. Recommended tools include road renovation, construction of wildlife crossings, watershed planning, habitat restoration, conservation easements, zoning, acquisition, and others. These recommendations are not exhaustive, but are meant to serve as a starting point for persons interested in becoming involved in preserving and restoring linkage function. We urge the reader to keep sight of the primary goal of conserving landscape linkages to promote movement between targeted core areas over broad spatial and temporal scales, and to work within this framework to develop a wide variety of restoration options for maintaining linkage function. To this end, we provided a list of organizations, agencies and regional projects that provide collaborative opportunities for implementation.

Public education and outreach is vital to the success of this effort – both to change land use activities that threaten species existence and movement in the linkage and to generate an appreciation and support of the conservation effort. Public education can encourage recreational users and residents at the urban-wildland interface to become active stewards of the land and to generate a sense of place and ownership for local habitats and processes. Such voluntary cooperation is essential to preserving linkage function. The biological information, figures and tables from this plan are ready materials for interpretive programs. We have also prepared a 3D animation (Appendix C on the enclosed CD) that provides a landscape perspective of the linkage.

Successful conservation efforts are reiterative, incorporating and encouraging the collection of new biological information that can increase understanding of linkage function. We strongly support the development of a monitoring and research program that addresses movement (of individuals and genes) and resource needs of species in the Linkage Design area. The suite of predictions generated by the GIS analyses conducted in this planning effort provides a starting place for designing long-term monitoring programs.

The remaining wildlands in southern California form a patchwork of natural open space within one of the world's largest metropolitan areas. Without further action, our existing protected lands will become isolated in a matrix of urban and industrial development. Ultimately the fate of the plants and animals living on these lands will be determined by the size and distribution of protected lands and surrounding development and human activities. With this linkage conservation plan, the outcome of land use changes can be tailored to assure the greatest protection for our natural areas at the least cost to our human endeavors. We envision a future interconnected system of natural space where our native biodiversity can thrive.

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South Coast Missing Linkages Workshop Minutes
July 29, 2002 at Franklin Canyon Park

Ray Sauvajot, National Park Service – *Welcome*

- Project goal is to identify, understand and protect habitat linkages across California
- Missing Linkages statewide conference (November 2000) allowed participants to map habitat linkages between remaining wildland areas using consensus-based approach
- Threats and scientific needs identified for each linkage area and compiled into conference proceedings, which has received attention from land planners and the media
- 69 linkages identified for landscape connectivity in the South Coast Ecoregion; 15 highest priority (most irreplaceable and vulnerable) linkage areas selected for immediate conservation action; this pilot planning project can be replicated across California
- Two workshops: biological perspectives (focal species information) and conservation design/delivery (land protection); thorough planning will attract conservation dollars
- Presentations will discuss connectivity needs for various groups of species and provide scientific framework for afternoon taxonomic working group sessions; datasheets will be used to collect linkage information and identify importance of corridor for focal species

Jonathan Levine, University of California Los Angeles – *How Does Habitat Connectivity Affect Rare Plant Persistence?*

Summary: It is commonly believed that dispersal is essential to the persistence of plant populations. Here, I present evidence from general ecological models identifying important caveats about the systems and species for which this notion is valid. By examining other mechanisms of persistence including dormancy and tolerance, I point out that the importance of dispersal, and ultimately habitat connectivity for the persistence of rare plant populations should not be assumed *a priori*.

Biography: Jonathan Levine in an assistant professor of conservation biology in the Department of Organismic Biology, Ecology, and Evolution, and the Institute of the Environment at UCLA. He received his doctoral degree at the University of California, Berkeley for his work on the relationship between native plant species diversity and biological invasions along the South Fork Eel River in northern California. Jonathan has written extensively on the controls over the success and impacts of biological invasions. Current interests include the importance of dormancy and environmental variation for the persistence of the rare annual plants on the southern California Channel Islands.

- Framework for choosing focal plant species: plant persistence dependent upon pollination and dispersal, often by animal vectors that require habitat connectivity
- Rare plant populations are threatened by demographic stochasticity (chance variation in birth rate, death rate, etc.) and environmental variation (such as drought); potential buffers against environmental variation: high tolerance (e.g. - special physiology allows Dudleya species to survive drought), dormancy (seeds can live for several years), and

dispersal (movement through shifting mosaic of favorable and unfavorable habitat locations); habitat connectivity is important for the dispersal of many plant species
- Dispersal is difficult way for rare plants to persist; dormancy is more flexible approach
- Theoretical model for rare annual plant populations on Channel Islands with variable climate, exotic annual grass competitors, and variable germination and dormancy - simulation shows population increase during periods of environmental fluctuation (which limits competition with exotic grasses allowing dormant seeds to flourish)
- Habitat linkages needed for movement of pollinators and dispersers; dispersal favorable for persistence of certain species according to three ecological models: evolution/natural selection, metapopulations in shifting environments, and neutral landscape/percolation in patchy environments; dispersal favors persistence if patch quality varies asynchronously (e.g. – Dudleya on rock outcrop might disperse seed to inappropriate chaparral habitat)
- Dispersal allows patches to be re-colonized by plants following disturbance, although after wildfire some species sprout from dormant seeds; habitat fragmentation and alteration may make plant dispersal more important than under natural conditions
- Plant dispersal takes place on a large scale; connectivity can potentially hurt plant populations by allowing invasion by non-native species
- Future regional climate is predicted to involve more extreme variations (severe floods and droughts); for non-rare plant species, connectivity may be important for dispersal into more favorable habitats, post-fire colonization, and seed dispersal by animals

Travis Longcore, The Urban Wildlands Group - *Invertebrates and Landscape-level Conservation Planning*

Summary: Invertebrates respond to landscape features across many scales, including much finer scales than vertebrates. While they can maintain viable populations in much smaller areas than charismatic megafauna, they are also perhaps even more sensitive to habitat degradation -- a simple footpath may constitute habitat fragmentation for some invertebrates. Corridors may funnel some mobile species between appropriate habitats, but inter-patch distance is equally if not more important. For flying insects such as butterflies, stepping stones of habitat may be more efficient than corridors in ensuring metapopulation viability. Landscape conservation planning for invertebrates must recognize their different scales of response, the value of relatively small and "isolated" habitat areas, and relative threats to population viability.

Biography: Travis Longcore completed his PhD in Geography at UCLA, and is an expert in urban conservation biology and restoration. His research has focused on the use of terrestrial arthropods to evaluate the success of ecological restoration in coastal sage scrub communities. Dr. Longcore has professional experience with urban habitat conservation and environmental education, having worked on efforts to conserve the Palos Verdes blue butterfly, and to develop butterfly garden programs for inner city schools. He is active in conservation planning for endangered species, serving on U.S. Fish and Wildlife Service Recovery Teams for the El Segundo blue butterfly and Quino checkerspot butterfly. He is currently Research Assistant Professor of Geography in the USC Sustainable Cities Program and Science Director of The Urban Wildlands Group, a Los Angeles-based conservation think tank.

- Incredible invertebrate diversity to consider for landscape-level planning
- Smaller scale for invertebrates when considering fragmentation: even dirt pathway may be movement barrier for certain species (e.g. – wolf spider); certain beetle species

remain in leaf litter under trees and will not leave favorable habitat patch; width of road/path and construction material (grass, gravel, pavement) influence beetle movement

- Flying insects: roads can still present dispersal barrier; butterfly species have different landscape mobility (only certain species will cross water/trees/path/road); some mobile butterflies use habitat corridors, while more sedentary species remain within habitat patches and may move less than ten meters (e.g. – remain at location of rare host plant); older female butterflies more likely to disperse long distances
- Patch size/distance matters; fragmentation can prevent habitat re-colonization by inverts
- Flightless habitat specialists (scorpions, land snails, trap door spiders): lifetime mobility only a few meters; require specific plants/soils; landscape-level connectivity already largely lost; poor linkage focal species - more important to preserve high quality habitat
- Mobile flightless inverts (certain beetles): move tens to hundreds of meters; connectivity compromised; poor linkage focal species – more important to preserve habitat mosaic
- Flying habitat specialists (butterflies, bees, moths, possibly grasshoppers): may move hundreds of meters up to few kilometers; require specific host plant, habitat type, or disturbance cycle; inter-patch distance influences colonization; good focal species - corridors must contain specific habitat qualities required by focal species
- Flying habitat generalists (mosquito, cabbage butterfly): no connectivity concern; can move between habitats as needed; poor focal species
- Recommended focal species are flying habitat specialists mobile enough to utilize linkages; for invertebrates, management of internal habitat quality in linkage areas is extremely important; must prevent irrigation (which leads to abundance of exotic invertebrates), artificial night lighting (some invertebrates use lights to navigate), chemical pollution (pesticides and fertilizers), and statutory habitat destruction for fire clearance/fuel modification (200 feet = approx. three acres habitat lost per structure)

Robert Fisher, United States Geological Survey, Biological Resources Division – ***Landscape Linkage Planning for Herpetofauna & Fish in the South Coast Ecoregion***

Summary: This presentation explores the contrasting habitat requirements of amphibian, reptile, and fish species found within the South Coast Ecoregion, and discusses the various types of barriers that preclude movement for each. The results of movement studies conducted in other parts of the Ecoregion will provide information on how to address these needs and issues with respect to linkage planning and design.

Biography: Robert Fisher completed his B.S. in Biology at University of California, Irvine, and both his M.S. in Zoology, and Ph.D. in Population Biology at University of California, Davis. His research interests include herpetology, including declining species, conservation biology, monitoring programs for vertebrates, and reserve design.

- Watershed boundaries are an important consideration for focal species; within linkage area, there are 6 fish species (arroyo chub, unarmored stickleback, partially armored stickleback, striped mullet, lamprey, and southern steelhead), 1 turtle, and many amphibians, lizards and snakes
- Focal species selection should be based on biological attributes: terrestrial breeding salamanders (riparian and upland chaparral); aquatic breeding newts (good indicator species, but difficult species to connect appropriate habitats across these linkages); frogs and toads (red-legged frog makes good focal species - once widespread and now

restricted to few locations; also arroyo toad and California treefrog); western pond turtle should be considered because it is capable of terrestrial movement
- Habitat specialist lizards – legless lizard (little movement), alligator lizard (resilient to fragmentation impacts), horned lizard (patchy distribution); recommended focal species is coastal whiptail, which is sensitive to fragmentation and utilizes various habitats
- Snakes: red racer uses scrub and grassland habitats; coast patch-nosed snake inhabits riparian areas; south coast garter uses various habitats and its range has been reduced
- Regional aquatic systems contain dams and other barriers; wild habitats must be reconnected; movement through urbanized landscape of linkage areas may involve use of low quality habitat, allowing exposure to artificial lighting, fish parasites, and exotic species; current herpetological studies focus on stickleback and frog exposure to fungus and disease; USGS is conducting amphibian distribution surveys with pitfall traps across southern California, investigating species-specific connectivity needs, and observing habitat recovery after wildfire

Kimball Garrett, Los Angeles County Natural History Museum – *An Ornithological Primer for Ecologists*

Summary: Birds are often not the focus of wildlife habitat connectivity planning because of their perceived ease of movement across barriers and unsuitable habitats. Nevertheless, birds vary greatly in their dispersal ecology, ability to cross unsuitable habitats, and tolerance of fragmented or modified habitats. My presentation is largely intended to be an ornithological primer for ecologists. In it I will review some of the important bird species in riparian, scrub, woodland, and grassland habitats in Ventura County and western Los Angeles County, with a focus on sensitive and declining species and their dispersal ecology. As with most groups, birds are poorly studied with respect to habitat connectivity needs and even basic life history traits that impact dispersal ability.

Biography: Kimball L. Garrett has been the Ornithology collections manager at the Natural History Museum of Los Angeles County since 1982; he obtained his undergraduate degree in Zoology at University of California Berkeley and did graduate work in ornithology at UCLA. He is co-author of "Birds of Southern California: Status and Distribution," published in 1981 by the Los Angeles Audubon Society, and served on the steering committee for the Breeding Bird Atlas of Los Angeles County, the results of which he is now co-authoring.

- Most birds are able to move across barriers and unsuitable habitat; biota of Baldwin Hills (isolated coastal scrub habitat in Los Angeles Basin) lost regional connectivity; Bewick's wren and spotted towhee remain (no historical density data or dispersal information available); cactus wren, a sedentary habitat specialist, disappeared from site
- Abundant/widespread birds (such as the house finch): no need to consider for avian connectivity planning; many already adapted to human landscape modification
- Artificially over-abundant/nuisance birds: plan to reduce or exclude; show accelerated population growth and range expansion; common raven and brown-headed cowbird, although native, can inflict negative impacts upon native species; also, do not plan for non-native species (European starling, parrots, parakeets)
- Water birds have evolved to travel great distances; excellent fliers adapted to interrupted habitats; migrate to breeding habitat; not important for linkage planning
- Focal bird species for linkage planning should be sedentary, habitat specific land birds; concentrate on sensitive, range-restricted or otherwise important species, including endemics (yellow-billed magpie and Clark's marsh wren found in region but not linkages)

- Riparian restoration and cowbird control have benefited migratory least bell's vireo, but poor focal species as re-colonization is not defined by habitat linkages; migratory willow flycatcher is also poor focal species, and not responding as well to recovery efforts
- Recommended focal species is rapidly declining loggerhead shrike, sensitive to landscape modification because young disperse (neither migratory nor sedentary)
- Some endangered species not appropriate focal species for habitat connectivity – more threatened by loss of prey base, declining habitat quality, pesticides, and exploitation
- Focal species should be non-migratory; consider keystone species (large predators, cavity nesters) and habitat specialists (acorn woodpecker and spotted owl in woodlands, Say's phoebe in arid open country, wrentit in low scrub/chaparral, non-migratory sparrows in low scrub, common ground dove in riparian/agricultural habitat, California gnatcatcher in dry desert washes, coastal horned lark and burrowing owl in grassland)

Seth Riley, National Park Service - *Fragmentation, Urbanization, Connectivity, and Mammalian Carnivores in the Santa Monica Mountains to Sierra Madre Mountains Region*

Summary: Maintaining habitat and landscape connectivity is particularly important for wide-ranging and low-density species such as mammalian carnivores. In the area of the Santa Monica to Sierra Madre linkage, we are fortunate to have detailed existing information on the movements and ecology of carnivores, specifically bobcats, coyotes, and, very preliminarily, mountain lions. While both coyotes and bobcats occur in the fragmented, urban landscape of the Simi Hills and northern Santa Monica Mountains, even at high densities, they are affected in various ways by urbanization and fragmentation. Most adult female bobcats, the group responsible for successful reproduction, rarely utilize developed areas or cross major urban roads. Male bobcats and coyotes do so more, particularly at night, but even the home ranges of coyotes and male bobcats in this landscape are made up of mostly (75%) natural habitat. In addition, a specific study of freeway undercrossings showed that while different mammals used them to varying extents, bobcats and coyotes were more likely to do so when natural habitat was present on both sides of the crossing point. Natural habitat is critical both for the maintenance of reproducing carnivore populations in this landscape, and for the maintenance of movement between regional habitat blocks. Genetic analyses are also underway to determine whether freeways have already resulted in detectable barriers to gene flow. Certainly the most difficult species to maintain in the Santa Monica to Sierra Madre area over the long-term is the mountain lion. A recently initiated study of lion movements and home range use in the region will help us learn more about what may be required to conserve even the largest carnivores.

Biography: Seth Riley graduated in 1988 from Stanford University with a B.A. in Human Biology, concentrating in Animal Behavior and Ecology. From 1988-1990 Seth worked as a wildlife biologist for the National Park Service at the Center for Urban Ecology in Washington. Seth attended the University of California, Davis graduate school, where he graduated with a Ph.D. in Ecology in 1999. After graduating, Seth worked as a post-doctoral fellow at Davis, and began his current position as Wildlife Ecologist with the National Park Service at Santa Monica Mountains National Recreation Area in 2000, where current projects include a bobcat and coyote study that addresses home range and habitat use, reproduction, food habits, and genetics, a mountain lion GPS telemetry study, stream surveys for amphibians, pitfall/drift fence trapping to determine terrestrial reptile and amphibian distribution and abundance, and bat inventory and monitoring.

- Connectivity extremely important for wide-ranging, terrestrial, territorial, low-density mammalian carnivores; best to choose focal species for which dispersal needs have been studied to provide biological foundation for linkage design
- NPS has studied bobcats and coyotes in the Santa Monica Mountains and Simi Hills using radio collars, focusing on movement across the 101 freeway to measure impacts of urbanization and study habitat use; bobcats are dimorphic (average home range in this region is 3 square km male / 1.5 square km female – extremely small for this species); coyotes also dimorphic (average home range in this region 6 square km male / 3 square km female); adult female bobcats rarely enter developed areas; male bobcats and coyotes will utilize developed areas, but prefer natural areas
- One female coyote dispersed into San Fernando Valley, and often traveled between semi-natural habitat at Pierce College and Sepulveda Basin using the L.A. River channel; even in urban areas, animals are moving and finding the most suitable habitat
- Small roads can be crossed by wildlife, but are still sources of mortality; freeways are significant barriers, but can be crossed at certain sites (bridges and under-crossings)
- 101 crossed at Liberty Canyon by raccoons, spotted skunks, rodents, coyotes, bobcats, and a mountain lion; monitored with remote camera and tracks in gypsum; carnivores preferred to cross at sites with natural habitat on both sides of freeway; tracking data for bobcats and coyotes used to compare mortality (roadkill, mange, etc.) and fragment size
- Mountain lion is difficult to maintain in fragmented landscape; NPS recently captured 140 lb. male lion; GPS collar is now collecting movement data; long-term estimate for this area is less than ten lions; connectivity important; 600 square km available in Santa Monica Mountains (Beier 1993: 2200 square km needed to maintain lion population); NPS would like to also track lions in Santa Susana Mountains and Simi Hills
- Little known about habitat and connectivity requirements for rare carnivores - badger, ringtail, weasel, fox; studies needed to understand distribution

Claudia Luke, San Diego State University, Field Stations Program – *Considerations for Connectivity & Overview of Working Group Session*

Summary: This presentation describes the Santa Ana – Palomar Mountains linkage to allow workshop participants to understand purposes of the focal species groups, identification of critical biological issues regarding connectivity, and qualities of species that may be particularly vulnerable to losses in connectivity.

Biography: Claudia Luke received her Ph.D. in Zoology from U.C. Berkeley in 1989. She is Reserve Director of the Santa Margarita Ecological Reserve, an SDSU Field Station, and Adjunct Professor at San Diego State University. She is on the Board of Directors for the South Coast Wildlands Project and has been the lead over the last two years in conservation planning for the Santa Ana – Palomar Mountain linkage.

- At the November 2000 Missing Linkages conference, participants determined which areas within California needed to be connected to allow species movement
- South Coast Ecoregion workgroup selected criteria to prioritize linkages and connect largest protected lands; planning efforts have progressed for the Santa Ana – Palomar Mountains linkage area - workshops have been held to select focal species
- Global linkage role: preservation of biodiversity hotspot with concentration of endemic species (formed by gradients in elevation, lack of past glaciers, soil diversity)

- Regional linkage role: maintenance of habitat connectivity to prevent extirpations, and considerations for climate change (warmer wetter winters and drier summers may cause extreme floods and wildfires, drier vegetation types may expand to higher elevations)
- Local linkage role: connect protected parcels, considering dispersal methods of focal species, and impacts to habitat specialists, endemics, edge effects, and gene flow
- Focal species approach to functional linkage planning based on Beier and Loe 1992 corridor design (choose appropriate species, evaluate movement needs, draw corridor on map, monitor); focal species are units of movement used to evaluate effectiveness of linkages; wide diversity of species necessary to maintain ecological fabric; collaborative planning effort based on biological foundation and conservation design/delivery
- Choose species sensitive to fragmentation to represent linkage areas; Crooks and Soule 1999 showed that in San Diego as fragment size decreases, multiple bird species are lost; must consider associated species in planning, including keystone species important to survival of other species (e.g. - *Yucca whipplei* pollinated by specific invertebrates)
- Each taxonomic working group will choose a few species, delineate movement needs, record information on natural history, distribution, habitat suitability, current land conditions, key areas for preservation and restoration; consider metapopulation dynamics so that if a species disappears due to disturbance, habitat can be re-colonized
- Focal species data will be displayed on conservation design map and used to guide planning efforts; regional approach to linkages will help the South Coast Missing Linkages Project gain visibility and leverage to work with multiple agencies and organizations

Appendix C: 3D Visualization

South Coast Wildlands has produced several flyovers or 3D visualizations of the Santa Monica-Sierra Madre Connection and other linkages throughout the South Coast Ecoregion as part of the South Coast Missing Linkages Project.

The 3D Visualization provides a virtual landscape perspective of the local geography and land use in the planning area.

INSTRUCTIONS ON VIEWING FLYOVER

The flyover provided on this CD is an .mpg file (media file) which can be viewed using most popular/default movie viewing applications on your computer (e.g. Windows Media Player, Quick Time, Real One Player, etc).

Simply download the .avi file "3D_Visualization.mpg" from the CD onto your computer's hardrive. Putting the file on your computer before viewing, rather than playing it directly from the CD, will provide you with a better viewing experience since it is a large file.

Double click on the file and your default movie viewing software will automatically play the flyover.

If you cannot view the file, your computer may not have any movie viewing software installed. You can easily visit a number of vendors (e.g. Real One Player, Window Media Player, etc.) that provide quick and easy downloads from their websites.

Please direct any comments or problems to:

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37

Mountain Lion

Puma concolor

Becky M. Pierce
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NOMENCLATURE

COMMON NAMES. Mountain lion, puma, panther, catamount, and cougar
SCIENTIFIC NAME. *Puma concolor*

TAXONOMY

Mountain lions have a complicated taxonomic history. Numerous subspecies have been described, largely based on morphometric differences. For example, Young and Goldman (1946) listed a total of 30 subspecies, and Culver et al. (2000) noted that 32 named subspecies existed. Of those listed by Young and Goldman (1946), at least 13 occurred in Canada or the United States (and adjacent Mexico); the remainder had geographic distributions restricted to Mexico, Central America, or South America.

The mountain lion was first described from a specimen collected in Brazil (Marcgrave 1648); Linnaeus reclassified the mountain lion as *Felis concolor* in 1771. Jardine (1834) placed the species in the genus *Puma,* where it remains (Wozencraft 1993). The historical taxonomy of the mountain lion was reviewed in detail by Young and Goldman (1946) and Currier (1983).

Based on molecular and morphological investigations, the mountain lion is thought to have evolved from an ancestor in common with the cheetah (*Acinonyx jubatus*) and jaguarundi (*Herpailurus yaguaroundi*) (Van Valkenburgh et al. 1990; Janczewski et al. 1995; Johnson and O'Brien 1997; Pecon-Slattery and O'Brien 1998). Mountain lions are represented in the North American fossil record dating back 300,000 years (Turner 1997). Based on an extensive analysis of mitochondrial DNA haplotypes and microsatellite alleles from throughout the geographic range of *Puma concolor,* Culver et al. (2000) speculated that a mass extinction during the Pleistocene (Martin 1989), which eliminated the majority of large mammals in North America, was followed by a colonization of mountain lions of South American stock. Furthermore, Culver et al. (2000) concluded that mountain lions (north of Nicaragua) today represent a single subspecies, *Puma concolor couguar,* in lieu of the 15 that formerly were recognized. Five other subspecies of *Puma concolor* are recognized throughout their southern range (Culver et al. 2000).

DESCRIPTION

Although the sexes are similar in appearance, male and female mountain lions are dimorphic in size. Gay and Best (1995) examined specimens from throughout the range of mountain lions and reported that males were significantly larger than females in 14 cranial and 5 mandibular measurements. In California, mean body weight of adult (≥2 years of age) males was $\bar{X} = 53.4$ kg (±8.5 kg [*SD*]). Adult females weighed 30–40% less ($\bar{X} = 35.8 \pm 7.7$ kg) (Charlton et al. 1998). Based on a sample of 1076 specimens from Oregon, Kohlmann and Green (1999) reported that males averaged about 50% heavier than females of equivalent age. Gay and Best (1995) found no evidence that sexual dimorphism among mountain lions varied geographically. Data compiled by Anderson (1983) show that similar degrees of sexual size dimorphism occur among mountain lions throughout their range. Although the degree of sexual dimorphism did not vary geographically, the size of mountain lions generally increased with an increase in latitude (Kurten 1973; Iriarte et al. 1990).

The dorsal pelage of a mountain lion is tawny, and they generally are white on the ventral surface (Fig. 37.1). Slight variation in color is common, and their coats can have reddish, yellowish, or grayish tinges. There are no obvious contrasting markings on the coats of adult lions, other than black markings at the base of the vibrissae on the muzzle, on the dorsal surface of the ears, and on the tip of the tail. In Latin, the specific epithet *concolor* means "single color."

In contrast to adults, young mountain lions have darker facial markings and are heavily spotted at birth (Fig. 37.2), but that pattern fades as kittens mature. The spotted pelage of kittens becomes less obvious at about 9 months of age. By the time young are approximately 2 years old, the spotting has largely disappeared (Russell 1978). The eyes are closed at birth, but open by 2 weeks of age (Young and Goldman 1946). Logan and Sweanor (1999) reported that the light blue eye color of kittens changes to the amber color typical of adults when kittens are as young as 5 months.

Despite the large difference in body weight typical of adult males and females, distinguishing the sexes from a distance can be difficult. Unless males are in an older age category, with well-developed shoulder, neck, and facial musculature, body conformation of young adult males can be confused with that of older adult females. Genders can be distinguished by observing the genitalia, but male lions frequently are misclassified as females, even by professional wildlife biologists and law enforcement personnel, because the scrotum and penis are not obvious to the untrained observer. Dark coloration is associated with hair surrounding the penis sheath of males, and is an important clue to the gender of lions (Logan and Sweanor 1999).



FIGURE 37.1. Adult mountain lion (*Puma concolor*). SOURCE: Photo by Becky M. Pierce.



FIGURE 37.2. Three-week-old mountain lion (*Puma concolor*) kittens in the birth nursery. SOURCE: Photo by Becky M. Pierce.

As with all felids, except cheetahs, mountain lions have retractable claws (Fig. 37.3) at the terminus of each digit. These claws function primarily to grasp prey, rather than as an aid in locomotion (Dixon 1982). The rostrum of felids is short and the orbits are large (Fig. 37.4) compared to those of canids. These skull adaptations allow for a more powerful bite, and felids are more dependent on sight than are canids to detect prey (Vaughan et al. 2000). The adult dental formula is I 3/3, C 1/1, P 3/2, M 1/1.

DISTRIBUTION

Although they occur at low densities, mountain lions are the most abundant large felid occupying North America and are second in size only to the jaguar (*Felis onca*) (Russell 1978). Historically, mountain lion distribution encompassed most of the western hemisphere (Young and Goldman 1946). They occurred from the Atlantic to the Pacific oceans and from approximately 50° N to 50° S latitude, and from near sea level to about 4000 m elevation (Young and Goldman 1946). In essence, mountain lions ranged from approximately the Cassiar Range of northern British Columbia to southern Chile and Argentina, and from ocean to ocean on the continents of North and South America.

In North America, the distribution of mountain lions has been reduced by as much as two thirds of its historical range (Fig. 37.5), largely because of conflicts with humans as settlers migrated westward (Ross et al. 1997). Currently, mountain lions occur in suitable habitat throughout Mexico, in the majority of the western United States, and in western Canada; a small population also occurs in southern Florida

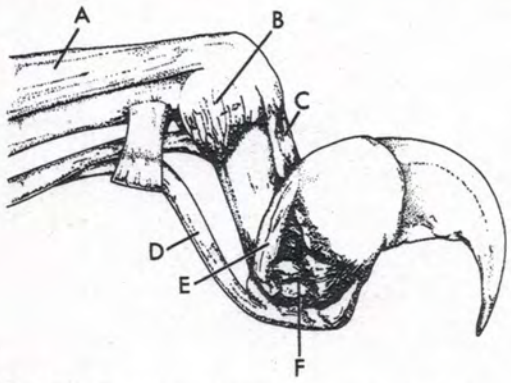

FIGURE 37.3. Retractile claw mechanism of the mountain lion (*Puma concolor*). A, Extensor expansion; B, middle interphalangeal joint; C, extensor tendon; D, flexor digitorum profundus tendon; E, lateral dorsal elastic ligament; F, distal interphalangeal joint. SOURCE: Adapted from Gonyea and Ashworth (1975).

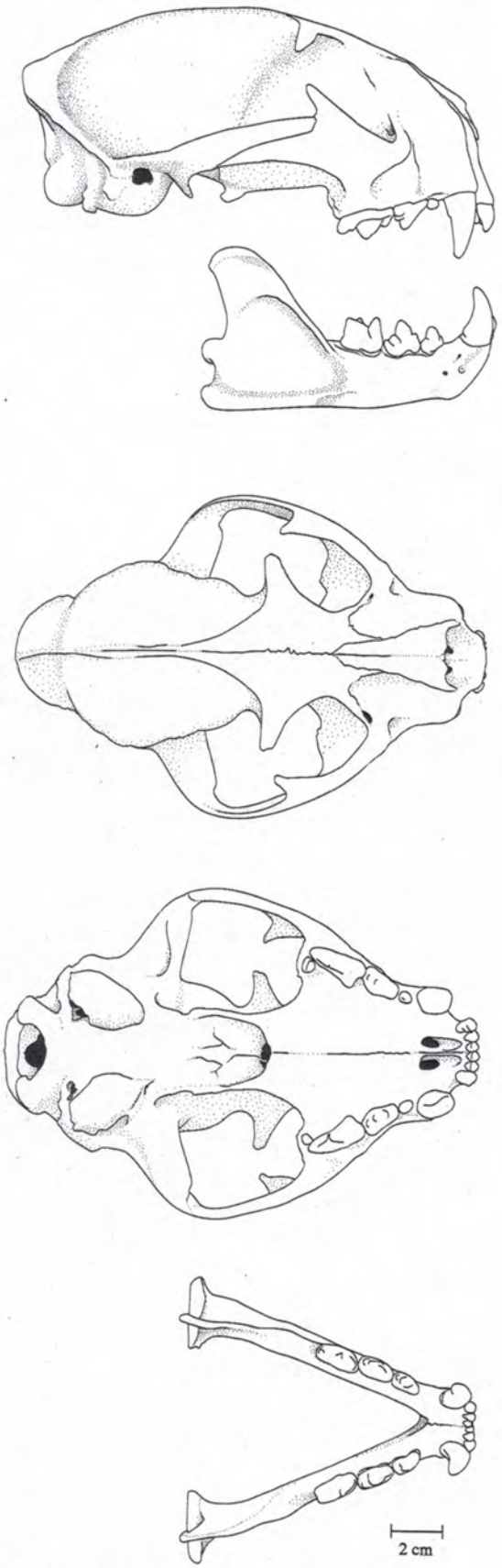

FIGURE 37.4. Skull of the mountain lion (*Puma concolor*). From top to bottom: lateral view of cranium, lateral view of mandible, dorsal view of cranium, ventral view of cranium, dorsal view of mandible.

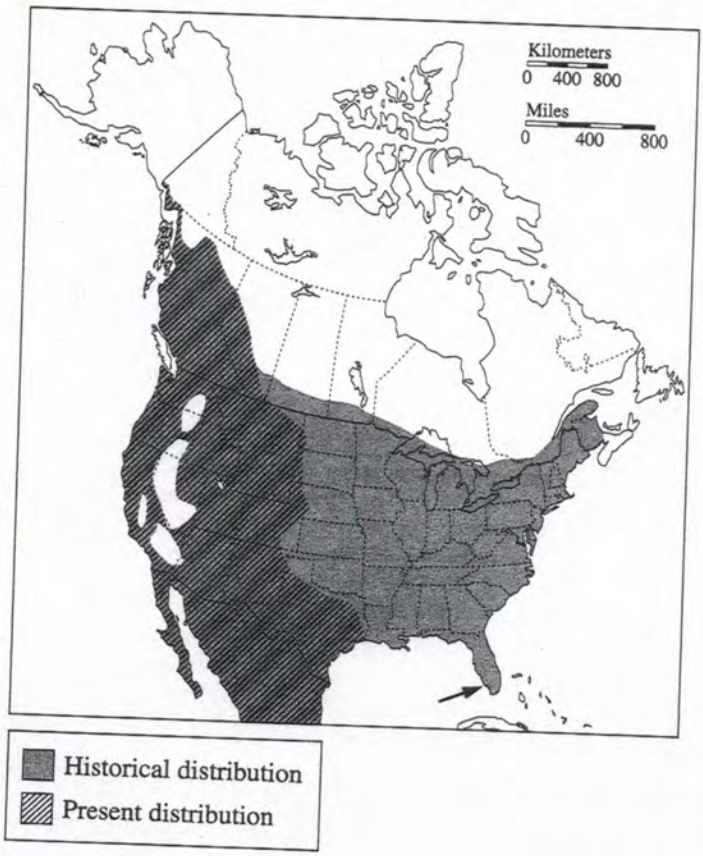

FIGURE 37.5. Past and present distribution of the mountain lion (*Puma concolor*).

(Fig. 37.5). Recently, mountain lions have been observed in southeastern Alaska and southwestern Minnesota (Nowell and Jackson 1996), and they inhabit western North Dakota (Jensen 2001) and Nebraska (Genoways and Freeman 1996) and are thought to be colonizing previously occupied habitat in Oklahoma (Pike et al. 1997). Recent evidence of a mountain lion in New Brunswick, Canada, was indisputable, but it could not be ascertained whether the animal had escaped from captivity (Cumberland and Dempsey 1994). The persistence of mountain lions in the maritime regions of Canada and the United States remains speculative (Hansen 1992). Anderson (1983) provided a detailed compilation of distributional records for mountain lions in the United States and Canada.

PHYSIOLOGY

There has been a paucity of information on blood parameters for free-ranging mountain lions. Anderson et al. (1992) sought to rectify this by providing hematological and biochemical reference values for ≤7 adult mountain lions from Colorado. Prior to that, information was limited to reports by Currier and Russell (1982) or Hawkey and Hart (1986). Paul-Murphy et al. (1994) provided serum biochemical reference ranges for 19 free-ranging mountain lions from throughout California, and concluded that the values were similar to those in domestic cats and captive exotic felids. Dunbar et al. (1997) described hematological and serum biochemical values for mountain lions from Florida. Most values were consistent with those established for mountain lions in Colorado (Currier and Russell 1982) and California (Paul-Murphy et al. 1994), but some differences were apparent (Table 37.1).

Dunbar et al. (1997) attributed higher packed cell volume, hemoglobin, and red blood cell values reported by Currier and Russell (1982) to the higher elevations in Colorado than in Florida. They also reported higher values for these three parameters within one "population" of Florida panthers compared to a nearby "population," and speculated that differences could be a result of generalized differences in health and nutritional status between the two groups. It may prove useful for mountain lion researchers to examine hematological and serological data from their study animals, given differences reported within localized areas as well as among widely separated populations (Dunbar et al. 1997). For example, mountain lions that use high-elevation passes to follow migratory prey (Pierce et al. 1999b) may exhibit differences that are not evident in mountain lions from the same population(s) that do not use high-elevation habitats. Further, data on hematological and serological parameters may reflect the general health status of mountain lions existing under different nutritional regimes (e.g., abundant vs. uncommon primary prey) that may occur as lion populations fluctuate with populations of mule deer (*Odocoileus hemionus*).

Mountain lions, like most cats, are well adapted to approaching prey closely and then rushing forward quickly to subdue their intended target (Guggisberg 1975). As such, they are not adapted to running long distances. Harlow et al. (1992) investigated the effects of pursuit on mountain lions. Animals responded physiologically to stresses experienced during pursuit by a depression in adrenal responsiveness. They suggested that frequent pursuit could result in deleterious physiological changes and urged caution by wildlife agencies in setting pursuit seasons until more information becomes available.

BEHAVIOR

Activity Patterns. Most felids are nocturnal predators (Kitchener 1991), and mountain lions are most active during crepuscular periods (Ackerman 1982; Hopkins 1989; Sweanor 1990). That pattern appears to shift to a more nocturnal pattern for mountain lions in the proximity of human disturbance (Van Dyke et al. 1986). Mountain lions will

TABLE 37.1. Blood serum biochemical values for free-ranging mountain lions from California ($n = 19$) and Florida ($88 \leq n \leq 94$)

Parameter	Units	Location ($\bar{X} \pm SD$)	
		California	Florida
Albumin	g/dl	3.13[a] ± 0.32[b]	3.70 ± 0.36
Alanine aminotransferase	IU/L	58.8 ± 16.7	60.2 ± 35.0
Alkaline phosphatase	IU/L	22.6 ± 11.3	35.4 ± 38.6
Aspartate aminotransferase	IU/L	—	73.4 ± 77.8
Calcium	mg/dl	9.53 ± 0.66	9.92 ± 0.66
Carbon dioxide	mEq/L	12.53 ± 1.75	14.33 ± 4.00
Cholesterol	mg/dl	155.1 ± 29.9	147.9 ± 26.7
Chloride	mEq/L	—	115.5 ± 4.3
Creatine phosphokinase	IU/L	—	515.6 ± 415.1
Creatinine	mg/dl	2.05 ± 0.45	1.84 ± 0.54
Gamma glutamine transferase	IU/L	—	1.6 ± 1.4
Globulin	g/dl	3.45 ± 0.41	—
Glucose	mg/dl	110.6 ± 37.3	154.4 ± 51.0
Inorganic phosphorus	mg/dl	5.66 ± 1.15	5.77 ± 1.51
Iron	μg/dl	—	65.1 ± 33.5
Lactate dehydrogenase	IU/L	—	269.7 ± 173.2
Potassium	mEq/L	—	4.60 ± 0.48
Sodium	mEq/L	—	152.6 ± 3.4
Total bilirubin	mg/dl	0.30 ± 0.25	0.26 ± 0.61
Total protein	g/dl	6.58 ± 0.67	7.35 ± 0.67
Triglycerides	mg/dl	—	54.9 ± 103.4
Urea nitrogen	mg/dl	32.9 ± 6.4	37.7 ± 14.1
Uric acid	mg/dl	—	0.55±0.59

SOURCE: Data have been adapted from Paul-Murphy et al. (1994) and are reported directly from Dunbar et al. (1997).

[a]The number of digits to the right of the decimal point has been reduced by rounding, for consistency with the data reported by Dunbar et al. (1997) for mountain lions from Florida.

[b]Paul-Murphy et al. (1994) reported means and two standard deviations for serum biochemistry values. Standard deviations reported here were calculated by halving, and rounding as appropriate, data from Paul-Murphy et al. (1994) for mountain lions from California.

repeatedly move and wait in ambush during the night when hunting (Beier et al. 1995), but that behavior is suspended when cached prey is available (Beier et al. 1995; Pierce et al. 1998). Movement to prey caches at night occurs earlier for females with small young than for other social categories of mountain lions (Pierce et al. 1998). That behavior could be a strategy to avoid adult males, a response to greater energetic needs of the mother, or a tendency to kill prey closer to the daytime resting location of the young. Female mountain lions without young cover more area and make longer movements than females with young (Sweanor 1990). Males make the longest movements (Sweanor 1990; Beier et al. 1995), cover the greatest area (Seidensticker et al. 1973; Logan et al. 1986a; Pierce et al. 1998), and are more likely to leave a prey cache before it is completely consumed (Ross 1994). The more extensive movements of males likely are necessary to monitor as many females as possible and result in large home ranges.

Adult mountain lions spend a majority of time resting during a diel cycle (Beier et al. 1995). The long periods of rest exhibited by most felids may reduce energy expenditure for a species that often kills prey as large as or larger than itself and frequently has prey caches available. Mountain lions will gorge when a large amount of food is available (Danvir and Lindzey 1981; Ross 1994) and move more frequently when they are unsuccessful at making a kill (Beier et al. 1995). Mountain lions also inhabit regions of extreme temperatures: resting may be the most efficient way to prevent overheating in desert environments or conserving fat stores in extremely cold climates. The negative relationship between mass-specific metabolic rate and body size likely influences the behavior patterns of large carnivores (Robbins 1993) and accounts for long periods of inactivity by mountain lions.

Communication. Mountain lions are the largest felid that make the low rumbling noise called a "purr." Purring, chirping, and whistling vocalizations have been described for adult females when they return to their offspring (Logan et al. 1996). Defensiveness and aggression are expressed by a suite of similar behaviors shared among felids (Kitchener 1991): ears layed down in a flattened position, growling, opening the mouth wide while making a hissing sound, tail twitching, and piloerection. Female mountain lions in estrus make a loud "caterwauling" vocalization to advertise their condition to males, and this behavior continues throughout any resulting mating association (Rabb 1959; Padley 1991; Beier et al. 1995; Logan et al. 1996).

Home range areas of mountain lions are marked by scrapes made by pawing the ground in a backward motion, drawing dirt and ground litter into a small pile behind two parallel grooves (Seidensticker et al. 1973). Males make scrapes more frequently than females (Cunningham et al. 1995), and scrapes often have feces or urine deposits associated with them (Smith 1981; Logan et al. 1996). Scrapes occur most frequently in locations where topography funnels a number of mountain lions into the same area (Smith 1981) and may facilitate mutual avoidance among individuals with overlapping home ranges (Hornocker 1969). Mountain lions display a Flehman response when smelling urine deposits in scrapes (Seidensticker et al. 1973). Females may scrape only when in estrus (Maehr 1997) and, if so, such scrapes may be used by males to monitor the reproductive cycles of females as well as home range occupancy. Mountain lions also scratch logs and trees repeatedly with their front claws. Scratch marks may serve the purpose of marking home range areas (Schaller 1972), but may simply be for sharpening claws (Seidensticker et al. 1973). In addition, felids have glands in the cheek, which often are rubbed against objects and family members as another means of communication (Macdonald 1985).

Hunting and Feeding. Mountain lions can jump vertically ≥3 m (Anderson 1983) and are capable tree climbers (Hornocker 1970). When pursued by canids, mountain lions may seek refuge in trees or rocks (Hornocker 1970; Seidensticker et al. 1973; Davis et al. 1996). Most reports of mountain lions ambushing prey have described them stalking from the ground (Koford 1946; Hornocker 1970; Wilson 1984; Beier et al. 1995) with very few instances of attacking prey from an elevated perch (Connolly 1949). The effect of hunting by humans on the behavior of mountain lions is unknown. Pursuit of mountain lions with hounds for research does not appear to cause changes in home range use or abandonment of prey caches in most instances (Seidensticker et al. 1973; Maehr 1997; Pierce et al. 1998, 1999b). Mountain lions remain close to human activity directly after being pursued, captured, and then released for research purposes (Seidensticker et al. 1973; Beier et al. 1995). However, they also may avoid areas where they are repeatedly harassed (Hebert and Lay 1997; Janis and Clark 2002).

Mountain lions move quietly and low to the ground when hunting and stalking prey (Koford 1946; Wilson 1984; Bank and Franklin 1998). Ears also may be lowered to reduce detection while they move slowly and deliberately, frequently freezing in position while waiting to approach closely enough to ambush the intended prey (Leyhausen 1979). When prey is within a suitable distance, they rush at the target. Pursuit of prey by mountain lions is relatively short compared to the long chases of coursing predators, such as wolves (*Canis lupus*). If prey is caught, it usually is attacked at or near the neck. When attacking ungulates, mountain lions most frequently grip the anterior ventral portion of the neck, delivering a crushing bite to the trachea and causing suffocation (Kitchener 1991). The dorsal portion of the neck also may be bitten, and the spinal cord can be severed. After killing prey, it is usual for mountain lions to open the body cavity of the carcass and remove the digestive tract (Hornocker 1970). Other internal organs including the heart, liver, and lungs often are consumed first (Danvir and Lindzey 1981). Gorging on the most nutritious tissues during the first day may be an important strategy for mountain lions that can lose food to scavengers (Danvir and Lindzey 1981) or need to move to locate mates (Ross 1994).

In an examination of hunter-killed mountain lions, Robinette et al. (1959) reported that 30% had empty stomachs. Mountain lions may consume >10 kg of meat during a single feeding (Hornocker 1970; Danvir and Lindzey 1981; Ackerman et al. 1986), with more being consumed during the first day than on consecutive days following the kill (Danvir and Lindzey 1981). Results of field sampling and trials with captive animals suggest that mountain lions consume an average of 4.4 kg of meat/day (Danvir and Lindzey 1981; Ackerman et al. 1986). In most instances, prey carcasses are dragged, sometimes >200 m, to locations with vegetative or topographic cover (Beier et al. 1995). When lions finish feeding, they usually conceal the prey by covering it with sticks, grass, and other material until the carcass is consumed or abandoned. Mountain lions normally consume 73–79% of a deer carcass (Danvir and Lindzey 1981; Ackerman 1982). Covering caches may slow decomposition of the meat and hide it from scavengers (Beier et al. 1995). Prey caches may be guarded to protect them from scavengers, but mountain lions can use day-beds several kilometers from kill sites, returning only at night to feed (Beier et al. 1995; Pierce et al. 1998, 2000b).

REPRODUCTION

Mountain lions are polygynous and males do not contribute to rearing young. Like all felids, except African lions (*Panthera leo*), adult mountain lions are solitary except when raising young, dispersing with siblings, or mating. Males tend to have relatively large home ranges, which overlap with those of more than one female (Seidensticker et al. 1973; Logan et al. 1986a; Pierce et al. 1999b, 2000b). Male and female mountain lions likely rely on auditory and olfactory signals to locate each other for mating (Currier 1983) (see Behavior).

Estrous cycles in females with overlapping home ranges may be synchronous (Padley 1990). Associations for mating generally last 2–5 days (Beier et al. 1995), during which time the pair may copulate up to 70 times a day (Eaton 1976). Female estrous cycles last approximately 8 days (Rabb 1959; Eaton and Velander 1977) and gestation is 82–96 days (Young and Goldman 1946; Anderson 1983; Currier 1983). Mountain lions may reproduce during any season (Robinette et al. 1961; Ashman et al. 1983), but many studies have identified seasonal birth pulses (Robinette et al. 1961; Ashman et al. 1983; Barnhurst and Lindzey 1984; Logan et al. 1986a; Ross 1994). Timing of reproduction in mountain lions may be affected by climate or prey abundance (Logan et al. 1996; Pierce et al. 2000a).

Females have eight teats, but only six produce milk (Lechleitner 1969). The number of kittens born per litter typically ranges from two to four (Robinette et al. 1961; Ashman et al. 1983; Ross and Jalkotzy 1992; Logan et al. 1996), but this may vary with prey availability, demography, and population density. Females may average more offspring per litter during their first year of reproduction and fewer toward the end of their lives (Logan et al. 1996). Most studies of mountain lions have reported an equal sex ratio among young (Donaldson 1975; Anderson et al. 1992; Logan et al. 1996). Padley (1991), however, reported that for a population of mountain lions in California, with 12 adult females and seven litters, six of seven kittens whose sex he was able to determine were male. In that population, adult males were scarce, and estrous females were unable to locate an adult male with which to mate for almost a year.

Kittens are brought to kill sites by their mother as early as 8 weeks of age, but are not weaned until they are 2–3 months old. Canine teeth first appear between 20 and 30 days and molars at about 40 days of age. Some permanent teeth erupt at 5–6 months of age and permanent canines appear during the eighth month, when primary and permanent canines are present. At weaning, kittens may weigh 3–4 kg (Currier 1983) with little variation in weight between the sexes until about 30 weeks of age (Robinette et al. 1961).

Mountain lion dens generally are located in rocky terrain (Logan et al. 1996) or thick vegetation (Beier et al. 1995; Bleich et al. 1996). Dens are not elaborate, but do provide hiding cover (Ross 1994; Beier et al. 1995) and thermal benefits (Bleich et al. 1996). Females with kittens have restricted movement patterns until the young are old enough to travel away from the den (Beier et al. 1995). A mother may move her young to several different dens before they are weaned (Shaw 1989).

ECOLOGY

Habitat. The broad distribution of mountain lions attests to their ability to adapt to a wide variety of habitats. Because of their wide distribution (see Fig. 37.5), defining preferred habitat for mountain lions is limited to general characteristics specific to distinct regions, and tremendous variation occurs among populations. Despite the large range of habitats used by mountain lions, relatively few quantitative studies of habitat selection exist; many studies present descriptive information without reference to habitat availability. For those studies that quantified habitat selection, prey availability, vegetation, and topography are the general characteristics that determine suitability for mountain lions. Within regions where a variety of habitat types occurs, structure of the vegetation and topography appear to be the most important criteria for determining habitat use (Lindzey 1987).

Most studies of habitat selection for mountain lions in western North America suggest that vegetative and topographic cover, in addition to steep slopes and higher elevations, are preferred resting, hunting, and denning sites, whereas open agricultural lands, sagebrush (*Artemesia tridentata*) grasslands, and open meadows and pastures are avoided (Murphy 1983; Logan and Irwin 1985; Laing 1988; Lindzey et al. 1989). Ashman et al. (1983) suggested that thermal characteristics cause mountain lions to select north-facing slopes at high elevations, with more vegetation and cooler temperatures, in the summer. South-facing slopes with little snow cover were selected in winter. Those habitats were strongly correlated with the density of deer. Rugged or steep terrain, with adequate vegetative cover, may be critical for stalking and catching prey (Ashman et al. 1983; Logan and Irwin 1985; Laing 1988) or for providing hiding cover and protection from thermal extremes for young at denning sites (Belden et al. 1988; Ross 1994; Bleich et al. 1996).

Dense hiding cover is preferred by mountain lions for hunting (Russell 1978; Beier et al. 1995). Indeed, mountain lions were more successful hunting pronghorn (*Antilocapra americana*) that inhabited rugged terrain with more vegetation than pronghorn that occurred in open prairie habitat (Ockenfels 1994). Mountain lions, however, can inhabit open or sparsely vegetated habitats, such as the plateaus of Patagonia (Wilson 1984; Bank and Franklin 1998) and the deserts of the southwestern United States (Cunningham et al. 1995; Logan and Sweanor 2001), by successfully using the limited available cover to catch prey. In addition, Pierce (1999) noted that mountain lions were more successful killing mule deer in relatively open habitat compared to that in which deer foraged. The pursuit of deer by mountain lions likely began in areas with vegetative cover, but deer that fled into more open areas without obstacles during the chase were more likely to be caught than those that remained in heavier vegetation.

Mountain lions can thrive in extremely dry climates with limited rainfall (Shaw et al. 1987; Cunningham et al. 1995; Logan et al. 1996; Pierce et al. 2000a); however, the severely cold temperatures of northern Canada and Alaska may limit their distribution despite the availability of ungulate prey. Mountain lions may avoid human disturbance when possible (Van Dyke et al. 1986), but can persist near human development (Beier et al. 1995; Torres et al. 1996).

Laing (1988) suggested that habitat use by mountain lions did not differ significantly during a 24-hr cycle, but that pattern may depend on the availability of habitats. When habitat used by mountain lions for denning or for caching prey is different than that used for resting, then they will use different habitats during a diel cycle. Beier et al. (1995) reported that mountain lions with young hunted throughout the night, but returned to the den during the day. Den sites were located in nearly impenetrable vegetation. Pierce et al. (1998) found that mountain lions fed on cached prey primarily after sunset and often rested long distances from the cache site during the day. In addition, Beier et al. (1995) reported that, in some instances, mountain lions rested >4 km from their cached prey. This behavior also was consistent with the reported use of high-elevation cliffs during the daytime and use of lower elevations with flatter terrain for hunting deer at night (Pierce et al. 1998, 2000b).

Several studies have described seasonal changes in elevation and habitat use associated with changes in home range for mountain lions preying on migrating populations of deer and elk (*Cervus elaphus*) (Rasmussen 1941; Seidensticker et al. 1973; Ackerman 1982; Ashman et al. 1983; Murphy 1983; Anderson et al. 1992; Pierce et al. 1999b). Indeed, differences in forage availability associated with seasonal ranges of prey leads to potential differences in the tradeoff between foraging benefit and predation risk for deer and elk. Consequently, there may exist differences in the effects of mountain lion predation on the seasonal foraging behavior and habitat selection of those large ungulates (Pierce 1999).

Dispersal. Young remain with their mother for 12–18 months. Dispersal may result from the mother abandoning the young (Seidensticker et al. 1973), but it is likely that there is some aggression by the mother directed toward the young to prevent them from following her (Hansen 1992). Dispersal of young from the mother is coincident with the female coming into estrous; adult males will kill young (Young and Goldman 1946; Ackerman et al. 1984; Spreadbury 1989; Logan and Sweanor 2001). During the period of dispersal, mountain lions are often referred to as "transients" (Hornocker 1970). Transients, as opposed to "residents," are individuals that do not have a defined home range area within a population.

Dispersal is a relatively risky period during the life cycle for many species (Baker 1978), and survivorship likely declines for mountain lions during the dispersal period (Logan and Sweanor 2001). Transients are more likely than resident mountain lions to be involved in depredation incidents or conflicts with humans, as they attempt to locate food without the advantage of an established home range (Torres et al. 1996). Males are more likely to disperse from their natal ranges than are females, and males tend to disperse further (Anderson et al. 1992; Sweanor et al. 2000).

Mountain lions can disperse nearly 500 km from their natal home range (Logan and Sweanor 1999). Consequently, mountain lion habitat throughout North America is considered almost contiguous on a large scale, with the exception of the isolated populations in southeastern Florida. Nevertheless, mountain lion populations can be isolated by

residential development or geographic features such as desert basins. Reduction in the size of habitat "islands" for populations of any species increases the chance of extirpation for that population (MacArthur and Wilson 1967).

Sweanor et al. (2000) described a metapopulation structure (Levins 1970) for mountain lions living in basin and range habitats of the Southwest. Mountain ranges provide islands of suitable habitat that support semi-isolated populations of mountain lions. Those populations are maintained through immigration by dispersers (primarily male) from other mountain ranges and recruits (primarily female) from within the population. The basins between the mountains are not considered suitable mountain lion habitat (Germaine et al. 2000) and act as barriers that may limit gene flow. Protecting source populations and habitat stepping stones may be exceptionally important in conserving subpopulations of mountain lions that exist in a metapopulation structure (Sweanor et al. 2000). Although concerns about habitat fragmentation and interruption of gene flow are legitimate, Ernest et al. (2003) have cautioned that it has not been demonstrated that mountain lions conform to the assumptions inherent in basic metapopulation models.

Survivorship of adults likely varies within most populations on an annual basis (Lindzey et al. 1988), but can be affected significantly by hunting (Anderson 1983). Destruction of habitat also can have large impacts on the demography of mountain lion populations. For example, fragmentation of habitat can inhibit dispersal and increase competition for resources (Beier et al. 1995; Maehr 1997). Furthermore, real estate development may limit prey populations, increase depredation events (Shaw 1980; Cunningham et al. 1995; Torres et al. 1996), and increase collisions with automobiles (Maehr 1997; Beier et al. 1995).

Disease and Parasites. Anderson (1983) suggested that the widely held opinion that mountain lions are relatively free of parasites and diseases reflected a lack of specific research rather than reality. For example, based on his literature review, Anderson (1983) reported the occurrence of feline panleukopenia virus was low, but Paul-Murphy et al. (1994) detected titers to the virus in nearly 100% of the animals that they tested. Furthermore, Adaska (1999) reported the first case of coccidioidomycosis detected in a mountain lion, and Jessup et al. (1993) documented the first occurrence of feline leukemia virus infection in a free-ranging mountain lion. Evermann et al. (1997) reported on the occurrence of puma lentivirus specifically in mountain lions in the state of Washington. Yamamoto et al. (1998) found overall seroprevalance of bartonellosis in 26 of 74 mountain lions they examined from California, among the first evidence of this condition detected in wild felids. Hence, it appears that Anderson's (1983) admonition was insightful.

Mountain lions potentially are susceptible to many infectious agents that affect domestic cats (Paul-Murphy et al. 1994) as well as to other diseases (summarized by Anderson 1983). Some of these, including feline panleukopenia virus, have the potential to affect morbidity and mortality (Paul-Murphy et al. 1994), may limit growth of wild populations (Anderson 1983), and have implications for the conservation and persistence of a viable population of the endangered Florida panther (Roelke et al. 1993). Foley (1997) concluded that epizootic diseases likely are not a primary threat to populations of mountain lions in the western United States. From a human health perspective, rabies has been detected among mountain lions (Storer 1923) and should be of concern in all cases involving attacks on humans (Kadesky et al. 1998).

Parasitic infections among mountain lions are not uncommon; Anderson (1983) listed $\geq$40 species of parasites that have been collected. Forrester et al. (1985) and Waid (1990) listed additional internal parasites not noted by Anderson (1983). The majority of parasites recorded have been internal (protozoans, trematodes, cestodes, or nematodes), but mites, ticks, and insects are known to parasitize mountain lions. Pence et al. (1987) noted a high degree of overdispersion (i.e., a few mountain lions harbored the majority of parasites collected and most had few or no parasites) in helminth species collected from the viscera of mountain lions in Texas. In general, mountain lions have been described as remarkably free of external parasites (Currier 1983), but our experience has been that ticks are commonly encountered during handling.

FEEDING HABITS

Mountain lions kill and eat vertebrate prey almost exclusively (Lindzey 1987). Vegetation often is ingested because it adhered to a carcass or to help with passage of parasites and hair from the gut (Robinette et al. 1959; Anderson 1983). The historical distribution of mountain lions throughout North America coincided with the distribution of their primary prey—deer. Most studies in North America identified deer as the most frequent prey in diets of mountain lions (Hornocker 1970; Shaw 1980; Ackerman 1982; Logan et al. 1996; Ross et al. 1997; Pierce et al. 2000a).

Despite the congruence of deer and mountain lion distributions in North America, lions are generalist predators (Anderson et al. 1992; Logan and Sweanor 1999). They do prey on other large ungulates including moose (*Alces alces;* Ross and Jalkotzy 1996), elk (Hornocker 1970), feral horses (*Equus caballus;* Turner et al. 1992), feral pigs (*Sus scrofa;* Harveson 1997; Sweitzer 1998), and wild sheep (*Ovis canadensis;* Cronemiller 1948; Harrison 1990; Wehausen 1996; Ross et al. 1997; Schaefer et al. 2000). Mountain lions also feed on smaller prey such as lagomorphs (Shaw 1980; Ackerman et al. 1984); ground squirrels (*Spermophilus* spp.; Seidensticker et al. 1973); beavers (*Castor canadensis;* Padley 1991); porcupines (*Erethizon dorsatum;* Sweitzer et al. 1997); small carnivores including raccoons (*Procyon lotor*), gray foxes (*Urocyon cinereoargenteus*), and skunks (Cashman et al. 1992; Beier et al. 1995); and birds such as wild turkeys (*Meleagris gallopavo*), grouse, and quail (Ashman et al. 1983; Ackerman et al. 1986; Maehr et al. 1990). Currier (1983) listed 41 nondomestic species of vertebrates identified in the feces of mountain lions from North and South America. Domestic sheep, goats, cattle, horses, dogs, and cats also are consumed when populations of mountain lions are in proximity to livestock operations or areas of human habitation (Shaw 1980; Torres et al. 1996). Attacks on humans by mountain lions are rare (Beier 1991); however, in most instances, victims of fatal attacks were treated as prey and either dragged to cover or partially consumed (Beier 1991; J. Banks, California Department of Fish and Game, pers. commun., 1996). Remains of bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and other competing carnivores occasionally occur in feces of mountain lions. Also, species that scavenge on lion kills, including eagles and turkey vultures (*Cathartes aura*), can be killed by mountain lions guarding a prey cache. Although intraspecific aggression leading to death in mountain lions may occur as a result of competition for resources or mating opportunities (Robinette et al. 1961; Hornocker 1970; Sweanor 1990; Pierce et al. 1998), instances of cannibalism by mountain lions, in which the carcass has been largely consumed, have been reported frequently (Lesowski 1963; Donaldson 1975; Ackerman et al. 1984; Spreadbury 1989).

Selection of Prey. Numerous authors have described the sex, age class, and condition of prey killed by mountain lions. Hornocker (1970), Spalding and Lesowski (1971), Shaw (1977), Ackerman (1982), Ackerman et al. (1984), and Murphy (1998) all suggested that vulnerability of individual prey may be the most important factor in their selection by mountain lions. Those investigations identified individuals in younger or older age classes or in poorer condition as being selected by mountain lions. Among adult deer and bighorn sheep, mountain lions also may prey on males selectively (Hornocker 1970; Ackerman 1982; Harrison 1990), especially when males are in a weakened condition following the rut (Robinette et al. 1959; Shaw 1977; Harrison 1990) or during drought conditions (Logan and Sweanor 2001). Studies of prey selection, however, require comparisons with availability of prey. Most studies of prey selection by mountain lions have been limited by lack of information on availability of prey or by biases in detecting prey.

Anderson (1983) attempted to compare sex and age ratios of deer killed by mountain lions to the estimated ratios in the populations of deer for six study areas, and concluded that the sampling methods used in those studies prevented clear testing of any hypothesis regarding prey selection. Since then, Ross et al. (1997) reported selection for young bighorn sheep by mountain lions. Pierce et al. (2000a) reported that mountain lions selected deer in young and old age classes, and that females were selected among adult deer. Preference for females among

adult mule deer also has been reported for other populations of mountain lions (Bleich and Taylor 1998). More recent investigations suggested that mountain lions do not select prey in poor condition (Kunkel et al. 1999; Pierce et al. 2000a); however, bone marrow fat has been the primary index used to determine prey condition by most investigators. Although percentage bone marrow fat was not related to prey selection by mountain lions (Kunkel et al. 1999; Pierce et al. 2000a), they selected for older animals. Thus, percentage marrow fat may not adequately reflect other forms of weakness detected by mountain lions (Pierce et al. 2000a).

Kunkel et al. (1999) determined that mountain lions killed deer with shorter diastemae than those killed by wolves or hunters, but values of marrow fat did not differ between deer killed by mountain lions and wolves. Size of prey also appears to affect selection by mountain lions. They selected deer over elk, and elk over moose in Montana (Kunkel et al. 1999). Ross and Jalkotzy (1996) reported that male mountain lions were more likely to kill moose than were females. Body size, however, did not appear to be important for selection of mule deer preyed on by mountain lions when compared with those killed by coyotes during winter, when young deer were unavailable (Pierce et al. 2000a).

Sex and age of mountain lions likely affect their diet. Solitary mountain lions may be more likely to eat smaller prey than do females with kittens (Ackerman 1982). Ackerman suggested that killing large prey to provide for their offspring would be a necessary strategy for mothers, and that populations of mountain lions could not exist in areas devoid of large ungulate prey. Pierce et al. (2000a), however, reported that female mountain lions with kittens (≤6 months old) were significantly more likely to kill young deer (<1 year of age) than were single adult females or males. Birth pulses of mountain lion populations often coincide with the birth pulse of their primary prey (Logan and Sweanor 2001; Pierce et al. 2000a), suggesting that timing of reproduction in mountain lions may be dependent on the availability of vulnerable, young prey. Adult females that are lactating may not be able to fast for extended periods between unsuccessful attempts to catch larger prey (Pierce et al. 2000a).

Latitude correlates strongly with size of prey selected by mountain lions (Iriarte et al. 1990; Maehr et al. 1990). In temperate zones, they tend to kill larger ungulates, whereas mountain lions in tropical environments have a higher frequency of small prey in their diet. The complicating effect, however, of competition with the jaguar on this pattern of latitudinal prey variation is unknown. Additionally, variation in prey selection is notable for some populations of mountain lions as vulnerability or availability of prey changes. During the wet season in coastal California, mountain lions increased predation rates on feral pigs (Craig 1986) and, in Utah, they killed twice as many black-tailed jackrabbits (*Lepus californicus*) during winter (Ackerman et al. 1984) than during summer. Adult male deer may be taken at a higher rate during winter when they are in weakened condition from the rut (Robinette et al. 1959; Shaw 1977). The vulnerability of newborn calves results in high depredation rates on cattle in Arizona (Shaw 1977; Cunningham et al. 1995).

POPULATION DENSITY AND DYNAMICS

Mountain lions coexist in a system of individual home ranges with varying amounts of overlap (Seidensticker et al. 1973; Hemker et al. 1984). Mean home range size and distribution of mountain lions can be affected by sex (Seidensticker et al. 1973) or availability of resources such as prey (Pierce et al. 1999b, 2000a). Anderson et al. (1992), however, concluded there was no relationship between prey density and frequency of use by mountain lions of areas inhabited by deer and elk. They felt that other factors, such as suitable habitat for hunting, may affect prey availability independently of prey density (Kruuk 1986) and may ultimately affect the home range size necessary for mountain lions to be successful.

Home ranges of mountain lions are delineated by visual and olfactory marking behaviors, and adult males tend to have larger home ranges than females (Seidensticker et al. 1973; Logan et al. 1986a; Pierce et al. 1998) (Table 37.2) (see Behavior). Male home ranges often overlap those of several females but have limited overlap with those of other males (Seidensticker et al. 1973; Murphy 1983; Logan and Sweanor 2001), whereas the home ranges of adult females often overlap those of other females extensively (Seidensticker et al. 1973; Sweanor et al. 1996; Pierce et al. 1999b, 2000b; Logan and Sweanor 2001). Extensive overlap among male home ranges (Anderson et al. 1992; Sweanor 1990) and limited overlap of female home ranges (Harrison 1990) also have been reported. Additionally, mountain lions may avoid each other temporarily, a behavior termed "mutual avoidance" (Hornocker 1969), but no investigations have tested for the dominance reversal necessary to demonstrate true territoriality in mountain lions (Kitchen 1974).

Hornocker (1969, 1970) and Seidensticker et al. (1973) suggested that mountain lion populations were self regulating (see Predator–Prey Dynamics). They described social behaviors such as mutual avoidance, territorial marking, and cannibalism as mechanisms that limited densities of mountain lions. Transient mountain lions were unable to secure permanent home range areas unless the home range area of a resident adult became vacant. This pattern occurred independently of prey densities. Lindzey et al. (1994) also concluded that the density of a mountain

TABLE 37.2. Estimated home range size and average density of mountain lions from North American studies using the minimum convex polygon method (Mohr 1947)

Study	Location	Males		Females		Lions/100 km^2
		n	Range (km^2)	*n*	Range (km^2)	
Ross and Jalkotzy 1992	Alberta	6	334	21	140	1.9 (RA, H), 4.2 (T)
Cunningham et al. 1995	Arizona	5	196	2	109	— (H)
Beier and Barrett 1993	California	2	767	12	218	1.1 (RA)
Hopkins 1989	California	4	199	7	84	3.6 (T)[a]
Anderson et al. 1992	Colorado	6	256	7	309	1.1 (RA, H)
Maehr et al. 1991	Florida	8	558	10	191	—
Seidensticker et al. 1973	Idaho	1	453	3	233	0.6 (RA[b], H)
Ashman et al. 1983	Nevada	7	574	6	178	— (H)
Logan et al. 1996	New Mexico	23	187	29	74	1.7 (RA)
Murphy 1983	Montana	2	462	5	202	7.1 (RA, H)
Pittman et al. 2000	Texas	6	349	5	206	0.4 (RA, H)
Pence et al. 1987	Texas	1	628	5	143	—
Hemker et al. 1984	Utah	1	826	4	685	0.4 (T)
Logan 1983	Wyoming	2	320	2	73	1.5 (RA, H), 3.9 (T)

NOTE: RA, Density of resident adults; T, density of total population; H, hunted population.
[a]From Anderson et al. (1992), Table 23.
[b]Estimated from Seidensticker et al. (1973), Table 6, Fig. 16.

lion population in Utah was independent of the density of their primary prey, mule deer, because the population of mountain lions did not increase at the rate predicted by the increase in prey. Nonetheless, the population of mountain lions did increase by one third after an increase in the deer population. Long time lags between fluctuations in prey populations and responses in mountain lion populations make determining the true relationship between predator and prey difficult (Schaller 1972), and emphasize the need for long-term research when working with large carnivores (Pierce 1999).

To invoke social regulation for a population (Hornocker 1969, 1970; Seidensticker et al. 1973), it must be demonstrated that the population is not limited by competition for resources (Watson and Moss 1970). Mutual avoidance does not prevent passive competition for resources. Pierce et al. (2000b) demonstrated that competition for prey by mountain lions occurred in a pattern that would be expected for nonterritorial species that do not exclude each other from prey resources. Furthermore, if mountain lions engaged in a territorial system that excluded individuals from resources beyond what would be expected for a population limited by competition, such costly behavior could have evolved only if it maximized reproduction for individuals that were territorial and, ultimately, would not lead to population limitation (McCullough 1979). Hemker et al. (1984) concluded that population size of mountain lions was primarily limited by the population of prey, a conclusion supported by Pierce et al. (2000b) and Logan and Sweanor (2001).

The density of males may be limited by intraspecific aggression to maximize access to females, but mountain lion populations on a whole likely are not limited by social behavior. In addition, dispersal by young mountain lions appears to be independent of population density (Seidensticker et al. 1973; Hemker et al. 1984; Ross and Jalkotzy 1992; Logan et al. 1996), and mountain lion population numbers parallel their prey populations (Lindzey et al. 1994; Logan et al. 1996; Cox and Stiver 1997) (Fig. 37.6). Furthermore, Logan and Sweanor (2001) reported a pattern of density-dependent growth for a mountain lion population, providing additional evidence that competition is an important factor affecting their population dynamics.

PREDATOR–PREY DYNAMICS

Few long-term studies of predator–prey dynamics have been conducted that include mountain lions. Unfortunately, many studies have independently focused on either the predator or the prey, thereby limiting conclusions that can be drawn about interspecific effects (Pierce 1999). In most instances, viable populations of mountain lions are dependent on populations of large ungulate prey (Ackerman 1982; Anderson 1983). Most ungulates that are preyed on by mountain lions, including deer, elk, and moose, are affected by density-dependent processes (McCullough 1979; Boyce 1989; Bowyer et al. 1999; Keech et al. 2000). Therefore, determining the effect of predation by mountain lions on the population dynamics of their prey requires an understanding of those density-dependent processes and all factors potentially limiting the population including weather, resources, and other predators.

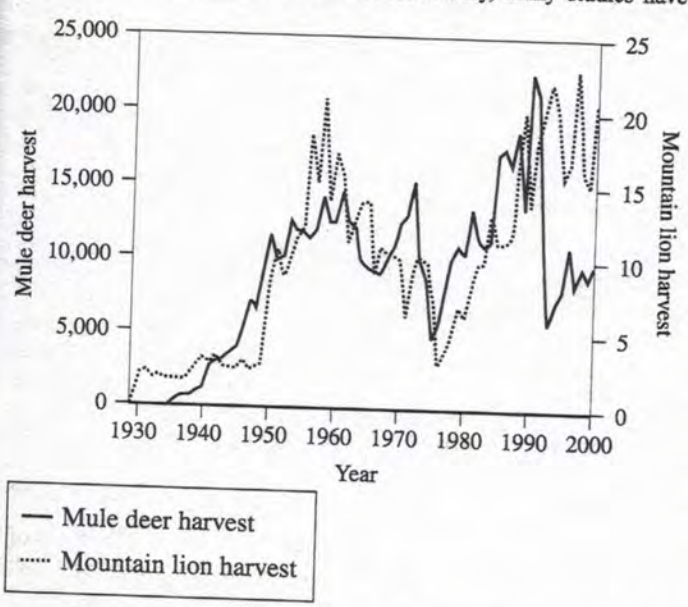

FIGURE 37.6. Harvest of mule deer (*Odocoileus hemionus*) and mountain lions (*Puma concolor*) in Nevada. Mule deer harvest shown includes males only. Mountain lion harvest shown includes depredation removals and sport hunting (sport hunting estimated to 1967). SOURCE: Data from S. Stiver, Nevada Department of Wildlife, pers. commun., 2001.

In the ecological systems that mountain lions inhabit, both exploitative and interference competition with other predators likely occur. Niches of wolves (Kunkel et al. 1999), coyotes (Pierce et al. 2000a; Harrison 1990), bears (Murphy 1998), bobcats (Koehler and Hornocker 1991), and jaguars (Iriarte et al. 1990) overlap extensively with that of mountain lions. Niche partitioning via habitat use and prey selection may allow for coexistence of mountain lions with those other carnivores. In some instances, scavenging of their food caches requires mountain lions to increase predation rates (Harrison 1990). In addition, mountain lions often kill smaller species of carnivores, such as bobcats, without feeding on them (Koehler and Hornocker 1991). Conversely, mountain lions have been killed by packs of wolves (White and Boyd 1989; Boyd and Neale 1992). Those observations also suggest that competition is an important factor affecting the predator–prey dynamics of multipredator systems that include mountain lions.

Mountain lions are an important limiting factor for some ungulate species (Hornocker 1970; Shaw 1980). Shaw (1980) estimated that lions annually removed 15–20% of the mule deer population on the Kaibab Plateau in Arizona. Anderson et al. (1992) estimated that mountain lions annually killed 8–12% of the mule deer population on the Uncompahgre Plateau, Colorado. In Alberta, a single mountain lion killed 8.7% ($n = 11$) of the early-winter bighorn sheep population and 26.1% ($n = 6$) of the young (Ross et al. 1997).

Mountain lion predation may reduce the severity of fluctuations in prey populations (Hornocker 1970) by slowing the growth rate and reducing overshoots of resource-based carrying capacity (K). Limitation and regulation, however, are distinctly different mechanisms. Limitation implies that the number of prey is reduced through decreased production or increased loss, and therefore any source of predation is limiting (Sinclair 1989; Boutin 1992). Limitation slows the increase of a population from the growth rate it would have achieved in the absence of the predator. However, if the prey population continues to increase, the proportion of prey removed by the predator is reduced. Consequently, prey populations limited by predators can continue to grow, although at a slower rate than in the absence of predation, until they reach K.

Regulation implies that rate of removal by the predator changes with the population of prey; as prey numbers increase, so does the rate at which predators kill prey. This phenomenon results from an increase in the number of predators (numerical response), the ease with which they find and kill prey (functional response), or a combination of both (Holling 1959). Regulation by a predator eventually stops the increase of the prey population and causes a decline to lower densities, which ultimately results in lower predation rates. Such feedback mechanisms can cause a prey population to fluctuate between low- and high-density equilibria, both of which are below K. This multiple-equilibria scenario is frequently termed a "predator pit" (Haber 1977; Bergerud et al. 1983; Messier and Crete 1985). Functional responses of the predator may ultimately determine whether a species has the capacity to regulate a prey population (Messier 1994). Nonetheless, determining the functional response curve for a species requires an unbiased measure of predation rate throughout the range of population densities of the prey, and controlled removal studies are necessary to determine the conditions that may cause multiple equilibria (i.e., regulation) to occur in predator–prey systems (Van Ballenberghe and Ballard 1994).

Attempts to measure predation rates of mountain lions have been made for static populations of prey. Using an energetics model, Ackerman et al. (1986) estimated that adult male mountain lions would kill

a deer every 8–11 days, adult females would kill every 14–17 days, and a female with three juveniles would kill every 3.3 days. Connolly (1949) reported that an adult mountain lion killed one deer every 9.7 days. Predation rates on bighorn sheep and mule deer by females with kittens ranged from 0.7 to 2.1 ungulates/week (Harrison 1990). Beier et al. (1995) determined that mountain lions killed 48 large and 58 small mammals/year. Rate of predation by mountain lions can vary extensively (Ross and Jalkotzy 1996), and is dependent on a number of factors including the number and age of young (Ackerman et al. 1986), season (Pierce 1999), and extent of competition from other predators (Kunkel et al. 1999) or scavengers (Harrison 1990). Those studies give insight into the behavior of mountain lions and their possible effects on prey populations, but the question of whether mountain lions can independently regulate a prey population remains unanswered.

Mountain lions have been implicated as regulating a wild horse population (Turner et al. 1992), and are thought to have caused populations of porcupines to decline through predation (Sweitzer et al. 1997). In addition, some bighorn sheep populations may have declined due to avoidance of high-quality forage in response to predation risk by mountain lions (Wehausen 1996). In those instances, mule deer were the primary prey for mountain lions. Systems with multiple predators and multiple prey are more likely to be regulated by predation and to produce predator pits (Gasaway et al. 1992). Mule deer populations can keep mountain lion numbers high. If populations of alternative prey increase, mountain lions encounter those species more frequently and predation rates may increase, causing alternative prey to decline. Bleich et al. (1997) noted, however, that unless female mountain sheep were killed in significant proportions, predation by mountain lions probably is not an important factor in the population dynamics of those ungulates.

Several studies examining the population dynamics of deer and mountain lions suggest that mountain lions do not determine the ultimate size of deer populations. Instead, other factors (especially forage resources) appear to be more important determinants of deer populations. For example, Logan and Sweanor (2001) determined that mountain lions were not responsible for the decline of mule deer in New Mexico, but that a lack of forage resources because of drought was responsible. Pierce et al. (1999a) came to a similar conclusion for a population of mule deer in the eastern Sierra Nevada of California. In that study, mountain lion numbers declined precipitously as did the deer numbers, but with a lag of 8 years. Long time lags between changes in prey populations and responses in mountain lion populations increase the difficulty of determining the relationships between mountain lion populations and prey populations (Schaller 1972), and emphasize the need for long-term studies (Pierce 1999).

MANAGEMENT AND CONSERVATION

Management Techniques. Demographic information is difficult to obtain for populations of large, cryptic predators like mountain lions. Track surveys have been a traditional method of determining presence or absence of mountain lions as well as establishing estimates of relative abundance. Various investigators have attempted to distinguish among lions using track characteristics unique to individual animals (Currier et al. 1977; Fitzhugh and Gorenzel 1985; Van Dyke et al. 1986) or track measurements (Currier et al. 1977; Shaw 1983; Fitzhugh and Gorenzel 1985) to recognize individuals. None of these investigators believed it was reliable to distinguish among individual mountain lions using only tracks.

Smallwood and Fitzhugh (1993) used a sophisticated statistical technique (multiple group discriminant analysis) in an attempt to develop a method to discriminate among individual animals based on measurements and characteristics of tracks. However, Grigione et al. (1999) determined that Smallwood and Fitzhugh (1993) had used an inappropriate method. Based on additional analyses, they concluded it was unlikely that individual mountain lions could be detected using discriminant analysis. Furthermore, Grigione et al. (1999) concluded that the most commonly used measurement (width of heel pad) for distinguishing among mountain lions based on their tracks was also the least variable, calling into question the utility of that measurement. Despite the problematic nature of discriminating among individual lions, Beier and Cunningham (1996) conducted several detailed analyses. They felt it is possible to detect changes in relative abundance of mountain lions using tracking techniques at the local level. Nonetheless, the migratory nature of some mountain lions makes it problematic to define populations (Pierce et al. 1999b), with serious implications for the use of track surveys for estimating changes in population size. Track surveys could be useful for estimating relative use of a specific geographic area by mountain lions, but inferences about population size over time are confounded because it is difficult to define an open population. The use of track surveys over large geographic scales to index relative abundance of mountain lions (Smallwood 1994; Smallwood and Fitzhugh 1995) has been attempted, but likely does not provide the power necessary to detect such changes.

Mountain lions frequently are captured to allow attachment of radiotransmitters. Capture techniques often involve the pursuit of animals with hounds, followed by chemical immobilization (Logan et al. 1986b; Jessup et al. 1986). Physical retrieval of immobilized animals (Hornocker 1970) is necessary if they are sedated in a location high above the ground. McCown et al. (1990) described a portable cushion that lessened the probability of injury to mountain lions falling from trees. Davis et al. (1996) developed a method to safely lower immobilized mountain lions from trees and cliffs. Foot snares have been used safely and successfully by some investigators (Logan et al. 1999; Pierce et al. 2000a), and are advantageous in some situations.

Radiotelemetry has been used extensively to determine the distribution of mountain lions in numerous studies, from which density estimates have been inferred. Capture and recapture methods also have been used to estimate population densities. Reliability of estimates obtained with those techniques is variable (Logan and Sweanor 1999), but densities have been estimated at 0.3–2.2 adult mountain lions/100 km^2. Pierce et al. (2000b) estimated the abundance of mountain lions by maintaining an intensive and constant effort to capture and radio-collar all lions detected on a mule deer winter range. They then used aerial telemetry to estimate the number of mountain lions present per aerial-telemetry day, and were able to determine their absolute abundance from year to year. Smallwood (1997) noted that most variation in densities of mountain lions can be attributed to the spatial extent of individual study areas, and suggested that field studies would be more meaningful if they spanned larger areas, a variety of land uses and habitats, and greater periods of time than most conventional studies.

Molecular techniques have been developed that allow investigators to identify individual mountain lions using DNA obtained from blood, tissue, or hair samples (Ernest 2000a, 2000b) and from feces (Ernest et al. 2000). These techniques depend on obtaining good-quality DNA, which is more difficult when using feces (Ernest 2000a). Fecal DNA has been used to identify individual lions occurring within certain geographic areas (Ernest et al. 2000) or associated with particular kill sites for large mammals (Hayes et al. 2000). Use of this technique to determine the absolute number of mountain lions occurring in a particular geographic area is subject to biases associated with their distribution and frequency in the area. Although it is possible to estimate minimum numbers of individuals present, the probability of detecting all individuals using molecular techniques is a function of sampling effort.

The literature is replete with estimates for home range sizes of mountain lions that have been determined using land-based or aerial telemetry. However, global positioning system (GPS) technology raises questions regarding previous studies. Bleich et al. (2000) described the results from GPS collars on two adult male mountain lions. Patterns of movement were vastly different and home ranges were much larger than were estimates from simultaneous aerial telemetry flights conducted on a weekly basis. Some GPS collars incorporate switches (Bleich et al. 2000) that have the potential to be useful in predicting mountain lion activity; Janis et al. (1999) described and quantified the use of traditional very high frequency transmitters equipped with tip switches to estimate activity of mountain lions.

Translocation of mountain lions as a technique for managing "problem" lions (i.e., animals that have preyed on livestock or that occupy areas adjacent to human habitation) is controversial and is inconsistent with management policies in some states because of potential liabilities. Generally, survival of translocated lions is very low. For example, Ruth et al. (1998) described an experiment in which 14 animals were moved and released different distances ($\bar{X} = 477$ km) from their locations of capture. Nine of those individuals died and, overall, survival was lower than that of reference animals that remained within their original home ranges (Ruth et al. 1998). They concluded that translocation was most successful when mountain lions were 12–27 months old. Translocation as a management technique for mountain lions is not widely implemented, but may become increasingly important as a result of changing attitudes toward predator control (Hancock 1980) and loss or fragmentation of habitat (Nowell and Jackson 1996).

Conservation. Conservation of a large carnivore that preys on other large mammals, frequently is involved in the killing of domestic livestock, and occasionally is a threat to human safety presents challenges that seem overwhelming in contemporary times. The primary prey of mountain lions require large tracts of open and undeveloped land, both of which are becoming increasingly uncommon. Mountain lions themselves similarly depend on large tracts of land to meet their needs. Indeed, the conservation and management challenge for the future will be to assure the presence of mountain lions and their prey, despite the certain loss of habitat and increases in human numbers and activity (Torres 1997).

In western North America, mountain lion populations generally remain healthy (Hornocker 1992), but conservationists will be faced with the task of maintaining large, contiguous tracts of suitable habitat that are linked to other such areas. Populations of mountain lions may occur in a metapopulation structure (Sweanor et al. 2000; but, see Ernest et al. 2003). Islands of habitat suitable for supporting permanent populations sometimes are separated by vast areas of habitat that are not permanently occupied, but instead provide opportunities for movement between habitat islands. Thus, habitat fragmentation is a major concern. Beier (1993) and Beier et al. (1995) described a situation where mountain lion habitat in the Santa Ana Mountains of southern California had become isolated from other suitable areas and immigration likely was reduced as a result of human development. Immigration and emigration of individuals are necessary for the maintenance of genetic diversity. Further, opportunities for recolonization must be provided in the event of extirpations from islands of suitable habitat. Maintaining adequate space for mountain lions and their prey as well as linkages between such areas clearly is a pressing issue that must be addressed if mountain lions are to retain their current status.

Depredations on livestock and other domestic animals likely will increase in frequency, especially as the human population expands (Torres 1997). Depredation may be coincident with increases in lion populations (Torres et al. 1996), but may also be a function of declines in populations of primary prey (Pierce et al. 1999a, Kamler et al. 2002). Whatever the cause, management of depredating mountain lions will remain an important issue. Current management of depredating individuals usually involves killing of the offending animal, a strategy unlikely to change in the immediate future. Even in densely populated areas, such events are relatively uncommon (Torres 2000), and such removals likely do not present a threat to existing populations of mountain lions.

Mountain lion populations apparently have expanded during recent years, and there has been increasing concern about the potential for an increase in human encounters. Indeed, such concerns have resulted in publication of pamphlets and books (Torres 1997) designed to minimize the probability of such incidents. Young mountain lions, dispersing between areas of suitable habitat, may be most apt to encounter humans; indeed, the majority of attacks on humans have involved subadult or apparently underweight lions (Aune 1991; Beier 1991). As human populations increase and expand into currently occupied lion habitat, the rate at which such encounters occur may be expected to increase. Meeting human safety objectives while simultaneously providing habitat for viable populations of mountain lions will become increasingly important (Torres 1997).

Sport hunting of mountain lions occurs in the majority of states that have viable populations of mountain lions, and harvest is a method by which wildlife managers attempt to control lion numbers. Increasingly, however, the concept of sport hunting has come under criticism, and hunting of mountain lions has been eliminated in California, and made extremely difficult in other states such as Oregon and Washington by restrictions on the use of hounds to bring animals to bay. Nonetheless, carefully regulated sport hunting remains an important recreational pursuit and is employed as a method of sustaining mountain lion populations at viable levels in a majority of western states (Logan and Sweanor 1999).

Conservation of mountain lions has a long and varied history, and has been couched largely in terms of political expediency (Torres 1997). Efforts to control or eliminate these obligate carnivores by unrestricted harvest and bounty systems were unsuccessful throughout much of the United States, but their efficacy has been attested to by the absence of mountain lions from much of their historical range. In those areas, such as western North America, where large tracts of essential habitat remained in relatively pristine conditions, intensive methods of controlling mountain lions gave way to regulated sport hunting, with an emphasis on ensuring viable populations with the capability of maintaining a sustainable harvest. Selective removal of individual lions that have preyed on livestock or domestic animals has been compatible throughout much of the range of mountain lions during the recent past. Elimination of lions involved with human safety incidents largely has achieved public acceptance.

RESEARCH NEEDS

Mountain lions occur at low densities and are secretive and cryptic; thus, they are among the most difficult large mammals to study. Furthermore, costs of research associated with the study of large carnivores are great, confounding efforts to obtain meaningful answers to difficult questions. Although many aspects of the ecology of mountain lions have been investigated, few authors have conducted the long-term investigations necessary to begin to understand the relationships among habitat, prey densities, and the dynamics of the populations of these secretive predators and their prey.

Mountain lions have been implicated as factors important in the dynamics of some populations of mountain sheep (Kamler et al. 2002), including two population segments (Wehausen 1996; Hayes et al. 2000) listed as endangered by the federal government. Impacts of lion predation on mountain sheep populations are most probable where mule deer and mountain sheep occur sympatrically (Schaefer et al. 2000; Kamler et al. 2002). Nonetheless, clear linkages among the dynamics of populations of primary prey (mule deer), mountain lions, and secondary prey (mountain sheep) are yet to be established, and warrant serious investigation. Such investigations must, however, be conducted over a temporal scale adequate to elucidate changes in habitat quality and resultant responses among prey and predators in such systems (Pierce 1999). As a result, population modeling may become an even more useful predictive tool, (Beier 1993) with more potential for application than currently recognized.

The genetic structure of populations of mountain lions has been examined only recently (Walker et al. 2000; Ernest et al. 2003), and additional opportunities to define populations from a genetic perspective are needed. Furthermore, the spatial structure of lion populations has been reported only on a local scale (Germaine et al. 2000; Sweanor et al. 2000), and landscape-level efforts to more clearly define populations of mountain lions clearly are warranted. Moreover, the potential metapopulation structure (Sweanor et al. 2000) of mountain lions warrants further investigation, and has important implications for the conservation of these large felids (Ernest et al. 2003). GPS technology can be incorporated into telemetry collars for investigations of mountain lion movements and habitat selection (Bleich et al. 2000; Anderson and Lindzey 2003) and can be combined with sophisticated genetic

analyses (Ernest 2000a; Ernest et al. 2000) to enhance the probability of obtaining meaningful results in landscape-level investigations of lion ecology.

Efforts to improve methods of estimating relative numbers of mountain lions in specific geographic areas should continue. Although investigators have developed a number of indirect methods of assessing abundance (Germaine et al. 2000; Pierce et al. 2000b) and some of these are robust (Beier and Cunningham 1996), they are not without problems associated with the definition of populations (Pierce et al. 1999b). Moreover, methods that rely on indirect evidence, such as tracks to identify individuals, are problematic and subject to statistical vagaries (Grigione et al. 1999). Efforts to determine relationships between indirect evidence of mountain lion abundance and genetic evidence from individuals known to be present in specific geographic areas (Ernest et al. 2000) may be a productive field of endeavor, and should be initiated.

As the human population increases, encounters between humans and mountain lions will occur more frequently (Torres 1997). The potential development of nonlethal methods to decrease such encounter rates has implications for the conservation of mountain lions in urbanized areas as well as for some endangered taxa on which they prey. Indeed, the question of aversive conditioning of mountain lions has not been adequately explored, and warrants investigation.

Preliminary findings (Foley 1997) have suggested that epizootic processes are not likely to affect populations of mountain lions in the western United States. Anderson (1983) felt that the relative absence of pathogens among wild mountain lions has largely reflected insufficient efforts to detect diseases, and the results of recent investigations have been consistent with that notion. Nonetheless, some diseases detected among mountain lions are similar to those affecting domestic cats, and further research is needed to determine whether they are the same as those carried by domestic cats or are endemic in wild populations.

Research on mountain lions has often been considered only in a management context, with publications limited to agency reports. Investigators have frequently failed to incorporate concurrent research on prey populations (Pierce 1999) or approach questions from the evolutionary perspective necessary (Pierce 1999; Bleich and Oehler 2000) to ensure that their findings have widespread applicability. The most meaningful knowledge provided by future investigations of mountain lion ecology will incorporate large-scale spatial and temporal components. Investigators will continue, however, to face challenges posed by the high costs and logistical constraints associated with working on a large, cryptic predator (Pierce 1999). Nonetheless, as mountain lions become a more significant and controversial management challenge, funding for the long-term, landscape-level research necessary to meet both proximate and ultimate conservation needs could be forthcoming. Investigators must be ready and willing to proceed along the most meaningful lines of endeavor.

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RESEARCH ARTICLE

Beyond the least-cost path: evaluating corridor redundancy using a graph-theoretic approach

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Abstract The impact of the landscape matrix on patterns of animal movement and population dynamics has been widely recognized by ecologists. However, few tools are available to model the matrix's influence on the length, relative quality, and redundancy of dispersal routes connecting habitat patches. Many GIS software packages can use land use/land cover maps to identify the route of least resistance between two points—the least-cost path. The limitation of this type of analysis is that only a single path is identified, even though alternative paths with comparable costs might exist. In this paper, we implemented two graph theory methods that extend the least-cost path approach: the Conditional Minimum Transit Cost (CMTC) tool and the Multiple Shortest Paths (MSPs) tool. Both methods enable the visualization of multiple dispersal routes that, together, are assumed to form a corridor. We show that corridors containing alternative dispersal routes emerge when favorable habitat is randomly distributed in space. As clusters of favorable habitat start forming, corridors become less redundant and dispersal bottlenecks become visible. Our approach is illustrated using data from a real landscape in the Brazilian Atlantic forest. We explored the effect of small, localized disturbance on dispersal routes linking conservation units. Simulated habitat destruction caused the appearance of alternative dispersal routes, or caused existing corridors to become narrower. These changes were observed even in the absence of significant differences in the length or cost of least-cost paths. Last, we discuss applications to animal movement studies and conservation initiatives.

Keywords Agroecosystems · Atlantic forest · Brazil · Functional connectivity · Corridors · Cost distance · Dispersal · Fragmentation · Graph theory · Matrix · Migration · Shortest path

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Introduction

Animal movement can occur at a range of temporal scales, influencing foraging, migration, and gene flow (Crooks and Sanjayan 2006). The dispersal routes associated with these processes can be strongly constrained by the landscape matrix. Thus models specifying the effect of matrix heterogeneity on movement rates can more successfully predict patch occupancy (Ricketts 2001; Verbeylen et al. 2003), metapopulation dynamics (Vandermeer and Carvajal

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2001), genetic structure (Stevens et al. 2006), and persistence in fragmented landscapes (Laurance et al. 2002). The role of behavior and natural history in shaping species' responses to the matrix has recently motivated the concept of functional connectivity (Calabrese and Fagan 2004). While many connectivity studies have described the influence of different land cover types in channeling or repelling movement of particular species (e.g., Burel 1996; Lees and Peres 2008), few tools are available to integrate data on matrix heterogeneity and species' habitat preferences to model dispersal routes.

A challenge in modeling animal dispersal routes is that individuals rarely use a single optimum route (e.g., Driezen et al. 2007), and connectivity measures focusing on optimum routes fail to incorporate variation in individual behavior (Belisle 2005). In this paper, we model the location of multiple dispersal routes across a heterogeneous matrix. We employ a movement model that assumes successfully dispersing organisms are more likely to use the route of least resistance when moving between two points, or the least-cost path. Despite its simplifying assumptions, the least-cost path has been successfully used to predict patch occupancy (Chardon et al. 2003; Verbeylen et al. 2003) and inter-patch movement rates (Sutcliffe et al. 2003). The least-cost path is identified using a graph theory algorithm, Dijkstra's breadth-first search (Cormen et al. 2001). Many GIS software packages have functions to locate the least-cost path between two points. Although only one path is obtained, Dijkstra's algorithm can be easily modified to output multiple paths with similar costs. We describe this modification and its two outputs, the Conditional Minimum Transit Cost (CMTC) and the Multiple Shortest Paths (MSPs).

We propose that corridors are heterogeneous structures that may contain multiple dispersal routes. However, we do not advocate a method for designing corridors (including few or many dispersal routes), neither do we attempt to quantify corridors' role in conserving biodiversity. Rather, our goal is to integrate information on species' habitat preferences into regional-scale depictions of habitat connectivity. This paper has three parts. First, we applied our method to artificial landscapes in order to illustrate the effect of matrix heterogeneity on the cost and spatial distribution of dispersal routes. Second, we studied the effect of small, localized disturbance on large-scale dispersal routes. This was performed using data from the highly fragmented Brazilian Atlantic forest (Morellato and Haddad 2000). Last, we discussed how the approach proposed here can be refined and incorporated in animal movement studies and conservation initiatives.

Methods

The landscape graph

In this section, we describe the approach routinely employed to perform any type of distance calculations on grids. Most GIS software packages use graphs (Urban and Keitt 2001) to represent grid maps. Graphs are composed of vertices (V) placed on cell centers, and edges (E) that connect each vertex to its eight nearest neighbors (Fig. 1). Using this representation, we define two cost grids:

(a) Relative cost grid (Figs. 2a, 3a), also referred to as a friction layer (Verbeylen et al. 2003). Each vertex contains the relative cost to cross it in any direction.

(b) Cumulative cost grid (Figs. 2b, 3b). Consider a source (S) composed of one or more vertices. Each vertex in the cumulative cost grid contains the minimum cumulative cost to reach S. This is calculated in two steps: first, the cost to move between pairs of vertices is stored as edge weights. The weight *W* for an edge connecting vertices V1 and V2 is calculated as:

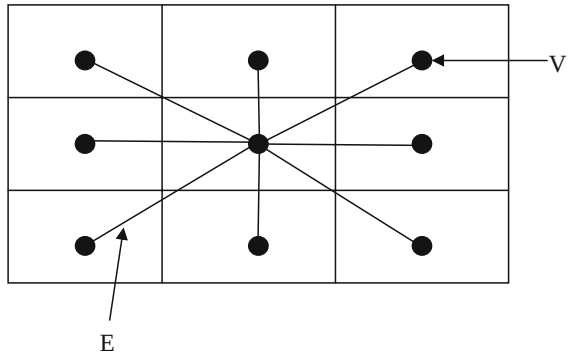

Fig. 1 The landscape graph. In most software packages, grid maps are internally represented as a graph. Vertices (V) are located in cell centers. Each vertex is connected to its eight nearest neighbors by an edge (E). Edge weights (not shown) hold information on the cost to move between pairs of vertices

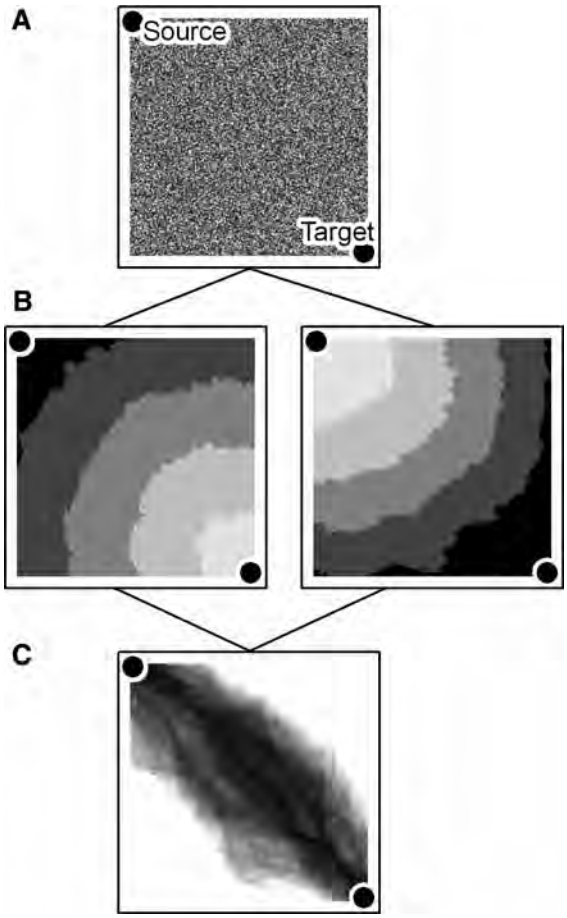

Fig. 2 Illustration of the procedure for calculating the CMTC. **a** Relative cost grid. **b** The cumulative cost grid for the target (*left*) and the source (*right*). Lighter shades indicate lower cumulative cost. **c** The two grids from (**b**) are added to produce the CMTC grid

$$W = [\text{Relative Cost}\,(\text{V1}) + \text{Relative Cost}\,(\text{V2})]/2 \quad (1)$$

For diagonal edges, edge weights W' are calculated as:

$$W\prime = W \times \sqrt{2} \quad (2)$$

Second, Dijkstra's breadth-first search algorithm (Cormen et al. 2001) is used to calculate the least-cost path between S and each vertex in the graph. The minimum cumulative cost between S and a given vertex (V) is the sum of all edge weights in the least-cost path connecting S and V. To calculate the

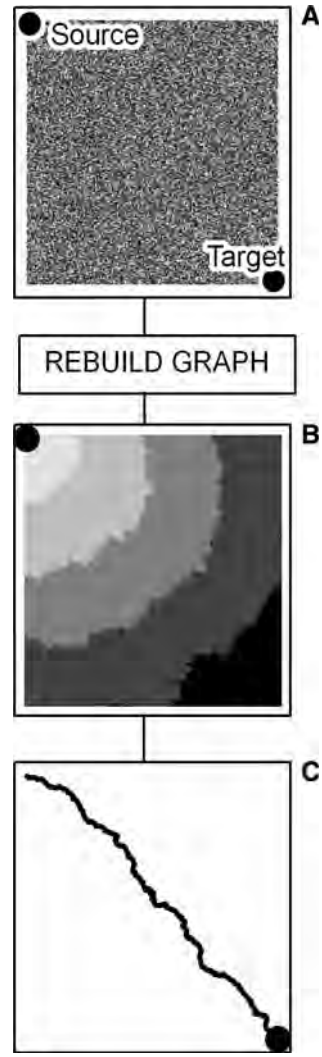

Fig. 3 Illustration of the procedure for locating MSPs. **a** Relative cost grid, **b** cumulative cost grid for the source. *Lighter shades* indicate lower cumulative cost. This was calculated after rebuilding the graph that represents the landscape, **c** with the cumulative cost grid, we trace the least-cost path between source and target, **b** and **c** are repeated 100 times to produce 100 least-cost paths

least-cost path between two habitat patches P1 and P2 we define all vertices in P1 as sources and all vertices in P2 as targets. The least-cost path between patches P1 and P2 will most likely link the two patches' most external vertices.

In the next two sections, we build on the above representation and describe two methods that extend Dijkstra's breadth-first search algorithm.

Conditional minimum transit cost (CMTC)

Consider a vertex (V) located between groups of source vertices (S) and target vertices (T). The Conditional Minimum Transit Cost (CMTC) for V is the cost-weighted distance to move from S to T, conditional on the route forming the shortest passage between S and T while passing through V. It is calculated as (Fig. 2):

$$\begin{aligned}\mathrm{CMTC}(\mathrm{V},\mathrm{S},\mathrm{T}) = {} & \text{Cumulative cost}(\mathrm{V},\mathrm{S}) \\ & + \text{Cumulative cost}(\mathrm{V},\mathrm{T}) \end{aligned} \quad (3)$$

The final CMTC grid was obtained by masking out all cells with CMTC values larger than the minimum CMTC value plus 10% (Fig. 2c). The remaining values were then divided by the grid's maximum CMTC. According to Forman (1995), a corridor is "a narrow strip of land that differs from the matrix on either side". We assume that areas within the 10% threshold form corridors, but emphasize that our choice of corridor width was arbitrary.

Our analysis generates corridors that are highly heterogeneous. Visually inspecting the CMTC grid (Fig. 2c) enables identification of contiguous cells with low CMTC value. We refer to these cell groups as "dispersal routes", while recognizing that distinction between routes that are close together is arbitrary. The least-cost path is invariably located within one dispersal route.

In practice, obtaining a CMTC grid is straightforward with modules such as spatial analyst within ArcGIS (Esri, California). Some conservation biologists strongly advocate the CMTC approach for designing wildlife corridors (Majka et al. 2007). But to our knowledge, the relationship between matrix heterogeneity and the distribution of dispersal routes as predicted by the CMTC has not yet been explored.

Multiple shortest paths (MSPs)

We developed a stochastic version of Dijkstra's algorithm (Fig. 3) that outputs multiple realizations of the least-cost path, or Multiple Shortest Paths (MSPs). As described above, the least-cost path is obtained from a relative cost grid. Dijkstra's breadth-first search algorithm (Cormen et al. 2001) proceeds by iteratively marking vertices in the order of their cumulative distance from the source. At each step, the algorithm must identify the set of neighbors associated with the marked vertices. Standard algorithms use a static definition of the neighborhood, typically the nearest eight cells on a rectangular grid (Fig. 1). Our approach is to redefine the neighborhood as a stochastic function such that adjacency is non-deterministic and is instead determined randomly in proportion to edge weights. The algorithm proceeds as follows (Fig. 3):

1. Draw a number (U) between 0 and 1 from a random uniform distribution.
2. Delete edges in the graph. An edge with weight W connecting two adjacent vertices V1 and V2 is deleted if $W > U$. That is, connections with lower costs are more likely to be maintained.

A program implementing Dijktra's algorithm (with the above modification) was run 100 times in order to produce 100 MSPs for each study case (Fig. 3c shows one path). The cumulative cost associated with each path is a measure of effective distance and is calculated by adding the weights of all edges in the path. The programs used to obtain both CMTCs and MSPs were written in the Java programing language.

Applications to artificial landscapes

We generated artificial landscapes with different degrees of spatial autocorrelation using the method of wavelet synthesis (Keitt 2000). We started with a grid containing values between 0 and 1, drawn from a random uniform distribution. Using this grid, each landscape was created in four steps: (a) apply the discrete Haar wavelet transform; (b) obtain wavelet coefficients; (c) multiply coefficients by $2 \wedge (L \times \beta)$, where L is the coefficient level (higher levels representing low-frequency variation); (d) apply the inverse Haar wavelet transform on the modified coefficients; (e) map results to a random uniform distribution ($\min = 0$; $\max = 1$). The last step is taken to ensure that the distribution of quality values is consistent across all landscapes. The values of the parameter β were 0, 0.25, 0.50, 0.75, and 1. A β value of zero generates a white noise landscape with no spatial autocorrelation. Increasing β produces autocorrelated landscapes, where clusters of favorable habitat can be identified. Each artificial landscape represents one relative cost grid that served as input in calculations of CMTC and MSPs (Fig. 4a). We used ANOVA to test for differences among landscapes, in terms of

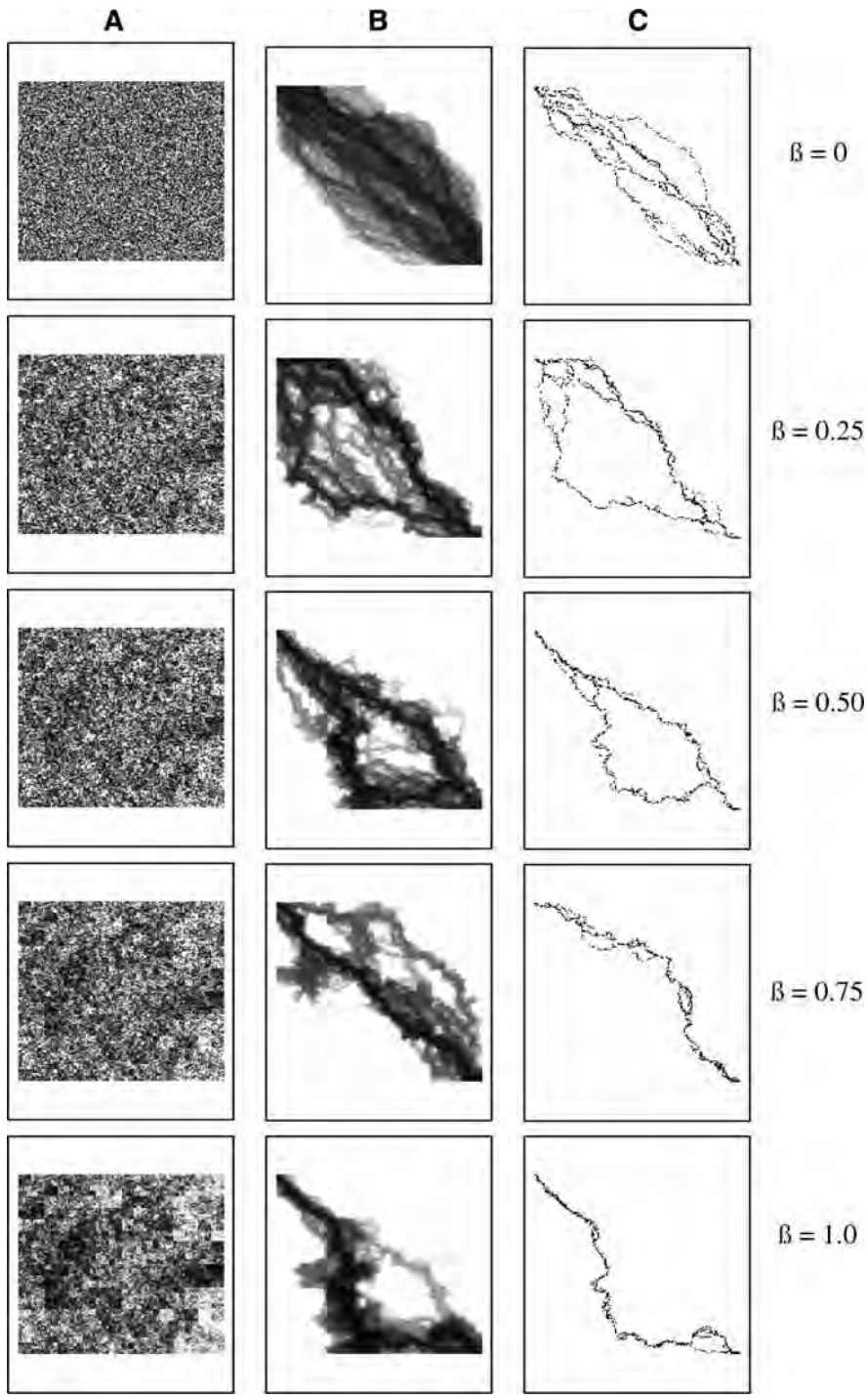

Fig. 4 Relative cost grids generated with the use of wavelet transforms (**a**), and the values of CMTC (**b**) and location of MSPs (**c**) for each landscape. A β value of 0 is a landscape with no spatial autocorrelation in habitat quality values, and landscapes become "patchier" as β values increase

cumulative costs associated with MSPs and mean CMTC. The generation of artificial landscapes and ANOVA tests were performed using the R programing language (R Core Development Team 2008).

Applications to real landscapes

We studied a real landscape (Fig. 5) that covers 111 km^2 of the Brazilian state of São Paulo (upper

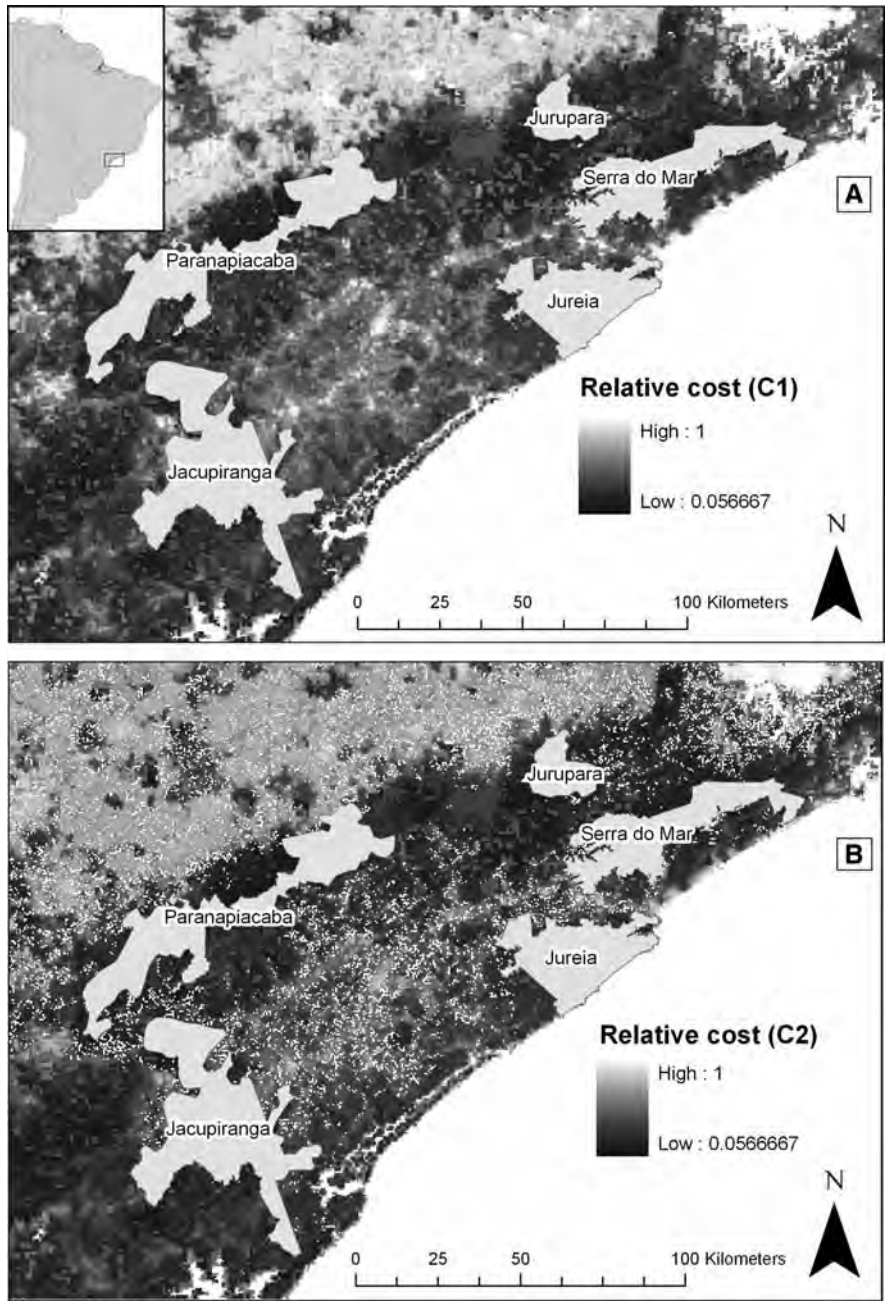

Fig. 5 Study site in the Brazilian Atlantic forest, showing conservation units in Sao Paulo State. **a** Relative cost values for scenario C1. **b** Relative cost values for scenario C2 (after deletion of small forest fragments)

left coordinates: 23.60S, 49.00W; lower right coordinates: 25.40S, 46.20W). Remaining forests are part of the Atlantic forest biome (for a description, see Oliveira-Filho and Fontes 2000). Despite its location in highly industrialized São Paulo state, the study area still contains large forest tracts and rural properties. A recent vegetation map (Eva et al. 2002) estimates that 11.1% of the study area is devoted to intensive agriculture, 7% contains a mix of agriculture and degraded vegetation, 23% is a mix of agriculture and degraded forest, and 46% is covered with forest. Excluding São Paulo's metropolitan area, human populations per municipality range in size from 3,403 to 412,243 (mean = 60,410; IBGE 1991). Five conservation units are considered here: Pedro de Toledo Nucleus within Serra do Mar State Park (868 km^2), Juréia-Itatins Ecological Reserve (801 km^2), Jurupara State Park (259 km^2),

Jacupiranga State Park (1,552 km^2), and the contiguous units Intervales State Park, Carlos Botelho State Park, Ecological Station Xitué, and Alto do Ribeira Touristic State Park (1,282 km^2), referred together here as "Paranapiacaba" due to their location along the Paranapiacaba Valley.

Our analyses consisted of modeling dispersal routes between all pairs of conservation units. We have built a relative cost map in an attempt to capture the habitat preferences of species that move in forested areas and suffer higher mortality when crossing disturbed habitat. In the discussion, we describe how more detailed models can be built and refined to reflect the habitat preferences of a particular species. Three land use/land cover maps were the main input for our analyses (Table 1).

1. The Modis continous fields, (Hansen et al. 2003) contains estimates of percent tree cover. Values were manipulated (Table 1) in order to obtain a grid with values ranging between 0 (=100% tree cover) and 1 (=no tree cover).
2. The human footprint map (Sanderson et al. 2002) is a global dataset with estimates of anthropogenic impact ranging from 0 (pristine land) to 100 (most disturbed land), normalized per ecosystem. These estimates were based on patterns of human population density, land use, and transportation networks. We divided original values by 100 (Table 1) to obtain a grid with values ranging from 0 (=pristine land) to 1 (=most disturbed land).
3. The South American vegetation map (SAVM; Eva et al. 2002) contains information on forest distribution, degree of forest disturbance, and mixture with agricultural lands. We assigned each class in the SAVM grid (Table 1) a relative cost value ranging from 0 (=closed or dense forest) to 1 (intensive land use or non-forested ecosystems).

The Footprint and SAVM grids were rescaled so as to bring their spatial resolution to 500 m. The first relative cost map (C1; Fig. 5a) was obtained by averaging the values in the three grids described above (Table 1). As a result, we obtained a grid where cell values ranged from 0.057 (minimum relative cost to cross) to 1 (maximum relative cost to cross).

The second cost map (C2; Fig. 5b) simulated the removal of small forest fragments from C1, which could result from clear cutting, selective logging, or road construction. Results do not necessarily reflect actual land cover changes taking place in the Atlantic forest, but they enable us to explore the effect of small, localized disturbance on regional connectivity patterns. The C2 map was built in three steps. First, we produced a binary map with areas classified as "forest" or "non-forest" based on the SAVM map. This binary map was eroded and dilated (Serra 1982) by 0.5 pixel, resulting on the deletion of fragments with area <5 ha and linear elements (such as riparian corridors) <500 m wide. Last, C2 was obtained by assigning the maximum relative cost (1) to the deleted cells. All other cells contained the same values as C1, and the range of relative cost values for the entire grid remained unchanged (0.057–1). It was assumed that individuals could not move through water, thus a cost value of positive infinity was assigned to cells representing water bodies in both C1 and C2 scenarios. Finally, we calculated the CMTC and MSPs for both C1 and C2 scenarios. All GIS layers were processed using programs written in Java

Table 1 Grids used to construct the relative cost maps used in the present study, their original spatial resolution (pixel size), period of data collection, and operations performed on original grid values

Layer	Resolution (m)	Years	Operations performed on the original raster values
South America vegetation map	1,000	1995–2000	0 = closed, dense, transitional forest
			0.25 = open forest
			0.5 = mosaic agriculture/degraded forest
			0.75 = shrubland, savannah, grassland
			1 = intensive agriculture, mosaic agriculture/degraded vegetation, desert, urban
Human footprint	1,000	1960–2001	Final value = (original value)/100
Modis continuous fields, % tree	500	2000–2001	Final value = (100 − original value)/100

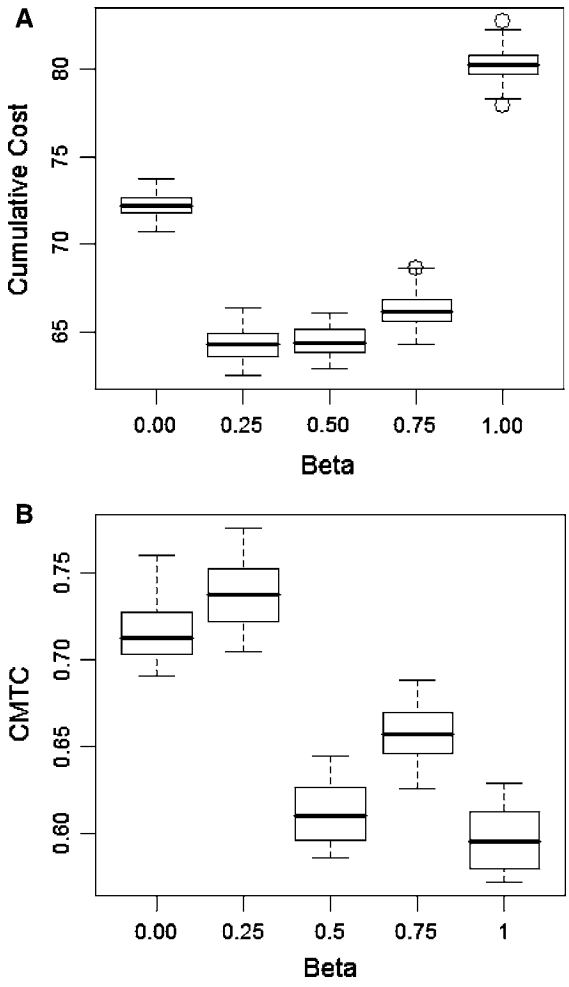

Fig. 6 The distribution of values of **a** Multiple Shortest Paths **b** and Conditional Minimum Transit Costs. A β value of 0 is a landscape with no spatial autocorrelation in habitat quality values, and landscapes become "patchier" as β values increase

programing language, and illustrations were produced in ArcMap (Esri, California).

Results

Artificial landscapes

The two graph theory approaches proposed here outlined the influence of matrix heterogeneity on dispersal routes. We detected a significant difference in mean cumulative costs associated with Multiple Shortest Paths (MSPs) among the five artificial landscapes (ANOVA, $F = 6{,}934.5$; $P < 0.001$). MSPs with lowest costs were observed when landscapes had intermediate patchiness (Fig. 6a; Tukey multiple comparisons of means, 95% family-wise confidence level, $P < 0.001$). We also observed significant differences in mean Conditional Minimum Transit Cost (CMTC) values (ANOVA, $F = 474{,}104$; $P < 0.001$). The most autocorrelated landscapes produced the lowest CMTC values (Fig. 6b; Tukey multiple comparisons of means, 95% family-wise confidence level; $P < 0.001$). In addition, we observed differences in the spatial distribution of dispersal routes. Landscapes with little autocorrelation in relative habitat quality produced redundant corridors with more alternative dispersal routes (Fig. 4; β closer to 0). As clusters of favorable habitat started to form, corridors became restricted to fewer routes (Fig. 4; β closer to 1). This was evidenced in the outputs of both the CMTC and MSPs calculations.

Real landscapes

We tested the influence of small, localized disturbance on corridors connecting five conservation units in the Brazilian Atlantic forest (Fig. 5). There were no significant differences in mean cumulative path costs calculated from MSPs, or in mean CMTC values (t-test, $P > 0.05$) between scenarios C1 and C2. But in most cases, simulated fragment removal influenced the spatial distribution of dispersal routes. Since small fragments were not homogeneously distributed in the study area, corridors obtained under scenario C1 were differentially affected by simulated fragment removal in scenario C2 (Table 2).

Table 2 Conservation units included in the present study

	Jacupiranga	Jurupará	Serra do Mar	Paranapiacaba
Juréia	72.321	35.391	6.905	3.993
	5	3.6	10.4	5.5
Jacupiranga		115.502	104.800	7.868
		4.0	5.0	21.0
Jurupará			7.263	43.739
			2.0	1.2
Serra do Mar				51.183
				2.3

Each unit in a pair can serve as a source or a target for dispersing organisms. The first line contains the straight-line distance between units (in kilometers), and the second line shows the percentage of 500-m^2 cells deleted from the corridor as a result of simulating fragment removal

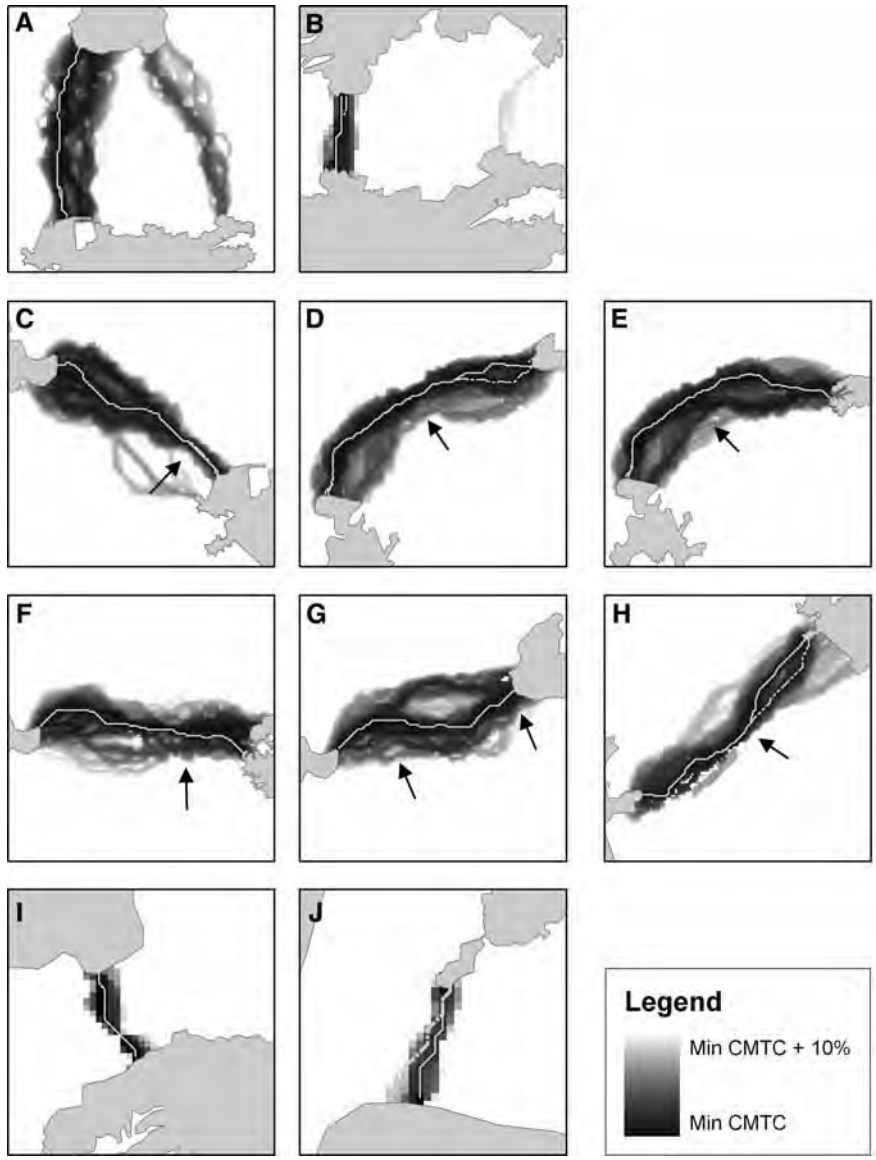

Fig. 7 CMTC grids for the corridor connecting conservation units in São Paulo, Brazil. The pairs are: **a** Jurupará–Juréia, **b** Juréia–Serra do Mar, **c** Juréia–Paranapiacaba, **d** Jacupiranga–Jurupará, **e** Jacupiranga–Serra do Mar, **f** Paranapiacaba–Serra do Mar, **g** Paranapiacaba–Jurupará, **h** Juréia–Jacupiranga, **i** Serra do Mar–Jurupará, **j** Paranapiacaba–Jacupiranga. *Gray lines* show the least-cost path. *Solid lines* represent least-cost paths obtained for scenarios C1 and C2, whereas *interrupted lines* represent sections of the least-cost path obtained for scenario C2 only. *Arrows* indicate potential dispersal bottlenecks

In most cases, the CMTC grid displayed more than one alternative route between conservation units, one of them being the least-cost path (Fig. 7a–h). When conservation units were close, the distance between them was small with respect to the variation in their shape. In this case, the CMTC grid produced narrow corridors, coinciding with the links representing the shortest Euclidian distance (Fig. 7b, i, j). When corridors contained alternative routes, these were rarely disjoint (Fig. 7a, b). The constriction zones where dispersal routes merged represented potential dispersal bottlenecks (Fig. 7c–h). In most cases, the location of the least-cost path did not change substantially as a result of small fragment removal (Fig. 7a–c; e–g; i, j). But in two cases, the least-cost path for scenario C2 was displaced to an alternative route located a few kilometers away from the least-cost path for scenario C1 (Fig. 7d, h).

We also identified the MSPs between pairs of conservation units. Compared to the CMTC calculation, this tool provided a better assessment of the impact of fragment removal on corridor redundancy. Examining the MSPs produced for the scenarios C1 and C2, we observed two trends. In some cases,

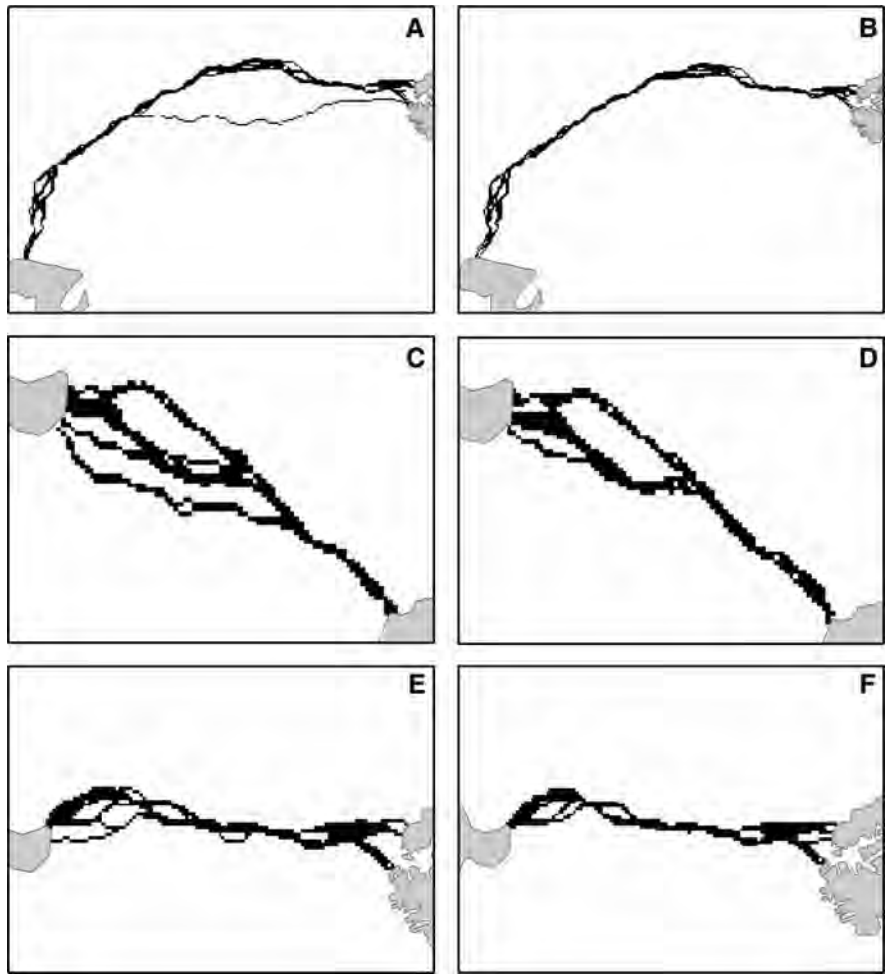

Fig. 8 Location of the first 100 least-cost paths connecting conservation units in São Paulo, Brazil. **a** Jacupiranga–Serra do Mar, scenario C1; **b** Jacupiranga–Serra do Mar, scenario C2; **c** Juréia–Paranapiacaba, scenario C1; **d** Juréia–Paranapiacaba, scenario C2; **e** Serra do Mar–Paranapiacaba, scenario C1; **f** Serra do Mar–Paranapiacaba, scenario C2

fragment removal led to the disappearance of external dispersal routes; corridors became narrower and less redundant (Fig. 8). In other cases, new, more external routes emerged after fragment removal (Fig. 9).

Discussion

Analyses of artificial landscapes show the influence of matrix heterogeneity on landscape connectivity. Redundant corridors with multiple alternative dispersal routes emerged in white noise landscapes, where favorable habitat is randomly distributed (Fig. 4, β closer to 0). As patches of favorable habitat started forming, corridors became narrower and less redundant (Fig. 4, β closer to 1). The cumulative cost of MSPs was on average lower in landscapes with intermediate degree of autocorrelation (Fig. 6a). This is because paths in white noise landscapes will often cross areas of high cost, whereas the presence of contiguous habitat patches in autocorrelated landscapes can lead to longer, more tortuous paths (Fig. 4c). The CMTC was on average lower in autocorrelated landscapes (Fig. 6b). This follows from our choice of CMTC value used to delimit corridors—under a 10% threshold, white noise landscapes produced wider corridors with higher CMTC values.

In addition to studying artificial landscapes, we illustrated our methods using data from a real landscape in the Brazilian Atlantic forest. In this region, a complex landscape matrix produced dispersal routes that were not apparent in land use/land cover maps (Fig. 7a–f, h–j), with the exception of the pair Paranapiacaba–Jurupará that is separated by an artificial dam (Fig. 7g). CMTC maps revealed highly

heterogeneous corridors displaying bottlenecks to animal movement (indicated by arrows in Fig. 7c–h). Removing small fragments did not produce a significant increase in the mean cumulative cost of MSPs but led to changes in their spatial distribution (Figs. 8, 9). Our work illustrates two possible large-scale effects of small, localized disturbance on the landscape matrix. Narrower corridors were produced (Fig. 8), and the importance of external dispersal routes increased (Fig. 9). The latter case included the two pairs of conservation units with the largest amount of deleted habitat in the scenario C2 (Table 2; Fig. 9c–f).

Results of least-cost path analyses are strongly dependent on the selection of relative cost grids (Adriaensen et al. 2003; Rae et al. 2007). Our choice of relative cost grids (Table 1) was made as an attempt to approximate the habitat preferences of a forest specialist. Relative cost grids can be further refined and validated for a particular species using patch occupancy data (Verbeylen et al. 2003) or from ecological niche modeling and tools such as the Mahalonobis distance (Farber and Kadmon 2003). In addition to habitat preference estimates, an important issue is the time scale over which individuals are expected to disperse. Here, we were not concerned with the time interval or number of generations that individuals (or populations) took to move between source and target fragments (conservation units). More realistic models can be obtained by adjusting the maximum Euclidian distance allowed between source and target fragments so as to match the maximum distance that can be crossed by a species given a particular time interval (Keitt et al. 1997). The issue of time scale is related to the question of whether corridors should function as habitat or as

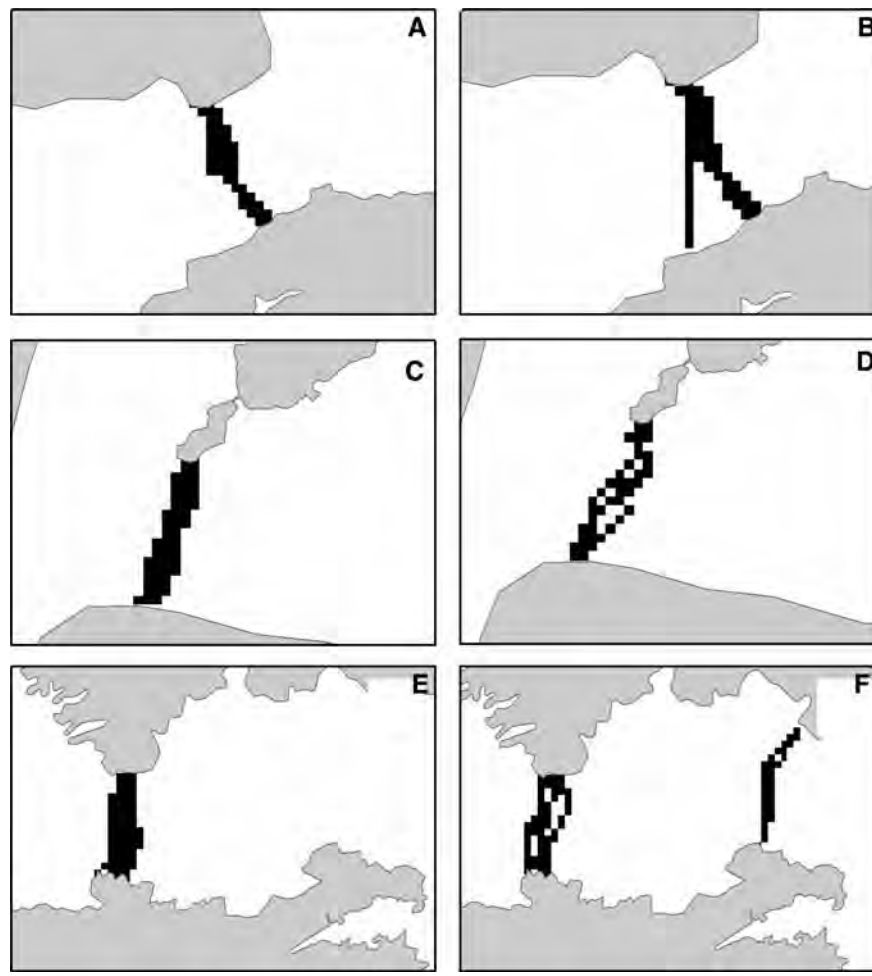

Fig. 9 Location of the first 100 least-cost paths connecting conservation units in São Paulo, Brazil. **a** Serra do Mar–Jurupara, scenario C1; **b** Serra do Mar–Jurupará, scenario C2; **c** Paranapiacaba–Jacupiranga, scenario C1; **d** Paranapiacaba–Jacupiranga, scenario C2; **e** Juréia–Serra do Mar, scenario C1; **f** Juréia–Serra do Mar, scenario C2

conduits (Hess and Fischer 2001)—i.e., individuals are expected to spend more time in habitat corridors. Corridor width can be adjusted by increasing the CMTC threshold to ensure that corridors contain minimum habitat requirements.

The ability to identify multiple dispersal routes can be desirable in conservation studies, for three main reasons. First, least-cost paths have been employed in the design of linked reserve systems (Hoctor et al. 2000; Schadt et al. 2002; Larkin et al. 2004). This approach, however, can lead to very narrow linkages (Alagador and Cerdeira 2007) that might not be located in land tracts available for purchase. Second, dispersal routes that appear similar may differ in terms of their conservation value. For example, field studies in Canada (Clevenger et al. 2001) show that drainage culverts can act as habitat linkages for several mammal species, but culverts near roads with higher traffic volume and noise levels are less commonly used. Third, the approach shown here enable the visualization of functionally unique landscape structures (Manning et al. 2006): narrow corridors or dispersal bottlenecks within corridors (e.g., Fig. 7).

Considerable attention has been given to quantifying the role played by agroecosystems in conservation (i.e., Bestelmeyer and Wiens 1996; Reitsma et al. 2001; Mas and Dietsch 2003). Agricultural lands can help support wild populations by providing critical habitat (Moguel and Toledo 1999) and influencing neighboring fragments, in which case potential outcomes depend on the spatial configuration and degree of mixture with pristine habitat (Perfecto and Vandermeer 2002; Perfecto et al. 2003; Tscharntke et al. 2005). Our study of the Brazilian Atlantic forest shows that private lands can collectively influence ecological processes occurring at large spatial scales and supports the assertion that small fragments can potentially shape regional patterns of gene flow (Bodin et al. 2005). This raises the necessity to view agricultural lands' contribution to biodiversity in a larger context.

Movement behavior is a key aspect in functional connectivity studies, but detailed data on animal movement remains hard to collect, especially for large spatial scales. In fact, the ability to produce accurate movement models has long been recognized as one of the main challenges of population biology studies (Turchin 1998). There is no consensus on the amount of biological detail that should be used in functional connectivity studies. It has been suggested that movement models ought to increase in complexity in order to capture the behavior of particular species (Goodwin 2003). At the same time, conservation biologists have raised the need for rigorous methods that predict the location of dispersal routes for many species (Boitani et al. 2007). Clearly a compromise is needed, which requires determining how much simplification can be made before losing predictive power (Baguette and Van Dyck 2007). Least-cost path predictions can be derived for many species, given the ever growing maps of habitat quality produced by ecological niche modeling. Also, rigorous protocols already exist to compare least-cost predictions with field data (Driezen et al. 2007).

Conclusions

In the present paper, we extended the graph theory algorithm that serves as the basis for least-cost path calculations. The two outputs are the Conditional Minimum Transit Cost (CMTC) and the Multiple Shortest Paths (MSPs). Our goal was to integrate information on habitat preferences to model dispersal patterns across a heterogeneous matrix. In addition to the path of least resistance between two points, the methods presented here outlined additional paths with similar length and relative cost. Results from artificial landscapes show that the location and relative cost of dispersal routes are strongly influenced by the spatial distribution of favorable habitat in the matrix. In addition, study of a real landscape shows that small, localized disturbance such as removal of small fragments can affect large-scale dispersal routes. Models producing multiple dispersal routes present a practical advantage over models assuming optimum behavior. Although the choice of number of dispersal routes or their location is application specific (and beyond the scope of this paper), our results suggest that the least-cost path is a flexible approach with a wide range of applications.

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How the West is Learning to Live with Mountain Lions – Bitterroot

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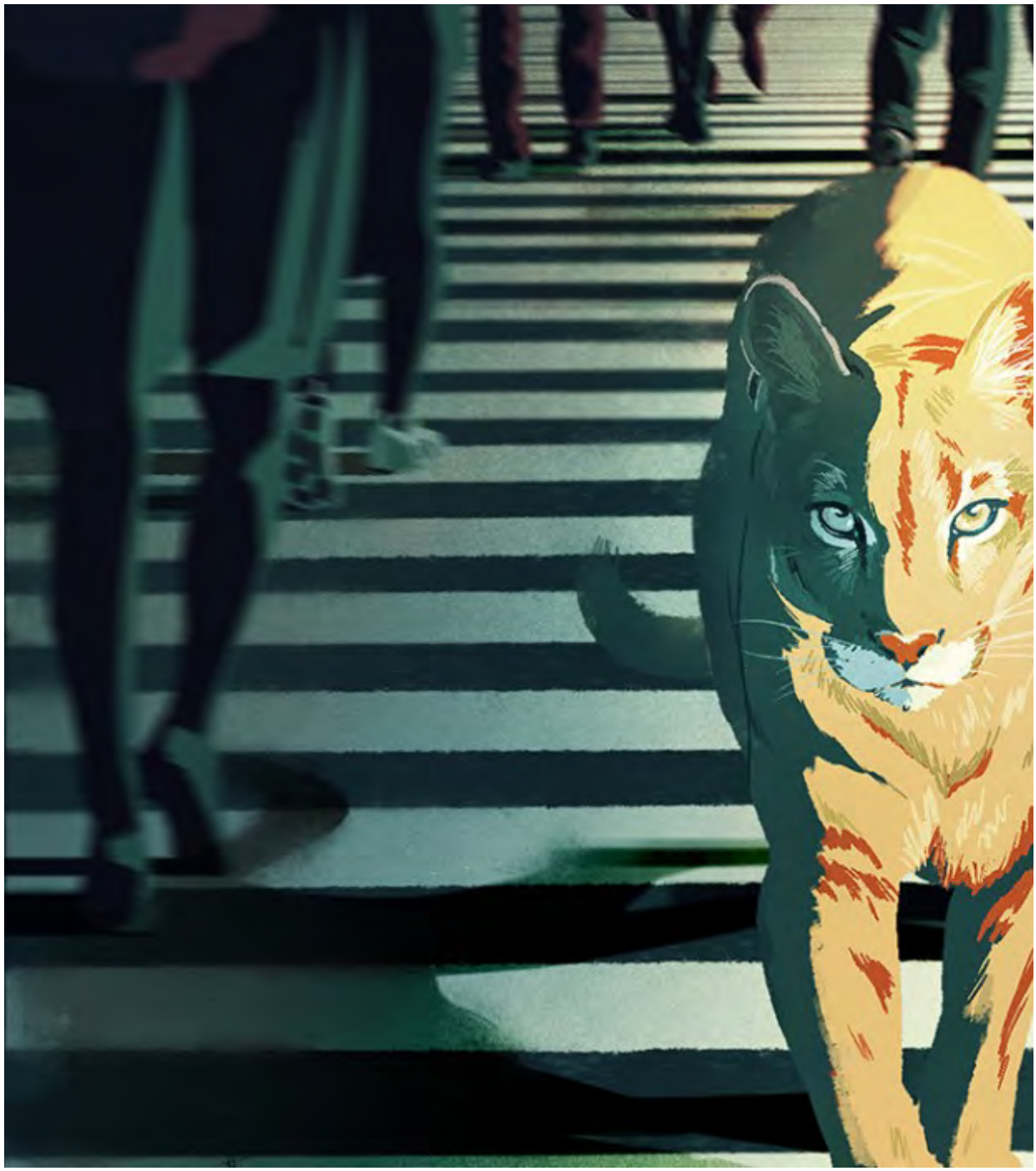

As the footprint of our cities expands into mountain lion territory, researchers say we must learn to live with the big cats — or they could go extinct in some areas. | *Illustration by Morgan Krieg*

Last August, months before the coronavirus pandemic accustomed us to seeing

wildlife in empty city streets, a mountain lion walked into San Francisco. Not much is known of the carnivore's journey to the city, but one can imagine. The young male, likely searching for territory of his own, may have snuck out of the Santa Cruz Mountains south of the city. From there, he ventured quietly through the parks, golf courses, neighborhoods, and commercial districts of Daly City and the Peninsula. Then, hitting the row houses near Lake Merced like a wall, he headed west, met the coastline at Ocean Beach, and followed it north. With the ocean to his left and the hotels, cafes, and bars of the Sunset District to his right, he finally reached a break in the city at Golden Gate Park, where a manicured grove of Monterey pine and cypress beckoned.

That's where city park officials spotted him and alerted the community. Then the cat disappeared, resuming his stealthy journey through the Bay Area.

"They just need protected cover — traveling at night and lying low during the day," said Chris Wilmers, a wildlife ecologist and cougar expert, as he traced the Golden Gate Park mountain lion's speculative path on a map in his office at the University of California, Santa Cruz. During a decade of research, Wilmers has collared more than 100 cougars in the Santa Cruz Mountains. The GPS-equipped collars plot the cougars' movements as they wander the landscape in search of food and mates. For the most part, these lions stay within redwood forests or chaparral canyons. But sometimes they wander through parks and backyards, across highways, or, like the Golden Gate cougar, into urban areas.

Mountain lions that cross these unseen boundaries can fall into trouble. Each year, about 90 California cougars are killed after they prey on livestock, according to data from the California Department of Fish and Wildlife. Collisions with cars kill another 100 — though, according to Justin Dellinger, a state mountain lion biologist, that number is significantly underreported. "It could be twice that," he said.

Biologists say these untimely outcomes are caused by highways and suburbs that fragment the habitat of a highly mobile species. The barriers between cougar populations present another threat: restricted genetics. Cats that can't move around inbreed, which can cause susceptibility to disease and reproductive abnormalities.

"When you put all that together, it's a recipe for a population at risk," said Winston Vickers, a University of California, Davis veterinarian who studies cougars in southern California. Some of these populations, Vickers explained, could face extinction in a matter of decades.

More protection could be on the way. In April, the state Fish and Game Commission granted six marooned populations of cougars temporary protection under state law. But the potential for jurisdictional protection begs a practical question: how can cougars be safe in the West's ever-expanding urban areas? For Wilmers in the Bay Area, Vickers in southern California, and researchers and conservationists throughout the West, the question of mountain lion protection hinges on how we perceive and interface with them, especially as our habitat — in the form of livestock yards, highways, and suburban sprawl — blends with theirs. "More and more development means more threats to habitat and connectivity," Wilmers said.

Solutions are emerging. Wildlife overpasses and tunnels, smarter and denser development, and nonlethal methods to mitigate predator-livestock conflict could save hundreds of cougars each year. In sum, they are emblematic of a shift in how

we view the divide between nature and cities. In his 1995 essay "The Trouble with Wilderness," environmental historian William Cronon lambasts the idea that nature exists solely within wilderness areas or national parks. "If wildness can stop being (just) out there and start being (also) in here, if it can start being as humane as it is natural, then perhaps we can get on with the unending task of struggling to live rightly in the world," he wrote.

As Western states address threats to mountain lions, many are finding the task requires a much bigger frame of conservation than previously thought. We're discovering there isn't wilderness just for cougars and cities just for people. Rather, there is only, as Cronon wrote, "the home that encompasses them both."

Puma concolor goes by many names: mountain lion, cougar, panther, catamount. Widespread as they are — pumas range from the Yukon to the southern reaches of the Andes — they've earned the nickname "ghost cat" pretty much everywhere because they're so elusive. Wilmers has never seen one in the wild "fair and square," as he phrased it — he's always needed the assistance of baited traps or hounds to locate them for research.

But the ghosts seem to be showing up more often. During the current pandemic, Boulder, Colorado residents have seen them wandering neighborhoods and napping in backyard trees. Cougars, of course, hung out in cities well before COVID-19 drove us all indoors. For the most part, they steer clear of people, but some conflicts do occur. In February, a mountain lion reportedly attacked a 6-year-old girl at a park near San Jose, and another attack took place a month earlier in Orange County. In 2018, a bicyclist in North Bend, Washington, was killed by a mountain lion in the state's first fatal cougar attack in almost a century. A trail runner encountered a mountain lion just outside Fort Collins, Colorado, last year, and killed the cat in self defense.

Such incidents, though rare, can stoke a collective fear of predators, and they'll likely become more common — especially in California. "We're on our way to 40 million people in California, and about 40 percent of this state is regarded as suitable mountain lion habitat," said Quinton Martins, a mountain lion ecologist based in Sonoma County. "Inevitably, we'll have more overlap between mountain lions and people."

Human-cougar interactions typically end poorly for the lion, particularly when our livestock or pets are involved. In the summer of 2019, Martins received a GPS collar in the mail at his office near Santa Rosa. Martins leads a study of mountain lion behavior for the nonprofit Audubon Canyon Ranch, and he had previously affixed the collar to a young male, labeled P14, near the coastal town of Jenner. For seven months, Martins traced the cougar's movements through a landscape of coastal redwoods and river basins. Somewhere in the coniferous forests around the town of Point Arena, 50 miles up the coast from Jenner, the GPS signal went dark.

In California, landowners can acquire a depredation permit to lethally remove a mountain lion that has preyed on livestock. The young lion, it turned out, had killed a dozen sheep, and was killed in turn by the landowner.

"Mountain lions are timid," Martins said. "But they do kill livestock and pets. That's where the conflict really lies in California."

Martins is from South Africa, where he worked in the safari industry and studied how leopards and humans interact. As in the West, ranchers there often hunted big cats that killed their livestock. Martins wanted to address carnivore conflict in ways that didn't result in a dead leopard, so he started the Cape Leopard Trust to educate ranchers about better livestock enclosures and when and where to safely run livestock. He moved to northern California in 2016, and now directs the Audubon Canyon Ranch's Living with Lions project. The goal, Martins explained, is to change public perception of these animals and show that lions don't have to die for the sake of our livestock. "People have encroached on these animals' space," he said. "What we're trying to do now is learn how to live with lions, to coexist."

Historically, coexistence with predators hasn't been a priority of many landowners in the West. Alongside wolves and grizzlies, mountain lions once represented an impediment to the ethos of manifest destiny. In 1907, California officially classified mountain lions as "bountied predator," incentivizing their eradication by offering $20 per carcass. When the program ended in 1963, state-deployed hunters had killed 12,461 mountain lions. "[Trappers] were doing such a good job that they worked themselves out of a job," said Dellinger, of the state Department of Fish and Wildlife.

No one knows for sure how many mountain lions were left in the state after the bounty period, but Dellinger says it's safe to assume the population recovered in the years since. State wildlife officials estimated in 1996 that about 5,000 cougars live in California, but Dellinger said that number could be wildly inaccurate. He's currently four years into a statewide mountain lion population survey expected to take a decade to complete.

The recovery keeps Martins and others in his field busy. "We've been killing [mountain lions] for centuries, and we still have problems," said Veronica Yovovich, a University of California, Berkeley biologist specializing in wildlife conflict mitigation. "We know that approach doesn't solve the problem, so we have to develop other tools."

In some instances, mitigating livestock-carnivore conflict nonlethally can be relatively simple. For many of the landowners in Martins' study area north of San Francisco, where most of the livestock in question are goats or alpacas, cougar problems can be avoided by putting animals in a roofed enclosure. It gets a little more complicated, however, with open rangelands and larger livestock operations. Ranchers might have to incorporate turboflaggery, electric fences, range riders, livestock guardian dogs, motion-controlled sprinklers, and so on.

Yovovich has a unique opportunity to test these methods on rangeland owned by the Midpeninsula Regional Open Space District, just west of San Jose. In November, Midpen decided that grazing lessees on its property would not be allowed to exercise lethal removal of mountain lions and coyotes, and the district pegged Yovovich to lead workshops with ranchers.

When I visited Yovovich at her office in Berkeley, she was excited — what she learns here could apply to numerous geographies. Midpen land is a mix of open rangeland and protected space, all on the edge of a burgeoning suburban area. "That mosaic represents anywhere in the West," she said. "All the information we get there can be extended to anybody else who's having problems with mountain lions."

Mountain lions contend with more than just ranchers defending their livestock. Take, for instance, 46M, a male lion tracked by Wilmers in 2014. The cougar gained notoriety when local officials discovered him in a parking garage in the middle of Silicon Valley. Police called Wilmers to safely capture and relocate the animal, but five months later, the cougar was hit by traffic in the hills above Stanford University and killed.

This is a common issue around the state. Vickers says a single culprit is responsible for killing half of his collared mountain lions in the Santa Ana Mountains southeast of Los Angeles: Interstate 15.

But it's the long-term impact of these highways that has researchers most worried. In 2018, a team led by University of Wyoming scientists (Wilmers and Vickers were co-authors) published findings that California's mountain lion population consisted of nine distinct genetic populations — a sign that habitat fragmentation has caused low genetic diversity.

"You look at other areas throughout the West, and you see that the genetic diversity is more spread out," said Tiffany Yap, a wildlife scientist at the Center for Biological Diversity. "The pattern here is that roads and development seem to be what shape those populations."

Take Wilmers' Santa Cruz Mountains population, one of the nine identified in the Wyoming paper. Its range falls within boundaries created by the coastline to the west and south, San Francisco to the north, and Highway 101 to the east. By nature, mountain lions — males in particular — tend to disperse from their home territories and spread their genetics throughout large swaths of habitat. But in his decade tracking mountain lions near Santa Cruz, Wilmers has never seen one make it outside their modern, hemmed-in territory.

That genetic isolation has drastic implications. Last March, Vickers published a study saying that some California cougar populations face extirpation within the next half-century. "It's remarkable to me that we can really cause potential extinction of such a highly mobile and capable animal," he said.

Genetic diversity has long been a mainstay of cougar conservation. In Florida, for instance, wildlife managers were so concerned with inbreeding among panthers that in 1995 they transported "new blood" from Texas to aid the panthers' recovery. In California, however, state biologists and researchers are focused on habitat restoration rather than relocating individual animals.

"If you want to protect a mountain lion, you need to protect the building block for that predator to be able to continue to exist," said Martins. "Conserving mountain lions is about broad habitat conservation."

The data that Wilmers, Vickers, Martins, and other researchers have been collecting on mountain lion dispersal patterns is helping conservationists target linkages between populations that can improve genetic diversity. For instance, the Center for Biological Diversity and other conservation groups convinced a superior court judge that a 270-acre mixed development and multilane highway in Temecula would block a corridor that links two lion populations, one in the Santa Ana Mountains and one in the Eastern Peninsula Range. The court's decision to pause the development could set a precedent throughout the southern part of the state.

Last year, the Center took its legal battle even further when it petitioned the state to list certain populations of mountain lions as threatened under the state Endangered Species Act. In April, the state Fish and Game Commission voted to move the petition forward, kicking off a yearlong review to determine whether these populations should be formally listed. If they are, "both state and local agencies would have a mandate to protect mountain lions," said J.P. Rose, an attorney with the Center who led the litigation against Temecula and other proposed developments in the Los Angeles area. "Local officials would need to coordinate closely with Fish and Wildlife to ensure that development projects don't block existing corridors."

Already, there are examples to draw from. The California Department of Transportation is building a wildlife tunnel beneath Highway 17, a known migration barrier that bisects the Santa Cruz Mountains. Nearby, the Peninsula Open Space Trust and the city of San Jose spent $93 million to preserve a wildlife corridor between the Santa Cruz Mountains and the Diablo Range. In the Santa Monica Mountains, engineers are designing what will be the largest wildlife bridge in the world over Highway 101. Advocates are quick to highlight smaller fixes, too: retrofitting culverts, restoring native vegetation, lowering highway median barriers, and so on.

"Southern California is providing an on-the-ground laboratory for identifying how to stop or repair the fragmentation of habitat that's causing wildlife species to be isolated," said Trish Smith, an ecologist with The Nature Conservancy. Sure, there are still plenty of challenges ahead for mountain lion conservation — land acquisition, the cost of wildlife-friendly infrastructure, and public acceptance of apex predators roaming freely to name a few. But Smith and others are hopeful about the recent progress.

"There's a potential to link these wildlife populations from the U.S.-Mexico border to the Oregon-California border," she said. "But we don't have much time to act. It's a major conservation challenge that requires that we work collaboratively and creatively."

In 2013, I woke up early to hike to the Numa Ridge Fire Lookout in Glacier National Park. The sun had already risen, but the cedars and hemlocks kept the trail shaded in a quiet dawn. A mile up the ridge, I rounded a switchback and came to a halt. There, perhaps 20 feet away, an adult cougar tread steadily up the trail with silent steps. I froze and tried to remember the protocol of staying calm, facing forward, and backing away slowly, but the golden cat gave nothing more than a lazy glance over its shoulder, turned off the trail, and faded from view.

"To see one in the wild is a life-changing experience. Very few people get that opportunity," Smith told me. "They seem to conjure up that feeling of wilderness."

But even more than wilderness, that mountain lion in Montana makes me think of the adaptability of creatures in our region. Cougars in Golden Gate Park and Glacier are reminders that these animals occupy the *whole* West, not just the preserved wildernesses and untouched landscapes with which we associate these charismatic species.

In her office, Yovovich, the Berkeley carnivore specialist, showed me a few photographs that she uses in workshop presentations. In one, a grainy security

image shows a young cougar standing on the hood of a Toyota Camry parked in a San Jose driveway. Another shows a family of mountain lions on a ridge in the Sierra Azul, the skyline of Silicon Valley stretched out before them. “This perfectly captures the Bay Area to me,” she said.

How different, really, is a mountain lion in a Silicon Valley driveway from the one I shared a trail with in Montana? Both feel the pressure of human presence on the landscape. Both are at the mercy of how we choose to perceive them. And both live here — in cities, wilderness, and everything in between.

Rapid growth of the US wildland-urban interface raises wildfire risk

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The wildland-urban interface (WUI) is the area where houses and wildland vegetation meet or intermingle, and where wildfire problems are most pronounced. Here we report that the WUI in the United States grew rapidly from 1990 to 2010 in terms of both number of new houses (from 30.8 to 43.4 million; 41% growth) and land area (from 581,000 to 770,000 km^2; 33% growth), making it the fastest-growing land use type in the conterminous United States. The vast majority of new WUI areas were the result of new housing (97%), not related to an increase in wildland vegetation. Within the perimeter of recent wildfires (1990–2015), there were 286,000 houses in 2010, compared with 177,000 in 1990. Furthermore, WUI growth often results in more wildfire ignitions, putting more lives and houses at risk. Wildfire problems will not abate if recent housing growth trends continue.

wildfires | housing growth | sprawl | development | fragmentation

The wildland-urban interface (WUI), defined as the area where houses are in or near wildland vegetation, is the area where wildfires pose the greatest risk to people due to the proximity of flammable vegetation (1). Wildfires frequently burn houses in the WUI (2, 3), and are most difficult to fight there. Furthermore, the WUI is where people often ignite wildfires (4), and the vast majority of fires are human-caused (5). While fires are an integral part of many ecosystems and the Earth system as a whole (6), humans have changed fire regimes globally (7) and throughout the United States (5), and climate change will increase fire frequency in the future, including in the WUI (8).

The close proximity of houses and wildland vegetation does more than increase fire risk (9). As houses are built in the WUI, native vegetation is lost and fragmented (10); landscaping introduces nonnative species and soils are disturbed, causing nonnatives to spread (11); pets kill large quantities of wildlife (12); and zoonotic disease, such as Lyme disease, are transmitted (13). Thus, understanding WUI patterns and WUI growth is important with respect to wildfires and many other environmental problems.

The WUI is widespread in the United States (1, 14) and in many other parts of the world (15, 16), including Argentina (17), Australia (18), France (19), and South Africa (20). Furthermore, both the annual area burned (8, 21, 22) and fire suppression costs (23) have rapidly increased in the United States. The area burned annually nearly doubled, from an average of 18,000 km^2/y in 1985–94 to 33,000 km^2 in 2005–14 (22). Concomitantly, federal wildfire suppression expenditures tripled from $0.4 billion/y to $1.4 billion/y (23), and exceeded $2 billion in 2017.

While there is ample evidence that houses in the WUI pose problems, it is not clear how fast the WUI is growing. Overall, the US population grew by 60 million people and 29.2 million homes from 1990 to 2010, but how much of that growth occurred in the WUI is uncertain. Previous assessments of WUI growth (24, 25) analyzed only housing data up to 2000, and did not account for changes in wildland vegetation. Post-2000 housing data are important, because the United States entered a recession after 2008, accompanied by a strong downturn in the housing market. Similarly, without data on vegetation change, the major cause of WUI growth is unclear. Areas where forests are regrowing on abandoned farmland, such as in the New England states (26), could see WUI growth without any additional houses. Fundamentally, two processes can create new WUI: construction of new homes in or near existing wildland vegetation, and an increase in wildland vegetation within and near previously developed areas. The prevalence of each process is unclear.

Knowing how the WUI is growing, and why, is essential when evaluating management and policy responses (3, 8). In the United States, federal wildfire management policy prioritizes fuel treatments and the promotion of fire-adapted communities in the WUI. Local jurisdictions use a variety of land use planning tools to limit the environmental impacts of housing growth in the WUI. The importance of the WUI for the environment and for national policy, accompanied by the lack of information about WUI growth in the most recent decade, highlight the need to both assess WUI growth and identify its causes. Thus, we addressed three major questions: (*i*) how much has the WUI in the conterminous United States grown from 1990 to 2010; (*ii*) whether WUI growth is caused mainly by housing growth or by vegetation growth; and (*iii*) how much WUI growth has occurred within recent wildfire perimeters.

The lack of consistent, fine-resolution longitudinal housing data has been the biggest impediment to a nationwide assessment

Significance

When houses are built close to forests or other types of natural vegetation, they pose two problems related to wildfires. First, there will be more wildfires due to human ignitions. Second, wildfires that occur will pose a greater risk to lives and homes, they will be hard to fight, and letting natural fires burn becomes impossible. We examined the number of houses that have been built since 1990 in the United States in or near natural vegetation, in an area known as the wildland-urban interface (WUI), and found that a large number of houses have been built there. Approximately one in three houses and one in ten hectares are now in the WUI. These WUI growth trends will exacerbate wildfire problems in the future.

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of WUI growth. The decennial US Census provides fine-resolution housing data for 1990, 2000, and 2010, but the boundaries of the smallest units for which housing units are reported (i.e., census blocks) often shift between decades, precluding direct change analyses (27). We have developed algorithms to convert the decennial Census data at census block resolution into a consistent dataset on housing growth across the conterminous United States (*Methods*), which we combined with 1992, 2001, and 2011 National Land Cover Data (NLCD) on wildland vegetation: forests (classes 41–43), shrublands (classes 51 and 52), grasslands (class 71), and woody wetlands (class 90). We mapped decadal WUI change from 1990 to 2010 within 2010 census block boundaries, based on the WUI definitions in the *Federal Register* and our previously developed WUI mapping algorithms (1, 14), and conducted several robustness checks of our new dataset (*Supporting Information*). Because of concerns about housing growth and wildfire management, we calculated housing growth for 1990–2010 within WUI burned areas identified in Landsat imagery between 1990 and 2015 (22).

We found that the WUI was widespread in 2010, covering 9.5% of the conterminous United States (Fig. 1), and that the WUI grew rapidly from 1990 to 2010 in all its aspects (Fig. 2).

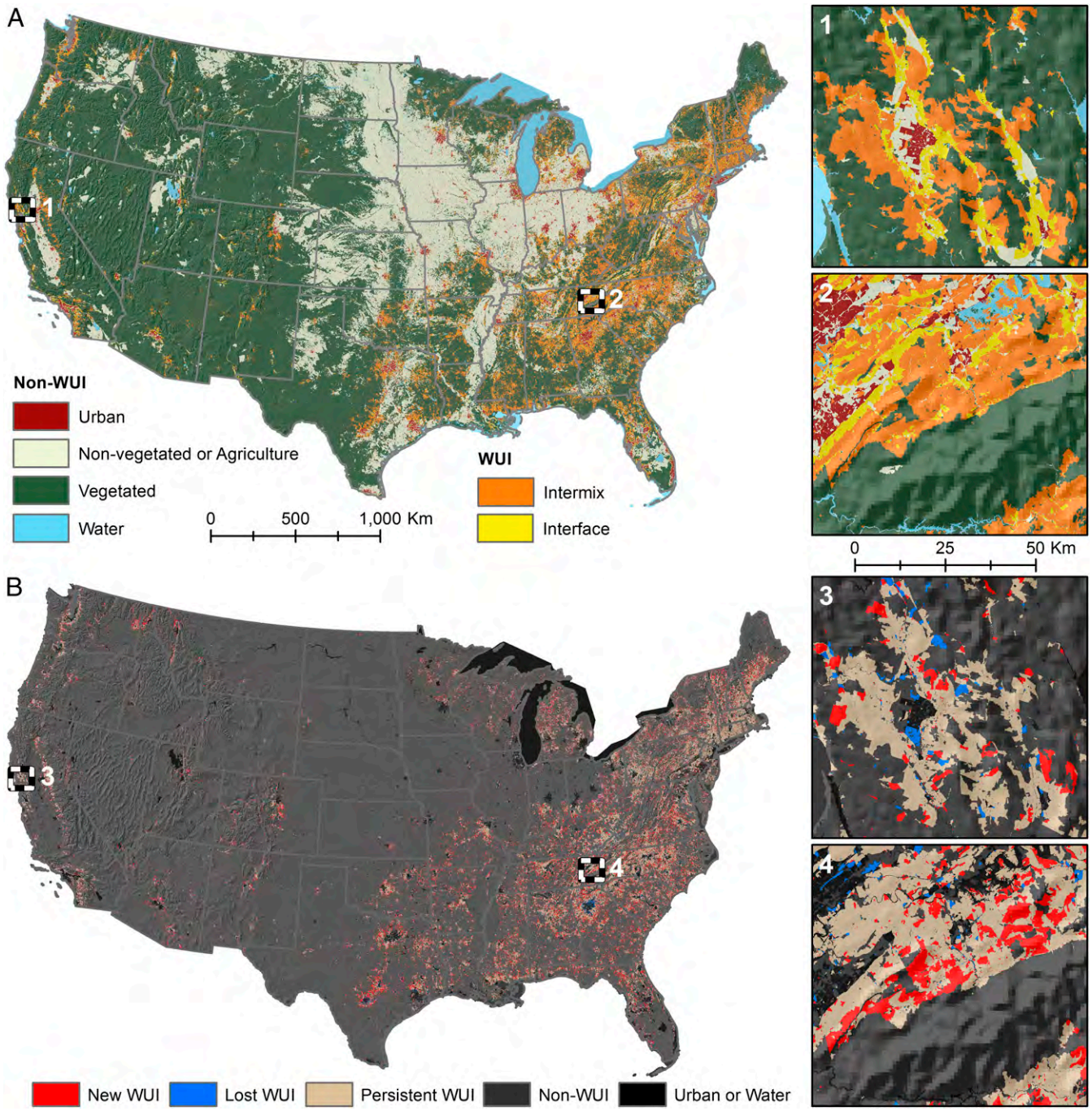

Fig. 1. The WUI in the United States was widespread in 2010 (*A*), as were changes in WUI area (*B*), for example, in and around Santa Rosa, California (1, 3), and Gatlinburg, Tennessee (2, 4), areas where wildfires destroyed many homes in 2017 and 2016, respectively.

The number of housing units ("houses" hereinafter) in the WUI grew fastest, followed by the number of people in the WUI and then WUI area (Fig. 2*B* and Table S1). New WUI area totaled 189,000 km^2, an area larger than Washington State. At 33%, WUI area growth is faster than that of any of the level I land cover categories included in the NLCD (28). Increases in houses and people were also strong, with 12.7 million more houses and 25 million more people in the WUI in 2010 compared with 1990. The overall combination of more WUI area (7.2% of the conterminous United States in 1990 vs. 9.5% in 2010; Fig. 2*C*) and higher growth rates for both houses and people in the WUI, compared with the nationwide averages (Table S1), increased the percentage of houses (from 30.3% to 33.2%) and people (from 29.4% to 31.9%) in the WUI from 1990 to 2010 (Fig. 2*C*). Even though the WUI occupies less than one tenth of the land area of the conterminous United States, 43% of all new houses were built there, and 61% of all new WUI homes were built in areas that were already in the WUI in 1990 (and remained in the WUI in 2010) (Tables S1 and S2).

There are two main types of WUI: intermix WUI, the area where houses and wildland vegetation directly intermingle, and interface WUI, where settled areas abut wildland vegetation (1). We found that intermix WUI was both more extensive and expanded much more rapidly in area (from 5.6% to 7.5% of the conterminous United States from 1990 to 2010) than interface WUI (from 1.6% to 2.0%). However, interface WUI had higher housing growth rates (43% from 1990 to 2010) than intermix WUI (38%) and non-WUI areas (23%; Table S1). In absolute numbers, there were 4.7 million more houses in the intermix WUI and 8.0 million more in the interface WUI in 2010 than in 1990.

Regional differences in WUI growth were striking (Fig. 3). The highest absolute gains in WUI area occurred in the East, whereas high gains in houses and people in the WUI were most common in the South and Southwest. Absolute gains are most relevant for management agencies, because they indicate how much area and how many people and houses may require management actions; however, rapid growth often garners the most attention. Across the United States there is an interesting dichotomy in that states in the East had large absolute gains, but relatively low WUI growth rates, largely because WUI was already so widespread in 1990. In contrast, states in the northern Rockies saw much smaller absolute gains in WUI area and houses, but rapid WUI growth rates.

New WUI areas arise either when new houses are built in or near wildland vegetation or when wildland vegetation regrows in or near settled areas. Between these two possible causes, housing growth was unambiguously the main cause for new WUI areas, with increases in vegetation contributing minimally. Of all new WUI areas, 97% were caused by housing growth in sparsely settled areas, pushing these areas over the threshold of 1 house per 40 acres (6.17 homes/km^2). Only 2% of new WUI area was due to vegetation growth alone, and 1% was due to the combination of both housing and vegetation growth (Table S2). Similarly, new houses were the cause of >80% of WUI growth in all states except Delaware, the District of Columbia, Maryland, and New Jersey (Fig. S1).

Among areas that were WUI in 1990, the vast majority were still WUI in 2010, and both homes and population increased in those areas over that time (Table S2). A small proportion (6%) of the 1990 WUI areas dropped out of the WUI by 2010. Among all WUI changes (i.e., gains and losses combined), 13% of the changes in WUI area and 23% of the changes in WUI houses from 1990 to 2010 were losses. In terms of the causes of WUI area loss, reduced housing density was the most important (65.0%), whereas the loss of vegetation accounted for 32.6%. Housing density may have declined due to actual removal of housing units, or possibly due to enumeration errors in the Census data. Loss of vegetation was the dominant driver of loss of homes from the WUI (65.0%), which occurred largely in densely settled areas where additional housing development, deforestation, or fuel management may have removed wildland vegetation.

The number of houses within burned areas in the different decades is a strong indication of how much WUI growth can exacerbate wildfire problems. In 1990, there were 177,000 houses within the perimeters of the fires that occurred in the subsequent 25 y. By 2010, there were 286,000 housing units in the same fire perimeters, i.e., 109,000 more, which corresponds to 62% growth (far outpacing the average US housing growth rate of 29%). Of these new houses, those built before the wildfires occurred complicated firefighting because more houses had to be protected and more residents had to be evacuated. Similarly, houses built after fires occurred are of concern because new development in areas that burned recently, and thus are known to have a high fire risk, suggests that there is little adaptation to fire risk (2).

Our results provide compelling evidence that the WUI in the United States has grown rapidly, despite the risks that wildfires pose to homes and lives (3) and despite the other environmental problems caused by housing development in or near wildland vegetation (9). Our findings are generally in alignment with previous studies that found rapid previous WUI growth (24) and widespread potential for future WUI growth (25, 29), even though absolute numbers are not comparable because of differences in WUI definitions, datasets, and time periods (30). Furthermore, the WUI is not unique to the United States, but is widespread in many other countries as well (15, 16, 18–20). Rampant WUI growth demonstrates that the social and economic factors that together propel WUI growth are strong. WUI areas are attractive places to live because of affordability and ready access to natural settings and recreation (31). As WUI areas attract new residents, the number of houses per capita often increases as well, due to increasing rates of seasonal homeownership and declining family size (32). Indeed, despite the economic downturn after 2008, the absolute number of

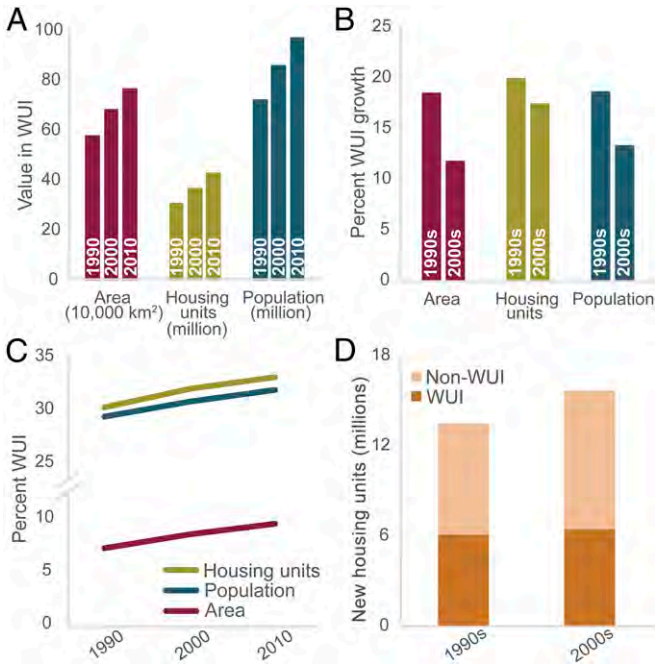

Fig. 2. WUI growth was rapid in terms of the absolute numbers of the area, houses, and people in the WUI in 1990, 2000, and 2010 (*A*); WUI growth rates during the 1990s and the 2000s (*B*); the proportion of all houses and people, as well as the land area in the WUI in 1990, 2000, and 2010 (*C*); and the absolute number of all new housing units within and outside the WUI during the 1990s and 2000s (*D*).

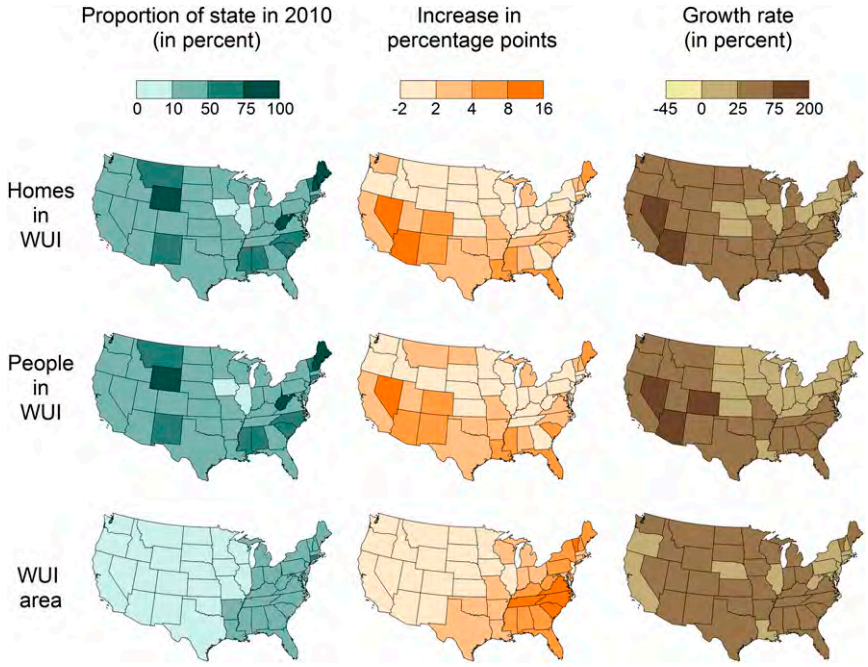

Fig. 3. WUI growth differed greatly among states, especially in the Southwest versus the Southeast, in terms of houses in the WUI, people in the WUI, and WUI area, calculated as the percentage of the state total in 2010, change in the WUI percentage from 1990 to 2010, and the growth rate (in percent) of the WUI from 1990 to 2010. Only the District of Columbia had negative absolute growth in the WUI (homes, people, and area). Fig. S2 summarizes these metrics at the county level.

houses built in the WUI, and in the United States as a whole, was higher between 2000 and 2010 than between 1990 and 2000 (Table S1). Demographic trends do not suggest slower future WUI growth. Furthermore, climate change projections indicate that conditions favorable for wildfires will occur more frequently in the future (8). Thus, increased wildfire ignition rates due to WUI expansion will initiate more wildfires in vegetation that is more susceptible to fire spread, leading to more widespread fires and possibly more severe fire behavior (33). This suggests that WUI growth and climate change together will compound the existing problems with wildfires in the WUI.

As WUI growth continues, there are many management options and policy tools to consider for addressing both wildfire and other environmental problems. Just as WUI-related problems involve actors (e.g., homeowners, community leaders) at many levels, so too must their solutions involve actors at multiple levels (i.e., local, regional, state, and national) (3, 8). Homeowners can reduce their individual fire risk by removing vegetation directly adjacent to their house (i.e., the home ignition zone; refs. 3 and 34), changing roofing and building materials, and following additional Firewise recommendations (35). To limit some of the other environmental problems associated with living in the WUI, homeowners can keep cats inside and dogs on a leash, limit fertilizer and pesticide use, and landscape with native plants (9). To reduce wildfire impacts, communities can coordinate fuel reduction efforts, educate homeowners, train firefighters, and establish wildfire management plans. Insurance companies can offer reduced premiums for communities taking mitigation action to incentivize community-level efforts to reduce wildfire losses. Communities and local jurisdictions could anticipate wildfires and environmental impacts more explicitly when planning future land use to avoid housing expansion in high-risk wildfire areas and other environmentally sensitive areas (36). State and federal agencies typically do not regulate development directly, but can allocate resources to areas experiencing rapid WUI growth, support local and regional planning efforts, and provide important research data and information to help communities adapt to fire-prone environments. Agencies managing public lands could consider targeted purchases of private inholdings to limit future housing growth within the administrative boundaries of public lands, which has been particularly rapid (37). In summary, there are many concrete management actions and policy responses that can limit the negative effects of WUI growth on wildfire risk and other environmental problems, but changes will require efforts at all levels by homeowners and community leaders, local and county governments, and state and federal agencies.

Housing development in the WUI greatly exacerbates wildfire problems and other environmental issues in the United States (1, 5, 8), and globally (16, 18–20). Our results highlight the magnitude and rapid rates of WUI growth in the US, underscoring the urgency of identifying what can be done to address WUI growth and its associated wildfire challenges (3). Past federal fire policy has focused largely on fighting and preventing wildfires and on fuel reduction, public outreach campaigns, and other actions (38). Although laudable, such efforts are unlikely to be successful by themselves, because housing growth is clearly the dominant cause of WUI growth, as well as a major factor contributing to wildfire occurrence and cost. As long as WUI growth is unchecked, wildfire problems will likely worsen. On a more hopeful note, to the extent that WUI growth reflects an affinity for nature, the evident consequences and costs of growth could prompt discussions on how to sustain those highly valued ecosystems in which so many people have chosen to live.

Materials and Methods

Our WUI definition is based on the definition published by the US government in the *Federal Register* (39) and that has been widely used for WUI assessments in the past (1, 14, 40). It specifies two types of WUI, intermix and interface. Intermix WUI is where houses and wildland vegetation intermingle, with both a housing density of >1 house per 40 acres (6.17 houses/km^2) and >50% of the area in wildland vegetation. Interface WUI represents settled areas that have <50% vegetation, but lie within

1.5 miles (2.4 km) of a densely vegetated area (at least 75% wildland vegetation) that is at least 5 km^2 in size (so that settlements near small urban parks are not included in the WUI).

Our WUI assessment was based on two main datasets: US Census data, which provided housing data (TIGER shape files for block boundaries, plus Census summary files for attribute data), and the US Geologic Survey's NLCD, which provided information on wildland vegetation. We derived housing data from the US Decennial Censuses for 1990, 2000, and 2010 at its finest resolution, the census block level. However, a major obstacle to conducting change analyses is that census block boundaries frequently change from one decade to the next, preventing direct change analyses (27). Indeed, 62% of all blocks changed their boundaries from 1990 to 2000, and 56% changed from 2000 to 2010, invalidating any housing density change analysis that does not account for these boundary changes. We used additional information available from the US Census Bureau as relationship files that details for each decade which blocks of the starting date were at least partly contained by which block in the second decade, and vice versa, to calculate the number of 1990 and 2000 housing units for the boundaries for each 2010 census block.

Based on the Census Bureau relationship files, we first allocated 1990 housing units to 2000 block boundaries by identifying the type of relationship for each 1990 block to 2000 block(s), classifying the relationship as one-to-one, one-to-many, many-to-one, or many-to-many. For one-to-one and many-to-one relationships, 1990 housing units were allocated directly to corresponding 2000 blocks. For one-to-many relationships, 1990 housing units were allocated proportionally based on the number of housing units in the 2000 blocks. For many-to-many relationships, we identified the least common denominator of polygons that fully contained groups of both 1990 and 2000 blocks. For each least common denominator polygon, we then summed the 1990 housing units and allocated them based on the proportion of the 2000 housing units. To minimize instances of many-to-many relationships and maximize direct relationships, we removed blocks that were classified as water in 1990 and as vacant in 2000, as well as all 1990 and 2000 blocks that intersected by <1% of their area. Once 1990 housing units were allocated to 2000 census block geometry, we repeated the process using the 2000–2010 relationship files to allocate 2000 housing units to 2010 block boundaries. We then joined the 1990 housing units allocated to 2000 block boundaries with the 2000–2010 relationship files, and repeated the process to allocate 1990 housing units to 2010 block boundaries. The end result of our algorithms are 1990 and 2000 housing units allocated to the 2010 block geometry across the conterminous United States, i.e., a dataset that permits valid analyses of housing growth across the United States at fine spatial resolution and that minimizes erroneous changes due to changing census block boundaries.

We further refined census block boundaries by integrating them with information on the boundaries of protected areas. The boundaries of protected areas were provided by the Protected Area Database, version 2. Where protected areas intersected census block boundaries, we assumed that the houses in that block were located in nonprotected areas only. However, where census blocks with houses were entirely within a protected area, we made no changes, and assumed a uniform housing density throughout the block.

The 30-m resolution NLCD provided us with data on wildland vegetation. We analyzed both the 1992/93–2001 and the 2001–2011 land cover change products and calculated the percentage of each NLCD land cover class within each census block after refinement by the protected area boundaries. We included forest and grass/shrub land cover classes as wildland vegetation and excluded open water, urban, barren, wetlands, and ice/snow.

For each decade, we mapped the WUI separately, by combining 1990 Census data with 1992/93 data from the 1992/93–2001 land cover change product, and 2000 and 2010 Census data with 2001 and 2011 data from the 2001–2011 land cover change product. We first identified all intermix WUI areas based on the housing and vegetation thresholds. We then identified contiguous vegetation areas that were at least 5 km^2 in size and had >75% wildland vegetation, selecting areas within 2.4 km that were above the housing threshold (but below the 50% vegetation threshold), and labeling these as interface WUI. When census blocks were only partly within this distance, we split them.

The NLCD change products are not fully consistent, in that the 2001 land cover in the 1992/93–2001 change product differs from the 2001 land cover in the 2001–2011 change product. Thus, we conducted a sensitivity analysis and mapped the 2001 WUI twice, based on the two representations, and then compared the resulting WUI maps. The differences between the two WUI maps were very minor.

To calculate the number of homes within fire perimeters over time, we analyzed all fire perimeters of fires that burned between 1990 and 2015 according to the Monitoring Trends in Burn Severity (MTBS) dataset, which includes all fires >404 ha (1,000 ac) in the West and 202 ha (500 ac) in the East. We then assessed which census blocks were at least partially within these fire perimeters and calculated an area-weighted estimate of the number of housing units within the fire perimeters in 1990 (177,000), 2000 (210,000), and 2010 (286,000). We note that this is a conservative estimate of the number of houses affected by wildfires because the MTBS dataset does not include small fires.

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FAST-TRACK

A southern California freeway is a physical and social barrier to gene flow in carnivores

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Abstract

Roads present formidable barriers to dispersal. We examine movements of two highly mobile carnivores across the Ventura Freeway near Los Angeles, one of the busiest highways in the United States. The two species, bobcats and coyotes, can disappear from habitats isolated and fragmented by roads, and their ability to disperse across the Ventura Freeway tests the limits of vertebrates to overcome anthropogenic obstacles. We combine radio-telemetry data and genetically based assignments to identify individuals that have crossed the freeway. Although the freeway is a significant barrier to dispersal, we find that carnivores can cross the freeway and that 5–32% of sampled carnivores crossed over a 7-year period. However, despite moderate levels of migration, populations on either side of the freeway are genetically differentiated, and coalescent modelling shows their genetic isolation is consistent with a migration fraction less than 0.5% per generation. These results imply that individuals that cross the freeway rarely reproduce. Highways and development impose artificial home range boundaries on territorial and reproductive individuals and hence decrease genetically effective migration. Further, territory pile-up at freeway boundaries may decrease reproductive opportunities for dispersing individuals that do manage to cross. Consequently, freeways are filters favouring dispersing individuals that add to the migration rate but little to gene flow. Our results demonstrate that freeways can restrict gene flow even in wide-ranging species and suggest that for territorial animals, migration levels across anthropogenic barriers need to be an order of magnitude larger than commonly assumed to counteract genetic differentiation.

Keywords: carnivores, conservation genetics, gene flow, habitat fragmentation, road and anthropogenic barriers, territoriality

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Introduction

Roads are the primary threat to dispersal between habitat patches in urban landscapes (Forman & Alexander 1998) and, without dispersal, isolated populations may be doomed to extinction (Brown & Kodric-Brown 1977; Hanski *et al*. 1996). Roads can also isolate populations previously in genetic communication, and the resulting genetic erosion may contribute to population decline (Saccheri *et al*. 1998; Westemeier *et al*. 1998). Empirical data on the frequency of dispersal across roads and its effect on genetic variation and population persistence are few and limited to small and relatively abundant species with low vagility (e.g. frogs, Reh & Seiz 1990; voles, Gerlach & Musolf 2000; beetles, Keller & Largiadér 2003). In contrast, the ability of large carnivores to disperse long distances could mitigate the effects of genetic isolation. However, for carnivores, population densities are low and home range

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sizes and dispersal distances are large (Sunquist & Sunquist 2001), so their persistence should be strongly influenced by the isolating effects of roads and development. Additionally, carnivores are susceptible to the deleterious genetic effects of inbreeding in small populations (O'Brien *et al.* 1985; Roelke *et al.* 1993; Vila *et al.* 2003; Liberg *et al.* 2005). Although conservation biologists have focused on the importance of connectivity for carnivores, actual demonstrations of the genetic consequences of roads for such long-lived and mobile species have been lacking.

We studied dispersal and genetic differentiation in coyote (*Canis latrans*) and bobcat (*Lynx rufus*) populations separated by a wide and heavily travelled freeway in the highly urbanized landscape of southern California. To obtain a direct estimate of dispersal, we radio-tracked animals on both sides of the freeway over seven years, from 1996 to 2003. To obtain a genetic estimate of dispersal, we genotyped individuals using highly variable microsatellite loci and then used genetic assignment tests based on the composite genotypes to assign animals genetically to each side of the freeway. We then assessed levels of genetic differentiation between populations on the same and different sides of the freeway to measure the effect of the road on gene flow (genetically effective migration). Finally, we determined whether levels of observed migration were consistent with levels of gene flow estimated by a coalescent model based on the number of generations since the freeway was established. The use of both radio-tracking information and genetic data to monitor migration and gene flow allows an assessment of the long-term genetic consequences of roads and other anthropogenic barriers on genetic diversity and can lead to the development of plans to mitigate their effects.

Materials and methods

We studied coyote and bobcat populations separated by the Ventura Freeway (US101), a congested 10–12 lane road in the San Fernando Valley 40 km from downtown Los Angeles. More than 150 000 vehicles use the road daily and the presence of a meridian fence largely restricts dispersal to underpasses and culverts (Fig. 1A) (Ng *et al.* 2004). The freeway was established in 1949 from a relatively undeveloped secondary road with minimal traffic (B. Marquez, personal communication), and there are no other natural barriers such as rivers or topographic features following the freeway that would have historically restricted gene flow. The study area consisted of 358 km^2 of chaparral, grassland, and oak woodland habitat (Table S1, Supplementary material) interspersed with secondary roads and housing developments. The 28.4-km length of the freeway connects the towns of Agoura Hills and Thousand Oaks that have a combined population of 200 000. The area is considered a critical habitat corridor connecting the Santa Monica Mountains with extensive natural habitat to the north (Penrod *et al.* 2001).

Animal capture and radiotelemetry

Bobcats and coyotes were captured with padded foothold traps in 1996–1998 and with box traps (bobcats) and neck snares (coyotes) in 2000–2003. We also genotyped a population of bobcats from northern California where bobcats were captured with box traps from 1992 to 1995 (Riley *et al.* 2004). Captured animals were aged, sexed, weighed, measured, ear-tagged, radio-collared, and released at the capture site. Blood, hair, scat, and in some cases tissue samples were taken for genetic analyses.

Animals were radio-located by triangulation using three consecutive or two simultaneous compass directions obtained with a peak directional antenna. Locations were obtained throughout the 24-h daily cycle. We computed 95% minimum convex polygon home ranges for animals with at least 20 locations. Home range overlap was computed for animals that were radio-tracked concurrently. We computed overlap as the total percentage of the home range that intersected with any other animals of the same sex.

Genetic sampling

All bobcat and coyote DNA samples were extracted from blood or tissue (ear punch) samples taken at time of capture. Standard phenol–chloroform extraction methods were utilized. Seven dinucleotide microsatellite loci developed for the domestic cat (Menotti-Raymond *et al.* 1999) and validated for polymorphism in the bobcat (Ernest *et al.* 2000) were used to genotype all bobcat specimens (FCA026, FCA043, FCA045, FCA077, FCA090, FCA096, and FCA132). Seven tetranucleotide microsatellite loci developed for the domestic dog (Breen *et al.* 2001) and validated as polymorphic for the coyote by the authors were used to type all coyote specimens (FH2001, FH2137, FH2422, FH2062, FH2226, FH2293, and PEZ19). Polymerase chain reactions (PCR) utilized either (i) a fluorescent dye-labelled forward primer, or (ii) a hybrid combination of forward primers consisting of the published forward primer with the M13F (–20) sequence (16 bp) added to the 5′ end and a fluorescent dye labelled M13F (–20) primer. The unlabelled reverse primer was used in both cases. We used the PCR conditions for the hybrid combination primer (a two-step cycle) (Boutin-Ganache *et al.* 2001). Primer dye labelling utilized BeckmanCoulter dye D4 and PCR products were sized on the BeckmanCoulter CEQ2000XL DNA Analysis System.

Genetic analysis

Observed and expected heterozygosities, allelic diversity, and deviation from Hardy–Weinberg equilibrium were assessed with GENEPOP (Raymond & Rousset 1995; Table S2, Supplementary material). Bonferroni corrections to significance levels were applied to account for multiple

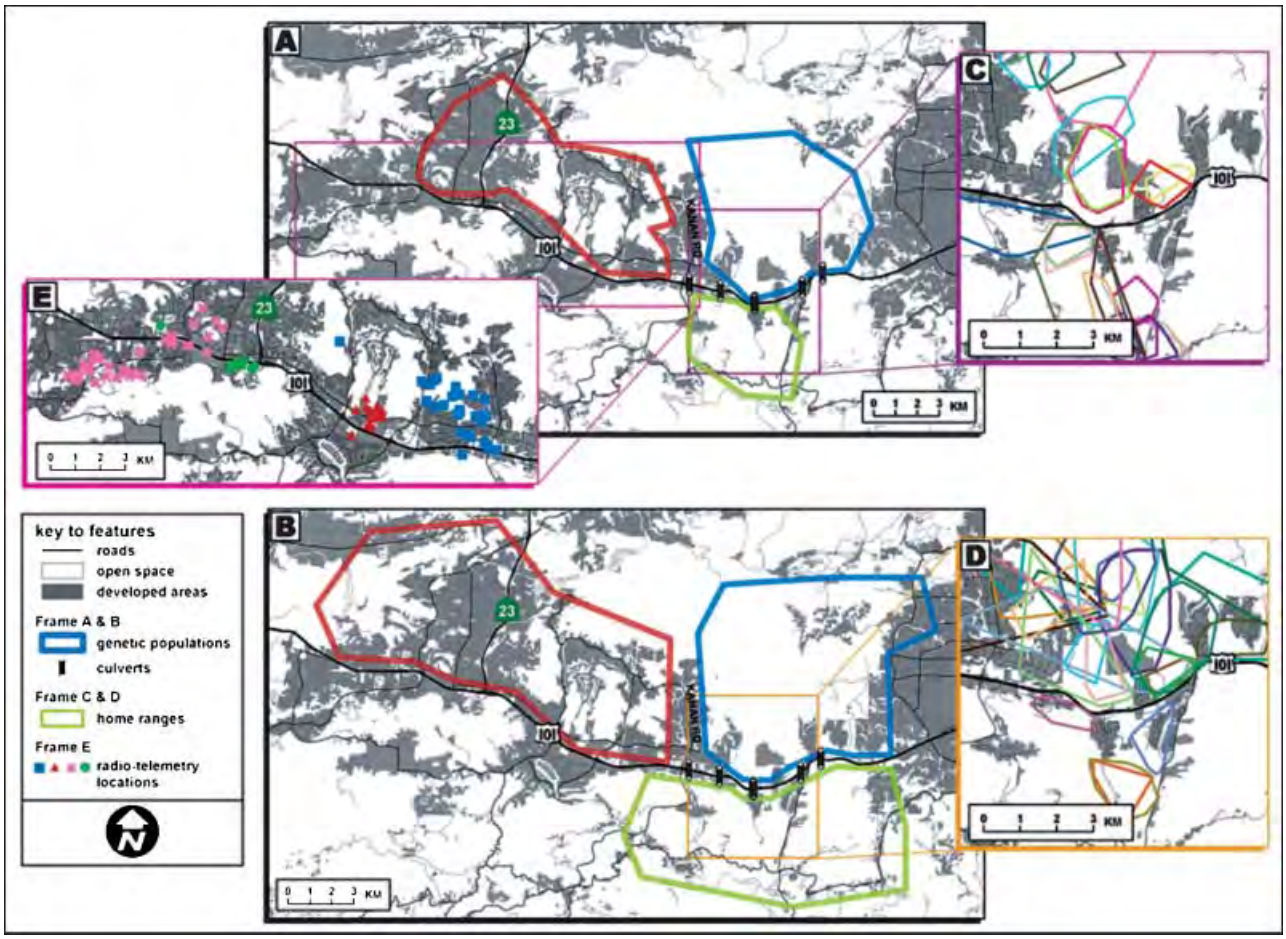

Fig. 1 Study populations, home ranges and radio-locations of bobcats and coyotes near the Ventura Freeway in southern California. Bobcat (A) and coyote (B) study populations are located north and south of the Ventura Freeway. The north side populations are further divided by Kanan road into northeast and northwest populations. 95% minimum convex polygon (MCP) home ranges are shown for all radio-tracked bobcats (C) and coyotes (D) near the freeway between the south and northeast populations. In (E), radio-telemetry locations are shown for four bobcats with locations north and south of the freeway that were captured north of the freeway but assigned genetically to the population south of it (see Fig. 2).

tests in the determination of heterozygote deficiency/excess (Rice 1989). Coyote samples were grouped into two populations north and south of the freeway, whereas bobcats were divided into three populations, two north and one south of the freeway according to STRUCTURE results (see Results and discussion).

To obtain a genetic estimate of dispersal, we used assignment tests based on the composite microsatellite genotypes. Assignment tests identify the population of origin for each individual, and thus individuals assigned to a population other than the one in which they were caught can be considered migrants (Berry *et al*. 2004). We used the program STRUCTURE (Pritchard *et al*. 2000) to assign individuals to populations. STRUCTURE is a Bayesian clustering algorithm that uses multilocus genotypes to infer population structure and assign individuals to populations. All individuals were combined into one data set for analysis, without any a priori population assignments. We utilized a burn-in of 50 000 iterations, followed by 500 000 iterations of the Gibbs sampler. Admixture was allowed. We evaluated K values, the number of assumed populations, from 1 to 6. Each value of K was run a minimum of three times to evaluate stability. For the highest likelihood K value, we then evaluated the cluster assignment results for each individual with respect to its capture location.

For potential migrants identified in the initial STRUCTURE analysis, we modified the STRUCTURE input data file to reassign them to their putative population of genetic origin based on the cluster assignment results. We then calculated the posterior probability of correct population assignment with this revised data set in STRUCTURE using the ancestry model with admixture, incorporating population information with the migration parameter set to $v = 0.1$ (Table S5, Supplementary material).

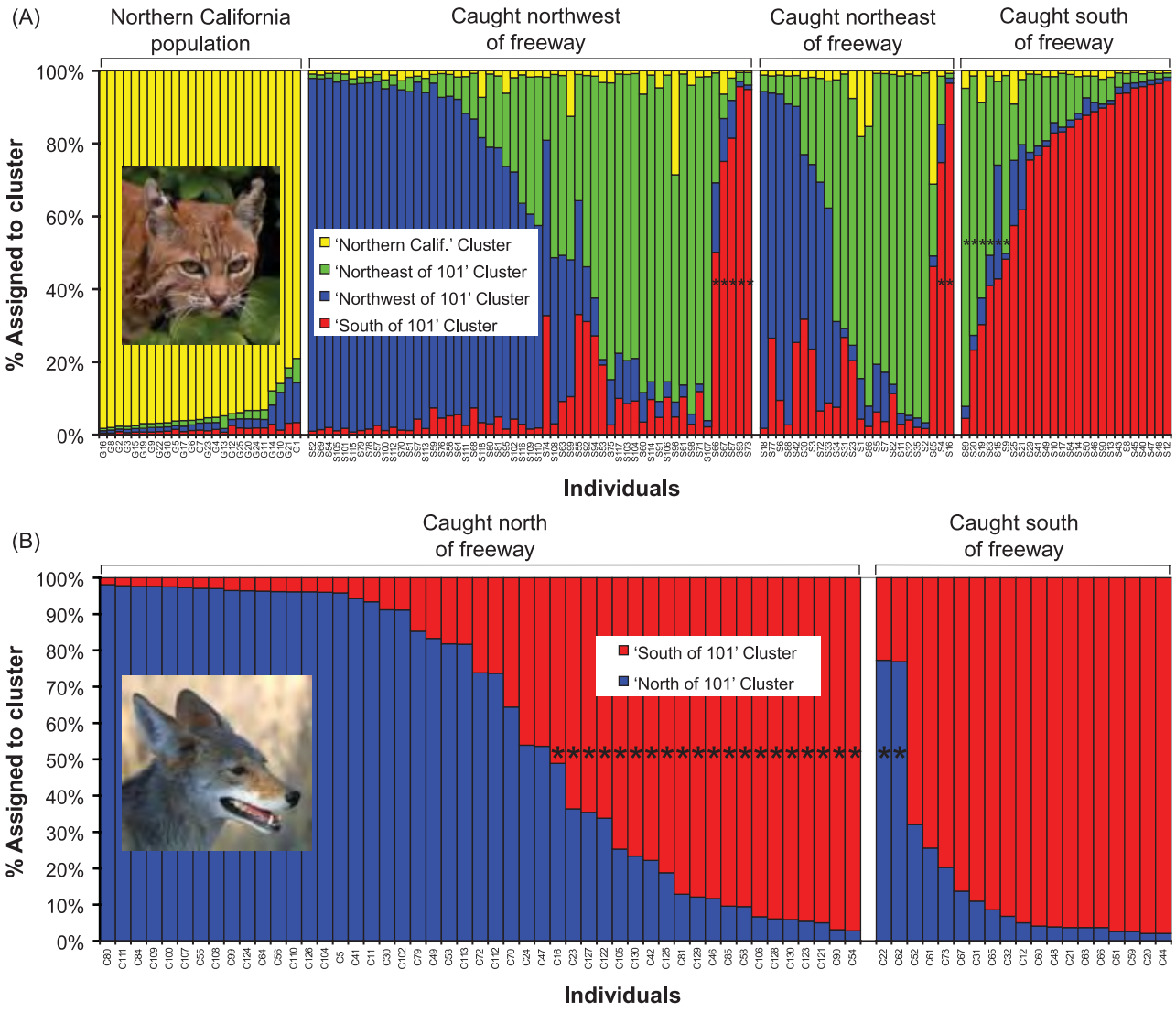

Fig. 2 Genetic assignment results from the program STRUCTURE for bobcat (top) and coyote (bottom) populations. Individuals are grouped according to capture location. Genetic population clusters are coded with different colours and the fraction of colour for each individual represents the probability of assignment to the cluster with that colour. Four clusters were found in bobcats, corresponding to a northern California group (yellow), two groups on the north side of the freeway (blue and green) and one group on the south side of the freeway (red). In coyotes, two clusters are supported by STRUCTURE, corresponding to a north (blue) and south (red) cluster. Asterisks denote misassigned individuals (individuals with greater than 50% assignment to a cluster different from the capture location) that are potential migrants.

We measured population differentiation by calculating population pairwise F_{ST} values and significance (*g*-test) using the program FSTAT (Goudet 2002). We estimated gene flow as the number of genetic migrants (*Nm*) between populations from F_{ST} values [$F_{ST} \approx 1/(1 + 4Nm)$; Wright 1921]. Population membership was based on the capture location north or south of the Ventura Freeway. The northern population was additionally split into northwest and northeast populations to measure differentiation between populations on the same side of the freeway. Computing F_{ST} between these two populations north of the freeway allows us to compare the amount of genetic differentiation across the freeway with that over the same or greater distance without the barrier. The east and west populations were divided by Kanan Road, a secondary road, and surrounding development (Fig. 1A,B).

We also computed the pairwise relatedness coefficient, *R* between individuals, (Queller & Goodnight 1989) using the program KINSHIP (Goodnight 2005). We identified pairs of individuals significantly related ($\alpha = 0.05$) at the $R \geq 0.25$ level by first performing a simulation in KINSHIP using the complete population data set at $R = 0.25$, followed

by log-likelihood calculations for all possible pairs. Based on the three defined populations, two north and one south of the freeway, for both bobcats and coyotes, we then determined the percentage of number of close relatives ($R \geq 0.25$) across the freeway, across a similar distance on the same side of the freeway, and within each population (Fig. S1, Supplementary material).

We used coalescent simulation to generate predicted levels of genetic differentiation based on a population isolation event with the program SIMCOAL (version 1.0) (Excoffier 2004). SIMCOAL is a computer program for the simulation of molecular genetic diversity in an arbitrary number of diploid populations based on a retrospective coalescent approach. SIMCOAL was utilized to estimate expected population pairwise F_{ST} values for both bobcat and coyote microsatellite results, based on the time since the freeway was built. A sensitivity analysis was performed on the parameter space of inference for the simulations by varying population effective sizes, sample sizes, migration rates, number of generations since a historical event (population separation), and microsatellite mutation rate. The microsatellite mutation rate was varied from 10^{-3} to 10^{-2} based on observed mutation rates for dinucleotide and tetranucleotide microsatellites for the domestic dog (Francisco *et al*. 1996). Effective population sizes (N_e) were estimated as the number of territorial adults in the study area based on telemetry observations. This calculation assumes that all territorial individuals reproduce equivalently; however, sensitivity analysis showed that results were not sensitive to small changes in N_e or sample size. One thousand analysis iterations were performed for each combination of input parameters. SIMCOAL output results were then analysed using ARLEQUIN (Schneider *et al*. 2000) for pairwise population F_{ST} estimation. F_{ST} values were determined by averaging the F_{ST} values of all 1000 iterations. Because sensitivity analysis showed that population effective size and sample size had minimal effect on F_{ST} within the range of our study values, they were held constant at 200/50 (population effective size/sample size) for bobcats and 75/25 for coyotes. The number of generations since separation was varied from 25 to 100, and migration rate was varied from 0 to 10% of source population. We assume a 2-year generation time for coyotes and bobcats (Knick *et al*. 1985; Bekoff & Wells 1986).

Results and discussion

We captured bobcats and coyotes on the north and south sides of the freeway and placed radio-telemetry collars on 110 (92 north side, 18 south side) coyotes and 87 (64 north side, 23 south side) bobcats. Using radio-telemetry, from 1996 to 2003 five (4.5%) radio-collared coyotes and 10 (11.5%) radio-collared bobcats were observed to cross the freeway, whereas 58 (52%) coyotes and 40 (45%) bobcats crossed major secondary roads. Because a principal study objective was to understand the effects of roads, and in particular the freeway, on carnivore movement, all radio-collared animals were captured within dispersal distance, and many within an average home range diameter, of both the freeway and secondary roads. However, only 213 (2.3%) of 9311 bobcat locations and 19 (0.4%) of 4565 coyote locations were on the opposite side of the freeway from the capture location of the individual.

Home range perimeters followed but did not cross roads such as the freeway, implying that they functioned as artificial territorial boundaries (Fig. 1C, D). For both male and female bobcats, home ranges that bordered on hard boundaries such as the freeway or development were significantly smaller than those that did not (males: $t = -1.919$, one-sided $P = 0.033$; females: $t = -2.186$, one-sided $P = 0.018$). Also, for adult female bobcats, the age class most important for reproduction, home range overlap was three times higher among individuals with home ranges adjacent to development and the freeway than in those with nonadjacent home ranges (38.8% vs. 12.4% overlap; $t = -1.77$, one-sided $P = 0.045$). For coyotes, we did not radio-track a sufficient proportion of territorial individuals throughout the study area to reliably measure territory overlap. Overall, the freeway was a significant barrier to movement as only about 5–10% of individuals crossed in the 7 years of observation, and home range boundaries, overlap, and size were affected by its proximity.

We genotyped 68 (49 north side, 19 south side) coyotes and 108 (82 north side, 26 south side) bobcats for variation in seven microsatellite loci. Microsatellite loci were highly polymorphic for both species (Table S2, Supplementary material). We also typed a population of 25 bobcats from Golden Gate National Recreation Area in the San Francisco Bay Area, a geographically remote and genetically distinct population (Riley *et al*. 2004). For bobcats, the STRUCTURE assignment test results determined that four populations best fit the data (Table S3, Supplementary material), with the northern California population clearly separated from those in southern California and two populations located north and one south of the freeway (Fig. 2A). All bobcats from northern California were assigned correctly to that population. However, seven bobcats caught north of the freeway, five to the west and two to the east, were assigned genetically to the south side population with assignment probabilities and posterior probabilities of greater than 50% (Fig. 2A; Table S5, Supplementary material). We had radio-telemetry observations on six of these seven bobcats, and four of the six were located south of the freeway at least once (Fig. 1E), corroborating their status as migrants. Six bobcats assigned north of the freeway were captured to the south (Fig. 2A). None of these bobcats were found north of the freeway based on

radio-telemetry observations, although three were located within 500 m of it, and two within 100 m. Therefore, based on genetic assignment and in part supported by telemetry observations, 9% (7 of 80) of the bobcats sampled from the north side of the freeway and 23% (6 of 26) of the bobcats sampled from the south side are putative migrants (see Fig. 2A). Considering the limited sampling of activity provided by radio-telemetry, the genetically derived estimate of migration (13 of 106 individuals or 12.3%) and that based on telemetry (10 of 87 individuals or 11.5%) are remarkably similar and suggest that about 12% of the sampled bobcat population crossed the freeway over the 7-year study period, or 3.4% per generation.

For coyotes, the assignment test determined that two populations best fit the observed data, one north and one south of the freeway (Fig. 2B; Table S3, Supplementary material). Two of 19 individuals (11%) captured south of the freeway were assigned to the north side population with assignment probabilities and posterior probabilities of greater than 50% (Fig. 2B; Table S5). Radio-telemetry observations were available for one of these two coyotes, and none of the 107 locations were north of the freeway, although six of the first seven locations were within 1.5 km of it, indicating that this coyote may have dispersed from the north. Twenty of the 49 coyotes (41%) captured on the north side of the freeway were assigned to the south side. We had radio-telemetry observation on 18 of these coyotes, and none showed evidence of crossing the freeway, although 11 of 18 were observed within 1 km of it. Consequently, the genetic results suggest that 10% of the South side population and as much as 41% of the north side population may be migrants. This implied migration fraction of 32% (22 of 68 individuals) or 9.1% per generation is much larger than the value of 4.5% or 1.3% per generation based on telemetry observations. Considering higher assignment thresholds of 80% and 90%, 21% (14 of 68) or 5.9% per generation and 10% (7 of 68) or 2.9% per generation, respectively, are still misassigned and likely to be migrants. The discrepancy between genetic- and telemetry-based estimates may reflect the unlikely probability of observing dispersal with limited radio-telemetry observations or the difficulty of classifying migrants in genetically similar populations. The use of assignment tests to measure dispersal requires a modest degree of genetic differentiation between populations, otherwise historical gene flow will confound the assessment of recent dispersal events (Berry *et al*. 2004). However, two observations argue for a higher dispersal rate than suggested by telemetry observations. First, coyotes generally disperse farther than bobcats (Van Vuren 1998), which had higher observed and implied rates of migration (see above). Second, of the 22 coyotes that were genetically misclassified, 14, or 64%, were juveniles or yearlings, the ages when coyotes typically disperse (Gese *et al*. 1989). This compares to 39% juveniles or yearlings in the population of coyotes that were not misclassified.

Although the freeway is a barrier to movement, rates of migration of 3.4% per generation for bobcats and from 1.3% to 9.1% per generation for coyotes as suggested by telemetry or genetic data imply high rates of gene flow sufficient to counteract drift (Mills & Allendorf 1996; Vucetich & Waite 2000). To assess levels of differentiation, we measured F_{ST}, the fixation index, for the seven microsatellite loci. For both species, we found that F_{ST} values between populations on different sides of the freeway were two to nine times larger (and *Nm* 2–9 times smaller) than those between populations on the same side, although the latter populations were separated by greater distances (Figs 1A, B and 3). Additionally, 39.2% of alleles for coyotes and 23.6% of alleles for bobcats were unique to one side of the freeway (Table S4, Supplementary material). For coyotes, both pairwise F_{ST} values across the freeway (F_{ST} = 0.030 northwest-south, F_{ST} = 0.037 northeast-south) were significantly different from zero ($P < 0.003$), whereas the F_{ST} values between the two subpopulations on the same side of the freeway (0.004, northwest-northeast) was not ($P = 0.134$). For bobcats all three pairwise F_{ST} values were significantly different from zero (F_{ST} = 0.064 northwest-south, F_{ST} = 0.039 northeast-south, F_{ST} = 0.018 northwest-northeast) ($P < 0.003$), suggesting that Kanan Road, a busy secondary road, and the wide development corridor flanking it, may also be a significant barrier to gene flow for bobcats

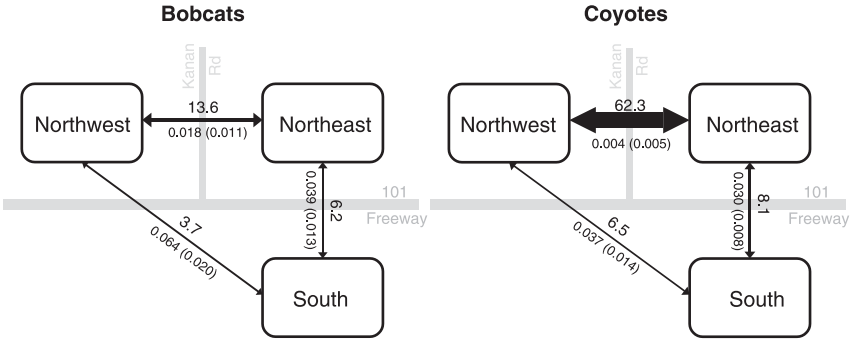

Fig. 3 The number of genetic migrants (*Nm*, above line) and levels of genetic differentiation (F_{ST}, below line, standard error in parentheses) between populations across the freeway (northwest vs. south and northeast vs. south) and on the same side of the freeway (northeast vs. northwest) for bobcats and coyotes. Arrow widths are proportional to *Nm* values.

(Fig. 3). Relatedness values also indicated substantially more closely related pairs of animals ($R \geq 0.25$) between populations on the same side of the freeway (northeast vs. northwest) than across it (northeast vs. south) (Fig. S1, Supplementary material). Overall, these results clearly show that the Ventura Freeway is an imposing barrier to gene flow for both species.

To assess if these levels of genetic differentiation were consistent with population history and the observed and implied migration rates, we used coalescent simulation modelling to estimate north side–south side pairwise F_{ST} indices resulting from the division of a single population by the creation of the freeway in 1949. The simulation results (Fig. 4) showed that a genetically effective migration rate of approximately 0.5% per generation or less is required to explain the observed level of population differentiation for both carnivore species. Consequently, given

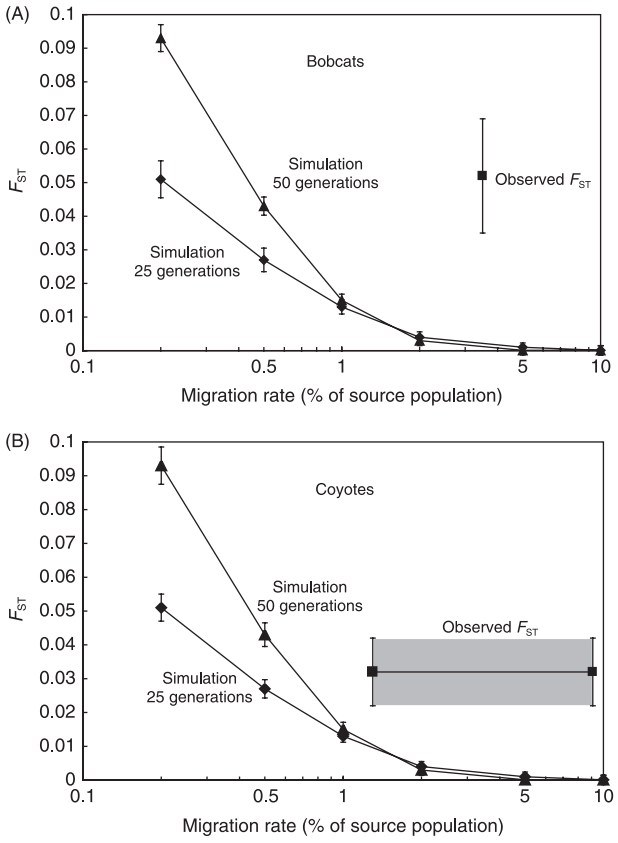

Fig. 4 Comparison of predicted genetic divergence (F_{ST}) using coalescence simulations (*Y*-axis) with observed F_{ST} values as a function of migration rate (*X*-axis) between bobcat (A) and coyote (B) populations north and south of the freeway. Migration rates for observed F_{ST} values are based on radio-tracking observations and genetic assignment tests (see text). Error bars for F_{ST} values represent one standard error. Observed genetic differentiation is consistent with a migration rate of 0.5% or less for both species given 25 or 50 generations since isolation.

that our observations span a period of about three generations (Knick *et al*. 1985; Bekoff & Wells 1986), the genetically effective migration rates estimated by the coalescent simulation are approximately 3–18 times lower than migration rates between populations separated by the freeway based on direct observation or genetic population assignment.

The disparity between observed migration rates and inferred gene flow likely reflects the lack of reproductive success of migrants. For example, 6 of the 10 bobcats that were found on both sides of the freeway were located across it less than four times, and of the four that stayed across, the two females were known not to have produced kittens the following spring. Of the five coyotes radio-tracked across the freeway, four did not reproduce since they were located six or fewer times across the road and over only a short period of time outside the reproductive season. Further, of the potential migrants observed by telemetry and implied by genetic results, 54% were classified as less than 2 years old. In undisturbed populations, young dispersers enter a matrix of occupied and unoccupied territories, reflecting natural mortality of territorial adults. However, in our study area, home ranges follow the freeway boundary (Fig. 1C, D) and consequently, territorial and reproductive individuals contribute genes to the population on one side of the freeway only. Additionally, in our urban study area, mortality from hunting and trapping is low or nonexistent, and carnivore survival rates were high (Riley *et al*. 2003). High survival rates, small home ranges, high home range overlap, and the barrier effect of roads and development all resulted in territory packing along hard boundaries such as the freeway. This territory pile-up likely produced a formidable social and behavioural barrier to genetically effective dispersal because dispersers are unlikely to obtain and hold territories near the freeway. This unique genetic-isolating effect of roads and other artificial boundaries likely applies to other territorial species.

Conceivably, genetic differences may also correspond to changes in habitat composition across the freeway. For example, continent-wide climate and habitat changes have been associated with genetic structure in grey wolves (*Canis lupus*; Geffen *et al*. 2004), and regional-scale biome changes, e.g. between mountainous regions and flat valley expanses, were associated with genetic structure in coyotes (Sacks *et al*. 2004). However, both the geographic scale and diversity in habitats sampled by these studies far exceed the habitat differences observed throughout the area that we studied. Both sides of the freeway consist of a similar mix of the three dominant types of vegetation in the Santa Monica Mountains and Simi Hills including mixed scrub (64–85%), grassland (8–26%) and riparian and oak woodland (2–11%; Table S1, Supplementary material). There is variation in the amounts of specific

types of scrub communities (e.g. coastal sage scrub, dominated by *Salvia* spp. and *Artemisia californica*, and chaparral, dominated by *Adenostoma fasciculatum* or *Ceanothus* spp.) across the entire study area, but coyotes and bobcats on both sides of the freeway used both of these scrub communities, indicating a lack of ecological specialization. Coyotes and bobcats are generalist carnivores, and we feel such small-scale ecological differences are an unlikely explanation of our results. Unfortunately, there are too few historical specimens from our study area in museum collections to directly assess genetic differentiation prior to the construction of the freeway.

Roads are a primary threat to the persistence of animal populations in urban landscapes. This threat is caused directly through vehicle mortality or indirectly by increasing the probability that isolated populations will become extinct through random demographic processes (Forman 2003). Our results show that the genetic effects of roads can also be substantial even for large, highly mobile species. Levels of differentiation between coyote and bobcat populations isolated for about 50 years are as large as those between coyote populations separated by several hundred kilometres (Roy *et al*. 1994). These levels of differentiation were found even between high-density populations of bobcats and coyotes. The isolating effects of roads would likely be even more severe for very small populations and rare species (Spielman *et al*. 2004). An additional insidious factor is the effect of roads in decreasing gene flow well below that expected from migration rates or existing between similarly spaced populations on the same side of the freeway. We suggest this decrease may be caused by: (i) roads acting as home range boundaries for terrestrial and reproductive individuals, and thus decreasing the migration rate of genes, and (ii) home range pile-up near roads that make it less likely that dispersing individuals can find territories. To counteract such genetic isolation, corridors across freeways could conceivably include more natural habitat so that home ranges could extend across the freeway and rates of genetic exchange might be increased. Five of the six potential crossing points in our study (Fig. 1A, B) were unvegetated culverts or paved underpasses. Finally, our results imply that observed migration rates across anthropogenic barriers may be poor surrogates for gene flow, and that molecular genetic studies of even recently isolated populations may provide new insights for conservation.

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Supplementary material

The supplementary material is available from http://www.blackwellpublishing.com/products/journals/suppmat/MEC/MEC2907/MEC2907sm.htm

Table S1 Percentage of different habitat types in the sampled areas, determined by overlaying the polygons for each population (Fig. 1) on a vegetation map of the Santa Monica Mountains and Simi Hills (Franklin 1997). Chaparral consists of scrub habitat dominated by chamise (*Adenostoma fasciculatum*) and ceanothus (*Ceanothus* spp.); coastal sage scrub consists of scrub habitat dominated by sage (*Salvia* spp.) and California sagebrush (*Artemisia tridentata*); grassland is mostly introduced annual grasses; woodland consists of oak and riparian woodlands and some walnut woodlands.

Table S2 Observed and expected heterozygosities, allelic diversity and deviations from Hardy–Weinberg equilibrium (significant deviations indicated by ±).

Table S3 Likelihood values for inferred number of genetic clusters (*K*) from STRUCTURE (3 iterations per value of *K*).

Table S4 Private alleles as percentage of total alleles per locus in each population.

Table S5 Cluster assignment and posterior probability of correct genetic population assignment of potential migrants.

Fig. S1 Comparison of the percentage bobcat and coyote pairs that were closely related genetically, as defined by having an *R* value of 0.25 or greater between populations across the freeway (south vs. northwest and northeast) and on the same side of the freeway (across Kanan road, northwest vs. northeast). Bar widths are proportional to percentage values.

Fig. S2 Sensitivity of the SIMCOAL simulation algorithm for F_{ST} as a function of microsatellite mutation rate (μ), migration rate, and number of generations since population separation (since construction of the freeway).

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Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park

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ABSTRACT

The strength of top-down forces in terrestrial food webs is highly debated as there are few examples illustrating the role of large mammalian carnivores in structuring biotic and abiotic systems. Based on the results of this study we hypothesize that an increase in human visitation within Zion Canyon of Zion National Park ultimately resulted in a catastrophic regime shift through pathways involving trophic cascades and abiotic environmental changes. Increases in human visitors in Zion Canyon apparently reduced cougar (*Puma concolor*) densities, which subsequently led to higher mule deer (*Odocoileus hemionus*) densities, higher browsing intensities and reduced recruitment of riparian cottonwood trees (*Populus fremontii*), increased bank erosion, and reductions in both terrestrial and aquatic species abundance. These results may have broad implications with regard to our understanding of alternative ecosystem states where large carnivores have been removed or are being recovered.

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1. Introduction

Humans can have a major role in food web dynamics by displacing or extirpating top predators. Over a half century ago, the iconoclast Aldo Leopold was among the first to argue that elimination of large mammalian predators had strong top-down influences on ecosystems (Leopold et al., 1947). Based on widespread empirical observations in the early to mid-20th century, when large carnivores were being extirpated from significant portions of the United States, Leopold and colleagues suggested that the loss of these carnivores set the stage for ungulate irruptions and ecosystem damage. Perhaps the most notable example was the Kaibab plateau in Arizona (Leopold, 1943; Leopold et al., 1947; Ripple and Beschta, 2005). Widely reported in early biology and ecology textbooks as a lesson in top-down importance, the Kaibab study was more recently deleted from textbooks after alternative hypotheses for ungulate irruptions were suggested (Caughley, 1970; Burke, 1973).

Within only one to two centuries the widespread effects of Euro-American settlement and development across the continental United States resulted in range collapse for most large mammalian carnivore species (Laliberte and Ripple, 2004). Yet, potential long-term cascading effects involving the loss of these large carnivores are largely unknown. A trophic cascade occurs when the presence of a top predator significantly affects consumers and this interaction alters or influences species composition, age structure, or spatial distribution of producers (plants). While current discussions on terrestrial food webs continue to question the relative strength of top-down forcing versus bottom-up controls (Estes, 1996; Pace et al., 1999; Terborgh et al., 1999, 2001; Polis et al., 2000; Borer et al., 2005), there is often little consideration beyond tri-trophic cascades, especially concerning potential pathways

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involving changes in the abiotic environment that could contribute to a loss of habitats, a loss of biodiversity, or regime shifts resulting in alternative states (Schmitz et al., 2006). Catastrophic regime shifts can occur when perturbations dramatically alter ecosystem structure and function (Holling, 1986; Scheffer and Carpenter, 2003). A regime shift typically occurs as a relatively abrupt restructuring of an ecosystem, but with prolonged consequences. The likelihood of a shift to a less desired state is increased when humans remove whole trophic levels (top-down forces), thereby reducing an ecosystem's capacity to generate services (Folke et al., 2004).

From a theoretical perspective, a major academic debate regarding trophic cascades was initiated when Hairston, Smith, and Slobodkin proposed the Green World Hypothesis, which indicated that predators maintain global plant biomass at high levels by limiting herbivore densities (Hairston et al., 1960). Yet even with recent advances in food web ecology, the debate about the Green World Hypothesis continues due to ongoing disagreement on the frequency and relative role of top-down versus bottom-up forces, as well as a paucity of studies regarding the effects of large mammalian predators on terrestrial vegetation (Pace et al., 1999; Polis et al., 2000; Shurin et al., 2002; Borer et al., 2005).

Ecosystem properties and processes in the presence or absence of large carnivores are not widely understood. For example, there is a lack of controlled, large-scale, and long-term studies of large carnivores, prey, and plant communities. This scarcity of research is attributable to a lack of functional populations of large carnivores, the cost of such studies, the need for relatively large spatial and temporal scales, the difficulty of experimentally manipulating populations of large carnivores, and the problem of separating confounding effects including the role of humans. To date, the vast majority of trophic cascades studies in terrestrial ecosystems have taken place at the scale of meters to hectares involving very small predators over short time periods. This limits the transfer of results to large landscapes, large carnivores, and long time scales (Schmitz, 2005).

A top-down trophic cascades model would predict an increase in consumer biomass and a decrease in producer biomass following predator removal, while the bottom-up model would predict little or no change in consumer or producer biomass after their removal (Ray et al., 2005). In addition to these basic top-down linkages, many other interaction pathways resulting from predator effects are likely, such as increased species interactions, improved nutrient cycling, limited mesopredator populations, and food web support for scavengers (Soulé et al., 2003, 2005; Côté et al., 2004; Reisewitz et al., 2006). One little known pathway is a linkage from predators to consumers to producers to streambank habitats to species abundance (i.e., how the change in abiotic environment due to trophic cascades affects the occurrence of native species).

Herein we report on a discovery that appears to link the loss of predators to a catastrophic regime shift via trophic cascades (cougar → deer → cottonwoods) and changes in abiotic environmental conditions (channel morphology). We took advantage of an unplanned landscape-scale experiment to document the status of an ecosystem where the presence of a large mammalian predator (cougar) had been greatly diminished in one of two landscape areas within Zion National Park, Utah. While an experimental design that includes spatial control of "predator rare" versus "predator common" areas seldom occurs in large carnivore-trophic cascades research (Terborgh et al., 2001), such a design greatly reduces the potential for confounding interactions associated with climate, natural disturbances, or habitat. An underlying hypothesis of this study is that Fremont cottonwood tree recruitment: (1) has been low in areas where cougars are scarce and mule deer abundant (treatment, Zion Canyon); and (2) has continued to occur in areas where cougars remain common and deer scarce (control, North Creek). Additionally, in the area with a reduced cougar presence, we hypothesized that reductions in riparian trees and other palatable hydrophytic plants caused increases in bank erosion, which in turn contributed to reductions in the abundance of riparian wildflowers, amphibians, lizards, and butterflies. We considered alternative hypotheses that might affect cottonwood recruitment including climate, human interventions to stream channels, and differences in geomorphology and runoff regimes between Zion Canyon and North Creek.

2. History of Zion Canyon

When Zion Canyon was first settled in 1862, ranchers and homesteaders found lush vegetation in the valley bottoms and excellent grass and browse in the uplands (Dixon and Sumner, 1939). During the next five decades agricultural use of bottomlands and heavy grazing eventually caused channels to destabilize and by 1915 most homesteads had been abandoned. By 1918, when Zion National Park was established, much of the natural vegetation in the canyon had been greatly diminished and the canyon deer population was at a very low level due to intense hunting (Presnall, 1938). However, by the late 1920s vegetation recovery in the canyon was underway and deer numbers had begun to increase (Presnall, 1938). Predators also returned during this 10-year period and thus kept the deer population at a low level (Smith, 1943).

Park development accelerated during the late 1920s resulting in a dramatic increase in the annual number of park visitors, from 8400 in 1924 to 68,800 in 1934. Consequently, a reduction in the canyon's cougar density was first noted in 1934. Zion Park Naturalist Presnall (1938) wrote "Human use of the park was, and no doubt always will be, concentrated in Zion Canyon, causing profound changes in the delicate balance between deer and their natural predators". National Park Service biologists Dixon and Sumner (1939) similarly indicated that "The presence of these hundreds of human visitors tended to drive out the cougars, which are the chief natural enemies of the deer". Superintendent Smith (1943) retrospectively wrote "A period of expansion in the park followed from 1924 to 1934 with the construction of highways and trails and a resulting heavy increase in visitor use which tended to frighten off the predators in the canyon due to the concentration of people".

3. Study areas

As cougars have been displaced from Zion Canyon by large numbers of human visitors since the 1930s, we used this as one of two primary study areas. Our second study area, the North Creek drainage immediately west and adjacent to Zion

Canyon, is a roadless area which, like other backcountry areas of Zion National Park, has a history of supporting a stable cougar population (Nile Sorenson, Utah Division of Wildlife, personal communication, 2005). Cougar hunting is prohibited within Zion National Park but occurs outside the park. Thus, canyons within the park like those along North Creek generally serve as refugia for cougars. According to Zion National Park archival files (Zion 16051, folder 15), after the 1930s tracks and other cougar sign were found in most every section of the park outside of Zion Canyon. Currently, the park is part of a Utah state wildlife management unit encompassing nearly 4500 km^2 with an estimated mule deer population of approximately 7200 (1.6 deer/km^2) and an estimated cougar population of 77–110 (17–25 cougar/1000 km^2; Utah Division of Wildlife files). Other predators in the Zion National Park include coyotes (*Canis latrans*) and a few black bears (*Ursus americanus*). Both of these species prey on mule deer, but mostly on newborn fawns in the spring of the year.

Present-day Zion Canyon resulted from geologic downcutting by the North Fork of the Virgin River through Jurassic rock units of the Markagunt Plateau. Modern terraces (former floodplains) along the canyon bottom contain a variety of dry-site grasses and herbaceous plants as well as Fremont cottonwood, boxelder (*Acer negundo*), and ash (*Fraxinus* spp.) trees. Scattered patches of Baccharis (*Baccharis* sp.) occur within the active channel. During the 1930s the National Park Service constructed rock and wire revetments (gabions) to stabilize streambanks in portions of Zion Canyon. These efforts tended to disconnect the river from its floodplain by reducing occurrence of overbank flows. Since bare substrates are typically important sites for cottonwood regeneration (Stromberg, 1998), this altered hydrologic connectivity of a river with its floodplain thus represents a potentially significant factor affecting cottonwood recruitment. A general lack of cottonwood recruitment (i.e., growth of cottonwood seedlings into trees) over a period of many years in Zion Canyon riparian areas (Fig. 1) has caused the Park Service to investigate channel alterations as a possible approach for improving cottonwood recruitment and reversing riparian degradation (McMahon et al., 2001; Steens-Adams, 2002).

We selected North Creek as a control for our study since its watershed is adjacent to Zion Canyon (North Fork of the Virgin River) and thus has similar geology, climate, and plant communities. The elevations for our study reaches, located ~15 km apart, were both ~1300 m; watershed areas were 760 km^2 and 170 km^2 for Zion Canyon and North Creek, respectively. High cliffs mostly impassable to mammals separate the North Creek watershed from the North Fork of the Virgin River watershed. Human use in the North Creek study area involves limited numbers of hikers annually, whereas nearly 3 million people currently visit Zion Canyon each year.

4. Methods

Historical mule deer population estimates were obtained from Zion Canyon census data. These estimates were adjusted (multiplied) by a factor of 2.4, an average from two population studies [2.2 from Presnall (1938) and 2.6 from Moorehead (1976)], to account for deer present but not observed.

Within Zion Canyon, an area with high human visitation and low cougar densities since the mid-1930s, we measured the diameter of all Fremont cottonwood trees $\geqslant$1 cm in diameter at breast height (DBH) in riparian areas along three 700–900 m reaches. These relatively long sample reaches were undertaken to encompass all cottonwoods within a given section of the river. The Riverwalk Reach occurs immediately upstream of the Temple of Sinawava parking lot, and has had no history of channelization or bank stabilization work. The



Fig. 1 – Photograph taken in 2004 of the historical floodplain along the North Fork of the Virgin River in Zion Canyon showing mature Fremont cottonwoods and a lack of cottonwood recruitment over a period of several decades.

Hereford Reach extends downstream of the parking lot and is generally free of revetments although fill from historical road construction has impinged on one streambank for a portion of the reach. Continuing downstream, the Big Bend Reach has had a history of revetment construction; however, over time the effectiveness of these structures has decreased as they have been eroded or partially buried by alluvial deposits.

In the North Creek drainage, where cougars have continued to inhabit the area, we measured the DBH of all cottonwoods ($\geqslant$1 cm) along three 200 m reaches, one each along the Left Fork, the Right Fork, and the main stem of North Creek. Roads and revetments are absent along study reaches in the North Fork area.

For both study areas we obtained increment cores from a subset of measured cottonwoods ($\geqslant$5 cm DBH), coring individual trees 1.4 m above the ground. We used this information to establish age–diameter relationships for estimating ages of uncored trees, adding 7 years to the number of rings to account for tree height growth from ground level to 1.4 m above the ground.

Measured tree diameters, in conjunction with an age–diameter relationship, were used to develop historical trends in cottonwood tree recruitment for both study areas (e.g., Beschta, 2005). Based on these trends (extending a century back in time), we quantified the strength of top-down forces in Zion Canyon in comparison to those in the North Creek drainage. To assess the strength of any potential trophic cascade, we used the natural log ratio (Borer et al., 2005) of cottonwood trees within each 10-year age class for the North Creek area (control) relative to the Zion Canyon area (treatment). The average log ratio ($\bar{u}$) of cottonwood frequencies was calculated by:

$$\bar{u} = \sum_{j=1}^{k} [\ln(y_j/z_j)]/k,$$

where y_j is the average number of cottonwoods per kilometer that established in "cougars common" reaches during the jth decade, z_j is average number of cottonwoods per kilometer that established in "cougars scarce" reaches during the jth decade, and k is number of decades. Decadal log ratios were averaged over two time periods: (1) before cougars became scarce (1910–1940); and (2) after cougars became scarce in Zion Canyon (1940–2000).

To further assess potential cascading effects, we undertook systematic surveys of channel dimensions, streambank condition, and hydrophytic vegetation along each study reach in late September 2005. Along the North Fork of the Virgin River in Zion Canyon, we determined wetted width, thalweg depth (deepest portion of water column), and active channel width at 10-m intervals within 400-m portions of each study reach in early September 2005, using these to calculate a wetted width/thalweg depth ratio for the reach. We took the same type of measurements in the North Creek drainage, but since these streams were smaller, the interval between measurements was 5 m along each 200-m study reach. During reach surveys, the presence of an eroding bank and the dominant hydrophytic vegetation was determined at the genus level [rushes (*Juncus* spp.), cattails (*Typha* sp.), scouring rush (*Equisetum* sp.)] within a 0.25 m^2 area of streambank at the edge of the channel. Both were recorded at 5-m intervals for each side of the channel.

To assess biodiversity, we determined the relative abundance of selected indicator species, using visual encounter surveys conducted along the bank on each side of the channel. All indicator species were easily observable and occurred in both study areas. We undertook these surveys on clear sunny days during the 16–20 September 2005, between 1000 and 1700 h. Species counts involved scanning the ground surface within 2-m wide transects along the streambanks of the study reaches (Heyer et al., 1994). Surveys were completed for cardinal flower (*Lobelia cardinalis*), Welsh aster (*Aster welshii*), red spotted toad (*Bufo punctatus*), canyon tree frog (*Hyla arenicola*), and all lizard species. To determine the relative abundance of deer, we recorded each hoofprint within these belt transects. Butterflies encountered within 10-m wide belt transects along the banks of each study reach were recorded at the subfamily level. Close focusing binoculars were used to help identify lizard species and butterfly subfamilies. To index the relative abundance of cougar, we conducted a survey of fecal droppings (scat) along ~4000 m of extant foot trails in both North Creek and Zion Canyon study areas, quantifying cougar droppings as number of droppings per linear kilometer of trail.

5. Results

With increasing numbers of park visitors and decreasing numbers of cougars throughout the 1930s, the Zion Canyon deer population irrupted from <80 in 1930 (<4 deer/km^2) to a peak of ~600 (30 deer/km^2) in 1942 (Fig. 2, Table 1). Because of impacts to vegetation, park officials trapped and removed 116 deer in 1938 (Dixon and Sumner, 1939) and shot and killed 180 more deer in 1943 (Fagergren, 1943). Between 1938 and 1947, 780 deer were killed or removed from Zion Canyon by the Park Service (National Park Service Archives, Zion 16051, folder 15). Since the 1940s canyon deer populations have declined to a recent estimate of ~200 animals (~10 deer/km^2), which is greater than the pre-1930 levels (Fig. 2) as well as current mule deer densities outside the park (1.6 deer/km^2).

The number of tree rings (t) was highly correlated with DBH (x) for cottonwoods in Zion National Park ($r^2 = 0.75$, $n = 51$, $t = -0.0096x^2 + 2.09x$). Based on estimated cottonwood ages from DBH measurements in the sampled reaches, two age structures are apparent when comparing the North Creek study reaches with those of Zion Canyon. The North Creek area (Fig. 3a) shows continuous recruitment over time with more young trees than old ones – a normal feature of functioning gallery forests (Beschta, 2005).

In contrast, study reaches in Zion Canyon (Fig. 3b) show a general paucity of young trees and a lack of recruitment since the 1930s as an apparent result of heavy browsing pressure since then. As an index of the relative strength of this potential trophic cascade, the average log ratio of cottonwood frequencies for the North Creek/Zion Canyon areas was near zero (−0.25) for the decades before cougars became scarce in Zion National Park and relatively high (3.85) afterward. While some young cottonwoods had established in Zion Canyon during the 1970s and 1980s (Fig. 3b), nearly all were observed growing in refugia sites inaccessible to deer, such as the base of steep slopes along the river (Fig. 4a) or within

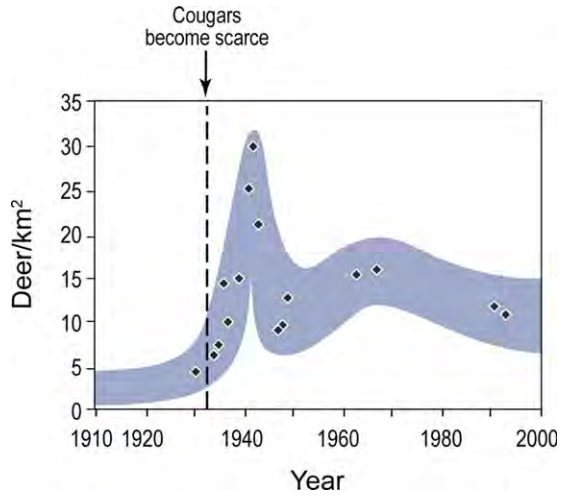

Fig. 2 – Estimated number of mule deer in Zion Canyon during the 20th century. Cougars became scarce in Zion canyon by the mid-1930s, a period of dramatic increase in park visitation. The shaded band represents an estimate of uncertainty. *Sources*: Mule deer data from Presnall (1938), Dixon and Sumner (1939), and the following reports located in the Zion National Park archives – 1930 Zion Park Superintendent report; 1943 chief ranger report by F.C. Fagergren; anonymous memorandum on resurgence of pink eye, 21 December 1993; National Park Service Archives, Zion 16051, folders 15 and 16.

the protection of Baccharis (a relatively unpalatable shrub) thickets (Fig. 4b).

As suggested by food-web theory, Fig. 5a shows an alternating pattern of biomass levels across trophic levels. In the North Creek area (control), human and consumer levels show low abundance while predator and producer trophic levels show high abundance. In Zion Canyon (treatment), the opposite pattern occurs. Although streams throughout Zion National Park experienced high flows (10–20 year return period) in January 2005, the occurrence of eroding banks for study reaches in Zion Canyon were >2.5 times as frequent as those in the North Creek area (Fig. 5a). Similarly, width/depth ratios for reaches in Zion Canyon are approximately double those in the North Creek area. For the Zion Canyon reaches active channel widths ($\bar{x} = 34.2$ m, standard error [SE] = 1.4 m) were more than double the wetted widths ($\bar{x} = 15.9$ m, SE = 0.4 m) as a result of bank erosion into historical floodplains, which created large areas of exposed gravels along these reaches.

The relative abundance of hydrophytic plants, wildflowers, amphibians, lizards, and butterflies observed along streams in the North Creek area was higher than in Zion Canyon (Fig. 5b). Neither of the wildflower species were observed within the belt transects in Zion Canyon, but both were found growing outside the belt transects in nearby side canyon areas, physically protected from deer browsing. Lizard species observed in both "cougars common" and "cougars rare" areas include: Eastern Fence Lizard (*Sceloporus undulatus*), Sagebrush Lizard (*Sceloporus graciosus*), and Plateau Whiptail

Table 1 – Reported observations regarding cougar, mule deer, and vegetation in Zion Canyon for 1932–1942

Date	Comment
1932	"The deer within the park are increasing in spite of hunting outside…"
1933	"Cougar signs were quite numerous within Zion Canyon this year".
1934	"Evidence of cougars within the park is more readily observed, indicating perhaps they are somewhat on the increase. However, they do not come into the valley of Zion Canyon, which is one of the factors assisting in the increase of the deer population here".
1935	"Deer are in the best of condition, and forage is plentiful, because of the large amount of moisture received during the winter and spring".
1936	"Evidence of [deer] overpopulation in the valley of Zion Canyon, however, continues to be seen … there are about 125 deer that winter here … the number of cougar within the park is increasing [outside of Zion Canyon]".
1937	"The over-population of deer in Zion Canyon, which was reaching the stage where plans for reduction were under discussion, was somewhat relieved by the severe winter of 1936–1937, which some of the less healthy animals were unable to survive".
1938	"The deer in Zion [canyon] are in very poor flesh and present a sorry spectacle. Professional wildlife visitors to the park this summer have been unfavorably impressed by the unbalanced deer forage situation here".
1939	"Deer became too numerous on the valley floor for the amount of forage available, so 130 of these animals were trapped and transported to outside areas".
1940	"The trapping and shipping of surplus Rocky Mountain mule deer from the floor of Zion Canon was carried on … 62 animals were removed from the park this year".
1941	[Report not available]
1942	"Overpopulation of deer in Zion Canyon, with consequent scarcity of feed, is one of the major problems at present in Zion National Park. During the winter of 1941–1942, 52 deer were trapped and removed … Vegetation is so over-browsed that it is in serious condition and there is danger of complete destruction".

Source: Annual reports by the superintendent of Zion National Park, Zion National Park Archives.

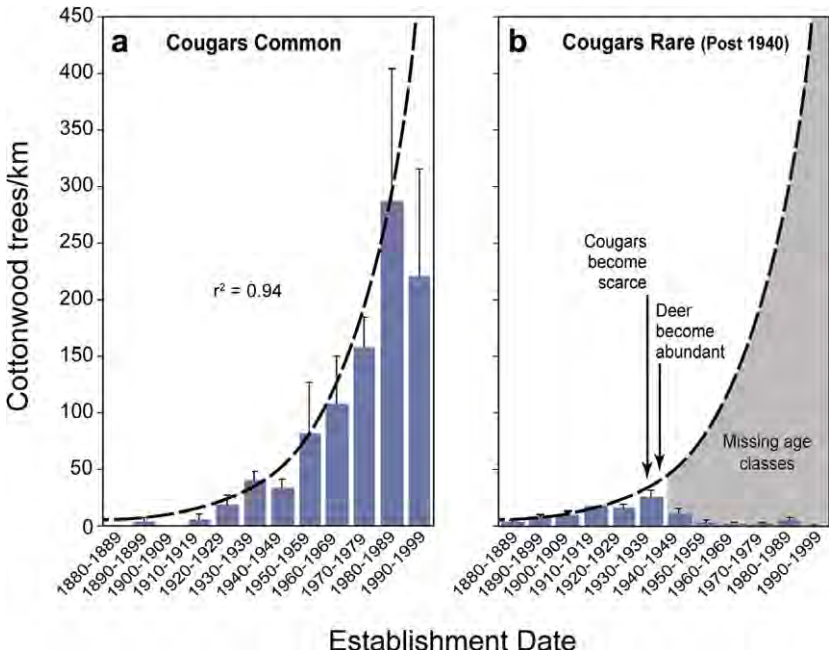

Fig. 3 – Cottonwood age structure for (a) the North Creek area where cougars are common and (b) Zion Canyon where they are rare. Both areas are within Zion National Park. The exponential function (dashed line) was fitted to measured tree frequencies for North Creek study reaches; this same relationship has been plotted along with tree frequencies for the Zion Canyon study reaches illustrating a general cessation of cottonwood recruitment (i.e., missing age classes) since ~1940. Error bars represent standard errors.

(*Cnemidophorus velox*). Additional lizard species observed in the "cougars common" area include: Desert Spiny Lizard (*Sceloporus magister*), Common Side-Blotched Lizard (*Uta stansburiana*), and Tree Lizard (*Uta ornata*). Butterfly subfamilies observed in both the "cougars common" and "cougars rare" areas include (scientific names listed as family: subfamily): Whites (Pieridae: Pierinae), True Brush-Foots (Nymphalidae: Nymphalinae), Admirals (Nymphalidae: Limenitidinae), and Grass Skippers (Hesperiidae: Hesperiinae). Additional butterfly subfamilies observed only in the cougars common area include: Swallowtails (Papilionidae: Papilioninae), Sulphurs (Pieridae: Coliadinae), Blues (Lycaenidae: Polyommatinae), Satyrs (Nymphalidae: Satyrinae), Monarchs (Nymphalidae: Danainae), and Spread-wing Skippers (Hesperiidae: Pyrginae).

6. Discussion

Our data confirm a major gap in the cottonwood age structure in Zion Canyon (cougars rare) occurred after 1940, where we found, on average, only 23 post-1940 cottonwoods per kilometer of stream (Fig. 3). This compares to 892 post-1940 cottonwoods per kilometer in the North Creek study reaches (cougars common). These results are consistent with a trophic cascade initiated regime shift in that the reduction in a large predator may have produced important ecosystem changes, including greater herbivore densities, decreased tree frequencies, more bank erosion, altered channel dimensions, and decreased riparian biodiversity (Fig. 6).

The geomorphic transformation of stream channels due to accelerated bank erosion can have serious ecological consequences (National Research Council, 2002). For example, plant loss on streambanks decreases shading on the surface of the water and allows width/depth to increase, thus contributing to high summertime water temperatures. Increased streambank erosion not only removes formerly deposited alluvium that serves as substrate for riparian vegetation, but reduces the capability of the stream to maintain hydrologic connectivity with its historical floodplain (Beschta and Ripple, 2006). Bank erosion also truncates allochthonous inputs from streamside vegetation, an important source of organic carbon for many aquatic organisms. An influx of finer sediments from accelerated bank erosion can decrease the median substrate size and sorting of sedimentary material in the bed, making it less inhabitable for many invertebrates that live within the interstices of the coarse bed materials (Smith, 2004). While large portions of the channel in Zion Canyon now have bare substrates normally favorable for cottonwood seedling establishment (Fig. 6b), it appears that annual herbivory since 1940 has effectively truncated the capability of seedlings to grow above the browse level of deer.

Not only do hydrophytic plants have a key role along channel margins in helping to maintain stable banks and performing other important functions, but they also provide food-web support and protective cover for amphibians, reptiles, and aquatic species. Both wildflower species assessed in this study grow in wet meadows and on moist streambanks and serve as host plants for several butterfly species. Relative low numbers of frogs, toads, and lizards associated with the "cougars rare" sites may be a result of both lower levels of invertebrate prey abundance, as well as degraded habitats with less cover for thermal regulation and protection against



Fig. 4 – Photographs taken in 2004 showing young cottonwood recruitment (2–4 m tall) at sites protected from deer browsing in Zion Canyon along the North Fork of the Virgin River. Refugia shown include (a) a site between the canyon wall and the channel, and (b) Baccharis thickets.

predators. Butterfly differences may be due to reduced diversity and abundance of flowering plants in Zion Canyon relative to the North Creek area. It should be noted that the results from our survey of amphibians, lizards and butterflies within the belt transects represent what we observed over a limited period of time and should not be considered an exhaustive inventory of these species groups. We also observed a wide range of woody browse species such as willow (*Salix* spp.), Squawbush (*Rhus trilobata*), and others in the North Creek drainage, which were absent or rare on comparable sites in Zion Canyon.

Our results are consistent with previous studies regarding the role of wolves (*Canis lupus*) in trophic cascades (McLaren and Peterson, 1994; Ripple and Larsen, 2000; Ripple and Beschta, 2004; Beschta, 2005; Hebblewhite et al., 2005). These studies and others (Rooney and Waller, 2003) indicate that ecosystems can be profoundly altered by ungulates after large carnivores are removed. Recent research has also connected wolves to stream channel and floodplain characteristics. For example, heavy elk browsing of willow communities after the loss of wolves ultimately generated major changes in floodplain functions and channel morphology (Beschta and Ripple, 2006). Other researchers have documented a reduction in abundance and diversity of birds in areas without wolves and with abundant ungulate populations (McShea and Rappole, 2000; Berger et al., 2001). Like wolves, cougars are a wide-ranging predator whose geographic distribution and predation effects have been greatly reduced

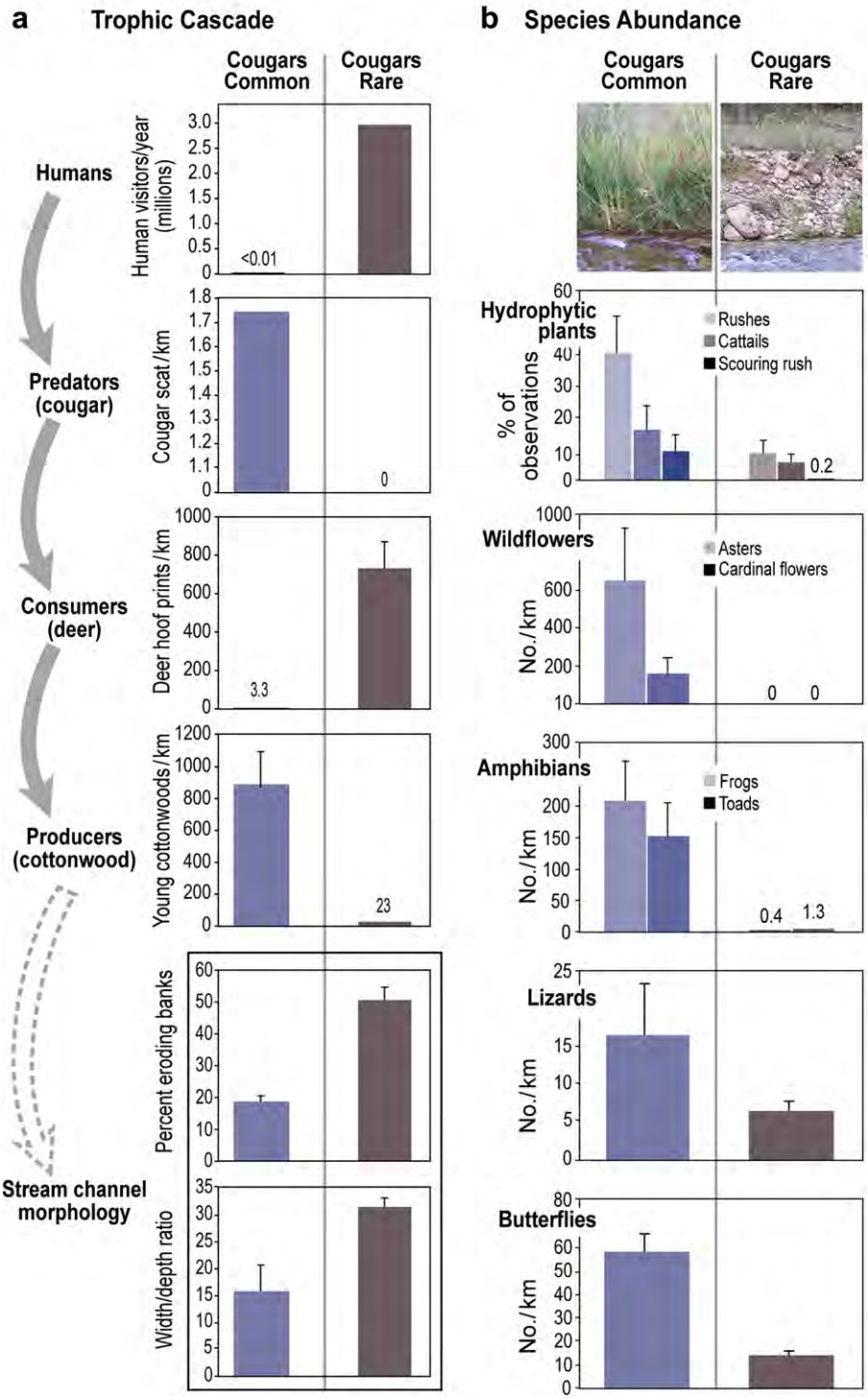

Fig. 5 – (a) Trophic cascade indicated by inverse patterns of abundance across trophic levels and (b) observed biodiversity indicators for "cougars common" and "cougars rare" areas of Zion National Park USA. Species include Fremont cottonwood originating since 1940 (*Populus fremontii*), rushes (*Juncus* spp.), cattails (*Typha* sp.), scouring rush (*Equisetum* sp.), Welsh aster (*Aster welshii*), cardinal flower (*Lobelia cardinalis*), canyon tree frogs (*Hyla arenicola*), red spotted toads (*Bufo punctatus*). See text for a list of observed lizard species and butterfly subfamilies. Error bars represent standard errors.

by humans. In contrast to wolves, cougars are solitary predators.

Mule deer represents the primary prey of cougars in southern Utah and are common across much of the region. However, cougars generally have avoided areas with high levels of human activity (Van Dyke et al., 1986), such as Zion Canyon. Thus Zion Canyon functions as refugia for mule deer from cougar predation due to high human presence, while

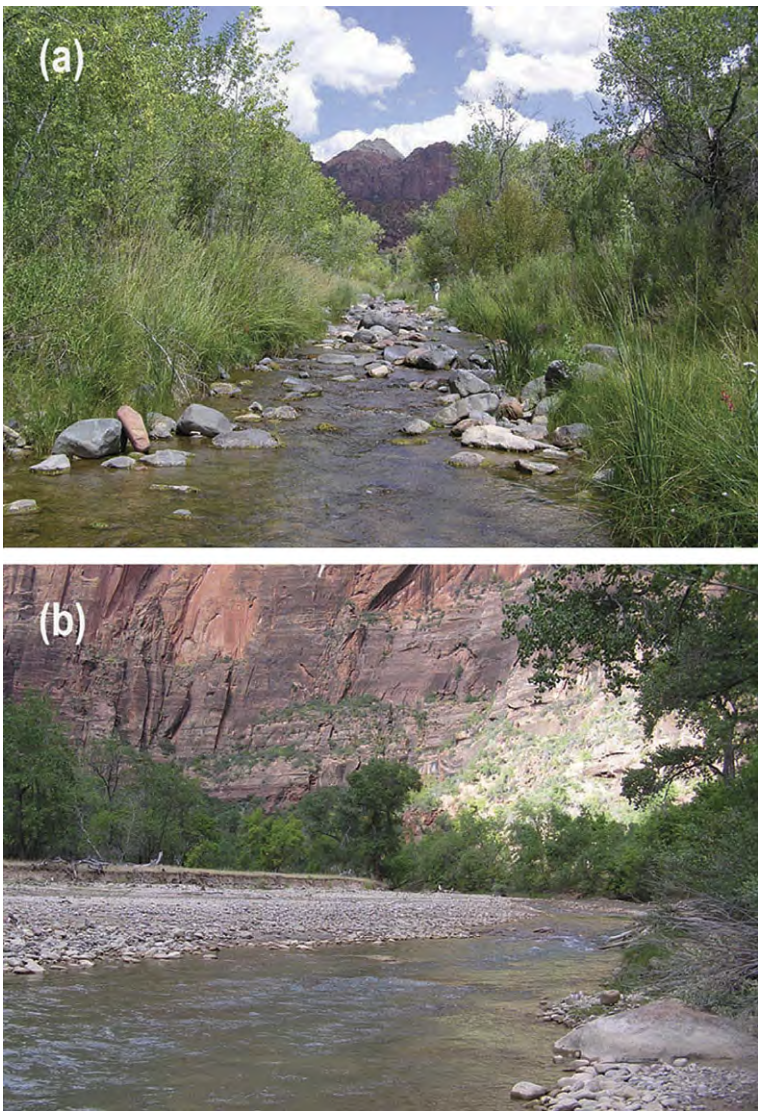

Fig. 6 – Photographs taken in 2005 showing stream channel and floodplain conditions along (a) North Creek, an area with cougars common, and (b) North Fork of the Virgin River in Zion Canyon, an area with cougars rare. The stream in (a) shows well vegetated and stable banks and a small width:depth ratio while the stream in (b) has a lack of bank vegetation, a large width:depth ratio, and a wide active channel (with banks continuing to erode).

areas such as the North Creek drainage provide refugia for cougars due to low human presence. These landscape-scale refugia are consistent with behaviorally mediated trophic cascades theory involving predation risk effects (Ripple and Beschta, 2004; Hebblewhite et al., 2005).

The natural log ratio of 3.85 (indicating a 47-fold difference) for young cottonwood frequencies in our control area (North Creek drainage) versus treatment area (Zion Canyon) ranks high compared to a recent meta-analysis of 114 trophic cascades studies from both aquatic and terrestrial systems, where such log ratios ranged from −0.7 to 3.2 (Borer et al., 2005). Thus, the diminishment of gallery cottonwood forests (and perhaps a wide range of other palatable species) reflects a potentially strong trophic cascade effect relative to other studies. Additionally, our results document an apparent catastrophic regime shift using a pathway spanning from trophic cascades to impacts on the abiotic environment, and ultimately, to a loss of native species abundance. Thus, the sustainability of functional riparian habitats and biodiversity may require the long-term effects of predation on herbivores, including lethal effects (densities) as well as nonlethal effects (predation risk).

Our findings on trophic cascades in Zion National Park are consistent with those of over a half century ago by Aldo Leopold regarding the Kaibab Plateau, located less than 100 km to the southeast. Zion serves as a replicate to the classic Kaibab study, since cougar/mule deer are the primary predator/prey combination in both areas. In addition, recent analyses of aspen tree rings from the Kaibab (Binkley et al., 2005) are consistent with Leopold's hypothesis of extreme deer herbivory following predator removal, as well as the importance of predation in controlling deer populations. Aspen recruitment on the Kaibab largely terminated following predator reductions, similar to the patterns of

cottonwood recruitment in Zion Canyon after cougars became scarce.

It is interesting to note that increased cougar sightings have occurred in Zion Canyon in recent years. This may be attributable to the dramatic decrease in vehicle traffic since a bus system was implemented in 2000. Reduced vehicle traffic may have positive effects on long-term riparian/aquatic biodiversity if cougars have an increasing presence in Zion Canyon. However, we are unsure how rapidly or to what extent any increase in cougar numbers in Zion Canyon might be able to reverse decades of direct impacts by deer upon riparian plant communities and subsequent impacts to the stream system.

While our results are consistent with trophic cascade theory, we nevertheless considered alternative scenarios that might affect cottonwood recruitment: (1) fluctuations in climate; (2) human interventions to channels (e.g., revetments in Zion Canyon); and (3) site attributes associated with differences in geomorphology or runoff regimes between Zion Canyon and North Creek. Both Zion Canyon and North Creek study areas had comparable cottonwood recruitment during the pre-1940 period (Fig. 3), indicating they were well-paired for comparative purposes. Thus, it would appear unlikely that any shifts in climate during the 20th century have been a significant factor associated with the post-1940 cessation of cottonwood recruitment in Zion Canyon, as a similar pattern was not observed in North Creek.

We considered the potential role of revetments constructed in the early 1930s along portions of the North Fork of the Virgin River in Zion Canyon. Such structures can diminish cottonwood recruitment by locally reducing: (1) availability of bare substrates (important for cottonwood germination); and (2) occurrence of overbank flows. Since construction of these structures decades ago, their capability to function has slowly deteriorated as they have been increasingly eroded or buried by alluvium during periods of high flow. Furthermore, our results indicated relatively low cottonwood recruitment since 1940, even in those reaches of Zion Canyon where revetments had not been constructed. Thus, some mechanism other than revetment construction appears to have been causing the post-1940 lack of cottonwood recruitment. This is further supported by observations in Zion Canyon which indicate that cottonwood recruitment is occurring, but only in localized places generally inaccessible to deer (e.g., steep canyon toeslopes, Baccharis thickets, Fig. 4). We generally observed extremely high levels of deer browsing on cottonwood seedlings in Zion Canyon, but very low levels of browsing on seedlings in the North Creek area.

Drainage areas and geomorphic features associated with Zion Canyon and the North Creek areas represent essentially constant conditions over our study period and thus are an unlikely candidate for causing a differential effect on cottonwood recruitment over time. However, to explore this issue further we measured cottonwood trees, channel width/depth ratios, and percent eroding banks along a 400-m reach of the East Fork of the Virgin River. Land use history in the East Fork during the late 1800s and early 1900s was similar to that which occurred in Zion Canyon. However, since inclusion into the Zion National Park in 1918, the East Fork has not had any roads or revetments, has experienced only a few human visitors annually, and has had continued presence of cougars. Although the East Fork has a drainage area approximately the same as that of Zion Canyon, annual peak flows average approximately 30% lower.

Along the East Fork we found 1216 young cottonwoods per kilometer (originating post-1940), with an exponential age-class distribution very much like that of study reaches in the North Creek drainage (i.e., Fig. 3a). The frequency of eroding banks averaged only 2% for the East Fork relative to 18.9% (SE = 1.3%) for study reaches in the North Creek drainage. Both were well less than the 51.0% (SE = 3.6%) eroding banks measured in Zion Canyon. In addition, the average wetted width/depth ratio of 12.9 m/m for the East Fork was similar to the North Creek study reaches ($\bar{x} = 15.6$ m/m, SE = 4.7 m/m), but considerably less than that for Zion Canyon ($\bar{x} = 31.1$ m/m, SE = 1.6). These findings support our contention that pre-park land use history as well as stream/watershed size did not cause the post-1940 lack of cottonwood recruitment in Zion Canyon.

We postulated that the apparent regime shift in riparian plant communities and channel morphology may have influenced native fish species abundance in the North Fork of the Virgin River. Therefore, we summarized recent fish surveys for North Creek, as well as for both the North and East Forks of the Virgin River. Annual monitoring of these streams has been ongoing since 1994 ($n = 11$ years) and is accomplished at one fixed area station per stream using electro-shocking methods (Morvilius et al., 2006). Summaries of these annual data show mean densities of native fish over three times higher in streams within areas with cougars common (North Creek and East Fork of the Virgin River) relative to the area with cougars rare (North Fork of the Virgin River, Fig. 7). Virgin spindace (*Lepidomeda mollispinis*), one of four native species found in these surveys, has been proposed for federal endangered species listing because of declining populations due to habitat degradation (Morvilius et al., 2006). These results

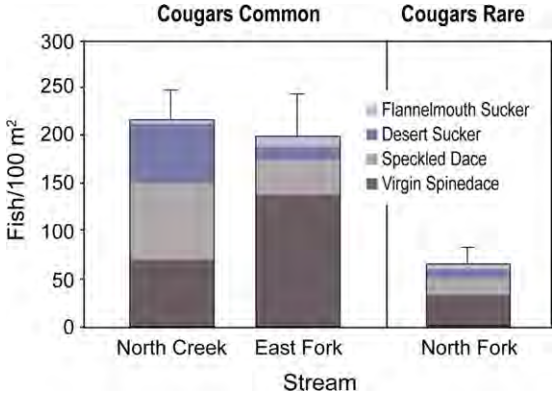

Fig. 7 – Native fish densities from two "cougars common" areas (North Creek and East Fork of the Virgin River) and one "cougars rare" area (North Fork of the Virgin River). Species include flannelmouth sucker (*Catostomus latipinnis*), desert sucker (*Catostomus clarki*), speckled dace (*Rhinichthys osculus*), and Virgin spinedace (*Lepidomeda mollispinis*). Error bars represent standard errors for all species combined. *Sources*: Morvilius et al. (2006) and Utah Division of Wildlife Resources (unpublished data).

provide additional evidence of potential connectivity between terrestrial and aquatic processes linked by a trophic cascade across ecosystems, a process rarely identified in the ecological literature (Knight et al., 2005).

We hypothesize that the lack of cottonwood recruitment associated with riparian areas in Zion Canyon indicates an altered trophic cascade involving decades of low cougar densities. Subsequent impacts to the riparian/aquatic systems appear to have included reduced bank vegetation, increased bank erosion and width/depth ratios, and decreased riparian biodiversity. Thus, removing or maintaining a large carnivore appears to have had profound effects on lower trophic levels, as well as multiple indicators of ecosystem status and native species abundance. Unless changes occur at the top of the food chain, Fremont cottonwoods in Zion Canyon may ultimately disappear. While loss of cottonwoods alone represents a major impact to biodiversity, it likely chronicles other functional losses already incurred by the larger community of riparian plants and animals. In contrast, where access by humans has been restricted and cougar populations have remained intact, as in the North Creek area, browsing levels have remained relatively low, as indicated by long-term patterns of cottonwood recruitment. Furthermore, streambank erosion was low, channels relatively narrow and deep, and relative abundances of hydrophytic plants and other indicator species of biodiversity were high in this area.

Understanding the historical context of various factors affecting Zion Canyon and North Creek ecosystems is fundamental to interpreting present-day ecosystem structure and functions. This indicates not only an important need to understand how ecosystems affected by humans currently function in comparison to relatively unaffected ecosystems, but that historical patterns of human disturbances and alterations leading up to the present need be understood so that on-going effects can be realistically evaluated. With the assistance of cottonwood age–diameter relationships and stand measurements of tree diameters, we were able to reach back over a century to help assess temporal stand structural dynamics of the gallery forests within our study sites. However, without the availability of control reaches (where cougar populations remained intact over time), we would have been unable to decipher the potential effects of predator removal on abiotic indicators of ecosystem conditions and on other biotic indicators with life cycles much shorter than cottonwoods.

Our results identify a central issue for ecological studies, since the presence or absence of a top predator may have a major influence on the outcomes of such studies. Following the loss of top-down control, succession may proceed via abrupt regime shifts and alternative states (Folke et al., 2004; Schmitz et al., 2006). Without an appreciation of this context, future studies, as well as many currently in the published literature, are likely to provide conflicting results regarding function and structure of perturbed ecosystems. This may be true not only for those in southern Utah, but also across many ecosystems in the United States and around the world, where key predators (large mammalian carnivores) have been removed and consumers (e.g., increased wild ungulate populations; high densities of domestic ungulates) have significantly affected native species biodiversity.

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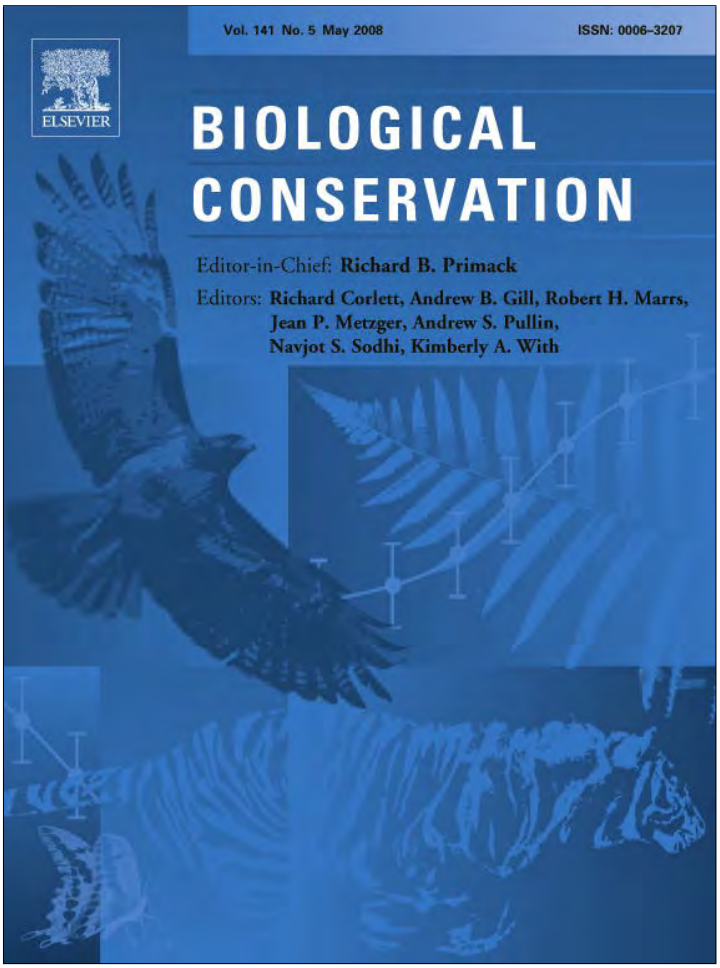

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Trophic cascades involving cougar, mule deer, and black oaks in Yosemite National Park

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ABSTRACT

Using a historical reconstruction, we discovered a potential trophic cascade involving cougar (*Puma concolor*), mule deer (*Odocoileus hemionus*), and California black oak (*Quercus kelloggii*) in the Yosemite Valley of Yosemite National Park in California. Our objective was to determine whether large deer populations in the absence of a top-level carnivore were suppressing tree regeneration. As human visitation increased in the early 1900s and cougar became increasingly scarce, the mule deer population irrupted in the 1920s. In August 2006, we undertook a retrospective study of black oak recruitment (i.e., growth of seedling/sprouts into tall saplings and trees) by inventorying all black oaks in stands accessible to deer and greater than 0.5 ha in size (18 stands, 2921 trees). We similarly inventoried oaks within sites representing refugia from deer browsing (4 stands, 481 trees). While significantly diminished oak recruitment has occurred since the 1920s in stands accessible to deer ($p < 0.01$), continuous recruitment of oaks was found in refugia sites. We also found less oak recruitment in areas of high human activity near the park's visitor center ($p < 0.01$), possibly due to behaviorally-mediated effects of lower cougar and higher deer densities. Overall our results are consistent with trophic cascade theory involving large predators, herbivores, and plants. The long-term lack of oak recruitment is also an indicator of a probable loss of biodiversity.

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1. Introduction

Historically, ecologists generally viewed food-webs as regulated by bottom-up forces (Ray et al., 2005). This view started to change when Hairston et al. (1960) initiated a continuing debate when they suggested that predators maintain plant biomass at high levels by limiting herbivore populations. Later termed trophic cascades, this "top-down" view of food-web interactions contradicted the prevailing bottom-up view that food-webs were nutrient-driven, as reflected in the classic food pyramid. More recently, ecologists have recognized that both top-down and bottom-up forces affect the abundance and diversity of flora and fauna within a food-web (Polis and Strong, 1996). Because interactions within a food-web can be complex and the relative strength of top-down vs. bottom-up forces can vary, the importance of trophic cascades in ecosystem processes and functions has remained controversial (Schmitz et al., 2000; Halaj and Wise, 2001; Shurin et al., 2002; Borer et al., 2005).

One source of controversy may be associated with the unraveling of ecosystems that often occurs whenever humans significantly affect trophic levels (Terborgh et al., 2001). Thus, the paucity of documented cases of terrestrial trophic cascades involving large predators may be an artifact

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of viewing seriously altered systems after carnivore extirpation, a situation which characterizes many current ecological investigations (Steneck and Sala, 2005).

Historical reconstructions of plant community dynamics may be particularly useful for understanding trophic cascades since they can provide direct evidence about the previous ecosystem states (Jackson et al., 2001). Furthermore, such assessments may be valuable for guiding interpretations of long-term trophic interactions following the removal or reduction of carnivores. Using tree rings as a basis for determining when trees became established, herein we report on a historical reconstruction of a potential trophic cascade involving cougar (*Puma concolor*), mule deer (*Odocoileus hemionus*), and California black oak (*Quercus kelloggii*) in the Yosemite Valley of California. Other than recent studies conducted by Binkley et al. (2005) and Ripple and Beschta (2006) on the Colorado Plateau, we are not aware of additional reports on the presence or absence of cougars triggering a trophic cascade.

Based on theoretical models of predator/prey dynamics, the overshooting of carrying capacity by ungulates would be rare or infrequent with an intact predator/prey system (Boutin, 1992; Ballard et al., 2001). Leopold (1943) in summarizing his research on this topic wrote,

> "We have found no record of a deer irruption in North America antedating the removal of deer predators. Those parts of the continent which still retain the native predators have reported no irruptions. This circumstantial evidence supports the surmise that removal of predators predisposes a deer herd to irruptive behavior".

More recently, Flueck (2000) reviewed literature from northern latitudes around the world and similarly found no reports of "deer [cervid] irruptions in unmodified continental environments containing complete large predator and prey communities". Furthermore, when predation is either eliminated or reduced, the subsequent decline in carrying capacity following an ungulate population irruption likely occurs because herbivores over-utilize their forage base (Leopold, 1943; McCullough, 1979; Ripple and Beschta, 2005). Our hypothesis (below) linking black oak recruitment (i.e., growth of seedling/sprouts into tall saplings and trees) in Yosemite Valley to the presence of predators is consistent with the above theory on the overshooting of carrying capacity as well as with Leopolds's (1943) and Flueck's (2000) findings.

Cougar were displaced from Yosemite Valley early in the 20th century and a deer population irruption followed in the 1920s (Wright et al., 1933; Dixon, 1934a). Thus, we undertook this study to evaluate any effects on the current age structure of black oak as mediated through potentially high levels of deer browsing. We hypothesized that any long-term gap in black oak recruitment is mainly associated with low density of predators and high browsing pressure by mule deer (see Fig. 1). We also considered alternative hypotheses for any reductions in black oak recruitment including: (1) fluctuations in climate, (2) lack of fires, (3) conifer invasion, (4) land use, and (5) loss of aboriginal influences.



Fig. 1 – Mature black oaks and a lack of young oaks near the visitor center in Yosemite Valley. The mule deer in the foreground is foraging for acorns and oak seedlings (W.J. Ripple, September 2006).

2. Yosemite Valley history

Humans occupied Yosemite Valley for at least the last 3000 years and paleoecological evidence suggests that aboriginals began burning in the valley about 650 years ago (Anderson and Carpenter, 1991). Coincident with this new burning practice, pollen from pond sediments showed a rapid shift from a conifer dominated forest to a more open oak system in the valley (Anderson and Carpenter, 1991). Prior to the 1850s, Yosemite Valley was occupied by a tribe of Miwok Indians that harvested black oak acorns and habitually used fire and hand-eradication methods to control brush and tree growth (Earnst, 1943; Reynolds, 1959). When Euro-Americans entered the valley in the 1850s, they found little undergrowth and a "park-like" setting, with clear open views throughout the valley (Earnst, 1943).

By the early 1860s, settlers in Yosemite Valley began plowing portions of the floodplain, planting crops, and grazing livestock. During the 1880s, settlers attempted to clear young trees and brush which, in the absence of fire, had proliferated throughout the Valley (Earnst, 1943). Mule deer were very scarce around the turn of the century since, in defiance of existing game laws, hunting of them was common (Dixon, 1934a). By the second decade of the 20th century, Yosemite National Park had an active predator removal program. Grinnell and Storer (1924) described professional cougar hunter Jay Bruce's success at killing cougar in the Yosemite area, "... a total of 31[cougar] being taken in the three winter seasons, 1915–1918". During this period of predator reduction, Yosemite ranger Forest S. Townsley wrote to Joseph Grinnell, "Coyotes, Lions, bob-cats seem to be very much on the decrease..." (Runte, 1990).

By the 1920s, the National Park Service began to note an increase in Yosemite Valley's mule deer population. Wildlife biologist Dixon (1934a) reported, "Through protection from predatory natural enemies and human hunters, the deer in Yosemite [Valley] increased so rapidly that they were numer-

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ous there by 1925". In addition to intense browsing on oak seedlings, Dixon (1934b) suggested that the deer were the cause of a decline of the evening primrose (*Oenothera hookeri*) in the valley. Other National Park Service wildlife biologists (Wright et al., 1933; Cahalane, 1941) similarly noted the absence of cougar, abundant deer, and browsing impacts to the vegetation. They suggested that vegetation was being threatened due to increases in the deer population following displacement of cougar from Yosemite Valley. In an attempt to preserve native flora, in 1930 and 1931 the Park Service trapped and removed 137 deer from Yosemite Valley (Dixon, 1934a). Although deer removals in the early 1930s provided temporary relief from overbrowsing, within a few years their numbers again increased and additional deer were removed in the 1940s.

To monitor deer impacts to vegetation, the park service constructed several deer-proof fenced exclosures in 1934. At the Bridal Veil meadow exclosure, Allen et al. (circa 1970) observed that a variety of plant species comprising the dense tall growth inside the fence were entirely absent in the immediate vicinity outside because of deer foraging impacts. At the El Capitan exclosure, they found oak seedlings to be much more numerous inside than outside the fence.

In a study of vegetation of Yosemite Valley, Heady and Zinke (1978), observed abundant black oaks in the seedling and mature size classes, but fewer oaks than would be expected in the intermediate size classes. They also noted relatively heavy browsing impacts by deer on woody browse species. Recently, Fritzke (1997) suggested a linkage between the lack of long-term black oak recruitment and deer browsing in the valley.

3. Study area

Yosemite Valley was originally shaped by glaciation, resulting in jagged peaks, rounded domes, waterfalls, and a U-shaped canyon. Following glaciation, the valley floor (comprising an area of $\sim$18 km^2) became largely covered with alluvial sediments.

The Mediterranean type climate of the central Sierras is characterized by hot, dry summers and cool, moist winters. Most precipitation occurs during the winter as either rain or snow. Yosemite Valley lies in the lower montane forest zone, with a prevalence of trees such as California black oak, interior live oak (*Quercus wislizeni*), ponderosa pine (*Pinus ponderosa*), incense-cedar (*Calocedrus decurrens*), and white fir (*Abies concolor*). Major predator species within the park include cougar, black bear (*Ursus americanus*), and coyote (*Canis latrans*), with ungulates represented only by California mule deer that are found in the valley year round. Among others, small mammal species include California ground squirrel (*Spermophilus beecheyi*) and western gray squirrel (*Sciurus griseus*).

California black oak reproduces by sexual and asexual mechanisms. Sexual reproduction consists of acorn crops after oaks are at least 30 years old. Asexual reproduction involves basal sprouting after disturbance, such as fire. Black oak is somewhat shade tolerant as a seedling, but less so as a sapling or small pole (McDonald, 1969). Initial seedling development is typically not limited by low light levels because acorns are relatively large and provide the bulk of carbohydrates for initial growth. Since the majority of a seedling's biomass lies in the roots, they are able to persist in low light for years until disturbance reduces overstory shade, thus allowing an oak seedling to continue its vertical growth. As black oaks grow they become increasingly shade intolerant, with the crown requiring full sunlight (McDonald, 1969).

Deer, small mammals, and insects consume black oak acorns, sprouts, and foliage. Gray squirrels disseminate acorns by burying them singly in the ground, a process that often results in the establishment of seedlings away from the parent trees. Black oak lives to 500 years, but in the absence of disturbance can be crowded out by conifer invasion or die because of shade intolerance. The spatial extent of black oak stands in Yosemite Valley has declined during the 20th century, and observers typically attribute this decline to lack of fire and conifer invasion (Earnst, 1943; Reynolds, 1959). Since 1970 the park service has implemented a prescribed burning program in Yosemite Valley. The visitor's center and nearly all other building and campground development (mostly <4 km from the visitor's center) occur near the east end of the valley. In contrast, the west side of Yosemite Valley and the Mirror Lake area on the far northeast end are relatively undeveloped except for some roads and/or trails.

4. Methods

We selected all black oak stands greater than 0.5 ha in size from a park service vegetation type map of Yosemite Valley. We only selected stands dominated by black oak, thus avoiding stands heavily invaded by conifers. A total inventory of tree diameters was conducted within the selected stands of all black oaks $\geqslant$1 cm diameter at breast height (DBH). Tree diameter measurements were made using a Biltmore stick. We inventoried oaks in all selected open-grown (accessible to deer) stands as well as those in refugia sites where there were physical barriers to deer access. These refugia included strips of land occurring between the main highway and river comprising terraces and other surfaces generally above the floodplain, often with high cutbanks. Our examination of the oak seedlings and saplings indicated very low levels of browsing in the refugia stands. Beschta (2005) described similar refugia along the Yellowstone River where he found low browsing levels on strips of land between the river and a highway. We compared oak age structure for the deer-accessible sites to that of the refugia sites (spatial control).

We obtained increment cores at breast height ($\sim$1.4 m above the ground) from 3 to 4 oaks in each inventoried stand and used these data to establish age–diameter relationships for estimating the breast height age of each inventoried tree. We mounted, dried, and sanded the cores before counting tree rings with the aid of a dissecting microscope. Cross dating of cores to identify ring anomalies was not accomplished due to low variability in ring widths. Based on sectioning young oak trees adjacent to the park, we added 11 years to this estimated age at breast height to account for tree height growth from ground level to 1.4 m above the ground. Measured tree diameters, in conjunction with the age–diameter relationship, were used for determining historical trends in black oak tree recruitment in Yosemite Valley (e.g., Beschta,

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2005). An exponential function was fitted to measured tree frequencies and establishment dates before the deer irruption (pre-1920) for deer-accessible stands and to all tree frequency and establishment data for refugia stands.

We established a 4 m wide belt transect through the centroid of each surveyed oak stand, along its long axis, within which the number and height of all oak seedlings were recorded. The total length of each transect was also recorded. Basal area measurements (using a 5 m^2/tree basal area factor gage) were obtained at up to 4 equally spaced points along the transect, with a minimum of 40 m separation between measurement locations. We searched for cougar fecal droppings in each oak stand while walking between measured trees. We surveyed evening primrose plants in order to obtain an estimate of deer browsing intensity that was independent of black oaks. Since evening primrose only grow in wet areas, a search and enumeration of this species was made at all oak stands growing in wet sites. Each evening primrose plant was classified as unbrowsed (buds intact) or browsed (buds browsed off).

Other covariates recorded for each stand included (1) distance from visitor center and (2) fire history. Since cougar generally avoid humans (Van Dyke et al., 1986), distance from the visitor center data were used to investigate whether more browsing and less oak recruitment occurred near the center of greatest human activity. In other national parks, researchers have found evidence of lower predation risk, higher ungulate densities, and more browsing on plants in areas of high human activities (Hebblewhite et al., 2005; Ripple and Beschta, 2006; Beschta and Ripple, 2007). Information on the number of times each stand burned since 1930 was obtained from a Park Service fire history map of Yosemite Valley.

We used *t*-tests (unequal variances) to determine any significant differences between covariates associated with deer-accessible oak stands vs. refugia oak stands, as well as for stands near the visitor center compared to stands farther away from the visitor center. The nonparametric Wilcoxon rank-sum test was used when data were not normally distributed. Since we were performing multiple comparisons, we applied the False Discovery Rate (FDR) procedure and adjusted the results as described by Benjamini and Hochberg (1995). We used the Palmer Drought Index (Cook et al., 2004) to examine general climatic patterns for the periods 1800–1919 vs. 1920–1999. We considered $p \leqslant 0.05$ from any test to represent a statistically significant outcome.

5. Results

We found and measured the diameters of 2921 black oak trees (DBH range 1–190 cm, $\bar{x} = 38$ cm) in 18 deer-accessible stands and 481 oak trees (DBH range 1–135 cm, $\bar{x} = 10$ cm) in 4 refugia stands. Deer-accessible stands ranged from 0.65 to 2.50 ha in size, while available refugia stands were smaller, ranging from 0.14 to 0.68 ha.

We obtained a total of 27 readable increment cores from black oaks occurring along Yosemite's valley bottom. Regression analysis indicated that the number of tree rings (y) was highly correlated with DBH (x) ($y = 5.35x^{0.795}$, $r^2 = 0.77$, $p < 0.01$). A statistically significant, but somewhat different relationship, was obtained for 13 readable cores from black oaks occupying hillslopes adjacent to canyon walls ($y = 14.94x^{0.592}$, $r^2 = 0.61$, $p < 0.01$).

The age structure of deer-accessible oak stands in Yosemite Valley was considerably different from that associated with refugia stands. The deer-accessible stands (Fig. 2a) show few young trees and lack of recruitment since the early 1900s. In contrast, oaks within the refugia stands (Fig. 2b) show continuous recruitment over time with more young trees than old ones, a normal feature of uneven-aged forest dynamics when recruitment is on-going. There were no significant differences in the number of fires since 1930 and oak seedling densities between the deer-accessible and refugia oak stands ($p \geqslant 0.14$, Table 1). We found a marginal difference in oak basal area between deer-accessible and refugia stands, but

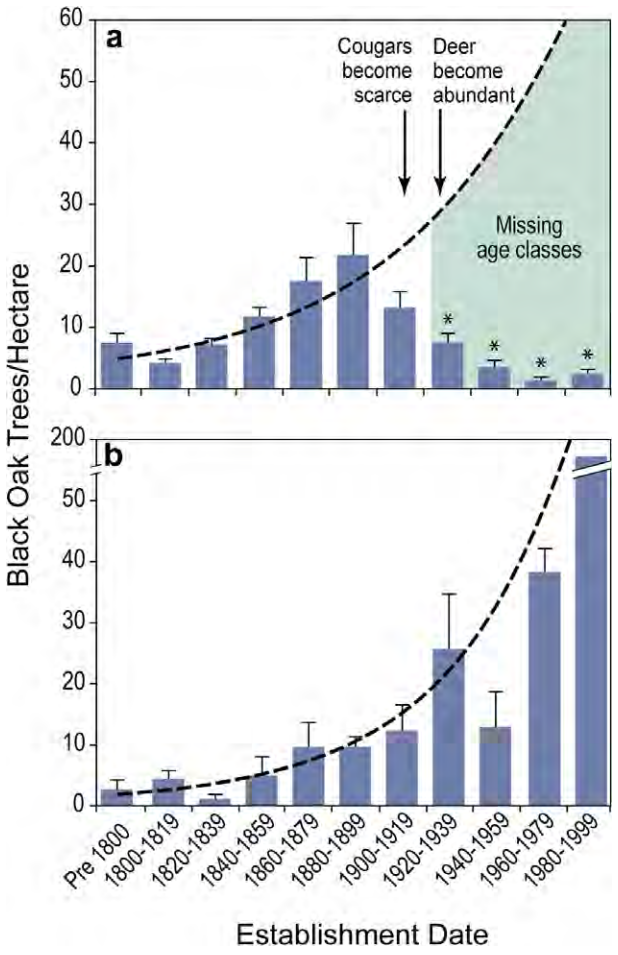

Fig. 2 – California black oak age structure (with standard error bars) for (a) deer-accessible oak sites and (b) refugia sites with low deer browsing; all sites are within Yosemite Valley. The exponential functions (dashed lines) are based on (a) tree frequencies and establishment dates before the deer irruption (pre-1920) and (b) tree frequency and establishment data between 1800 and 1999. The age structure in (a) illustrates a general cessation of oak recruitment (i.e., missing age classes) since the early 1900s, which is in contrast to generally continuous recruitment in (b). Age classes outside the lower 95% confidence interval of the exponential equation are represented by *.

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Table 1 – Summary statistics of covariates for deer-accessible oak stands (generally those experiencing intensive oak browsing by deer) and refugia oak stands (with little or no oak browsing by deer)

Covariate description	Deer-accessible stands ($n = 18$)			Refugia stands ($n = 4$)			p-value	Statistical test
	mean	min	max	mean	min	max		
Number of fires since 1930	1.8	0	5	1.8	0	4	0.98	t-test
Conifer basal area (m^2/ha)	10.5	0	22.4	22.7	17.6	33.9	0.05[a]	Rank-sum
Oak basal area (m^2/ha)	12.9	4.9	21.5	6	0.6	12.9	0.07	t-test
Oak seedlings (#/ha)	716	167	2567	897	639	1173	0.14	Rank-sum
Oak seedling height (cm)	17.2	9.7	38	57.6	47.6	65	<0.01	Rank-sum
Oak recruitment since 1920 (#/ha)	13.1	0	45.1	86.8	74	106.7	<0.01	t-test

a Not considered significant due to false discovery rate from multiple comparisons.

this was not statistically significant ($p = 0.07$). We also found marginally higher ($p = 0.05$) conifer basal area in the refugia stands when compared to the deer-accessible stands but this was not significant after conducting the FDR procedure. Mean oak seedling height and the mean number of oaks originating since 1920 was significantly lower in deer-accessible stands than for refugia stands ($p < 0.01$).

Since deer-accessible oak stands occurred up to 8 km from the visitor center, we classified all stands as either 0–4 km from the visitor center ($n = 11$) or 4–8 km from the visitor center ($n = 7$). There were no significant differences in number of fires since 1930, conifer and oak basal area, seedling density, and seedling height between oak stands 0–4 km vs. 4–8 km from the visitor center ($p \geqslant 0.18$, Table 2). However, significantly more oaks originated since 1920 in stands 4–8 km from the visitor center when compared to those 0–4 km from the visitor center ($p < 0.01$) where we found on average 20.1 vs. 2.1 oaks/ha, respectively. We found cougar scat in 3 of the 18 deer-accessible stands, all at distances 4.1–6.5 km from the visitor center. Mean recruitment of black oaks since 1920 in stands with observed cougar scat was higher than in stands without observed scat (35.6 vs. 8.4 trees/ha, $p = 0.02$).

A total of 91 evening primrose plants were found in 4 out of 7 wet-site oak stands of which approximately 98% had been browsed, as indicated by the absence of flower buds. The 4 wet-site stands with primrose were all located away (4.3–5.5 km) from the visitor center whereas the three wet-site stands with no observed primrose were all located near (0.8–2.1 km) the visitor center. For the 18 deer-accessible stands, we found significantly more oak recruitment since 1920 in dry-site ($\bar{x} = 18.8$ oaks/ha, $n = 11$) than wet-site ($\bar{x} = 4.2$ oaks/ha, $n = 7$) stands ($p = 0.03$).

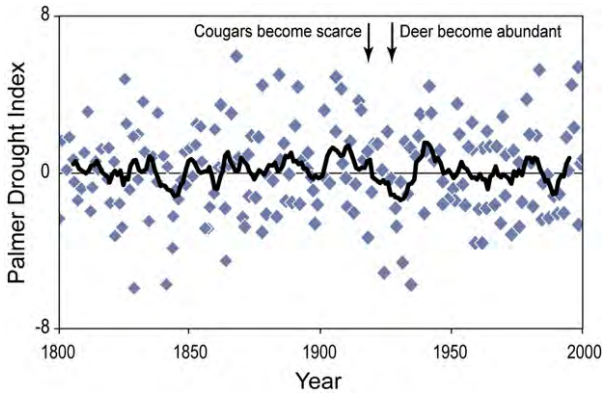

Fig. 3 – Annual values (closed diamonds) of Palmer Drought Index for Yosemite Valley and a 10-year moving average (continuous line) over a 200-year period of record ("point 47" data from Cook et al., 2004). Positive values of the index indicate wet periods and negative values dry periods.

There were no apparent differences in drought/wet period fluctuations in the Palmer Drought Index (PDI) data when comparing the periods before 1920 to those since 1920 (Fig. 3). We calculated the mean PDI for the periods 1800–1919 and for 1920–1999 and found that they were not significantly different ($p = 0.62$).

6. Discussion

Our age structure data for deer-accessible oak stands (Fig. 2a) illustrate a major recruitment gap in Yosemite Valley occurring after 1920 where we found, on average, only 13 oaks/km^2. This compares to 87 post-1920 oaks/km^2 in the browsing refugia

Table 2 – Summary statistics of covariates for oak stands near (0–4 km) the visitor center and those away (4–8 km) from the visitor center

Covariate description	0–4 km stands ($n = 7$)			4–8 km stands ($n = 11$)			p-value	Statistical test
	mean	min	max	mean	min	max		
Number of fires since 1930	1.1	0	3	2.2	0	5	0.18	t-test
Conifer basal area (m^2/ha)	7.3	0	18.7	12.5	0.3	22.4	0.15	t-test
Oak basal area (m^2/ha)	13.1	5.7	21.5	12.8	4.9	20.7	0.89	t-test
Oak seedlings (#/ha)	795	188	2567	665	167	1646	0.79	t-test
Oak seedling height (cm)	15.8	9.7	32.5	18	9.8	38	0.48	Rank-sum
Oak recruitment since 1920 (#/ha)	2.1	0	6.6	20.1	0	45.1	<0.01	t-test

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stands, representing nearly a 7-fold difference between these two groups of stands. Furthermore, oak recruitment rates for the deer-accessible stands decreased with time as the 20th century progressed, with very low recruitment occurring by the end of the century (Fig. 2a). The oak age structure data show the recruitment decline starting between 1900 and 1920, which is during the predator eradication period and just before the deer irruption of the 1920s. This downturn in oaks may have been due to browsing by an increasing deer population or, since oak grow slowly, the irrupting deer of the 1920s may have killed oak regeneration from the previous decade.

Overall, our results indicate a continuation of the high deer browsing intensities witnessed by early wildlife biologists and park managers after cougar, and perhaps other predators became scarce, and the deer population irrupted in Yosemite Valley (Wright et al., 1933; Dixon, 1934a,b; Cahalane, 1941; Allen et al., circa 1970). Such results are consistent with trophic cascades theory whereby a reduction in large carnivore predation can produce important ecosystem changes, including greater herbivore densities and relatively few young palatable trees.

Due to a lack of case studies, there have been questions in the literature about whether terrestrial trophic cascades driven by large carnivores generally occur (Borer et al., 2005). The results reported here support previous studies regarding the role of wolves (*Canis lupus*) in trophic cascades in Isle Royale (McLaren and Peterson, 1994), Yellowstone (Ripple and Larsen, 2000; Ripple and Beschta, 2004; Beschta, 2005), Banff (Hebblewhite et al., 2005), Wind Cave (Ripple and Beschta, 2007), and Jasper National Parks (Beschta and Ripple, 2007). Our findings in Yosemite Valley are consistent with other studies describing trophic cascades in cougar/mule deer systems on the Kaibab Plateau (Leopold, 1943; Binkley et al., 2005) and in Zion National Park (Ripple and Beschta, 2006). Aspen recruitment on the Kaibab largely terminated following predator reductions, similar to the patterns of reduced cottonwood recruitment and reduced biodiversity in Zion Canyon after cougar became scarce. Our findings also support Leopold's (1943) hypothesis of ungulate irruption and ecosystem degradation after the removal of large carnivores. Thus, this study and other recently published studies involving wolves as well as cougars indicate that terrestrial trophic cascades involving large carnivores may be relatively strong in areas with winter or year-round ungulate use.

In other parts of the United States, deer impacts to oak recruitment in the absence of large carnivores have been documented in a variety of ecosystems. For example, Healy (1997) suggested that high densities of white-tailed deer (*Odocoileus virginianus*) in Massachusetts reduced oak recruitment due to browsing on seedlings. He described these oak stands as having a poorly developed understory and midstory layers similar to what we observed in Yosemite Valley. Russell and Fowler (1999) suggested that browsing by high densities of white-tailed deer caused a lack of Texas live oak (*Quercus fusiformis*) and Texas red oak (*Quercus buckleyi*) recruitment in central Texas. White (1966) found that heavy browsing by mule deer on blue oak (*Quercus douglasii*) seedlings in the California foothills caused a lack of small diameter oak trees. Boyer and Bleich (1979) studied mule deer and California black oak in a state park in southern California where they found, in a system degraded by past domestic livestock grazing, even moderate densities of deer were able to prevent oak recruitment.

Our results of less cougar scat, oak recruitment, and evening primrose in areas near the Yosemite visitor center (low predation risk), compared to more distant locations (high predation risk), are consistent with trophic cascades theory involving behaviorally-mediated effects. This shift in the use of space by the herbivore is typically considered a behavioral effect, since it is a non-lethal mechanism, and occurs when ungulates, under the risk of predation, alter their foraging patterns and movements in a "landscape of fear" (Lima, 1998; Laundré et al., 2001). When predation risk is high, herbivores balance needs for both safety and forage as described by optimal foraging theory (Brown et al., 1999; Berger, 2007) and the effects on plants may be greater than those resulting from changes in predator or prey populations (Schmitz et al., 1997). Furthermore, recent research in carnivore/ungulate systems has found high ungulate densities and/or high levels of browsing near human developments in other national parks in the western North America including Denali (Wolff and Cowling, 1981), Banff (Hebblewhite et al., 2005), Zion (Ripple and Beschta, 2006), Jasper National Parks (Beschta and Ripple, 2007), and Grand Teton National Park (Berger 2007).

While our results are consistent with trophic cascade theory, we nevertheless considered alternative scenarios that might affect oak recruitment including: (1) fluctuations in climate, (2) lack of fires, (3) conifer invasion, (4) land use, and (5) lack of aboriginal influences.

Climate fluctuations do not appear to have caused the lack of oak recruitment as the Palmer Drought Index shows wet and dry periods throughout a 200-year period of record (1800–1999). We found no significant differences when comparing the average PDI before 1920 to that after 1920 and there has been continuous long-term recruitment of oaks in the refugia stands (Fig. 2b). Additionally, Angress (1985) studied Yosemite Valley oaks and soil moisture and suggested that varying levels of soil moisture did not have a significant effect on black oak germination and seedling growth. We found more oak recruitment since 1920 in dry-site than wet-site stands ($p = 0.03$) further indicating that available moisture was not a limiting factor for oak recruitment.

The lack of fire may be hampering black oak recruitment since fire can eliminate competing conifers, open the canopy, and allow asexual reproduction through basal sprouting. However, we do not believe that a lack of fire is the cause for reduced oak recruitment in our deer-accessible stands since we found on-going recruitment in the refugia stands, even though both groups of stands have a similar fire history (Table 1). Additionally, there has been little recruitment of oaks within the valley even with an on-going prescribed fire program implemented by the Park Service since 1970 (Fig. 2a).

Shading and competition from conifer invasion may be a factor in oak decline for large portions of Yosemite Valley, since various studies have documented a general increase in conifers during the 20th century (e.g., Gibbens and Heady, 1964), and oak stands may have been lost to this factor. However, we did not survey stands heavily invaded by conifers, and conifer basal area was greater in the refugia stands than in the deer-accessible stands. It appears that oak recruitment

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suppression can be nearly complete in the absence of significant conifer invasion as a result of intense deer browsing.

The variable land use history in Yosemite Valley complicates efforts to easily discern potential predator–herbivore effects on plants. Historically, aboriginal inhabitants may have kept carnivore and deer numbers to relatively low levels. Low deer densities in conjunction with frequent low-intensity fires (Reynolds, 1959; Angress, 1985) allowed oaks to recruit over time (our pre-1920 oak age structure data). When Euro-Americans arrived they also hunted deer and predators, thus keeping large mammal numbers down. Until the time deer irrupted, subsequent to the decline in cougar and other predators in the 1910s, black oak recruitment appears to have been on-going (Fig. 2a). While land use practices prior to the 1920s may have affected the overall distribution of black oak stands that are currently left in the valley, oak recruitment prior to the 1920s was occurring in the stands we measured.

Although the study of interactions of herbivory and disturbance events is in its infancy, research is beginning to show the importance of "coupling" press disturbances such as ungulate predation with pulse disturbances such as wildfire on the recruitment of woody browse species (Wisdom et al., 2006; Halofsky, 2007; Beschta and Ripple, 2007). Since the occurrence of fire with moderate-to-high herbivory can be detrimental to tree recruitment, decreased levels of herbivory may be required before some of the potential ecological benefits of fire (i.e., the maintenance of palatable woody species that are adapted to fire) can be attained (Wisdom et al., 2006). We observed essentially no recruitment of basal sprouts on 104 large oaks killed during relatively recent Park Service prescribed burns (authors' observations, 2006). Thus, our results suggest that prescribed burning in the presence of existing levels of ungulate herbivory is likely accelerating the decline of the overstory oaks in Yosemite Valley while providing no improvement in oak recruitment.

The paleoecological data suggest that Yosemite Valley was dominated by conifers before humans began burning the Valley 650 years ago. This perspective has implications for the current management of fire and oaks in understanding the valley's "natural state" before anthropogenic disturbances (Anderson and Carpenter, 1991). The more recent aboriginal peoples in Yosemite Valley probably influenced black oaks in at least two ways: (1) burning the valley which decreased conifers and increased oaks; and (2) killing or displacing large predators and deer. They appear to have modified natural ecosystem structure and processes to create a system that favored oak recruitment, acorn production, and acorn harvest (i.e., frequent burning and low predator/deer densities). Thus, the current park service policy of prescribed burning to remove conifers in conjunction with the current high deer densities is in contrast with both the conifer dominated system prior to 650 years ago as well as the more recent aboriginal system, which likely consisted of fewer conifers, more oaks, and fewer deer.

We did not study the effects of several factors that might influence oak recruitment such as variability in hunting pressure on deer, acorn predation by small mammals and birds, pathogens, periodicity of acorn crops, interaction of available light with browsing pressure, and direct impacts of human trampling on young oaks. However, we propose that they were unlikely to have been major factors affecting the oak recruitment gap documented in this study since our study design included both a temporal control (pre-1920s deer irruption vs. post-1920s deer irruption) and two types of spatial control (deer-accessible vs. refugia oaks as well as near visitor center vs. away from visitor center).

In Yosemite Valley, there are dozens of faunal species that rely on acorns for food and oak trees for nesting and cover. The lack of oak recruitment documented in this study likely indicates a substantial decrease in biodiversity (e.g., shrubs, wildflowers, birds, invertebrates) since early in the 20th century. Thus, in concert with a broader literature (e.g., Rooney and Waller, 2003; Côté et al., 2004), this study supports the concept that, in the absence of large carnivores or control by humans, ungulates can profoundly alter ecosystems.

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Status and Ecological Effects of the World's Largest Carnivores

William J. Ripple,* James A. Estes, Robert L. Beschta, Christopher C. Wilmers, Euan G. Ritchie, Mark Hebblewhite, Joel Berger, Bodil Elmhagen, Mike Letnic, Michael P. Nelson, Oswald J. Schmitz, Douglas W. Smith, Arian D. Wallach, Aaron J. Wirsing

Background: The largest terrestrial species in the order Carnivora are wide-ranging and rare because of their positions at the top of food webs. They are some of the world's most admired mammals and, ironically, some of the most imperiled. Most have experienced substantial population declines and range contractions throughout the world during the past two centuries. Because of the high metabolic demands that come with endothermy and large body size, these carnivores often require large prey and expansive habitats. These food requirements and wide-ranging behavior often bring them into conflict with humans and livestock. This, in addition to human intolerance, renders them vulnerable to extinction. Large carnivores face enormous threats that have caused massive declines in their populations and geographic ranges, including habitat loss and degradation, persecution, utilization, and depletion of prey. We highlight how these threats can affect the conservation status and ecological roles of this planet's 31 largest carnivores.

Advances: Based on empirical studies, trophic cascades have been documented for 7 of the 31 largest mammalian carnivores (not including pinnipeds). For each of these species (see figure), human actions have both caused declines and contributed to recovery, providing "natural experiments" for quantifying their effects on food-web and community structure. Large carnivores deliver economic and ecosystem services via direct and indirect pathways that help maintain mammal, avian, invertebrate, and herpetofauna abundance or richness. Further, they affect other ecosystem processes and conditions, such as scavenger subsidies, disease dynamics, carbon storage, stream morphology, and crop production. The maintenance or recovery of ecologically effective densities of large carnivores is an important tool for maintaining the structure and function of diverse ecosystems.

Outlook: Current ecological knowledge indicates that large carnivores are necessary for the maintenance of biodiversity and ecosystem function. Human actions cannot fully replace the role of large carnivores. Additionally, the future of increasing human resource demands and changing climate will affect biodiversity and ecosystem resiliency. These facts, combined with the importance of resilient ecosystems, indicate that large carnivores and their habitats should be maintained and restored wherever possible. Preventing the extinction of these species and the loss of their irreplaceable ecological function and importance will require novel, bold, and deliberate actions. We propose a Global Large Carnivore Initiative to coordinate local, national, and international research, conservation, and policy.



Ecologically important carnivores. Seven species of large carnivores with documented ecological effects involving (**A**) "tri-trophic cascades" from large carnivores to prey to plants, (**B**) "mesopredator cascades" from large carnivores to mesopredators to prey of mesopredators, and (**C**) both tri-trophic and mesopredator cascades. [Photo credits: sea otter (N. Smith), puma (W. Ripple), lion (K. Abley), leopard (A. Dey), Eurasian lynx (B. Elmhagen), dingo (A. McNab), gray wolf (D. Mclaughlin)]

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ARTICLE OUTLINE

Ecological Effects of Large Carnivores
Ecosystem and Economic Services
Anthropogenic Impacts
Climate Change
Outlook
A Final Word

SUPPLEMENTARY MATERIALS

Figs. S1 to S4
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ADDITIONAL RESOURCES

"Lords of nature: Living in a land of great predators"; www.youtube.com/watch?v=PagO3gmwmA0

George Monbiot, TED "For more wonder, rewild the world"; www.youtube.com/watch?v=8rZzHkpyPkc

Trophic Cascades Program, www.cof.orst.edu/cascades/

Large Carnivore Initiative for Europe, www.lcie.org/Home.aspx

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Status and Ecological Effects of the World's Largest Carnivores

William J. Ripple,[1]* James A. Estes,[2] Robert L. Beschta,[1] Christopher C. Wilmers,[3] Euan G. Ritchie,[4] Mark Hebblewhite,[5] Joel Berger,[6] Bodil Elmhagen,[7] Mike Letnic,[8] Michael P. Nelson,[1] Oswald J. Schmitz,[9] Douglas W. Smith,[10] Arian D. Wallach,[11] Aaron J. Wirsing[12]

Large carnivores face serious threats and are experiencing massive declines in their populations and geographic ranges around the world. We highlight how these threats have affected the conservation status and ecological functioning of the 31 largest mammalian carnivores on Earth. Consistent with theory, empirical studies increasingly show that large carnivores have substantial effects on the structure and function of diverse ecosystems. Significant cascading trophic interactions, mediated by their prey or sympatric mesopredators, arise when some of these carnivores are extirpated from or repatriated to ecosystems. Unexpected effects of trophic cascades on various taxa and processes include changes to bird, mammal, invertebrate, and herpetofauna abundance or richness; subsidies to scavengers; altered disease dynamics; carbon sequestration; modified stream morphology; and crop damage. Promoting tolerance and coexistence with large carnivores is a crucial societal challenge that will ultimately determine the fate of Earth's largest carnivores and all that depends upon them, including humans.

The order Carnivora consists of 245 terrestrial species inhabiting nearly every major habitat on Earth (*1*). These mammalian species, which we call carnivores, are generally unified by a shared heritage of subsisting largely on other animals and are naturally rare because of their position at the top of the food web. These are also some of the world's most revered and iconic species. Ironically, they are also some of the most threatened. During the previous two centuries, many carnivores have experienced substantial population declines, geographic range contractions, and fragmentation of their habitat (*2*, *3*).

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Carnivores of various sizes play an important role in regulating ecosystems (*4*–*7*). These roles, moreover, may not be redundant among carnivore species, because the strength and nature of their impacts are influenced by factors such as the carnivore's size, metabolic demands, density, sociality, and hunting tactics. The larger carnivores especially tend to have large energetic constraints, slow life histories, and low population densities and roam widely in search of larger prey (*8*–*10*). This conflation of low population densities and reproductive rates with high food requirements and wide-ranging behavior, bringing them into conflict with humans and livestock, is what makes them vulnerable and poorly able to respond to persecution.

Large carnivores can exert ecological effects despite existing at low densities (*11*), but persecution can affect their social structure and influence their ecological role (*12*). Classically, the effects of large carnivores are thought to extend down the food web to herbivores and to plants, but we are learning that their cascading influences propagate broadly to other species as mediated by their controlling effects on mesocarnivores (*4*, *13*, *14*). Large carnivores have the dual role of potentially limiting both large herbivores through predation and mesocarnivores through intraguild competition, thus structuring ecosystems along multiple food-web pathways. Together, these controls influence the nature and strength of ecosystem functioning. What makes the conservation of large carnivores exceptionally important, therefore, is both their vulnerability to extinction and their ability to structure ecosystems. With this in mind, our focus here is on the largest carnivores.

We review the conservation status and ecological effects of the 31 largest (average adult body masses ≥15 kg) species of Carnivora (not including pinnipeds). Although most of these species are obligate meat eaters, some are omnivorous and one is herbivorous (Table 1). The remaining 214 carnivore species with body masses <15 kg are not considered here, but we acknowledge they also can play important and varied roles in communities (*4*, *13*). The 31 largest carnivores belong to five families: Canidae, Felidae, Mustelidae, Ursidae, and Hyaenidae. They generally have small population sizes (Fig. 1 and table S1), often due to high levels of range loss (Table 1). Many of these species (61%) are listed by the International Union for the Conservation of Nature (IUCN) as threatened (vulnerable, endangered, or critically endangered) and are at risk of local or total extinction. Most (77%) are undergoing continuing population declines (Table 1). Estimates of range contractions for 17 of the 31 species revealed that they currently occupy on average only 47% (minimum <1%, maximum 73%) of their historical ranges (Table 1). These range losses can result in local population extinctions, which have implications for the maintenance of ecosystem and socioeconomic services. Thus, many of these species are gradually disappearing just as we are beginning to understand and appreciate their roles in ecosystems and the many societal benefits that accrue from their preservation (*5*, *15*).

We report our current understanding of the substantial ecological roles large-carnivore species play in ecosystems and how their population declines, extirpations, and recoveries stand to influence ecological communities and ecosystems across the globe. We further consider how those roles may change as environmental conditions become altered when humans cause habitat loss and climate change. We end by addressing the outlook for the future and the looming uncertainties motivating an urgent need for more research on carnivore interactions in food webs and the conservation of these species.

Ecological Effects of Large Carnivores

Seven of the 31 species of large carnivores are associated with documented trophic cascades. Therefore, we focus on these seven species with analysis and discussion. Each of the seven species is well studied in comparison to other large carnivores (fig. S2). In all cases, these seven species of large carnivores clearly have cascading influences on ecological communities and ecosystems. We assessed the general strength of these effects using available data to calculate the $\log_{10}(X_a/X_p)$ effect magnitudes, where X_a and X_p are the values for the response variables with the large-carnivore species absent and present, respectively [for methods, see (*6*)]. The effect magnitude of large-carnivore removal on the abundance of prey, plants, and mesopredators ranged from –2.3 to 2.3 (Fig. 2). These are considered large effects. For example, an effect size of 2 or –2 represents a difference of two orders of magnitude (100 times) in the effect

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between when carnivores are absent as compared to present. These values also rank relatively high when compared to a meta-analysis of 114 case studies of predators from both aquatic and terrestrial systems, where effects, expressed in $\log_{10}$ ratios, ranged from −0.3 to 1.0 (*16*). With the exception of the sea otter, all of the aquatic and terrestrial predators included in that study were ≤2 kg in body mass, suggesting a potential link between carnivore size and ecological influence. Below we provide a brief synthesis for each of the seven large-carnivore species. Following these species accounts is a general discussion of other large-carnivore species, for which less is known about their ecological effects.

Lions and Leopards

The African lion (*Panthera leo*) occupies 17% of its historical range and is listed as vulnerable by the IUCN. Its abundance has declined dramatically in recent decades because of habitat loss and indiscriminate killing in defense of humans and livestock (*17*). The leopard (*Panthera pardus*) is near threatened and occupies 65% of its historical range. When sympatric, lions and leopards exert control on mesopredators. In West Africa, olive baboons (*Papio anubis*) increased in abundance at rates most closely correlated with declines in these apex predators relative to seven other environmental variables that might explain baboon abundance and range occupancy (*18*). Increases in baboons correlated with accelerated declines in small ungulates and primates. Among large mammals, baboons pose the greatest threat to livestock and crops and they use many of the same sources of animal protein and plant foods as humans in sub-Saharan Africa. In some areas, baboon raids in agricultural fields require families to keep children out of school so they can help guard planted crops (*18*).

Dingoes

The dingo (*Canis dingo*), thought to have arrived in Australia around 5000 years ago (*19*), became the sole remaining mammalian apex predator on the continent after the extinction of the Tasmanian tiger (*Thylacinus cynocephalus*). With European settlement, dingo populations have been affected across the continent, notably by the erection of a 5500-km dingo-proof fence designed to keep dingoes out of Australia's major sheep-grazing region. The presence and absence of dingoes on either side of the fence, along with variation in dingo management practices among properties, has produced a continental-scale experiment. The most significant and well-understood effects of dingoes are in the control of populations of native

Table 1. Large-carnivore species list, body mass (in kilograms), diet, endangerment status, population trend, and percent of historical range occupied. Body masses are from Gittleman (*15*), Mammalian Species Accounts, and the Animal Diversity Web. Diet categories are from Hunter (*1*) as follows: M, meat eater; V, vegetation and/or fruit eater; O, omnivore. Species status and trend are from the IUCN Red List (*16*): LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered; CR, critically endangered.

Family/species*	Common name	Mass, diet	IUCN status (trend)	% of historical range	Reference for % of historical range
Canidae					
Canis lupus	Gray wolf	33, M	LC (stable)	67	(*1*)
Canis rufus	Red wolf	25, M	CR (increasing)	<1	(*91*)
Chrysocyon brachyurus	Maned wolf	23, O	NT (unknown)	68	(*2*)
Lycaon pictus	African wild dog	22, M	EN (decreasing)	10	(*17*)
Cuon alpinus	Dhole	16, M	EN (decreasing)	–	–
Canis dingo†	Dingo	15, M	VU (decreasing)	84	(*20*)
Canis simensis	Ethiopian wolf	15, M	EN (decreasing)	2	(*17*)
Felidae					
Panthera tigris	Tiger	161, M	EN (decreasing)	18	(*3*)
Panthera leo	Lion	156, M	VU (decreasing)	17	(*17*)
Panthera onca	Jaguar	87, M	NT (decreasing)	57	(*3*)
Acinonyx jubatus	Cheetah	59, M	VU (decreasing)	17	(*17*)
Panthera pardus	Leopard	53, M	NT (decreasing)	65	(*3*)
Puma concolor	Puma	52, M	LC (decreasing)	73	(*3*)
Panthera uncia	Snow leopard	33, M	EN (decreasing)	–	–
Neofelis nebulosa	Clouded leopard	20, M	VU (decreasing)	–	–
Neofelis diardi	Sunda clouded leopard	20, M	VU (decreasing)	–	–
Lynx lynx	Eurasian lynx	18, M	LC (stable)	–	–
Mustelidae					
Enhydra lutris	Sea otter	28, M	EN (decreasing)	–	–
Pteronura brasilliensis	Giant otter	24, M	EN (decreasing)	–	–
Aonyx capensis	Cape clawless otter	19, M	LC (stable)	–	–
Ursidae					
Ursus maritimus	Polar bear	365, M	VU (decreasing)	–	–
Ursus arctus	Brown bear	299, O	LC (stable)	68	(*3*)
Ailuropoda melanoleuca	Giant panda	134, V	EN (decreasing)	–	–
Ursus americanus	American black bear	111, O	LC (increasing)	59	(*35*)
Tremarctos ornatus	Andean black bear	105, O	VU (decreasing)	–	–
Ursus thibetanus	Asiatic black bear	104, O	VU (decreasing)	–	–
Melursus ursinus	Sloth bear	102, O	VU (decreasing)	–	–
Helarctos malayanus	Sun bear	46, O	VU (decreasing)	–	–
Hyaenidae					
Crocuta crocuta	Spotted hyena	52, M	LC (decreasing)	73	(*17*)
Hyaena brunnea	Brown hyena	43, O	NT (decreasing)	62	(*17*)
Hyaena hyaena	Striped hyena	27, O	NT (decreasing)	62	(*17*)

*Changes to taxonomic status have influenced the number of species included in this group, and some less-known and taxonomically ambiguous carnivores may be missing from this analysis because they have yet to be listed by the IUCN. †Currently incorporates the New Guinea singing dog, *C. hallstromi*, whose taxonomic and conservation status is yet to be elucidated.

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herbivores, introduced herbivores, and the exotic mesopredator the red fox (*Vulpes vulpes*). The suppression of these species by dingoes reduces total herbivory and predation pressure, in turn benefiting plant communities and smaller native prey (*12*, *14*, *20*, *21*). The dingo's social stability and associated behavior are thought to be key to its ecological effectiveness (*12*). Overall, the suppression of dingoes has probably contributed to the endangerment and extinction of small marsupials and rodents over much of the continent (*21*, *22*).

Eurasian Lynx

The Eurasian lynx (*Lynx lynx*) maintains an extensive distribution in eastern and northern Eurasia, but it has been extirpated from large parts of Western Europe (*23*). At the continental scale, the effects of lynx predation increase with harsh winter conditions (*23*, *24*). Lynx may limit both prey (roe deer *Capreolus capreolus*) and mesocarnivore (red fox) abundance, so changes in lynx status may trigger cascading effects along two pathways, of which the mesocarnivore-mediated cascade is the more explored (*25*). The recent recovery and enhanced conservation protection of Eurasian lynx in Finland were accompanied by a decline in red fox abundance and a commensurate recovery in the abundance of forest grouse (*Tetrao tetrix and T. urogallus*) and mountain hare (*Lepus timidus*) (*7*, *25*). Moreover, where lynx density had recovered to "ecologically effective" levels, the controlling effects of lynx on red foxes and prey increased with ecosystem productivity, indicating that the strength of predator control may vary as a function of the net primary productivity of the ecosystem (*26*, *27*).

Sea Otters

Sea otters (*Enhydra lutris*) were hunted to near-extinction during the Pacific maritime fur trade in the 18th and 19th centuries (*28*). Sea otter populations are presently stable or increasing from about Kodiak Island eastward, deeply depleted [presumably because of killer whale predation (*29*)] from about Kodiak Island westward through the Aleutian archipelago, and largely recovered in Russia. The earlier recovery of these populations and the more recent decline of recovered populations in southwest Alaska (*29*) offer natural experiments to study the sea otter's influences on coastal ecosystems. The best-documented cascade of effects involves sea otters limiting herbivorous sea urchins and, in turn, enhancing the abundance and distribution of kelp and other fleshy macroalgae in coastal inshore ecosystems (Fig. 3A) (*30*). As sea otter populations recover and decline, shifts between the kelp-dominated and urchin-dominated conditions can be abrupt (*31*). Once reached, these different ecological states tend to persist (*32*) unless the system is pushed strongly to the other state by substantial increases or reductions in otter abundance. The follow-on effects of these shifts influence numerous other species and ecological processes in coastal ecosystems through three basic mechanisms: the creation of biogenic habitat (i.e., created by living organisims), the enhancement of primary production, and the influence of kelp forests in dampening coastal waves and currents [reviewed in (*31*)].

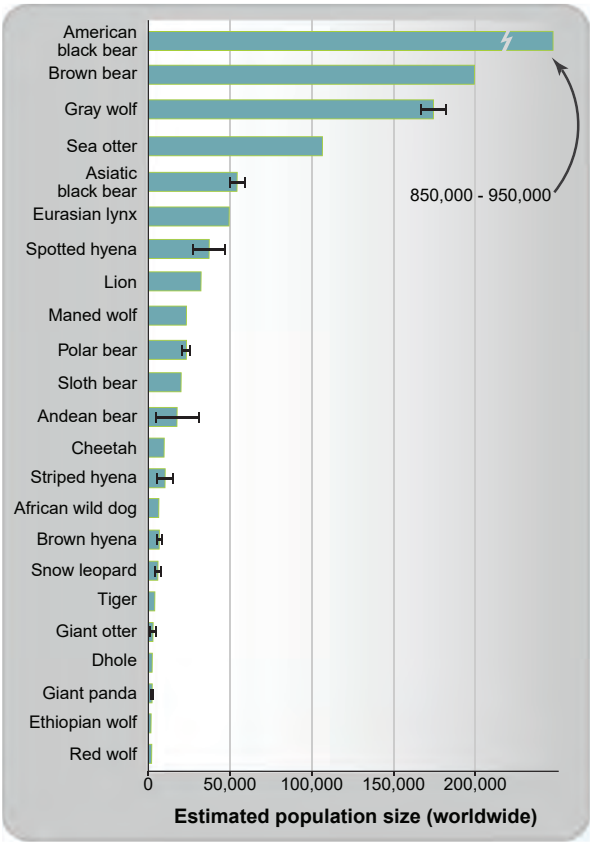

Fig. 1. Worldwide population estimates of large-carnivore species. Error bars represent the low and high range of the estimates when available. Population estimates were not available for all species. Species ranges vary widely, and range sizes can have a strong influence on species population levels (table S1). Sources: Gray wolf (*90*), all other species IUCN (*91*).

Gray Wolves

The gray wolf (*Canis lupus*) is one of the world's most widely distributed mammals and the most studied large carnivore (fig. S2). It has been extirpated from much of Western Europe, the United States, and Mexico, and its overall range has been reduced by approximately one-third because of persecution by humans and habitat fragmentation (*1*). In recent decades, wolf population declines have been arrested because of enhanced legal protection, reintroduction programs, and natural recolonization, resulting in population recoveries in portions of the Rocky Mountains, Great Lakes, and southwestern regions of North America, as well as in various parts of Europe. Other than humans, gray wolves, by virtue of their widespread geographic distribution, group hunting, and year-round activity, are the most important predator of cervids in the Northern Hemisphere (*33*). Predation by wolves with sympatric bears (*Ursus* spp.) generally limits cervid densities (*33*). In North America and Eurasia, cervid densities were, on average, nearly six times higher in areas without wolves than in areas with wolves (*34*). As early as the 1940s, cervid irruptions, after wolf and other predator declines, were first documented in various ecosystems of western North America (*35*). The shifts in plant communities consequent to the cascading effects of wolf extirpations and of recoveries have been found across a variety of areas of North America, representing a wide range of productivity (*6*). In Yellowstone National Park, wolves were reintroduced in 1995–1996, making this park one of the most predator-rich areas in North America. This reintroduction triggered various direct and indirect effects, as mediated by both mesopredators and cervid prey (Figs. 3B and 4).

Pumas

The range of the puma (*Puma concolor*) in the Western Hemisphere remains larger than that of any other terrestrial mammal, even though they have been extirpated from most of the eastern United States (*36*). In the absence of pumas and sometimes other large carnivores, hyperabundant cervids [such as the white-tailed deer (*Odocoileus virginianus*)] in the eastern United States and Canada now affect many aspects of ecosystem function, including plant recruitment and survival, endangered species status, forest stand structure, nutrient dynamics, and socioeconomics through vehicle collisions (*37*). Where pumas are present, they can be important drivers of cervid populations and associated trophic relations, as in canyon settings in western North America, where they locally limit mule deer (*O. hemionus*) densities, releasing woody plants from browsing suppression (*38*, *39*). Pumas also appear to influence processes affecting terrestrial and aquatic species, including hydrophytic plants, wildflowers, amphibians,

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lizards, and butterflies. Their presence may also help to stabilize stream banks and channels (*38*). Pumas may induce their prey to engage in "human shielding" as an antipredator strategy. Deer at risk from pumas, for example, associated themselves with human development at high densities, in turn causing plant damage (*38*, *39*).

Other Large Carnivores

Little is known about the ecological effects of the other large-carnivore species listed in Table 1, and questions remain about their potential roles in controlling food webs and ecosystem functioning, especially in the tropics and subtropics (Fig. 5). However, some valuable lessons come from the flooding of a forest region in Venezuela to generate hydroelectric power. This once-intact, productive tropical system was composed of a species-rich food web with multiple linkages among species. Flooding fragmented the region to produce mountaintop islands—the Lago Guri islands—resulting in the loss of an entire predator guild of jaguars (*Panthera onca*), pumas, lesser mammalian predators, large raptors, and snakes (*40*). This loss of predators had cascading effects on species of pollinators, seed dispersers, seed predators, folivores, and mesopredators, as well as on woody plant recruitment, bird abundance, and soil carbon/nitrogen ratios (*41*).

Predator species often co-occur, requiring consideration of their joint effects. Multiple predator effects on prey species and on ecosystems can be synergistic (*15*). Thus, in some cases, the strength of a trophic cascade may be due to synergisms owing to complementarity among species in the top carnivore guild of communities. This implies that the combined effects of predator species may need to be conserved to fully ensure control over communities and ecosystem functioning. For example, bears of northern latitudes (*Ursus* spp.) may control the recruitment of juveniles into populations of their prey species (*42*). Because bears are opportunistic omnivores and eat a variety of foods, their effects may complement those of gray wolves (*34*). In North America, both black (*U. americanus*) and brown (*U. arctos*) bears commonly prey on neonatal cervids, taking a large percentage of the annual offspring that are less than 1 month old, and these effects could be additive. In Yellowstone National Park, bears killed more elk (*Cervus elaphus*) calves than did gray wolves, coyotes (*Canis latrans*), and pumas combined (*43*). In Europe, roe deer densities were significantly lower in areas with sympatric wolves and lynx than in areas with wolves alone or areas where both predators were absent (*24*, *34*). The effect of multiple predators on prey, however, need not always be synergistic. Adult female elk mortality was similar in areas of western North America with pumas alone as compared to areas with sympatric pumas and wolves (*44*).

Questions persist about how large-carnivore effects interact with habitat productivity. Theory

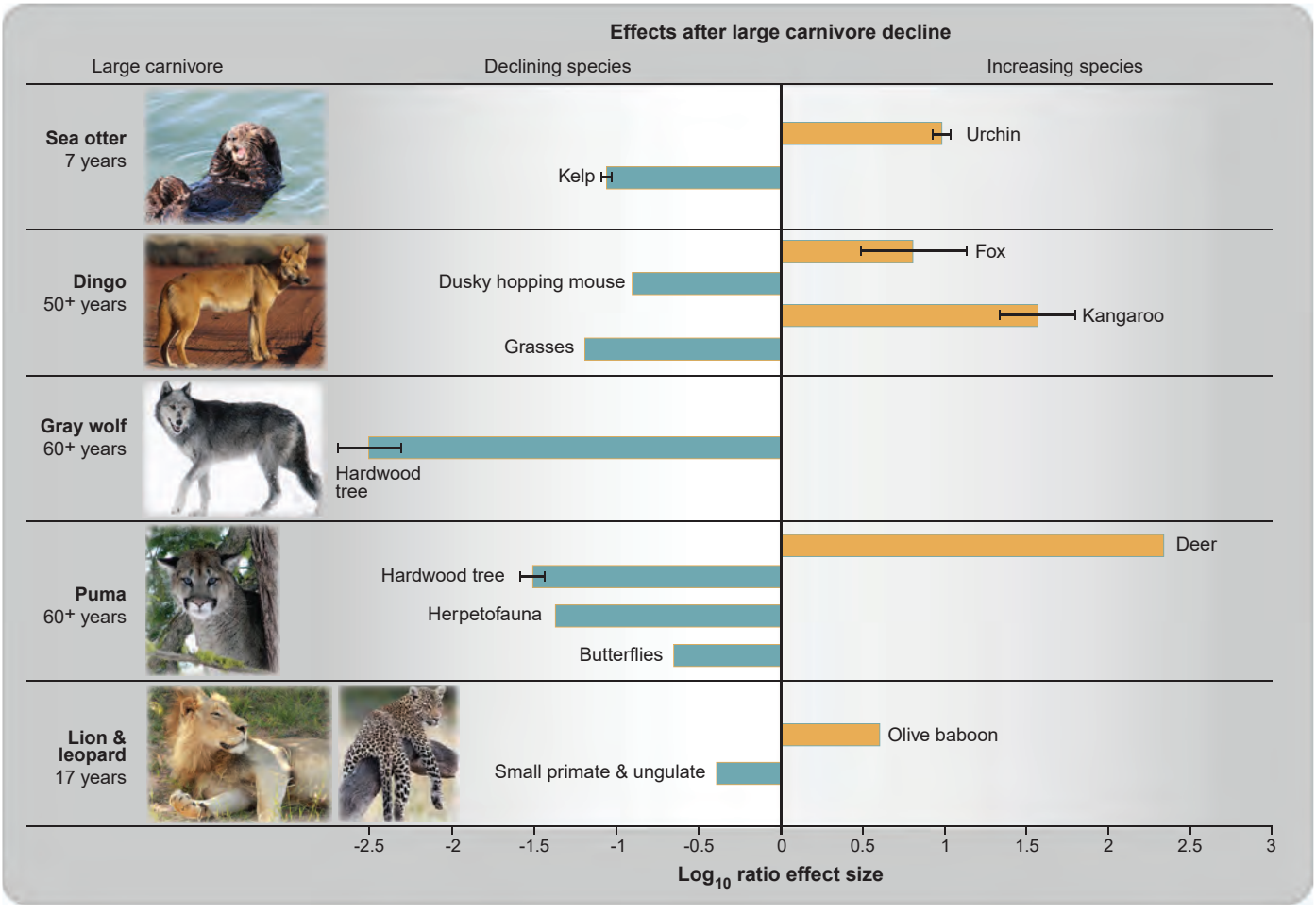

Fig. 2. Examples of effect sizes, shown as $\log_{10}$ ratios, after the removal of large-carnivore species. Sea otters (*29*, *92*), dingoes-foxes and dingoes-kangaroo (*21*, *93*), dingoes-mice (*Notonmys fuscus*) (*93*), dingoes-grasses (*20*), gray wolves–hardwood trees (*94*, *95*), pumas–hardwood trees (*38*, *39*), pumas-deer-herpetofauna-butterflies (*38*), and lions and leopards (*18*). The number of years refers to the time since large-carnivore extirpation. The $\log_{10}$ ratios were calculated by dividing the values of each response variable without predator by those with predator and then taking the $\log_{10}$ of that ratio. Positive log ratios$_{10}$ indicate a positive effect, and negative $\log_{10}$ ratios indicate a negative effect of removing large carnivores. For studies using time-series data, we used the final sampling date in our analysis. The orange bars indicate direct effects and the blue bars indicate indirect effects. Error bars represent standard errors and were only available in some cases. [Photo credits: sea otter (N. Smith), dingo (A. McNab), gray wolf (Yellowstone National Park), puma (Washington Department of Fish and Wildlife), lion (K. Abley), leopard (A. Dey)]

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predicts that the strength of cascading effects may vary with the productivity of ecosystems and should show a "humped relationship" with ecosystem productivity (*26*, *27*). That is, we might not expect to see strong trophic cascades in ecosystems such as extreme deserts, high elevations, or high latitudes, where low primary productivity limits herbivore populations and where there is insufficient energy available to support populations of large carnivores (*27*). The trophic effects of single carnivore species might also be diminished in extremely productive environments, because prey species diversity may also be high in such systems and, consequently, the strength of interspecific interactions is diffused across a greater number of interaction pathways (*20*, *41*, *45*). For example, in a productive tropical forest, Sunda clouded leopards (*Neofelis diardi*) had no measurable effect on the abundance of the main large ungulate prey species (*46*). Conversely, there is also empirical evidence indicating that some canids consistently limit prey densities regardless of ecosystem productivity (*34*, *47*). Accordingly, more analyses of how productivity interacts with trophic interactions are needed. To this end, regions harboring large-carnivore populations with different conservation statuses, including places without them, can be used as broad bioclimatic contexts for natural experiments.

Ecosystem and Economic Services

Large carnivores deliver economic and ecosystem services in a variety of direct and indirect ways. Because of their iconic and charismatic nature, large carnivores provide direct economic benefits associated with tourism. In both Minnesota and Yellowstone (*48*, *49*) and the African photo-safari industry (*50*), the opportunity to simply observe large carnivores can drive tourism revenue. In Yellowstone alone, wolf-related tourism expenditures range from $22 million to $48 million (in U.S. dollars) per year (*49*).

Large carnivores also have strong potential to indirectly deliver ecosystem services, such as carbon storage to buffer climate change, biodiversity enhancement, reestablishment of native plant diversity, riparian restoration, and even regulation of diseases. In some ecosystems, large carnivores may enhance carbon storage by limiting the numbers of their herbivore prey, thus allowing plants (all of which absorb and store CO_2) to flourish. Carnivore conservation and restoration might reverse declines in forests stands and production, thereby aiding carbon storage, especially in the highly productive tropics, where declines in plant biomass occur after predator extirpation (*40*, *41*). Maintaining gray wolf populations and their interactions with moose is estimated to help store significant amounts of carbon in boreal ecosystems (*51*). The restoration of sea otter populations can reduce sea urchin herbivores, thereby allowing kelp ecosystems to flourish at levels that can, in the North American range, lead to a 4.4- to 8.7-teragram increase in stored carbon valued at $205 million to $408 million (in U.S. dollars) on the European Carbon Exchange (*52*). Predators may enhance scavenger diversity (*53*) and thereby contribute to nutrient cycling, in addition to myriad other documented cascading and ramifying pathways (*15*). In riparian systems, large carnivores may reduce stream bank erosion through the growth of woody plants and enhance water quality and flood control through the restoration of beaver that benefit from the restored plants (*54*–*57*). Large carnivores help reduce disease prevalence in ungulate prey populations, thereby mitigating agricultural costs because of spillover effects on domestic livestock (*58*). Perhaps counterintuitively, large carnivores may also provide crucial services for the very industry they are perceived to be at most in conflict with: pastoralism. By limiting the density of wild herbivores and promoting productivity, large carnivores may enable pastoral activities that are sustainable (*12*, *59*). This is not to deny that large carnivores also have direct costs, often associated with livestock losses (*60*), and balancing these costs against potential benefits for human-dominated ecosystems as a whole is a pressing challenge (*61*). Regardless, the potentially widespread beneficial ecosystem and economic services associated with large carnivores are underappreciated by society.

Anthropogenic Impacts

Large-carnivore population declines are typically precipitated by multiple, and sometimes concurrent, human threats, including habitat loss and degradation, persecution, utilization (such as for traditional medicine, trophy hunting, or furs), and depletion of prey. Globally, the strength of these threats varies substantially by region (Fig. 6 and table S2). These threats are sometimes localized to only parts of a carnivore's range and, in some cases, may extend beyond its range, thus acting to limit reoccupation of former habitats.

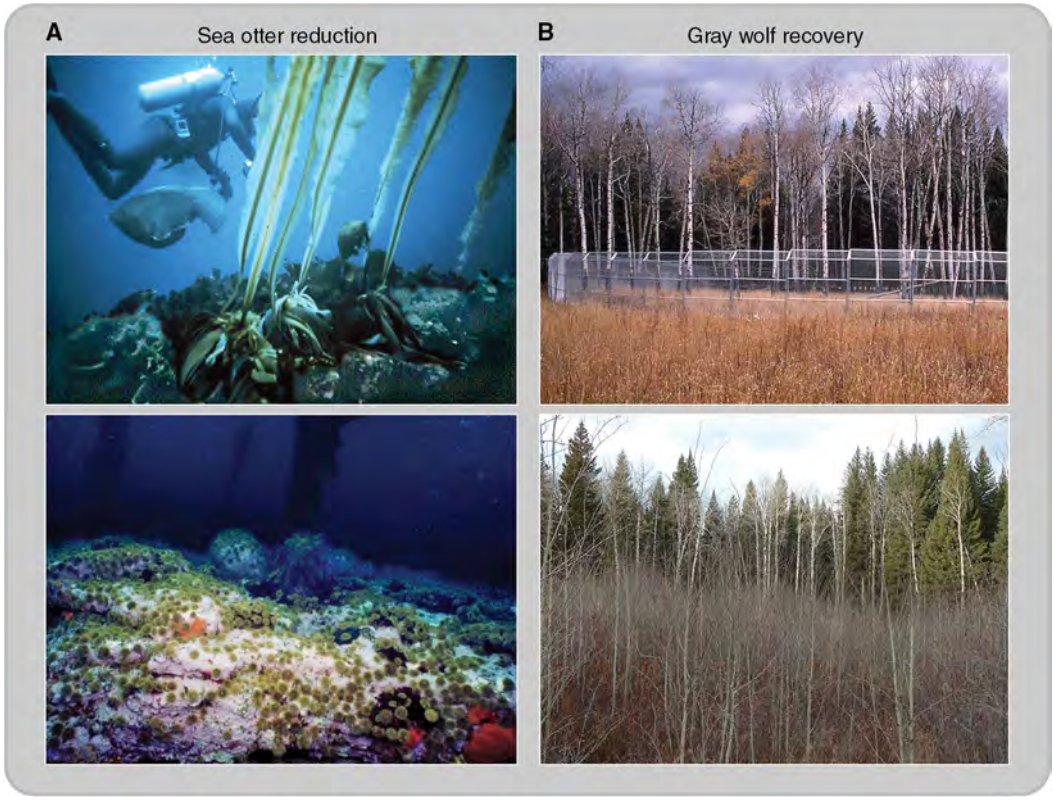

Fig. 3. Examples of plant response after sea otter reduction and after gray wolf recovery. (**A**) An area of seafloor near Kirilof Point, Amchitka Island, Alaska, in 1971 (upper left, photo by P. Dayton), at which time sea otters were abundant, and in 2001 (lower left, photo by M. Kenner) at which time sea otter numbers had been reduced by more than 90% by killer whale predation. (**B**) Photos of the Yellowstone Northern Range taken in October 1994 (top right, photo by National Park Service) and November 2012 (bottom right, photo by D. Mclaughlin), showing increased recruitment of aspen since wolf reintroduction in 1995–1996 at the site of the Crystal Creek gray wolf holding pen, which was removed in 1998. Young aspen in the 1994 photo were mostly less than 1 m tall and those in the 2012 photo were typically 3 to 4 m tall.

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Human actions may dampen or even eliminate cascading effects. For example, Mexican gray wolves in southwestern North America have not yet been restored to an ecologically effective density in relation to that of their main prey, elk, because of ongoing conflicts with livestock grazing and repeated management translocations (*62*). Likewise, recent wide-scale hunting of recovering gray wolf populations in parts of the Great Lakes region and the western United States may reduce wolf populations below sizes at which they are able to exert their effects on communities and ecosystems (*63*–*65*). Furthermore, wolves and other carnivores may have little influence on other species in areas where human hunters have disproportionate effects on prey densities (*66*). Few large carnivores can persist in parts of Latin America, Asia, and Africa because of the loss of wild ungulate prey species caused by activities such as hunting for bushmeat. The extraction of bushmeat, in turn, has created "empty forests" (*1*). Conversely, hyperabundant exotic ungulates (domestic livestock) are present in much of the world. These livestock are a potential prey base and thus a continuing source of conflict between humans and large carnivores (*17*).

Hunting by humans, whether legal as in North America and Europe or illegal as in the pantropical bushmeat trade, may itself cause trophic cascades, because humans are also predators with the potential for ecological impacts. Indeed, human hunting pressure on moose (*Alces alces*) has led to the release of control on willow (*Salix* spp.) shrub production and hence encouraged increases in neotropical migrant bird abundances (*42*). Although it is often claimed that human hunting substitutes for predators, it remains doubtful whether such substitution actually leads to the same functional consequences for communities and ecosystems. Effects may be different because of differences in the intensity and timing of predation by humans versus predators, as well as hunting effects on the behavior, age, and sex of prey (*67*). Many carnivores hunt year-round, day or night, and away from human access points. The behavioral responses of prey to predation risk caused by carnivores may create an "ecology of fear" with myriad cascading effects on ecosystems (*68*). In the end, it is not surprising that various human activities in Australia (*12*), North America (*13*, *34*), and Eurasia (*24*) have been unsuccessful in substituting for large carnivores to control populations of native and nonnative herbivores and mesopredators. The huge importance of carnivores is exemplified by the fact that humans typically cannot replicate the effects of carnivores on ecosystems.

Habitat fragmentation, and more generally the intensity of human uses of landscapes, continue to be persistent threats to larger-bodied carnivores, with the potential for cascading impacts on species diversity (*5*, *38*). There exists, therefore, an increasing need to understand the interacting effects of anthropogenic land-use changes and altered large-carnivore guilds on community structure and function. Because of differences in their ecology and human tolerance, pumas are able to persist in areas with much higher levels of human land use than are gray wolves, even though these two carnivores are of similar size. Such differential predator species loss in the face of landscape changes may be especially critical if synergism among multiple large carnivores within predator guilds is required to maintain control over prey populations (*34*, *43*). These and other carnivore species make kills in different habitats, or scavenge to supplement their diets, which can determine the nature and rates of prey kills and consumption (*53*, *69*). In addition to altering predator communities, increased human land use can alter nutrient and water availability, thereby mitigating natural controls over ecological communities and ecosystem functioning (*70*).

Perhaps one of the most insidious threats to carnivores is global human population size and its associated resource consumption, which are expected to continue rising significantly through at least 2050 (Fig. 7). Increased human population size can lead to increased demand for meat. Interestingly, human carnivory competes with

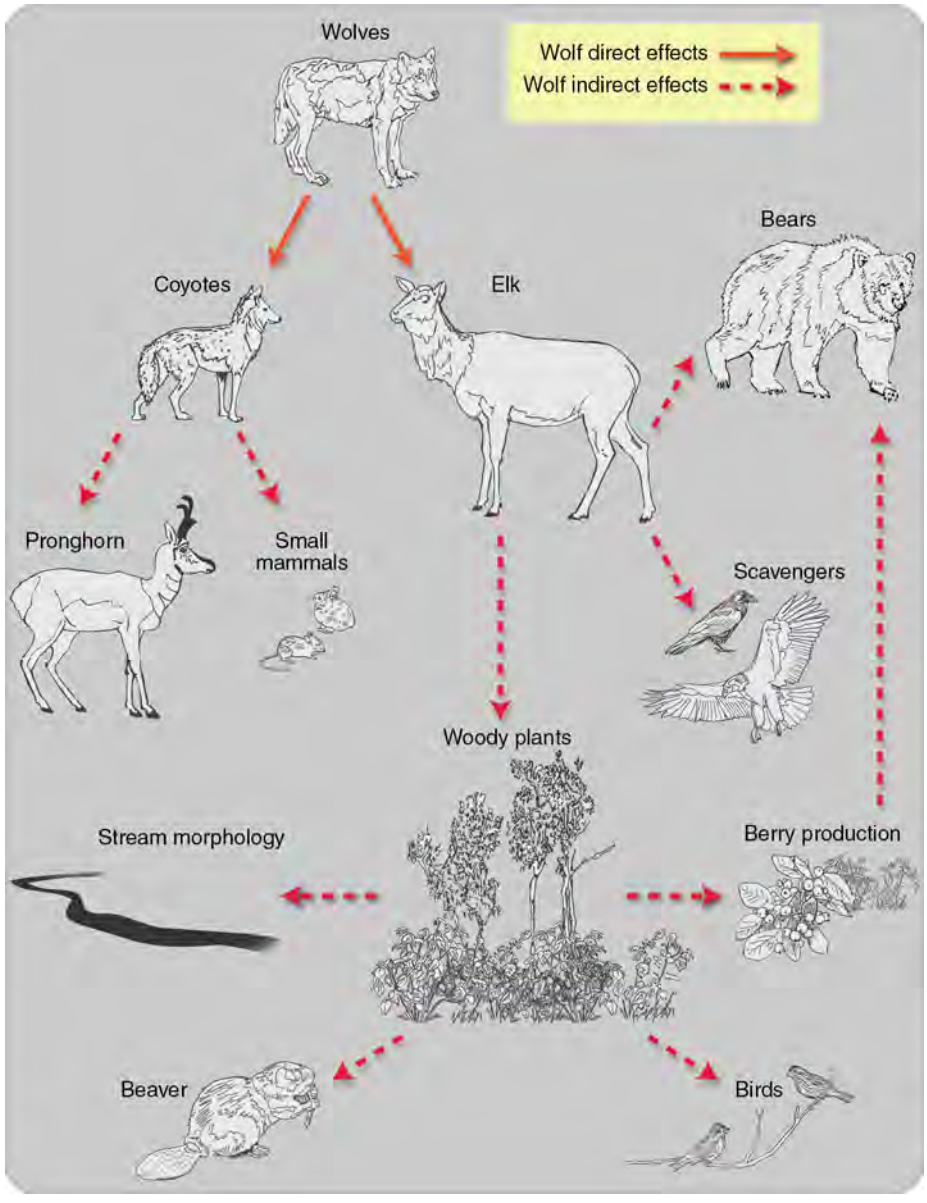

Fig. 4. Conceptual diagram showing direct (solid lines) and indirect (dashed lines) effects of gray wolf reintroduction into the Greater Yellowstone ecosystem. Wolf direct effects have been documented for elk (*96*) and coyotes (*97*), whereas indirect effects have been shown for pronghorn (*98*), small mammals (*99*), woody plants (*100*), stream morphology (*54*), beaver (*55*), birds (*101*), berry production (*63*), scavengers (*53*), and bears (*56*, *63*). This is a simplified diagram, and not all species and trophic interactions are shown. For example, the diagram does not address any potential top-down effects of pumas, bears, and golden eagles (*Aquila chrysaetos*), which are all part of the Yellowstone predator guild where juvenile or adult elk are prey.

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large carnivores. For example, the need for humans to either produce meat through livestock production or to exploit wild sources necessarily puts extra pressure on large carnivores on multiple fronts, including ongoing habitat loss from land conversion, depletion of prey, and direct persecution due to conflicts with livestock. In light of their slow life histories and requirement for large continuous habitat, such trends exacerbate the vulnerability of large carnivores to extinction (*9*). Increases in both human population and meat consumption can also affect biodiversity, greenhouse gas emissions, food security, deforestation, desertification, and water quality and quantity (*71*, *72*). Therefore, policy for carnivore conservation needs to be joined up with policy addressing these other converging issues having implications at the global scale (*71*, *72*). Ideally, discussions regarding potential decreases in both human fertility rates and per-capita meat consumption would be part of a long-term strategy for overcoming these concurrent challenges.

Climate Change

Looking forward, the status of large carnivores will influence the extent to which individual species, biotic communities, and ecosystems respond to climate change. For example, mesopredators that have been released from control by the loss of their carnivore predators may increase further in abundance wherever climate change relaxes limitations on their own prey (*23*). Large carnivores may instrumentally determine resilience against invading species, because both native and introduced species are less likely to become invasive in ecosystems in which food-web interdependencies remain intact (*7*). These potential buffering capacities remain both poorly appreciated and poorly understood. Widespread modeling approaches forecasting climate change effects on species still simplistically assume that such interactions and interdependencies do not require consideration, let alone quantification (*73*). Furthermore, climate change is already causing species geographic range shifts that stand to disrupt existing species interactions (*74*, *75*). As species move at different rates and in different directions, novel communities are likely to be created as new combinations of predator and prey species assemble on landscapes. The recently documented change in hunting locations and food habits among polar bears (*Ursus maritimus*) is a case in point. With receding sea ice, polar bears have more difficulty hunting seals, their traditional prey, and are now feeding onshore on the eggs of migratory waterfowl (*76*).

As climate change progresses, large carnivores might serve as important buffers or amplifiers of effects on ecosystems (*77*). In Yellowstone National Park, reintroduced gray wolves control the timing and abundance of ungulate carrion resources, on which a suite of scavenger species, ranging in size from grizzly bears to magpies (*Pica hudsonia*), depend for winter survival and reproduction. The return of wolves has buffered the influence of climate change on late-winter carrion availability (*77*) by shifting the dynamics of carrion availability from a boom–and-bust cycle, linked to climate variability, to a more dependable resource based on shifting patterns of wolf pack size (*53*). Large carnivores might also help augment ecosystem carbon storage by suppressing herbivores, thereby allowing plants to flourish (*34*). For instance, the decline of large carnivores in western North America was followed by a decline in hardwood tree recruitment in riparian areas of over two orders of magnitude (*6*). In northern North America, gray wolves limiting moose populations may be responsible for increased net ecosystem uptake of carbon due to decreased browsing and increased net primary productivity (*51*). Likewise, the presence of sea otters in nearshore environments suppresses sea urchins, allowing macroalgael kelp to thrive and thereby

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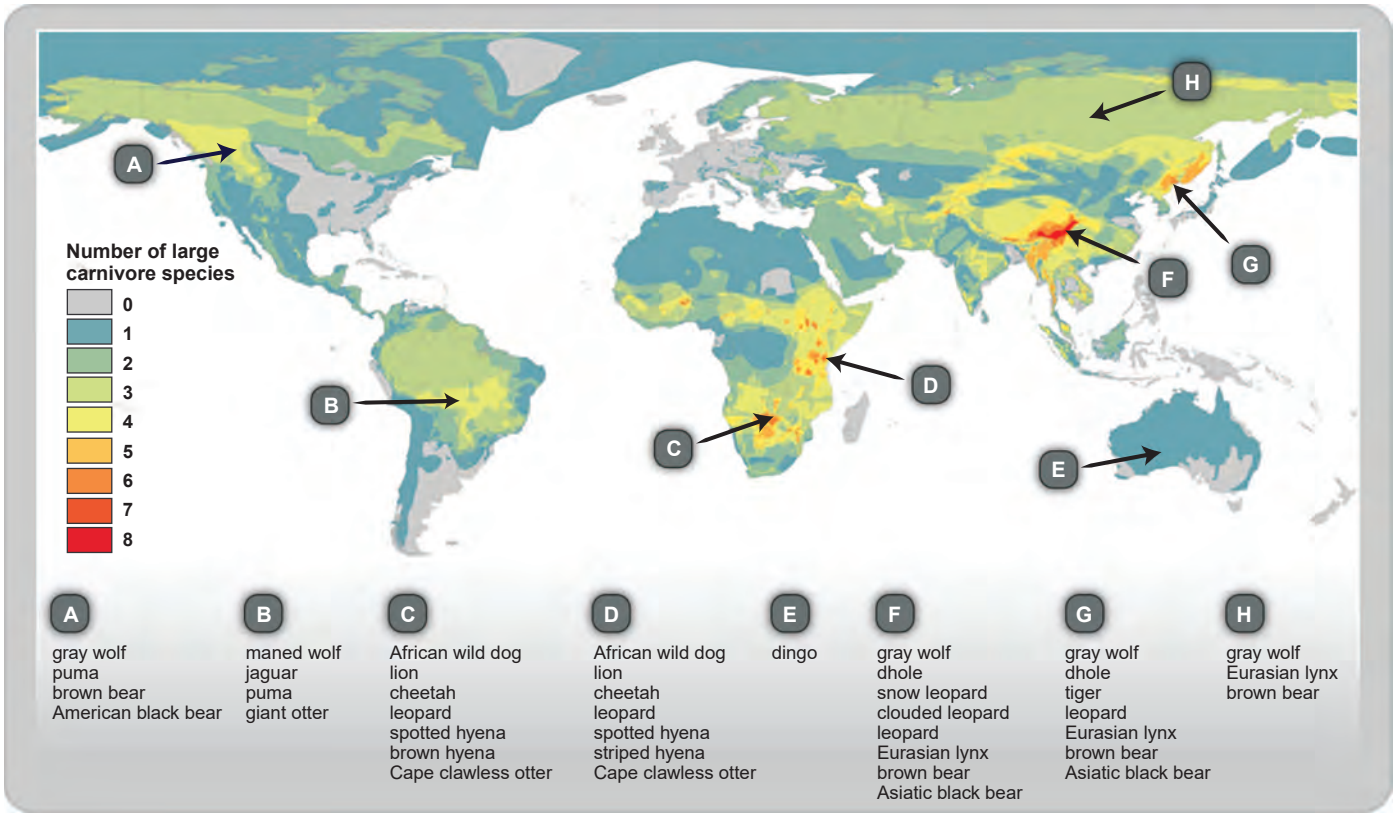

Fig. 5. Contemporary overlap of large carnivore ranges throughout the world. Compared to historical times, large-carnivore range contractions have been most extensive in Europe, southeastern North America, and western and central Africa. The areas with the highest number of species and with intact large-carnivore guilds are some of the best regions for research and conservation (e.g., southeastern Asia, eastern and southern Africa, and northwestern North America). Northern Eurasia is the region with the most expansive range for a three-species guild (gray wolves, Eurasian lynx, and brown bear). The percent of the total terrestrial land area in each of the eight classes in the map includes 0, 13.3%; 1, 29.1%; 2, 23.5%; 3, 20.5%; 4, 9.1%; 5, 2.8%; 6, 1.1%; 7, 0.4%; 8, 0.1%. Only ~5% of Earth's land surface currently contains more than four overlapping large-carnivore species. See fig. S4 for individual range maps. Source: IUCN (*91*).

increasing ecosystem carbon production and storage by one to two orders of magnitude (*52*). Globally, several billion head of ruminating livestock affect global climate change by contributing significant amounts of methane, nitrous oxide, and carbon dioxide (~5.7 gigatons of CO_2 equivalent per year) to the atmosphere, making domestic ruminants a significant contributor to climate change (11.6% of all anthropogenic emissions of greenhouse gases) (*72*). Decreasing global livestock numbers to reduce greenhouse gas emissions would both mitigate climate change and benefit large-carnivore conservation by reducing ongoing worldwide conflict between large carnivores and livestock.

Outlook

The loss of large carnivores across global ecosystems is predicted to lead to two general outcomes. First, as apex predators are lost, we should expect continued change in cascading controls over communities and ecosystem function. Although these effects will differ with the variation in precipitation, temperature, productivity, diversity, and overall landscape features, the continued loss of carnivores nonetheless will be accompanied by changes in plant species diversity, biomass, and productivity. In forest and arid ecosystems, the loss of palatable perennial plant species may interact with global warming to increase the rate of desertification. Because plants are the trophic foundation of all ecosystems, these vegetation changes can be expected to have wide-ranging influences on virtually all other species. The growing list of case studies, some of which we presented above, may well represent the tip of the proverbial iceberg. Changes in species abundance resulting from the loss of large carnivores can be expected to influence numerous other ecological processes, including disease dynamics (*78*, *79*), wildfire (*80*), and carbon sequestration (*51*). Furthermore, the effects of large carnivores are now known to have wide ramifications through highly interconnected food-web networks within their associated ecosystems (*81*). Second, we should expect surprises, because we have only just begun to understand the influences of these animals in the fabric of nature (*82*).

The classic conception of large-carnivore influences on ecosystems held that predators were responsible for depleting resources such as fish, wildlife, and domestic livestock. This assumption is still used to justify wildlife management practices aiming to limit or eradicate predators in some regions (*83*, *84*). This conception of carnivore ecology is now outdated and in need of fundamental change. Indeed, evidence shows that their roles are far more complex and varied, and their myriad social and economic effects on humans include many benefits. Conservation decisions must begin to account for these integral roles and the attendant economic costs of carnivore species losses.

Currently, the IUCN Species Survival Commission (SSC) action plan series represents perhaps the most comprehensive attempt to establish priorities for individual species or taxa (*84*, *85*). These action plans not only provide assessments of threats but recommend conservation monitoring and actions for each large-carnivore species (table S3). Action plans are compiled by the taxonomically organized SSC's Specialist Groups (for example, the Canid Specialist Group compiles action plans for all canid species). Large carnivores, however, also share common conservation challenges that cross taxonomic boundaries: slow life histories, requirement for extensive and continuous habitat, low densities, complex

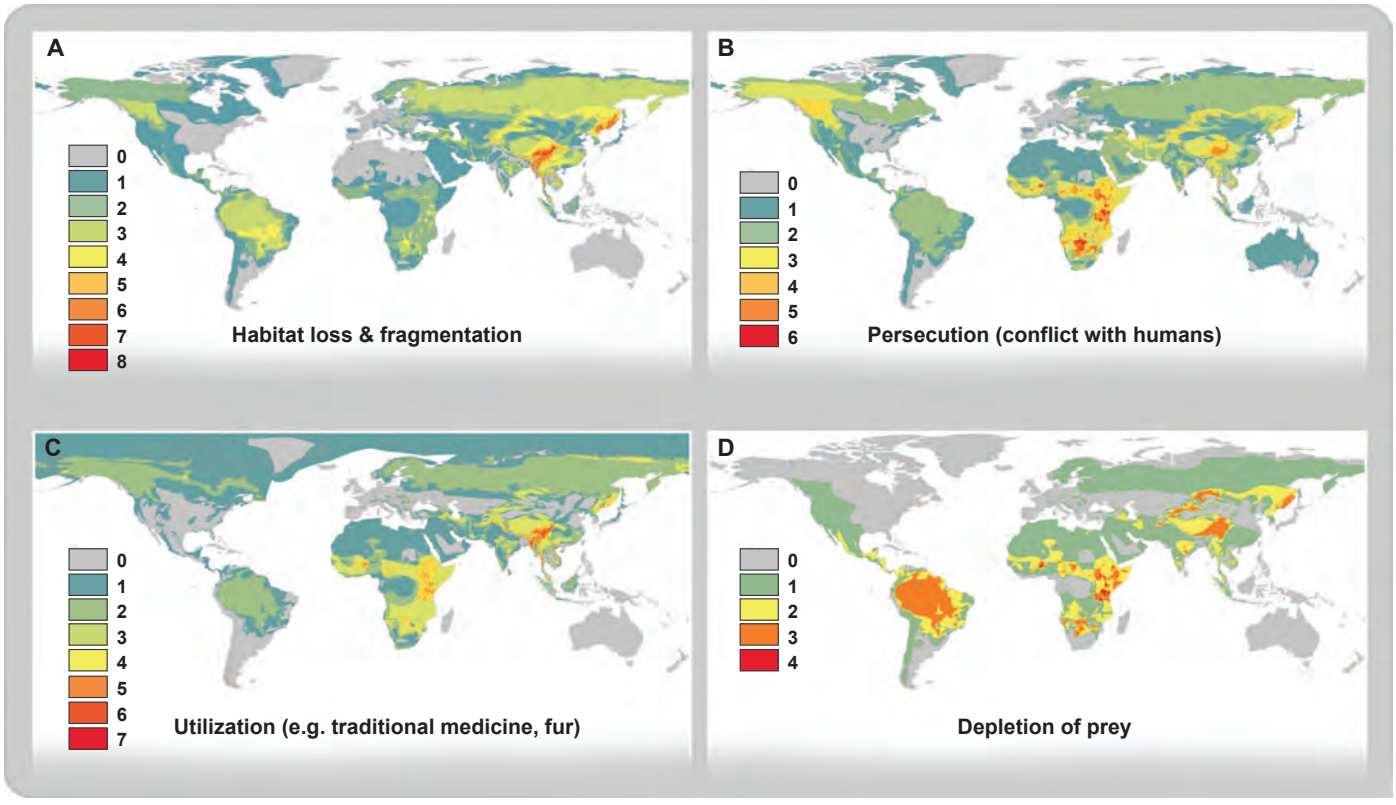

Fig. 6. Maps showing the the spatial overlap for the ranges of large-carnivore species by threat category for habitat loss and fragmentation, persecution, utilization, and depletion of prey. The number of large-carnivore species affected by specific threats is shown in the map legend. Threat catgories include: (**A**) Habitat loss and fragmentation. Forest logging and/or the development of urban, agricultural, and road infrastructure reduces land available to large carnivores and creates barriers between and within populations. (**B**) Persecution. Culling (poison baiting, trapping, and shooting) for the purpose of removal or reduction, in some cases reinforced with a government-subsidized bounty system, in response to real or perceived threat to pastoral and agricultural activities and human lives. (**C**) Utilization. Large carnivores are killed for sport, body parts for traditional medicine, fur, and meat for human consumption, and live animals are captured and sold. (**D**) Depletion of prey. The decline of prey populations due to human hunting, competition with livestock, habitat loss, and other factors reduces the prey base for large carnivores. See table S2 for raw data. Source: IUCN (*91*).

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social structures, importance to ecological function, and conflict with humans. These common traits and challenges have given rise to the creation of the Large Carnivore Initiative for Europe, a Specialist Group whose vision is "to maintain and restore, in coexistence with people, viable populations of large carnivores as an integral part of ecosystems and landscapes across Europe" (86). We propose the expansion of this initiative, to establish a Global Large Carnivore Initiative (GLCI).

There is now a substantial body of research demonstrating that, alongside climate change, eliminating large carnivores is one of the most significant anthropogenic impacts on nature (5). Unlike climate change, however, large-carnivore conservation has yet to become a focus of widespread public recognition, possibly because they are rare, remote, and in some cases perceived to be dangerous and a threat to economic prosperity. The formation of a GLCI would be an important step for the advancement of international public recognition of the ecological role and inherent value of large carnivores, and for developing and coordinating strategies for conservation actions that promote human/large-carnivore coexistence. Such an organization could be modeled, in part, after the Global Tiger Initiative, which is coordinating local, national, and international tiger conservation policy across their distribution and was endorsed in 2010 by the leaders of all 13 tiger-range countries, with funding from the World Bank (87). These 13 countries and partners have moved well beyond words to accomplishments on the ground, including securing funding, establishing new tiger reserves, passing laws on tiger conservation, creating high-level commissions to improve wildlife law enforcement, addressing habitat loss and fragmentation, promoting connectivity, and more (87). The success of any future GLCI would probably include these types of authoritative actions, orchestrated by politically bold commitments from nations around the world.

A Final Word

One of the main ecological arguments for the conservation of large carnivores is that they are often capable of exerting strong regulatory effects on ecosystems (5, 15). Although we present evidence that seven of the top carnivore species we reviewed here have such trophic effects, we know much less about the trophic impacts of the 24 other species of large carnivores. More research directed at these species is needed. Also, we need a better understanding of minimum required densities for large carnivores to maintain trophic cascades in different ecosystems, and when and where the strength of those effects is likely to be large versus small. It is also important to understand which human activities are most in conflict with the conservation of specific large carnivores.

A crucial societal challenge is finding creative solutions to maintain viable populations of large carnivores in the face of alternative land uses (7, 59). This is most urgent because global livestock production continues to encroach on land needed by large carnivores, particularly in the developing world, where livestock production tripled between 1980 and 2002 (88). If the world continues to transition into one that replaces top carnivores with livestock and mesopredators, it is incumbent on us to understand more about the ecological effects of such a downward ratcheting on ecosystems. More large and livestock-free protected areas are needed, especially in regions such as southeastern Asia, where large-carnivore richness (Fig. 5) remains the highest in the world. Yet even in these regions, carnivore populations are decreasing (Table 1) and few large reserves exist (fig. S3). More protected areas alone will not be sufficient, so strategies are also needed to facilitate human coexistence with these animals across working landscapes (59).

Large-carnivore conservation might best be served by a two-pronged approach. First, there is a need for increased recognition of and focus on conserving the full range of the potential effects provided by large carnivores, because this may lead to broader biodiversity, as well as social and economic benefits (5, 15, 89). In areas where large carnivores have been displaced or locally extirpated, their reintroduction may represent a particularly effective approach for passively restoring those ecosystems. However, harnessing the positive effects of large carnivores while (i) minimizing their impacts on humans and (ii) getting humans to adapt to large-carnivore presence, represents a major sociopolitical challenge. Biodiversity conservation programs intended to retain or reintroduce large carnivores must ultimately address both of these challenges if they are to succeed. Second, large-carnivore conservation might also be seen as a moral obligation—the recognition of the intrinsic value of all species. A 40-year history of the field of environmental ethics has both rigorous and systematic rationales for valuing species and nature itself. Large-carnivore conservation, therefore, might benefit greatly from a more formal relationship with practitioners of environmental ethics. It will probably take a change in both human attitudes and actions to avoid imminent large-carnivore extinctions. A future for these carnivore species and their continued effects on planet Earth's ecosystems may depend upon it.

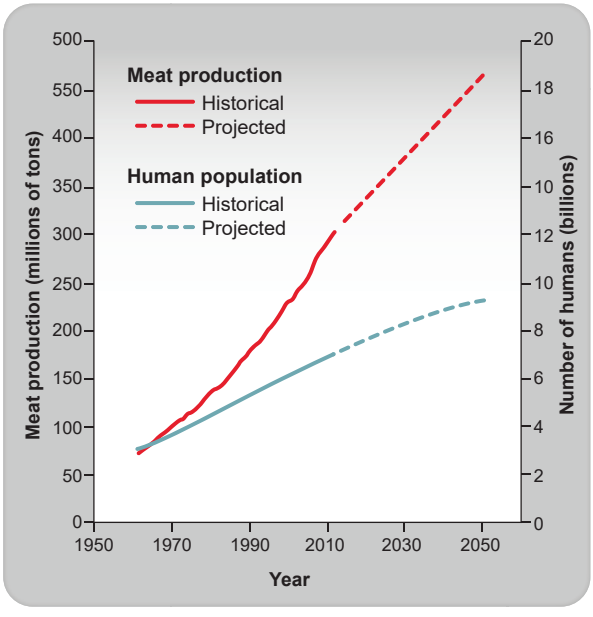

Fig. 7. Historical and projected global human population and global meat production from 1961 to 2050. Source: FAOSTAT (102) and (103) for projected meat production.

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Supplementary Materials

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Science

Status and Ecological Effects of the World's Largest Carnivores

William J. Ripple, James A. Estes, Robert L. Beschta, Christopher C. Wilmers, Euan G. Ritchie, Mark Hebblewhite, Joel Berger, Bodil Elmhagen, Mike Letnic, Michael P. Nelson, Oswald J. Schmitz, Douglas W. Smith, Arian D. Wallach and Aaron J. Wirsing

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Preserving Predators

Large-bodied animals play essential roles in ecosystem structuring and stability through both indirect and direct trophic effects. In recent times, humans have disrupted this trophic structure through both habitat destruction and active extirpation of large predators, resulting in large declines in numbers and vast contractions in their geographic ranges. **Ripple *et al.*** (10.1126/science.1241484; see the Perspective by **Roberts**) review the status, threats, and ecological importance of the 31 largest mammalian carnivores globally. These species are responsible for a suite of direct and indirect stabilizing effects in ecosystems. Current levels of decline are likely to result in ecologically ineffective population densities and can lead to ecosystem instability. The preservation of large carnivores can be challenging because of their need for large ranges and their potential for human conflict. However, the authors demonstrate that the preservation of large carnivores is ecologically important and that the need for conservation action is immediate, given the severity of the threats they face.

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behaviour of the various complexes is the same, but they exhibit profoundly different emission properties, we conclude that the specific nature of the bridge is the key to the colour switching phenomenon. It is well known that electron conduction, stabilization and delocalization on such bridging ligands depend on the geometry, energetics and structural features of the molecules[19–21]. Furthermore, use of different polymers with a higher-energy LUMO level (the HOMO level is chosen to be the same)—so that electron transfer mediated by the Ru complex cannot populate their excited state—did not result in green emission at reverse bias.

Symmetric devices with Au as anode and cathode have symmetric emission properties (that is, they show red emission at both forward and reverse bias), clearly indicating that an asymmetry in the device's charge injection behaviour is needed for the differentiation of the two possible mechanisms of light emission in the $[Ru(ph)_4\text{-}Ru]^{4+}$ PPV system. As the work functions of the ITO and Au contacts are energetically comparable, and the red/green switching behaviour is also seen when Au is replaced by Al, influences other than simple energetics must also have a role in allowing the stepwise electron transfer at reverse bias; we intend to study these influences in greater detail in the near future. □

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Fingerprints of global warming on wild animals and plants

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Over the past 100 years, the global average temperature has increased by approximately 0.6 °C and is projected to continue to rise at a rapid rate[1]. Although species have responded to climatic changes throughout their evolutionary history[2], a primary concern for wild species and their ecosystems is this rapid rate of change[3]. We gathered information on species and global warming from 143 studies for our meta-analyses. These analyses reveal a consistent temperature-related shift, or 'fingerprint', in species ranging from molluscs to mammals and from grasses to trees. Indeed, more than 80% of the species that show changes are shifting in the direction expected on the basis of known physiological constraints of species. Consequently, the balance of evidence from these studies strongly suggests that a significant impact of global warming is already discernible in animal and plant populations. The synergism of rapid temperature rise and other stresses, in particular habitat destruction, could easily disrupt the connectedness among species and lead to a reformulation of species communities, reflecting differential changes in species, and to numerous extirpations and possibly extinctions.

Many studies have examined biological changes in relation to climatic change[4,5], but generally they are concentrated in particular regions or examine a limited set of taxa. To test whether or not a coherent pattern exists across regions and taxa that is consistent with predictions of expected change, we used two types of meta-analyses on these studies: vote counting and the regression-slope model (see Methods). One advantage of meta-analyses is that a broad spectrum of findings can be combined, including those for which statistical significance has not been shown. We examined thousands of articles, including those assembled by Working Group II of the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC TAR WGII)[6]. Of these, we included in our analyses only those that (1) examined a span of at least 10 years, (2) found that a trait of at least one species shows change over time, and (3) found either a temporal change in temperature at the study site or a strong association between the species trait and site-specific temperature. Because we were looking for trends, we also excluded studies examining climatic cycles, such as North Atlantic Oscillation and El Niño/Southern Oscillation. We divided 143 studies that met our criteria into two 'tiers': those demonstrating a statistically significant trend for at least one species examined (tier 1, most of which were used as the methodological basis for conclusions in the IPCC TAR WGII[6,7]) and those in which statistical significance was not shown by the study's authors (tier 2), usually because no statistical tests were applied. We performed our analyses for each tier taken separately and for the two combined. Appendices 1 and 2 of the Supplementary Information provide the data and citations

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Table 1 **Summary statistics for meta-analyses**

	Significant species	Nonsignificant species	Combined species
Number of species changing	586	882	1,468
Number changing in expected direction	482	708	1,190
Percentage in expected direction	82.3%	80.4%	81.1%
90% confidence interval for percentage in expected direction	73.4–88.6%	70.5–87.4%	74.2–86.5%
Effect size (δ)	−0.09	−0.23	−0.23
90% confidence interval for δ	−0.12 to −0.06	−0.30 to −0.14	−0.29 to −0.17
Standard error for δ	0.0004	0.0023	0.0014
Correlation coefficient (r)	−0.05	−0.12	−0.12
90% confidence interval for r	−0.06 to −0.03	−0.16 to −0.07	−0.15 to −0.09
Standard error for r	0.0002	0.0012	0.0007

A breakdown of values for those species or groups of species that were found, in the studies examined, to have statistically significant trends for various traits and for those that were not statistically significant. In addition, values are listed for the combination of these two categories of species or species groups.

for all of the studies used in our meta-analyses.

We focused on temperature change and ignored other climatic changes, such as precipitation, because the biological effects of temperature are often better understood for most of the organisms examined. Explicitly considering drought in our analyses would have allowed us to include many more studies, particularly from the Southern Hemisphere, but attributing local droughts to globally coherent patterns of climatic changes can often be difficult. We do, however, recognize that factors influencing populations interact in complex ways: temperature can exert its influence, for example, by affecting moisture availability.

Four types of change in species' traits due to warming may be possible. First, the density of species may change at given locations, and the ranges of species may shift either poleward or up in elevation as species move to occupy areas within their metabolic temperature tolerances. Second, because many natural history traits of species are triggered by temperature-related cues, changes could occur in the timing of events (phenology), such as migration, flowering or egg laying. Third, changes in morphology, such as body size, and behaviour may occur. Fourth, genetic frequencies may shift.

Attributing observed changes in populations of plants and animals to climatic change, specifically temperature increases, is possible because we expect the trends created by the large-scale pressure of global warming to show widespread, predictable and concordant patterns of change. In addition, we expect these changes to be concentrated in areas where temperature changes are largest (that is, at higher latitudes and altitudes) and for changes to be less evident elsewhere. Climate change is only one of a long list of pressures that influence the distributions and health of populations, as well as traits such as timing of activities and processes. These other pressures (for example, habitat modification, pollinator loss and exotic species introductions) often result in localized (often around centres of human populations) or multidirectional patterns of alterations to populations of species. To document a strong role for climate change in explaining many of the observed changes in animal and plant populations, we looked for repeated examples occurring over long temporal and broad spatial scales that showed unidirectional changes predicted by our understanding of the physiological tolerances of species to temperature. The predicted result, or fingerprint, of an underlying consistent shift in a large-scale pattern shown by many species around the globe, coupled with an understanding of the possible causal mechanisms, provides confidence in attributing observed species changes to climatic change. The 85 tier 1 studies and 58 tier 2 studies found strong changes occurring around the globe in various types (taxa) of animals and plants (see Supplementary Information). The meta-analyses we used to analyse the findings of these studies were the vote-counting method[8] and the regression-slope model[9]. We applied the vote-counting method to three different categories of data: 1) the 587+ species or groups of species ('+' because some studies do not provide numbers) in tier 1 (see Methods) that show statistically significant change; 2 the 886+ species or groups of species in both tier 1 and tier 2 that show statistically nonsignificant change or where the significance was unknown; and 3) the combined species (1,473+) showing change. For all three categories, the percentage of species changing in the expected direction was around 81% with a 90% confidence interval ranging from 71% to 89% (Table 1). The meta-analysis results of effect sizes and correlation coefficients were statistically different from zero ($P < 0.05$), which means that we can reject the null hypothesis of equal change in both the expected and opposite directions. Consequently, even this fairly low-powered vote-counting meta-analysis indicates that most changes are consistent with our understanding of how temperature change influences various traits of a variety of species and populations from around the globe. Hence, we can safely state that there has probably been a discernible impact of recent global warming on animals and plants.

The actual amount of change shown can be determined for those studies that examined shifts in spring phenologies. The 61 studies that investigated the change in timing of events occurring within the

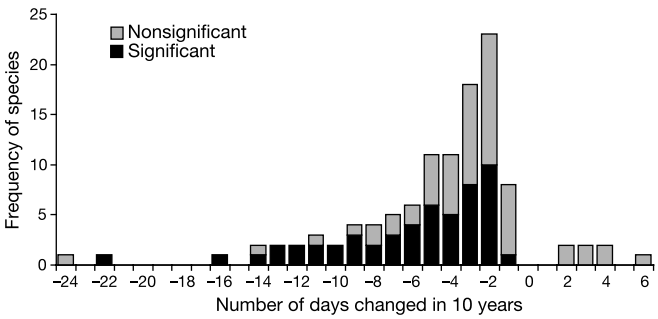

Figure 1 Frequency distribution of species and groups of species (see text) with a temperature-related trait changing by number of days in 10 years. No data were tabulated for species showing zero days changing in ten years (see Methods).

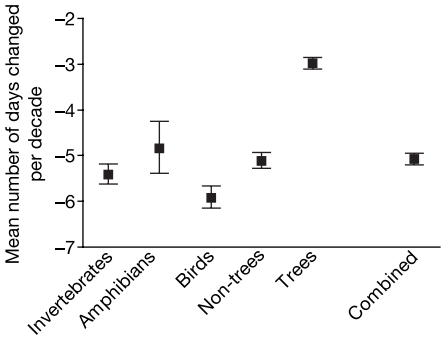

Figure 2 Means ± s.e.m. of days changed for the given groups of species. The 'Combined' category includes only those species tallied in the groups of species (that is, data for the one mammal, two fish and zooplankton are not included).

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past 50 years examined a total of 694 species or groups of species. Our meta-analyses of these species indicate that over an average decade within the past 50 years, a statistically significant change towards earlier timing of spring events has occurred. The number of days changed per decade for a given species or species group ranges from 24 days earlier per decade for the breeding of North American common murre (*Uria aalge*) to 6.3 days per decade later for the breeding of North American Fowler's toad (*Bufo fowlen*) (Fig. 1). Using the regression-slope model[9] (see Methods), we found that the estimated mean number of days changed per decade for all species showing change in spring phenology is 5.1 days earlier (s.e.m. $\pm$ 0.1; Fig. 1). When the data are grouped by statistical significance, the estimated mean of the species with nonsignificant findings is closer to zero than that for species with significant findings (-3.4 ± 0.1; -6.9 ± 0.1, respectively; negative numbers indicate an earlier shift). The latter mean is understandably earlier than the former, given that regression analysis is more powerful at discriminating steeper slopes than shallower ones. However, all three estimated averages are statistically significantly different from zero, which means that these species are all showing a marked shift towards earlier spring events.

Given that higher latitudes have warmed more than the lower latitudes in the past half century (see Fig. 3d of ref. 1), we expect phenological responses to be larger nearer the poles and not as pronounced closer to the equator. (Unfortunately, our pool of literature did not allow us to test elevational changes.) The latitudes of the spring phenology studies in the Northern Hemisphere extend from 32° N to 72° N, with one study in the Southern Hemisphere at 39°. Because of the unevenness of the location of the data (for example, a preponderance of studies in the United Kingdom), we were able to have large enough sample sizes in each group only by dividing them into two groups along 50° latitude circles. The sample size from 32° to 49.9° was 24 +, which includes the one Southern Hemisphere study. From 50° to 72° N latitude, 85+ species or species groups were examined. As expected, the estimated mean and s.e.m. of the phenological shifts (see Methods) from 32° to 49.9° latitude is smaller (-4.2 ± 0.2) than that between 50° and 72° N latitude band (-5.5 ± 0.1). These two means are statistically significantly different from each other (Kruskal–Wallis test, ($P < 0.0001$), which strongly suggests that species at higher latitudes are indeed reacting more strongly to the more intense change in temperature.

Our spring phenology data set consists of species and populations from major taxa from molluscs to mammals. We had large enough sample sizes to examine the estimated means of the phenological shifts separately for invertebrates, amphibians and birds, and for trees and other plants (Fig. 2). Four of the five means cluster around an earlier shift of 5 days, which is the estimated mean for all taxa combined. Trees, however, show an estimated mean that is later than the cluster (-3.0 ± 0.1). This estimated mean is statistically different from the other means (Kruskal–Wallis test), and the other four means are not statistically different from one another.

Our study shows that recent temperature change has apparently already had a marked influence on many species. Meta-analyses provide a way to combine results, whether significant or not, from various studies, and to find an underlying consistent shift, or fingerprint, among species from different taxa examined at disparate locations. The findings for the nonsignificant species, when aggregated, show nearly as much significant change as the group of species showing statistical significance (Table 1 and Fig. 1). Hence, for the studies we examined, the balance of evidence suggests that a significant impact of recent climatic warming is discernible in the form of long-term, large-scale alterations of animal and plant populations. For example, the average shift in spring phenology (timing) of events, such as breeding or blooming, for temperate-zone species is 5.1 $\pm$ 0.1 days earlier in a decade. The observed consistent broad-scale patterns of changes in the expected directions (80% of species showing change) strongly suggest that recent temperature trends are the most likely explanation for these observed phenomena. Clearly, if such climatic and ecological changes are now being detected when the globe has warmed by an estimated average of only 0.6 °C, many more far-reaching effects on species and ecosystems will probably occur in response to changes in temperature to levels predicted by IPCC[1], which run as high as 6 °C by 2100.

Projected future rapid climate change could soon become a more looming concern, especially when occurring together with other already well-established stressors, particularly habitat destruction. During rapid climatic changes in the past, species showed differential movements[10], rather than shifting together as suggested by many authors, including Darwin[11]. Such differential movement could result in a disruption of the connectedness among many species in current ecosystems (for example, a tearing apart of communities[7]). Research and conservation attention needs to be focused not only on global warming and each of the other stressors by themselves, but also on the synergism of several pressures that together are likely to prove to be the greatest challenge to animal and plant conservation in the twenty-first century[3,12]. Because anticipation of changes improves the capacity to manage—by acting proactively rather than reactively—it behoves us to increase our understanding about the responses of plants and animals to a changing climate. This understanding, coupled with further documentation of change, may well indicate a need for actions to modify conservation efforts and future planning to account for climate change, and to slow the projected rate of warming. □

Methods

We used results from 143 studies, each of which found some trait of a species showing a trend over a span of at least 10 years. The geometric mean of the time span for all studies was 30.3 years and the average was 34.5 years. Gaps between years were allowed. Several studies investigated more than one species and some species showed no change. The relative number of species exhibiting change compared with all species reported in the literature sources we examined is not the relevant metric we consider, because we are not trying to determine what percentage of species is responding to current climatic changes. Given that all species examined in this study (and indeed by the entire scientific community) represents only a small proportion of the total number of species that exist in the world (itself unknown), such percentage claims are untenable by any analysis. Rather, a relevant metric to detect a discernible influence of global warming on plants and animals is the fraction of those species exhibiting change that have changed in the direction expected given a temperature trend at their location. For those studies finding change in more than one species and reporting the change as an average for several species, only one entry is used in the various tests performed. For example, Fleming and Tatchell[13] reported the change in flight period of five aphids as 2.6 days earlier per decade. To be conservative, for all our analyses, this group of aphids (and all similarly grouped species) is considered as one entry, rather than as five.

Meta-analyses used

We used two types of meta-analysis, vote counting and regression slope, to determine whether changes observed are consistent with the possibility that one force, global warming, is instigating a noticeable change in species. The vote-counting method is explained in detail in ref. 8. This method is biased towards finding zero or no effect[14]—of global warming, in our case. The various studies have different sampling lengths (K_i) and so we use a geometric mean of these numbers to determine K, the mean length of years the studies examined traits of species or populations. In all three vote-counting analyses that we used—species showing statistically significant change, species showing nonsignificant change, and the combined species that showed change—the value of K is 30.

The regression-slope meta-analysis provides a way to examine directly the shift in spring phenological changes. For this method to work, the various studies examined must have used the same measurement of change, which in these meta-analyses is the number of days changed per decade. We included only those studies that examined more recent spring shifts, from 1951 to 2001. Details of the methods we used here to derive estimated slopes are given in ref. 9. Our only deviation from this formulation is that we did not include the sampling variance term in the calculation of the variance of the slope parameter. This is because most studies examined do not report some of the data necessary to derive the sampling variance. This term acts to reduce the size of the variance of the regression slope. Consequently, the variances presented here are slight overestimates, making our inferences more conservative.

Potential biases

Apart from the problems inherent in summarizing information from diverse studies of numerous subjects and methods, potential biases in the data are also of concern in analyses like ours. We do not claim that all authors of studies in the literature we cite report all

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species they observe, and there may be a bias to report primarily those species that show change. Even if there were such a bias, however, it would have no influence on our claim of a discernible impact of warming on plants and animals, because our metric of investigation is what fraction of those species that exhibit change has changed in the direction expected with local temperature trends, not what fraction of all species has exhibited change. The only way that observer bias could influence our metric would be if there were a systematic bias among the scores of studies we examine for researchers to select as study subjects only species showing changes in the direction preconceived by the authors to reflect temperature change. In addition, these many authors would have to have deliberately and systematically suppressed reporting on those species that changed in directions opposite to that expected. We find this possibility of widespread and systematic biases far-fetched, and thus believe that the metric we use is adequate for examining in an unbiased manner the existence of a discernible climatic signal in the traits of many plants and animals.

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True navigation and magnetic maps in spiny lobsters

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Animals are capable of true navigation if, after displacement to a location where they have never been, they can determine their position relative to a goal without relying on familiar surroundings, cues that emanate from the destination, or information collected during the outward journey[1,2]. So far, only a few animals, all vertebrates, have been shown to possess true navigation[3]. Those few invertebrates that have been carefully studied return to target areas using path integration, landmark recognition, compass orientation and other mechanisms that cannot compensate for displacements into unfamiliar territory[4,5]. Here we report, however, that the spiny lobster *Panulirus argus* oriented reliably towards a capture site when displaced 12–37 km to unfamiliar locations, even when deprived of all known orientation cues *en route*. Little is known about how lobsters and other animals determine position during true navigation. To test the hypothesis that lobsters derive positional information from the Earth's magnetic field, lobsters were exposed to fields replicating those that exist at specific locations in their environment. Lobsters tested in a field north of the capture site oriented themselves southwards, whereas those tested in a field south of the capture site oriented themselves northwards. These results imply that true navigation in spiny lobsters, and perhaps in other animals, is based on a magnetic map sense.

In the context of homing behaviour, an animal capable of true navigation must possess both a positional sense to determine its location and a directional or compass sense to orient in the appropriate homeward direction[6,7]. Many animals, both vertebrate and invertebrate, possess diverse compasses based on the Earth's magnetic field, the position of the Sun, patterns of skylight polarization and the positions of stars[4,8]. In contrast, few animals are known to possess the ability to determine position relative to a goal after being displaced to unfamiliar areas under conditions in which

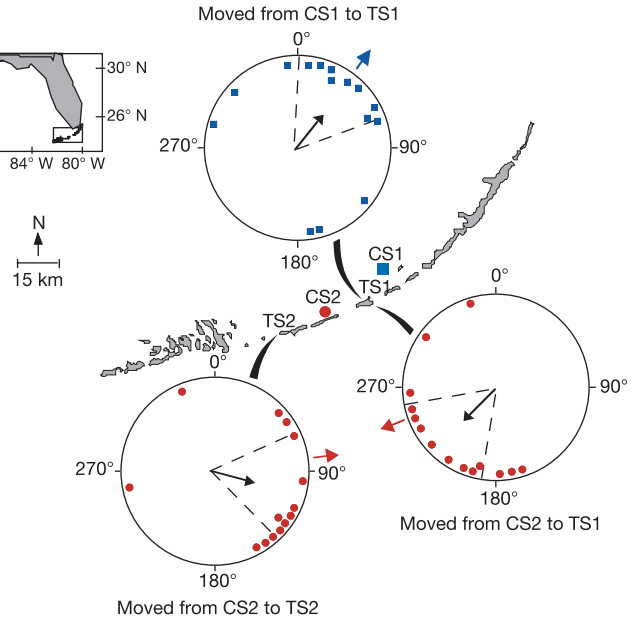

Figure 1 Orientation of displaced lobsters. Lobsters were transported by boat from two capture sites (CS1, CS2) via circuitous routes (see the text) to one of two test sites (TS1, TS2). In the orientation diagrams, each small symbol represents the mean angle of a single lobster. Blue squares indicate lobsters captured at CS1, whereas red circles indicate lobsters captured at CS2. The arrow in the centre of each orientation diagram indicates the mean angle of each group; the arrow length is proportional to the mean vector **r**, with the radius of the circle corresponding to $r = 1$. Lobsters transported from CS1 to TS1 were significantly oriented ($r = 0.51$, $Z = 3.92$, $P < 0.02$, Rayleigh test) with a mean angle of 38°. Lobsters transported from CS2 to TS1 were significantly oriented ($r = 0.65$, $Z = 5.96$, $P < 0.01$) with a mean angle of 222°. Lobsters displaced from CS2 to TS2 were also significantly oriented ($r = 0.51$, $Z = 3.89$, $P < 0.02$) with a mean angle of 105°. In all orientation diagrams, the dashed lines represent the 95% confidence interval for the mean angle. Data are plotted relative to magnetic north. The blue or red arrow outside each orientation diagram indicates the direction from the test site to the capture site. In each case, the mean angle of orientation coincided closely with the direction towards the capture site (see the text) and the 95% confidence interval encompassed this 'homeward' direction.

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Research Article

Cougar Survival and Source-Sink Structure on Greater Yellowstone's Northern Range

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ABSTRACT We studied survival and causes of mortality of radiocollared cougars (*Puma concolor*) on the Greater Yellowstone Northern Range (GYNR) prior to (1987–1994) and after wolf (*Canis lupus*) reintroduction (1998–2005) and evaluated temporal, spatial, and environmental factors that explain variation in adult, subadult, and kitten survival. Using Program MARK and multimodel inference, we modeled cougar survival based on demographic status, season, and landscape attributes. Our best models for adult and independent subadults indicated that females survived better than males and survival increased with age until cougars reached older ages. Lower elevations and increasing density of roads, particularly in areas open to cougar hunting north of Yellowstone National Park (YNP), increased mortality risks for cougars on the GYNR. Indices of ungulate biomass, cougar and wolf population size, winter severity, rainfall, and individual characteristics such as the presence of dependent young, age class, and use of Park or Wilderness were not important predictors of survival. Kitten survival increased with age, was lower during winter, increased with increasing minimum estimates of elk calf biomass, and increased with increasing density of adult male cougars. Using our best model, we mapped adult cougar survival on the GYNR landscape. Results of receiver operating characteristic (ROC) analysis indicated a good model fit for both female (area under the curve [AUC] = 0.81, 95%CI = 0.70–0.92, $n = 35$ locations) and male cougars (AUC = 0.84, 95%CI = 0.74–0.94, $n = 49$ locations) relative to hunter harvest locations in our study area. Using minimum estimates of survival necessary to sustain the study population, we developed a source-sink surface and we identify several measures that resource management agencies can take to enhance cougar population management based on a source-sink strategy. © 2011 The Wildlife Society.

KEY WORDS cougar, infanticide, elevation, Greater Yellowstone Northern Range, Program MARK, *Puma concolor*, road density, source-sink dynamics, survival, wolf.

Cougars (*Puma concolor*) are considered habitat generalists and their broad distribution is a testament to their ability to persist in a variety of habitats that provide adequate cover and prey (Cougar Management Guidelines Working Group [CMGWG] 2005). Nonetheless, habitat quality may vary spatially and temporally and affect cougar survival and production. Ultimately, survival of individuals and population resiliency may be strongly influenced by various factors including land use (i.e., roads, livestock, homes), management through hunting and depredation removal, and likely by competition with other carnivores (Murphy 1983, Torres et al. 1996, Creel et al. 2001, CMGWG 2005, Schwartz et al. 2010). Across western North America, large areas of contiguous habitat support cougar populations managed primarily through sport hunting within hunting districts, game management units (GMU), or data analysis units (DAU), except where harvest is prohibited, such as in California (California Wildlife Protection Act of 1990, CMGWG 2005). Management with sport hunting typically identifies areas where cougars are targeted for population reduction in hopes of increasing prey populations, reducing conflicts with humans, or for stable population growth while providing sport hunting opportunity (CMGWG 2005, Stoner et al. 2006). Within this management structure parks and wilderness are often assumed to function as refugia and

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source habitats for cougars, yet those areas may not always operate in such a manner (CMGWG 2005). The difficulties associated with monitoring cougar populations has challenged management at landscape scales and biologists' understanding of factors that explain variation in survival and other population characteristics of cougars (Stoner et al. 2006).

Cougars immigrate and emigrate via dispersal that strongly influences population dynamics and regional source-sink structures (Sweanor et al. 2000, Robinson et al. 2008). Furthermore, cougar movements within their large annual home ranges potentially overlap boundaries of state management units and refuges such that individuals might not reside exclusively in either source or sink habitats. Recently, the CMGWG (2005) suggested mapping habitat and landscape features and managing subpopulations of cougars using source and sink structure that may or may not conform to delineated boundaries of GMUs or DAUs. Such an approach acknowledges large movements of individual cougars and incorporates habitat heterogeneity: a local demographic surplus arises in good quality habitats (source), and a local demographic deficit (sink) occurs in habitats of poor quality or in high quality habitats that pose high risk of death (attractive sinks or ecological traps; Dias 1996, Delibes et al. 2001, Robinson et al. 2008). Thus, the source-sink model implies that some habitat patches may be more important to the long-term survival of a cougar population and alterations of the availability of source habitat could greatly affect production and survival in other nearby habitats (Pulliam and Danielson 1991). An understanding of source-sink dynamics requires not only identifying quality habitats but also identifying risks that influence production and survival in various habitats (see Schwartz et al. 2010).

Accurate characterization of local populations in different habitats as sources or sinks and their relative contributions to the larger population (i.e., metapopulation) at a landscape level is important in an increasingly fragmented world (Runge et al. 2006). In the Greater Yellowstone Ecosystem (GYE), rural residential development is increasing rapidly because of the area's natural amenities (Hansen et al. 2002). People attracted to lands surrounding reserves may impact natural buffers and alter ecological process within reserves (Hansen et al. 2002). Several authors have noted the combined effects of roads, hunters, and conflicts with humans along reserve boundaries, which have contributed significantly to the extinctions of large carnivores, particularly in small reserves (Woodroffe and Ginsberg 1998, Revilla et al. 2001, Sunquist and Sunquist 2001, Woodroffe 2001). Competition with wolves (*Canis lupus*) reintroduced in 1995 and 1996 may also influence and affect cougar behaviors, survival, movements, and habitat use in the GYE. Because wolves are pack animals, and tend to be dominant in direct interactions, wolf reestablishment may alter the behavior and population dynamics of cougars (Ruth 2004*a*,*b*). Wolves kill cougars and steal their kills, and cougars show avoidance of wolves (Ruth 2004*a*,*b*; Kortello et al. 2007). Thus, associated energetic costs from these interactions may affect cougar reproductive and survival rates. Whether wolf reestablishment influences vital rates of sympatric cougars has not been documented, yet is relevant to cougar management and conservation in many western states.

Although numerous authors have examined survival rates of hunted and non-hunted cougar populations, none have used probabilistic analyses to examine temporal, spatial, and environmental factors that explain variation in survival and constructed a map of survival at a landscape scale (Beier and Barrett 1993, Logan and Sweanor 2001, Lambert et al. 2006, Stoner et al. 2006, Robinson et al. 2008). We studied survival and mortality of radiocollared cougars on the Greater Yellowstone Northern Range (GYNR) prior to and after wolf-reintroduction. Our objectives were to: 1) estimate and use survival rates to assess the effect of wolf reintroduction on cougar survival on the GYNR, 2) identify individual, temporal (i.e., environmental), and spatial (i.e., landscape) factors that explain variation in adult, subadult, and kitten survival, and 3) use estimates of survival that incorporate landscape heterogeneity to construct a source-sink surface that allows managers to evaluate probability of cougar survival on the GYNR.

STUDY AREA

We conducted our study on the GYNR, Montana, and Wyoming, including the northern range and adjacent backcountry areas in Yellowstone National Park (YNP), the adjoining Absaroka-Beartooth Wilderness, and the Gardiner Basin north of YNP (3,779 km^2). Fifty-seven percent of the study area fell within the northern range of YNP with the remainder of the study area to the north of the YNP boundary. Elevations increase from west to east from 1,500 m to >2,400 m (Despain 1990, Cook et al. 2004). Vegetation was primarily grassland and sagebrush steppe at lower elevations, dominated by Idaho fescue (*Festuca idahoensis*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and big sagebrugh (*Artemesia tridentata*; Despain 1990). At higher elevations, conifer forest of Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*) covered about 41% of the northern range (Houston 1982, Wright et al. 2006). Mean annual precipitation varied from 24 cm in the Gardiner basin to 35 cm in the upper Lamar River valley (Coughenour and Singer 1996) with average monthly temperatures ranging from −12° C to 13° C. Vegetation, climate, and geology of the area were described in detail by Houston (1982) and Despain (1990).

The GYNR was occupied year-round by cougars prior to and after wolf reintroduction in 1995–1996 (Murphy 1998). A cougar hunting season occurred in Montana outside the north boundary of YNP. Hunting season length was December through February during 1987–2000 and was extended to December through April in winter 2000–2001. Our study area overlapped Montana hunting unit 313 and the southern portion of unit 314. Hunter-killed cougars were sexed and age-estimated by Montana Department of Fish, Wildlife and Parks (MDFWP) Wildlife Laboratory (Aune and Schladweiler 1995). During 1988–2005, 55% of annual hunter harvest in these

units occurred in the north portion of our study area and averaged 1.4 (range 0–2) adult females (≥3 yr old) and 0.6 (range 0–1) yearling–subadult females (1–2 yr old) per year. During the same time span, annual hunter harvest averaged 1.8 (range 0–3) adult males (≥3 yr old) and 0.9 (range 0–1) yearling–subadult males (1–2 yr old).

Wolves were protected under the Endangered Species Act, which allowed no hunting of wolves except for lethal removal following livestock depredation (Bangs and Fritts 1996). Grizzly bears (*Ursus arctos*), black bears (*U. americanus*), and coyotes (*C. latrans*) were sympatric with cougars and wolves on the GYNR.

Five ungulate species inhabited the northern range. Elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) were the most abundant ungulate prey for cougars and wolves (Murphy 1998). Minimum counts of elk and mule deer ranged between 9,400–19,000 and 1,600–2,500, respectively, prior to wolf reintroduction (1987–1994; Lemke et al. 1998, Murphy 1998). After wolf reintroduction (1998–2005), elk and deer numbered 8,300–14,500 and 1,600–2,300, respectively (Eberhardt et al. 2007, Cross 2009). Moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), and pronghorn (*Antilocapra americana*) were also documented as prey for cougars (Murphy 1998). Bison (*Bison bison*) numbered 2,000–4,000 but were not cougar prey (Murphy 1998). Wolves also preyed on moose, bison, and pronghorn (Smith et al. 2005, Smith and Bangs 2009).

METHODS

Cougar population characteristics were quantified pre-wolf (PW) reintroduction (1987–1994; Murphy 1998) and during wolf (DW) reestablishment (1998–2005) on the GYNR. We estimated population size and density of independent cougars during winter by surveying for cougar tracks in snow while traversing non-overlapping transects (approx. 1,500 km each winter during both PW and DW) and through intensive efforts to capture cougars ($\bar{x} = 228$ person-days/5 months winter during PW and 226 person days/4–5 months winter during DW) following Murphy (1998). Although cougars were constrained to winter range during months with snow, there was some movement across the study boundary. Thus, estimates represented the minimum number of cougars that used the study area.

Using trained hounds we captured and collared adult, independent subadult, and dependent kitten cougars (see individual covariates below) in and adjacent to YNP. Cougar capture and handling procedures followed Logan et al. (1986) and Quigley (2000) and were approved by the Hornocker Wildlife Institute/Wildlife Conservation Society Animal Care and Use Committee (no. 1998-YCW-502) and YNP (research permit no. YELL-SCI-0039). We backlogged cougars into the winter population and estimated proportion of adults marked each year using percent accuracy methods of Logan and Sweanor (2001). We radiomarked an estimated 77% of adult cougars by winter 1988–1989 during the PW study with 87–94% radiomarked in all subsequent years until the final year of study. We radiomarked an estimated 68% and 88% of adult cougars present in the DW study by winters 2000–2001 and 2001–2002, respectively, with 88–93% radiomarked in all subsequent years until the final year of study.

When possible, we ear tagged and radio-collared kittens at the den at 4.5–8.5 weeks of age following procedures described by Logan and Sweanor (2001). We generally captured kittens not marked during this time frame during the first winter after birth at 4–8 months of age. We radiocollared 57–78% of PW kittens and 60–70% of DW kittens prior to 3.5–4.8 months of age.

We estimated ages of cougars with unknown birthdays and >9 weeks of age by tooth development and wear, body weight, neck measurements, pelage characteristics, and gum-line recession (Ashman et al. 1983, Murphy 1998, Anderson and Lindzey 2000, Laundré et al. 2000). We fitted subadult collars with a biodegradable canvas spacer that ensured collar drop after dispersal and kitten collars were designed to expand to the neck size of adult cougars. All transmitters had a motion sensor that increased pulse rate if stationary for 4–6 hr, allowing for detection of mortalities and dropped collars. In addition to a Very High Frequency (VHF) mortality sensor, Global Positioning Satellite (GPS) collars we used during the DW study recorded the date and time the radio collar became stationary.

We located or monitored cougars for a mortality signal with radio telemetry every 1–5 days from the ground and every 7–14 days from an airplane. We investigated a site the day of or day following reception of the mortality signal unless another carnivore was present at the site, in which case we waited until the carnivore was no longer detected at the area. We determined causes of mortality through visual inspection of carcasses and through necropsies performed both in and out of the field. Necropsies were occasionally performed by a veterinarian in a laboratory. Pathology of tissue and blood samples was conducted by the Montana Veterinary Diagnostic Laboratory, Bozeman, Montana, USA or the Wyoming Game and Fish Laboratory, Laramie, Wyoming, USA.

We located cougars from close proximity (generally 100–300 m) and used tree cover and topography and assessed direction of air currents to avoid disturbing cougars as we took ≥3 compass bearings. Our telemetry error averaged 33 m (SD = 81) for 863 ground-based locations. Mortalities and dropped collars that were located aerially and investigated by site searches from the ground had average aerial telemetry error of 161.7 m (SD = 216.0, $n = 41$) in the PW study and 156.8 m (SD = 121.1, $n = 21$) in the DW study. Similar to Schwartz et al. (2010), pixel size accounted for telemetry error for some spatial layers. Although distance measurements were influenced by telemetry error, the overall magnitude should not have affected results (i.e., even with telemetry error, locations close to escape habitat would still have a small value compared to those that were distant).

Survival Analysis

We used Program MARK and the known fate data type to estimate mean survival and investigate the influence of cova-

riates on survival (White and Burnham 1999, Haroldson et al. 2006). We converted radio-location records into monthly encounter histories for each cougar in each year monitored during both study phases (White and Burnham 1999). Because no cougars died as a result of capture, availability began at the date of capture and continued through the end of the year, a change in reproductive status (from non-maternal to maternal or vice versa) for females, a change in age class (from subadult to adult), or until the cougar died or was censored. We followed methods of Haroldson et al. (2006) and censored data from an individual beginning with the day after its last location if time between telemetry locations exceeded 60 days. The median number of days between successive locations was 6 days ($\bar{x} = 7.4$, SD = 8.1) across both study phases. We assigned cougars that died a death date based on the median day between the last location and the date we received the mortality signal. Excluding hunter-killed cougars, we estimated the average number of hours between the last location and date of death at 65.8 hr (SD = 86.2, range = 4–336).

We defined a study area boundary for the survival analysis based on the 95% fixed kernel home range (Hawth's Analysis Tools for ArcGIS®, www.spatialecology.com/htools/, accessed 15 Aug 2005) for the combined location set of all adults monitored in both phases. We did not include in the analysis independent subadults that dispersed beyond the study area because we monitored them infrequently and often obtained no locations until their death. Additionally, we removed adult or independent cougars that moved beyond the defined study area boundary permanently or for periods >60 days for those time frames they were outside the boundary.

We analyzed kitten survival separately from adult and independent subadult cougar survival. Because we assumed each kitten record to be an independent random sample, we used data bootstrap analyses to evaluate if the distribution of mortalities among litter sizes was random and estimated the overdispersion parameter ($\hat{c}$) following methods of Bishop et al. (2008). We used Program MARK to run the bootstrap analysis with 10,000 replicate datasets generated by resampling litter size (1, 2, 3, and 4) with replacement. We used our most parameterized model and the mean value of individual covariates in the bootstrap procedure. The bootstrap option generated a mean and standard deviation of 10,000 survival estimates and we compared standard deviations of the replicate estimates with the theoretical standard errors obtained from our original kitten survival estimates. The ratio of the empirical (i.e., bootstrap) variance to the theoretical variance provided the estimate of overdispersion, $\hat{c}$. Following Bishop et al. (2008), we considered $1.0 < \hat{c} \leq 1.2$ as weak evidence of overdispersion. We used $\hat{c}$ to adjust the quasi-likelihood estimate for kitten survival in Program MARK.

Covariate Selection

We developed separate a priori sets of individual and temporal covariates hypothesized to affect survival for the 2 distinct age groups of 1) adults and independent subadults and 2) dependent kittens. We selected covariates after discussions with carnivore experts and from published information on cougars (see Tables S1 and S2 available online at www.onlinelibrary.wiley.com) and other large carnivores in North America (grizzly bears: Haroldson et al. 2006; Schwartz et al. 2006, 2010; wolves: Mech et al. 1988, Mladenoff et al. 1995, Smith and Bangs 2009).

Individual covariates.—We assigned each cougar individual covariates including sex, age class, and age (Tables S1 and S2). We included a quadratic term, age plus age^2, in some models because, similar to grizzly bears, we expected cougar survival to increase with age and then decline at older ages (Johnson et al. 2004). After we attributed locations with individual covariates, we calculated the mean value of attributes for all telemetry locations for each cougar each year (seasonal or annual); mean values for binomial covariates represented the proportion of locations in the area of interest (Schwartz et al. 2010). We then used mean values as individual covariates in the Program MARK input file.

We identified cougars as resident adults when they bred or reached the average age of known breeders in the population and showed fidelity to a home area (Logan and Sweanor 2001). Independent subadult cougars were pre-breeding and pre-dispersal age cougars that were immigrants to the study area or individuals that separated from their mother but remained within the study area (Logan and Sweanor 2001). Kittens were dependent on and generally remained with their mother (Logan and Sweanor 2001) between an average (SD) of 12.8 (3.2; PW) months and 17.1 (3.2; DW) months of age unless they were orphaned. One male and 2 female kittens in the PW study were separated from their mother at approximately 9.6 to 10.8 months old and remained as independent subadults on the study area. As a consequence, we included them as independent, pre-dispersal subadults, which resulted in overlap in independent, pre-dispersal ages and dependent kitten ages between our 2 survival analyses. We classified kittens orphaned prior to 9 months of age as dependent and included them in the kitten survival analysis. We assigned adult female cougars an additional covariate to indicate absence (0) or presence (1) of dependent offspring.

Reproductive rates of animals frequently improve with age due to changes in experience at breeding or raising young (see Clutton-Brock 1988). To evaluate the effect of a mother's age, thus increased experience, on survival of dependent young, we attributed each kitten year with the mean age of their mother in years.

Female cougars can give birth to young in all months of the year (Anderson 1983), yet numerous studies report a peak in births, often referred to as a birth pulse (Murphy et al. 1999, Logan and Sweanor 2001). Logan and Sweanor (2001) hypothesized that kittens born during the birth pulse of July–September would have increased survival. Laundré and Hernández (2007) found a greater number of litters were born during July–September, yet those authors did not find support for the hypothesis. We evaluated the effect of kitten birth during 2 pulses appropriate for our data set: a primary birth peak of May–July (35 of 59 litters documented

in PW and DW) and a secondary birth peak of September–October. We compared alternative models that included only the primary birth peak (Bpeak1) against those that included the primary through secondary birth peak (Bpeak2) of May–October (53 of 59 litters). We additionally evaluated whether Julian birth days of kittens would affect survival and predicted survival would be low earlier in the year, increase around peak birth months, and decline for births later in the year. Thus we included a quadratic term ($Julbirth^2$) in some models.

After reintroduction, the wolf population increased from 48 wolves/1,000 km^2 to a peak of 106 wolves/1,000 km^2 on the northern range of YNP between 1995 and 2003 (Smith et al. 2005, 2006). We evaluated the effect of increasing wolf density on cougar survival by comparing models with a temporal covariate of wolf density/1,000 km^2 per year with those that included an individual spatial covariate that indexed wolf density through intensity of wolf use. For each yearly season (e.g., winter 2001; winter: 1 Nov–30 Apr, snow free: 1 May–31 Oct) we generated 95% utilization distribution (UD) grids (30 × 30 m cell size) from the locations of all radio-collared wolves using Hawth's Analysis Tools with least-squares cross-validation bandwidth values. Regression analyses indicated that the number of radio collared wolves per pack was a good indicator of pack size over each year ($F = 131.83$, $P = 0.000$, $R^2 = 0.78$), thus high UD values occurred in areas with more wolves and reflected spatial variability in wolf use across the landscape. We then scaled each yearly seasonal UD by the number of wolves present to capture variability in the wolf population across seasons and years. We attributed cougar locations with the wolf use value for the matching date.

We evaluated the influence of landscape characteristics such as cover, elevation, and elk winter range on cougar survival (Tables S1 and S2). We calculated the average minimum distance (in meters) to either tree cover or areas of high topographic roughness, whichever was closest in any direction, as an index of escape terrain (index ranged from 0 to 100 with zero indicating flat and 100 indicating greatest heterogeneity in elevation; Ruth et al. 2003). We evaluated the impact of annual and seasonal elevation on cougar survival and attributed all telemetry locations with elevation (km) using 1:24,000-scale digital elevation models from the United States Geological Survey (USGS 2005).

In northern latitudes, cougars follow migrating elk to winter ranges of limited spatial extent, resulting in increased spatial overlap between predator and prey (Murphy 1998, Pierce et al. 1999). Increased access to prey on winter range could have positive influences on cougar survival. However, cougar and wolf overlap increases during winter as both carnivores seek access to prey on winter range (Ruth 2004*a*). Wolf detection of cougar-killed prey and movements of cougars away from high wolf activity may have energetic costs that reduce survival (Ruth 2004*b*, Kortello et al. 2007). The Northern Yellowstone winter range has long been defined by a static boundary based on winter distribution of elk (Houston 1982, Lemke et al. 1998). To investigate the effect of cougar use of elk winter range during winter, we attributed telemetry locations as in or out of elk winter range and then calculated the proportion of locations a cougar was in winter range for intervals entered in the survival analysis (Johnson et al. 2004).

Few if any cougar populations are untouched by human influences because few protected areas are big enough that cougars, with their large home ranges, are able to completely avoid humans (Beier et al. 2010). Based on findings for grizzly bears and hunted cougars, we hypothesized that measures of human disturbance help explain spatial heterogeneity of cougar survival (Table S1, Murphy 1983, Schwartz et al. 2010). For each cougar during each year, we calculated the proportion of telemetry locations inside YNP and the Absaroka-Beartooth Wilderness. Although hunting occurred in the Wilderness, few roads and deep snows during winter limited access and no cougars were removed from the Wilderness during the PW or DW studies (R. DeSimone, MDFWP, unpublished data).

Because the density of open and closed roads affect the probability that houndsmen will detect a cougar track and reach a treed cougar, road access increases the vulnerability of cougars to hunters during the cougar hunting season (Murphy 1983, Barnhurst 1986, Murphy 1998). We evaluated the impact of roads on cougar survival by comparing covariates of average annual and seasonal distance to roads (km), average annual total road density, and average total road density in hunt areas during the cougar hunting season. We calculated road density following Schwartz et al. (2010) using a thematic layer of motorized routes from the Cumulative Effects Model (CEM) database for the GYE created by the Interagency Grizzly Bear Study Team (IGBST; Schwartz et al. 2010). We based total motorized route density (TMRD) on all roads including those that were open, restricted (administrative access only), and closed to all motorized vehicular access. We attributed telemetry locations with annual and seasonal total road density at 2 scales using a 17 × 17-pixel (roaded 30-m cells/500 m^2, Trdann17) moving window and a 54 × 54-pixel (roaded 30-m cells/2.59 km^2, Trdann54) moving window (Table S2 available online at www.onlinelibrary.wiley.com). We used the estimated average length of road of 25.8 m per cell as found by Schwartz et al. (2010) and converted lengths to kilometers of road/km^2 when discussing road densities. Because all roads provide increased access for hunters during winter, we used TRMD to calculate the average density of roads for individual cougars in hunt areas (Hunttrd17 and Hunttrd54) during the cougar hunting season. Finally, we measured distance from each telemetry point to the nearest road (km).

To evaluate the influence of secure habitat on cougar survival (Tables S1 and S2), we attributed telemetry locations as in or outside of secure habitat and then calculated mean values for each cougar (annual and seasonal) as the proportion of locations in secure habitat. We compared this measure of security against the remoteness index from Merrill et al. (1999). We attributed locations with the remoteness index (0 to 1 floating decimal with 1 being most remote) and then calculated annual and seasonal mean values for each

cougar. We compared the amount of secure habitat and remote habitat to alternative models that included road density.

Since 1970, the human population in the 21 counties surrounding the GYE has grown by >60% with the current form of development consisting of large lot rural subdivisions (Hernandez 2004, Schwartz et al. 2010). We used a map of home distribution on private lands across 20 counties surrounding the GYE from Hernandez (2004) and which was updated to include incorporated cities and town sites by Schwartz et al. (2010). We used attribute fields for total homes present in 1990 and 2000 to assign housing estimates to telemetry data from the PW and DW studies, respectively. We attributed each telemetry location with the total number of homes within a 2.59 km^2 cell.

Temporal covariates.—We included phase (PW or DW), density of cougars and wolves, biomass of prey, climactic factors, and season (winter or summer) as temporal covariates (Tables S1 and S2). We used minimum population counts based on radio-marked individuals and tracks of unmarked individuals as an index to minimum population size each winter. We estimated summer population size each year by assuming that a new independent subadult present during a winter (Nov–Apr) had immigrated into the study area during the previous summer. During the PW study 95% (21 of 22) of offspring dispersed from their natal area June–August. During the DW study 90% (27 of 30) of offspring dispersed from their natal area April–July and in September. This time also coincided with post-dispersal localization of cougars on the GYNR winter range prior to the onset of the next winter. We then added the number of new independent subadults detected to the minimum population index of the previous winter to calculate the minimum summer population size. We used minimum population size as an index of cougar population density by calculating a density (cougars/1,000 km^2) for the total winter and total summer area (95% fixed kernel) used by all adult radio-marked cougars within each study phase.

Sexually selective infanticide (SSI) theory (Hrdy 1979) suggests that increased removal of adult males can increase kitten mortality through SSI by immigrating males (Stringham 1980). Through their use of large, defended territories, resident males may provide a spatial umbrella of protection for maternal females against newly establishing males or intruding adult males that could be infanticidal (Seidensticker et al. 1973; Logan and Sweanor 2001, 2010). The opposite effect also has been postulated; because adult males kill kittens, a reduction in the number of adult males should reduce kitten mortality (Miller 1990). Our PW study coincided with reestablishment and increase of the GYNR cougar population and included territorial instability as immigrant males established territories and dominance; 3 established males shifted territories from inside YNP to the north outside YNP (K. Murphy, Yellowstone National Park, unpublished data). Therefore, there was uncertainty in adult territorial boundaries as new males vied to establish residency, some males shifted home ranges, and females also exhibited lower home range fidelity (T. K. Ruth, Selway Institute, unpublished data). In contrast, the early to mid-years of our DW study represented a time of greater home range stability, thus stable social relationships, of resident adult females and dominant adult males (T. K. Ruth, unpublished data). Consequently, we hypothesized that instability of adult males, whether through removal (hunting or management related) or during reestablishment and population recovery, can result in increased kitten mortality. We lacked adequate sample sizes to calculate fidelity indices for early and later years in our PW and DW studies. To avoid dropping years with missing data from our analyses, we tested the influence of stability of adult males on kitten survival by comparing alternative models using adult male density and average annual age of adult males as indices of stability.

Because cougars preyed primarily on elk, particularly elk calves (66% of elk killed PW, Murphy 1998; 53% of elk killed DW, Ruth 2004*b*), we compared covariates of total elk biomass, adult elk biomass, and calf elk biomass in several a priori survival models. We hypothesized that dependent kittens would have increased survival in years when calves were abundant versus years when adult females supporting kittens might have reduced access to vulnerable calves (low calf abundance). We obtained estimates of minimum numbers of elk and sex–age ratios of elk from annual airplane and helicopter-based winter counts and classification conducted on the Northern Range of YNP (Lemke et al. 1998, Eberhardt et al. 2007, Cross 2009). The spatial extent of sampling matched our study area during both the PW and DW studies. We calculated calf elk, adult elk, and total elk biomass by multiplying average live weights (Houston 1982) for each sex–age class by number of individuals and then summing and converting to metric tons (metric ton = 1,000 kg). We interpolated estimates from surrounding years for counts missing in 1993 and 1994 (Haroldson et al. 2006).

We included a winter severity index (WSI; Farnes et al. 1999) and cumulative summer rainfall, which are both climatic factors that influence distribution and condition of ungulates and which may directly and indirectly affect cougar survival (Table S1). Because elk may be limited by the nutritive quality of summer forage as well as winter severity, we included summer precipitation separately from WSI in our seasonal models (Merrill and Boyce 1991, Cook et al. 2004). Although we know of no studies relating precipitation and vulnerability of elk to predation or cougar survival, vulnerability of deer appeared linked to limited food availability and cougars exploited deer as they concentrated at water sources during an extended drought in a desert environment (Logan and Sweanor 2001). We used climate data collected at four climatological (CLIM) stations distributed across the GYNR at Gardiner, Montana and Mammoth, Tower Falls, and Lamar Valley, Wyoming and from remote snow monitoring equipment (SNOWTEL sites) in and around the park (Despain 1990, Farnes et al. 1999). By combining monthly precipitation and temperature records, an index of relative winter severity was produced by Farnes et al. (1999) to provide a measure of winter influences on ungulate species. Values above zero typically correlate with

low winter mortality, higher reproduction and recruitment, and presumably, additional effort by predators to obtain prey that are in improved physical condition (Farnes et al. 1999). Values between −1.0 and −2.0 show some reduction in reproduction, but typically little mortality of older animals and yearlings occurs. Winter severity index values <−2.0 generally indicate significant mortality, low reproduction rates, weaker calves and lower birth weights, smaller or even negative herd recruitment rates (i.e., more animals die than enter the population), and increased predation. We averaged 3 WSI values from across the GYNR and attributed them to cougar locations. We attributed cougar locations with percentage of cumulative rainfall above or below the monthly rainfall average for the GYNR, 1948–2004 (Western Regional Climate Center, 2005).

Model Selection and Survival Surface

We used an information-theoretic approach (Burnham and Anderson 2002) and Akaike's Information Criterion (AIC) adjusted for small sample sizes (i.e., AIC_c) to rank models (Burnham and Anderson 2002) from the candidate list. We derived model-averaged covariate estimates (Burnham and Anderson 2002) from all a priori models and applied them to the best model to estimate annual survival of independent cougars and kittens and to develop survival surfaces for independent male and female cougars. We assessed model fit with receiver operating characteristic (ROC) curves (Boyce et al. 2002) performed with Program R package ROCR (Sing et al. 2005). Integrating the area under the ROC curve (AUC) provides an assessment of model performance (Swets 1988, Manel et al. 2001).

We assessed model fit for the study area and developed separate ROC curves for males and females contrasting known harvest locations with an equal, randomly selected number of known live cougar telemetry (VHF and GPS) locations. We attributed locations with the probability of survival (pixel size of 30 m) from the top model and with true survival (survival = 1, mortality = 0) from the harvest and telemetry data. We obtained harvest locations spanning the years 1989–2005 and recorded as township, range, and section from MDFWP. The study area boundary included portions of Montana Region 3 hunt units 313, 314, and 317. To further assess predictive capabilities, we applied our model an additional 50 km east and 80 km north of the study area boundary (including Region 3 hunt units 310, 311, 316, and 362 and remaining portions of units 313, 314, and 317) and again assessed model fit with ROC AUC for males and females.

We used the finite rate of increase function in the PopTools (PopTools version 3.0.5, www.cse.csiro.au/poptools, accessed 20 Jun 2008) extension for Excel (Microsoft Corporation, Redmond, Washington) to estimate population growth rates (λ) during the PW and DW studies. We used study phase specific maternity rates (m_x) and age specific survival estimates for females from birth (age class zero) to age 14 years as matrix inputs. Because the simple deterministic models we used assume closed population structure (i.e., no immigration or emigration), we adjusted survival rates for yearling females based on our estimates of immigration and emigration (T. K. Ruth, unpublished data). We used PopTools to evaluate the sensitivity and elasticity of lambda to changes in age-specific survival and reproductive rates (Caswell 2001). Following Harris et al. (2006, 2007) and Schwartz et al. (2010) we determined a threshold female survival rate that resulted in population growth ($\lambda \geq 1.0$) and chose this value of female survival to identify source and sink areas in the GYNR.

RESULTS

Adult and Independent Subadult Survival

We monitored 104 adult and independent, pre-dispersal cougars during the PW (30 F, 20 M) and DW (27 F, 27 M) phases of our study (Table 1) for a total 1,911 cougar months. Number of individuals monitored annually ranged from 1 to 16 and 0 to 12 for females and males, respectively, during the PW study phase and did not differ ($\chi^2_1 = 0.003$, $P = 0.958$) from the DW study in which number of individuals monitored per year ranged from 1 to 17 females and 0 to 8 males (Table 1, Fig. 1A). There was no difference in median length of monitoring for female (Mann–Whitney $U = 315.5$, $P = 0.152$) or male (Mann–Whitney $U = 233.5$, $P = 0.428$) cougars between study phases.

Six of 123 a priori models had $\Delta AIC_c < 2$ (Table 2), indicating similar support for these models (Burnham and Anderson 2002); they accounted for 89% of AIC_c weights among the candidate model set. Covariates common to these models were sex, age, age^2, km/km^2 of total roads during the cougar hunting season, and annual elevation.

Evidence ratios using AIC_c weights indicated weak support for the best model over other models in the set; model 1 had 1.4 times support over model 2 and 2.7 times support over

Table 1. Numbers of adult and independent, non-dispersing cougars, total and average months radio-monitored, and mortalities by study phase and sex for cougars on the Greater Yellowstone Northern Range, 1987–2005.

			Months available				Mortalities		
Phase	Sex	No. cougars	Total	$\bar{x}$	Median	SD	Human	Natural	Total
Pre-wolf	Female	30	578	19.3	10.0	20.4	2	6	8
	Male	20	285	14.3	7.5	17.3	3	2	5
	Subtotal	50	863	17.3	9.0	19.2	5	8	13
During wolf	Female	27	764	28.3	19.0	25.9	2	7	9
	Male	27	284	10.5	4.0	13.0	3	8	11
	Subtotal	54	1,048	19.4	11.5	22.2	5	15	20
Total		104	1,911	18.4	10.0	20.7	10	23	33

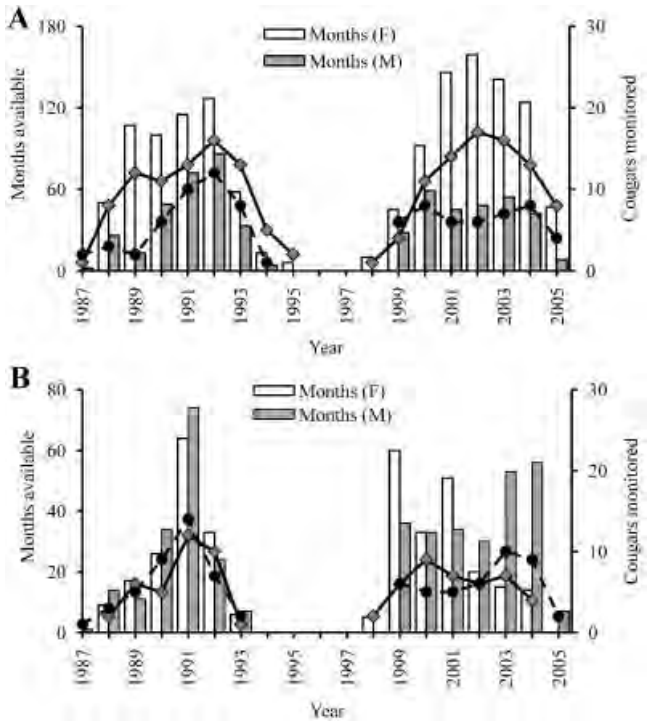

Figure 1. Number of independent cougars (A) and dependent kittens (B) we radio monitored, and total months of availability by sex, for pre-wolf (1987–1995) and during wolf (1998–2005) monitoring phases on the Greater Yellowstone Northern Range. We depict the number of females (F) with gray diamonds and males (M) with black circles.

model 6. The second through sixth models contained the same suite of top model covariates, as well as the additional covariates of annual wolf use, annual density of adult male cougars, season, and study phase. Survival was negatively affected by increasing annual wolf use and positively affected as the density of adult male cougars increased. Temporal covariates of season and phase had negative effects on survival with survival slightly lower during summer and in the DW study phase. Models 2–6 differed by 1–2 parameters from our best model (model 1), and likelihood ratio tests comparing nested models yielded $0.117 \leq P \leq 0.817$ suggesting that additional covariates did not add to the overall model. In addition, 95% confidence intervals for the β coefficients for annual wolf use, annual adult male cougar density, season, and study phase bounded zero, suggesting uncertainty in the predictive power of these covariates. These models (and covariates) were probably not strongly supported because they were influenced by the top 4 covariates (Burnham and Anderson 2002:131) and had confidence intervals that overlapped zero. We derived model averaged beta estimates (Table 3) for covariates in the top model to use in constructing survival surfaces.

Results from the best model (Table 3) indicated that survival of adult and independent, pre-dispersal cougars was influenced by 1) sex—females had higher survival rates than males; 2) age—survival increased with increasing age and females between 1 yr and 10 yr of age had survival >0.80, males 3–9 yr old had survival of 0.70–0.81 (Fig. 2A); 3) road density—survival declined with increasing km of road/km^2 during the cougar hunting season; and 4) elevation—cougars had improved survival at higher elevations.

Road density during the cougar hunting season was better supported than total annual road density. Road density calculated with a 2.59 km^2 moving window outperformed the 500-m^2 moving window. The β coefficients for all the road density covariates were negative and 95% confidence intervals did not bound zero (Table 3), indicating the influence of roads was well supported in our best model. Cougar survival decreased with increasing density of roads; however, road densities >1.58 km/km^2 had little additional effect on survival (Fig. 2B).

Annual elevation was an important covariate and it outperformed seasonal elevation by 8.84 ΔAIC_c. The 95% confidence intervals for the β coefficient did not bound zero (Table 3), indicating clear support for the positive influence of elevation on cougar survival (Fig. 2C).

Although the effects of study phase were not clear, model results indicated that PW females (0.880, SE = 0.002) and PW males (0.746, SE = 0.008) had slightly higher mean rates of survival than did DW study females (0.842, SE = 0.008) and males (0.676, SE = 0.027). Causes of mortality (human, predation, and natural or accidental) were similar between PW and DW phases ($\chi^2_2 = 0.878$, $P = 0.645$). During both studies and across all years, mortal-

Table 2. Top 6 of 123 a priori models* we used to assess impact of individual and temporal covariates on survival of adult and independent subadult cougars on the Greater Yellowstone Northern Range prior to (1987–1994) and during wolf reestablishment (1998–2005). All models also contain an intercept that accounts for one parameter.

Model[a]	AIC_c	No. parameters	ΔAIC_c	Model likelihood	AIC_c weights	Deviance
1. Sex + Age + Age^2 + Hunttrd54 + Elevann	301.719	6	0	1	0.260	289.675
2. Sex + Age + Age^2 + Hunttrd54 + Elevann + Wolfann	302.328	7	0.609	0.738	0.191	288.269
3. Sex + Age + Age^2 + Hunttrd54 + Elevann + Wolfann + Amcougann	303.066	8	1.347	0.510	0.132	286.990
4. Sex + Age + Age^2 + Hunttrd54 + Elevann + Amcougann	303.504	7	1.785	0.410	0.106	289.445
5. Sex + Age + Age^2 + Season + Hunttrd54 + Elevann + Wolfann	303.615	8	1.896	0.388	0.101	287.540
6. Phase + Sex + Age + Age^2 + Hunttrd54 + Elevann	303.680	7	1.961	0.375	0.097	289.621

* Difference in Akaike's Information Criterion adjusted for small sample size [ΔAIC_c] < 2.0.

[a] Sex = gender of cougar; Age + Age^2 = quadratic term for cougar age, which was calculated using midpoint of radio location interval and birth date of the individual; Hunttrd54 = total road density (roaded 30-m cells/2.59 km^2) in hunt areas during the cougar hunting season; Elevann = average elevation (km); Wolfann = average annual wolf use days; Amcougann = minimum annual density of adult male cougars per 1,000 km^2; Season = winter (1 Nov–30 Apr) or snow free (1 May–31 Oct). Model covariates are further described in Table S2 available online at www.onlinelibrary.wiley.com.

Table 3. Model averaged beta estimates on the logit scale for covariates in the top a priori model we used to assess impact of individual and temporal covariates on estimates of independent cougar survival on the Greater Yellowstone Northern Range, prior to (1987–1994) and during wolf reestablishment (1998–2005).

			95%CI	
Parameter[a]	**Beta coeff.**	**SE**	**Lower**	**Upper**
Intercept	−4.419	2.706	−10.331	1.493
Sex	−1.186	0.407	−1.986	−0.386
Age	0.559	0.194	0.174	0.944
Age^2	−0.050	0.013	−0.076	−0.023
Hunttrd54	−0.032	0.007	−0.046	−0.018
Elevann	3.925	1.248	1.458	6.392

[a] Sex = gender of cougar; Age = cougar age calculated using midpoint of radio location interval and birth date of the individual; Age^2 = included as quadratic term for cougar age; Hunttrd54 = total road density in hunt areas during the cougar hunting season; Elevann = average elevation (km). Model covariates are further described in Table S2 available online at www.onlinelibrary.wiley.com.

ities peaked in December ($n = 6$) and again in July with the highest number of deaths ($n = 4$) occurring in July in the DW study. Human hunting accounted for 38.5% of total mortality during the PW study and 25% of mortality in the DW study (Table 1). In the PW and DW phases 62% and 75% of mortalities, respectively, were due to natural causes. During the PW study, natural deaths included intraspecific killing (37.5%), death from an unknown predator (12.5%), and disease or accidents (50%). Intraspecific killing accounted for 33.3%, wolves for 26.7%, and disease or accidents for 40% of natural deaths in the DW study.

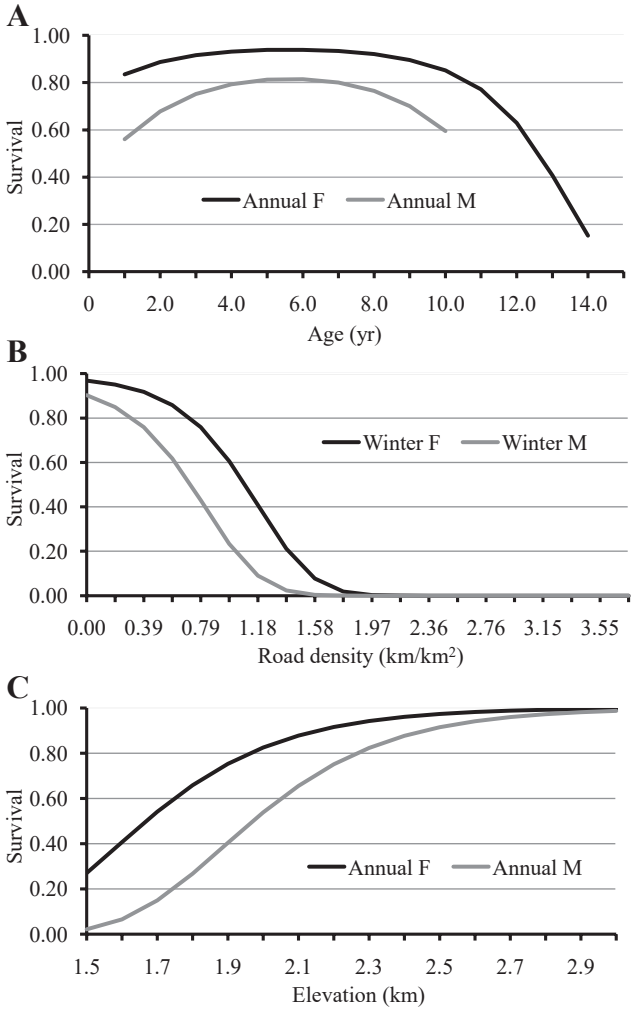

Figure 2. Annual, age-specific survival estimates of independent cougars (A); the influence of road density (km/km^2) during the cougar hunting season on winter survival estimates (B); and the influence of elevation (km) on annual survival estimates (C) of adult and independent, pre-dispersal female (F) and male (M) cougars on the Greater Yellowstone Northern Range, 1987–2005. We computed estimates using βs from the top model (Table 3).

Kitten Survival

Our survival sample contained 106 dependent kittens radio-monitored in 24 litters during the PW (27 F, 27 M) and 24 litters in the DW (24 F, 28 M) phases of our study for a total 767 cougar–months (Table 4). There was no difference between numbers of individuals monitored per year between study phases and sexes ($\chi^2_1 = 0.133$, $P = 0.754$). Number of kittens monitored per year ranged from 1 to 12 and 1 to 14 for females and males, respectively, during the PW study with 0–9 females and 0–10 males monitored in the DW study (Table 4 and Fig. 1B). There was no difference in median length of monitoring (Mann–Whitney $U = 645.5$, $P = 0.286$) for female kittens between study phases. Median length of monitoring was less for male kittens in the PW than in the DW study (Mann–Whitney U = 626.0, $P = 0.029$).

Our estimates of $\hat{c}$ for kitten survival ranged from 0.839 to 3.637 and averaged 1.527, indicating the fates of siblings were generally not independent, as evidenced by 9 litters in which kittens died at the same time and of similar causes. Littermates were killed in single events from wolves ($n = 1$ litter), infanticidal male cougars ($n = 5$ litters), or orphaning due to the death of their mother ($n = 3$ litters). Thus, we used the value of 1.53 for $\hat{c}$ to adjust the quasi-likelihood estimate in Program MARK.

Four of 90 candidate models with $\Delta QAIC_c < 2$ included the following covariates: age, age^2, season, and biomass of elk calves (Table 5). These models accounted for 80% of AIC_c weights among the candidate model set. Evidence ratios using the $QAIC_c$ weights indicated weak support for the best model over other models in the set; model 1 had 1.9 times support over model 2 and 2.7 times support over model 4. When we added annual adult male density to the model with age, season, and elk calf biomass and compared it against the model with seasonal adult male density, it lowered the former model by 1.245 $\Delta QAIC_c$ units. Adding seasonal wolf use to the top model did not improve model

Table 4. Number of cougar kittens, total and average months radio-monitored, and mortalities by study phase and sex for cougars on the Greater Yellowstone Northern Range prior to (1987–1994) and during wolf reestablishment (1998–2005).

			Months available				Mortalities			
Phase	Sex	No. kittens	Total	$\bar{x}$	Median	SD	Human	Natural	Undetermined	Total
Pre-wolf	Female	27	155	5.7	5.0	4.3	0	5	6	11
	Male	27	165	6.1	5.0	4.0	1[a]	7	2	10
	Subtotal	54	320	5.9	5.0	4.1	1	12	8	21
During wolf	Female	24	197	8.3	6.5	6.2	1	6	1	8
	Male	28	250	8.9	8.5	5.0	0	10	2	12
	Subtotal	52	447	8.6	7.0	5.5	1	16	3	20
Total		106	767	7.2	5.0	5.0	2	28	11	41

[a] Removed by Montana Fish, Wildlife, and Parks after mother was killed by hunters.

Table 5. Top 4 of 90 a priori models[*] we used to assess impact of individual and temporal covariates on survival of cougar kittens on the Greater Yellowstone Northern Range prior to (1987–1994) and during wolf reestablishment (1998–2005). All models also contain an intercept that accounts for one parameter.

Model[a]	$QAIC_c$	No. parameters	$\Delta QAIC_c$	Model likelihood	AIC_c weights	QDeviance
1. Age + Age^2 + Season + Calfbio + Amcougseas	144.412	6	0	1	0.112	132.301
2. Age + Age^2 + Season + Calfbio + Amcougann	145.657	6	1.245	0.537	0.060	133.546
3. Age + Age^2 + Season + Calfbio + Amcougseas + Wolfseas	146.253	7	1.842	0.398	0.045	132.106
4. Age + Age^2 + Season + Calfbio	146.392	5	1.980	0.372	0.042	136.313

[*] Difference in quasi-likelihood modified Akaike's Information Criterion adjusted for small sample size [$\Delta QAIC_c$] < 2.0.

[a] Age + Age^2 = quadratic term for cougar age, which was calculated using midpoint of radio location interval and birth date of the individual; Season = winter (1 Nov–30 Apr) or snow free (1 May–31 Oct); Calfbio = total calf biomass in metric tons; Amcougseas = minimum seasonal density of adult male cougars per 1,000 km^2; Amcougann = minimum annual density of adult male cougars per 1,000 km^2; Wolfseas = average wolf use days during winter and snow-free months. Model covariates are further described in Table S2 available online at www.onlinelibrary.wiley.com.

fit (likelihood ratio test, $\chi^2_1 = 0.195$, $P = 0.658$) yet $\Delta QAIC_c$ indicated similar support for this model with other top models (Burnham and Anderson 2002). Survival was negatively affected by increasing seasonal wolf use (model 3) and positively affected as annual density of adult male cougars increased (model 2). There was uncertainty in the predictive power of seasonal wolf use and annual male cougar density as 95% confidence intervals for the β coefficients bounded zero.

The best-fitting model (Table 6) had 6 parameters and detected variation in survival between ages of dependent kittens, season, biomass of elk calves, and seasonal minimum density of adult male cougars. Kitten survival increased rapidly and reached an asymptote of 0.90 between 0.6 yr and 0.7 yr (7–8 months) of age (Fig. 3A). Survival of kittens was lower during winter (0.755, Nov–Apr), a time when cougars and wolves were condensed on winter range, than during snow-free months (0.910, Mar–Oct, Fig. 3B). The primary cougar breeding season also occurred during late winter (Mar–Apr). The temporal covariate of elk calf biomass had a positive influence on kitten survival; survival increased with increasing minimum estimates of calf biomass (Fig. 3C). The top model included seasonal density of adult male cougars and it improved the model with age, season, and elk calf biomass by 1.98 $\Delta QAIC_c$ units. Kitten survival increased with adult male density (Table 6). The 95% confidence interval for the model-averaged β coefficient for adult male density bounded zero, suggesting uncertainty in the predictive power of this covariate. Prior to model averaging, however, the 95%CI (0.019–1.670) for the adult male density β coefficient (0.844) did not bound zero. Winter male density varied from 0.91/1,000 km^2 (1989) to 1.82/

Table 6. Model averaged beta estimates on the logit scale for covariates in the top a priori model we used to assess impacts of individual and temporal covariates on estimates of cougar kitten survival on the Greater Yellowstone Northern Range prior to (1987–1994) and during wolf reestablishment (1998–2005).

			95%CI	
Parameter[a]	Beta coeff.	SE	Lower	Upper
Intercept	−4.595	2.158	−8.824	−0.366
Age	13.917	3.046	7.947	19.888
Age^2	−6.024	1.966	−9.877	−2.171
Season	1.769	0.717	0.364	3.174
Calfbio	0.700	0.308	0.096	1.305
Amcougseas	0.853	0.455	−0.040	1.745

[a] Age = cougar age calculated using midpoint of radio location interval and birth date of the individual; Age^2 = included as quadratic term for cougar age; Season = winter (1 Nov–30 Apr) or snow free (1 May–31 Oct); Calfbio = total calf biomass in metric tons; Amcougseas = minimum seasonal density of adult male cougars per 1,000 km^2. Model covariates are further described in Table S2 available online at www.onlinelibrary.wiley.com.

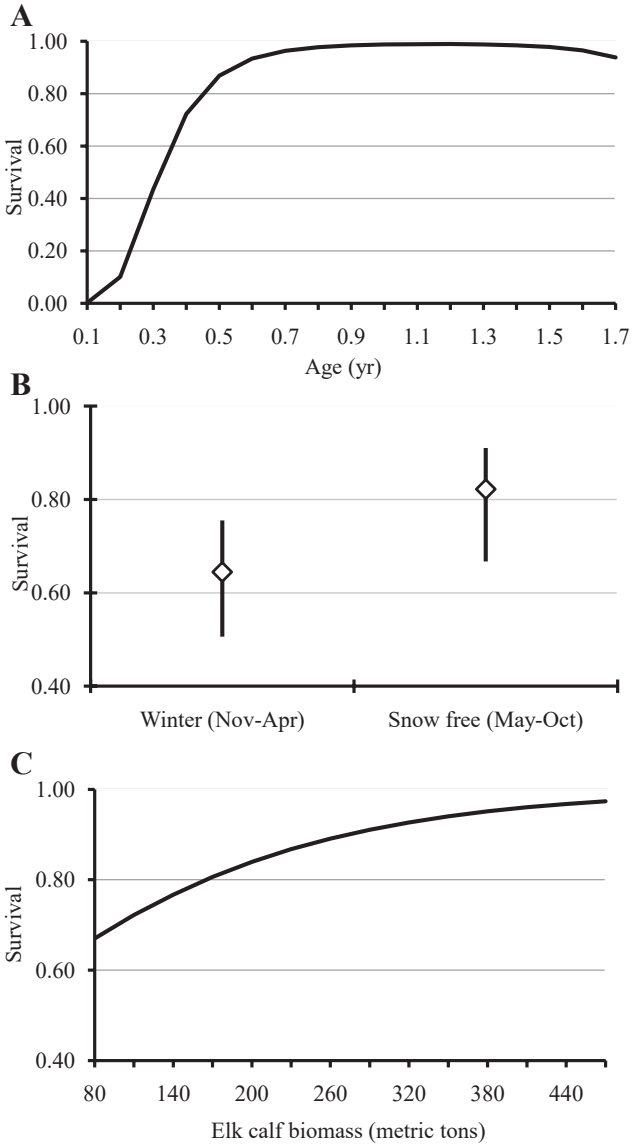

Figure 3. Annual, age specific survival estimates of cougar kittens (A), the effect of season (B) on estimates of kitten survival, and the influence of elk calf biomass (metric tons) on annual survival estimates of cougar kittens across the range of minimum estimates of elk calves (C) on the Greater Yellowstone Northern Range, 1987–2005. We computed estimates using βs from the top model (Table 6).

1,000 km^2 (1993) with annual mean age of 3.7–5.2 yr during the PW phase as males immigrated at an average rate of 1.7/yr and established home ranges. In the DW phase, male density increased from 1.76/1,000 km^2 in winter 1998–1999 to 2.93/1,000 km^2 in winter 2000–2001 and then declined to 1.03/1,000 km^2 by 2005 as adult males died. Annual mean age of adult males during the DW phase ranged from 4.2 to 7.1 yr and new males immigrated at an average rate of 0.9/yr.

Although phase was not included in our top model, annual kitten survival was slightly lower during the PW study (0.462) than the DW study (0.585). Causes of mortality (predation, orphaning or malnutrition, unknown) of kittens were similar between PW and DW phases ($\chi^2_2 = 5.932$, $P = 0.052$). In the PW and DW phases, 29% and 39% of total mortalities, respectively, were due to natural causes. However, during the PW study, 43% of kitten mortality (Table 4) resulted from infanticide and we suspected that 2 of the undetermined mortalities were related to infanticide. The DW study represented a time of greater territorial stability of dominant adult males and we documented only one (5%) kitten mortality due to infanticide. Orphaning and malnutrition accounted for 10% of natural deaths in the PW study and 40% of mortality during the DW study. Another 35% of mortalities during the DW study were due to predation by wolves or bears. One female kitten (14 months of age) was killed by hunters during the hunting season in the DW study. Most kitten mortality occurred in winter (PW = 81%, DW = 65%, $\chi^2_1 = 3.72$, $P = 0.05$) and was associated with infanticide in the PW study and wolves and orphaning or malnutrition in the DW study.

Survival Surface and Model Fit

We used model-averaged covariate estimates from our top model to create a survival surface for independent female and male cougars on the GYNR. Because our best model included road density during cougar hunting, we incorporated this seasonal effect when creating the survival surface. Thus, we created an annual surface by multiplying a surface that incorporated density of roads during the 4 months of the cougar hunting season (Dec–Mar) by a surface that removed the effect of roads for the 8 months when cougar hunting did not occur, such that:

$$\begin{aligned}\text{Annual survival surface} &= (\text{roads during hunt surface})^4 \\ &\times (\text{no roads during hunt surface})^8\end{aligned}$$

Results of ROC curve analysis indicated a good model fit for both female cougars (AUC = 0.81, 95%CI = 0.70–0.92, $n = 35$ harvest locations) and male cougars (AUC = 0.84, 95%CI = 0.74–0.94, $n = 49$ harvest locations) for our study area. When we applied our model further north and northwest beyond the study area boundary, our model provided a fair fit for female (ROC AUC = 0.73, 95%CI = 0.65–0.81, $n = 82$ locations) and male cougars (ROC AUC = 0.73, 95%CI = 0.67–0.80, $n = 137$ locations).

Mean survival for independent female cougars was 0.880 and 0.842 from our PW and DW studies, respectively. Using our survival estimates, PW $m_x = 0.75$ and DW $m_x = 0.44$, our estimates of population trajectory were $\lambda \geq 1.04$ in the PW study and $\lambda \geq 0.83$ in the DW study. Sensitivity and elasticity analyses (age specific sensitivity = 0.01–0.72, age specific elasticity = 0.01–0.11) supported the large influence of female survival on cougar population growth as found by Lambert et al. (2006). We found that $\lambda \geq 1.0$ when survival of 2–12-year-old independent females was $\geq$0.93 for the PW study and 1.00 for the DW phase. By assuming that maintaining $\lambda \geq 1.0$ across variation in m_x and emigration of 1-year old females requires female survival $\geq$0.93, we identified and mapped source (survival $\geq$0.93) and sink (survival $<$0.93) habitats from survival probabilities (Fig. 4; see Schwartz et al. 2010).

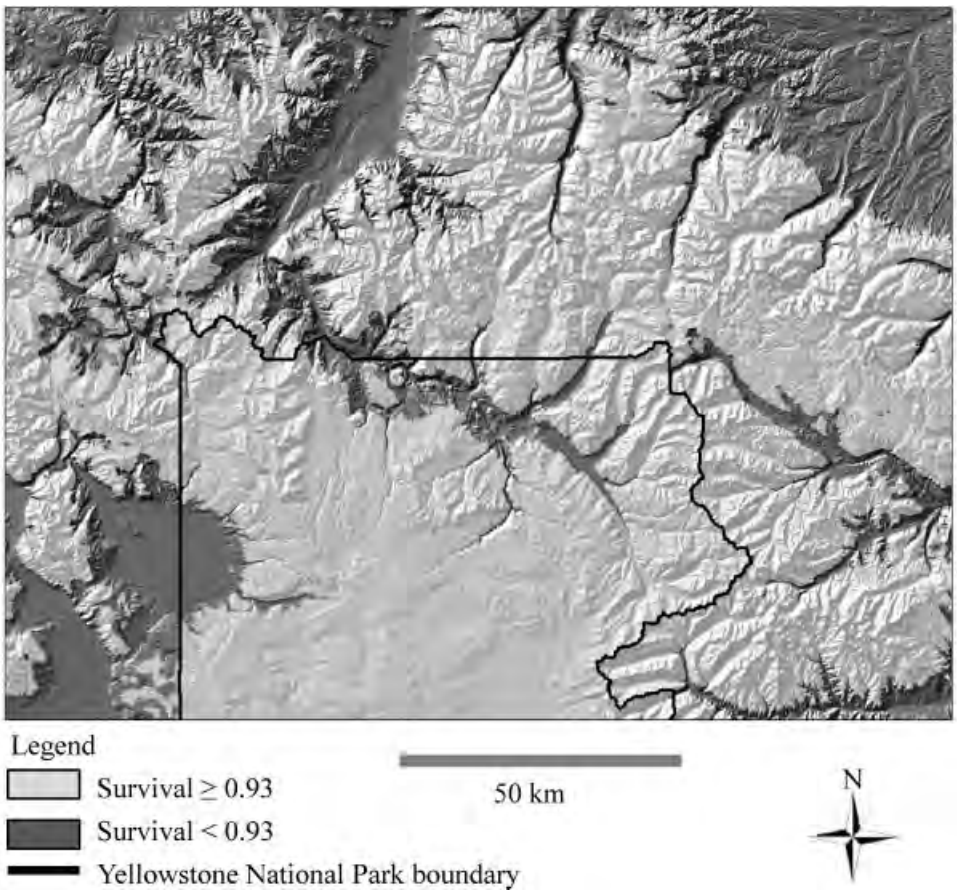

Figure 4. Survival surface reflecting threshold values of survival for independent female cougars; areas ≥0.93 indicate source habitat (white) and areas <0.93 indicate sink habitat (dark gray) on Greater Yellowstone's Northern Range, 1987–2005. We applied model averaged covariate estimates to the best model (Table 3) to estimate survival.

DISCUSSION

Quigley and Hornocker (2010:65) noted, "Two important extremes are evident in mortality factors for cougar populations, one human caused and one driven by internal strife (supplemented by other factors, such as disease and old age)." Cougar survival on the GYNR was largely a function of demography, density, and human influences stemming from sport-hunting.

Adult and Independent Subadult Survival

With the exception of the evaluation by Biek et al. (2006) of feline immunodeficiency virus (FIV) infection on cougar survival, our study is the first to evaluate factors influencing cougar survival in a multi-model approach. By far the most important determinants of survival were age and sex of the cougar, elevation, and density of roads in a cougar's home range during the cougar hunting season. Survival increased as females and males aged but then rapidly declined at older ages: >10 yr for females and >8 yr for males. Similar to other studies of hunted cougar populations (Cunningham et al. 1995, Lambert et al. 2006, Robinson et al. 2008) and in contrast to one non-hunted population (Logan and Sweanor 2001), female cougars in our study area had higher survival than males. Selective harvest of males could have contributed to observed differences in female and male survival in our study. Cougar hunters may selectively harvest males, particularly when competition between hunters is low, becoming less selective when demand exceeds harvest quotas and competition is high (Anderson and Lindzey 2005). During our PW study, 73% of harvest on the north end of our study area was males, suggesting selection for this gender, whereas males (55%) and females (45%) were harvested more equitably during the DW study. Because we combined adults and independent subadults for these analyses, our results do not reflect differences in harvest structure between these 2 age classes. Two female and 3 male cougars killed by hunters during the PW study were adults. In the DW study, 2 adult females and 3 subadult males were killed by hunters.

Annual elevation was important in our models, supporting the hypothesis that regardless of season, survival can be expected to be higher at higher elevations, a result similar to that found for grizzly bears in the GYE (Schwartz et al. 2010). For cougars outside or overlapping Park or Wilderness, elevation likely captured access to cougars by hunters starting from trailheads or roads originating in the Gardiner and Paradise valleys. Although a seasonal effect was not supported in our top model set, cougars are constrained to lower elevations where prey occurs during winter

and spatial overlap with wolves can increase as winter progresses (Alexander et al. 2006). Overall, elevation may represent a combination of factors that influence survival, perhaps including some that we did not consider or include in our analysis.

Road density outside YNP during the cougar hunting season was an important predictor of cougar survival. Road densities $\geq$1.58 km/km^2 had no additional effect on survival as estimated survival dropped to zero. On average, adult and subadult cougars in our sample only spent about 27% of their time in areas open to hunting during winter. Thus, although cougars spent proportionally more time in areas with no hunting access (Park or Wilderness), road access had a significant negative effect on survival for cougars that overlapped or lived outside the park during winter. Our study sample underrepresented independent subadults because we excluded them from analysis once they dispersed beyond the study boundary. Of 38 successful dispersers in the DW phase, 29% were killed prior to establishment during the hunting season at 18 months to 3 years of age and 18% were killed during the hunting season at >3 years of age. On the GYNR, survival rates for adult and subadult cougars combined were lower than mean survival estimates for adult males where no hunting occurred (0.91 M, 0.82 F, Logan and Sweanor 2001), were higher than heavily hunted populations (0.64 pooled adults on Monroe, Utah study area, Stoner et al. 2006; 0.33 adult M, 0.77 adult F, Lambert et al. 2006), and fell within annual estimates reported in other populations where mortality from hunting, vehicle collisions, and depredation removals were the leading causes of death (0.69–0.92 pooled M-F, Anderson et al. 1992; 0.75 pooled adults, Beier and Barrett 1993; 0.12–1.0 M, 0–0.81 F, Cunningham et al. 1995; 0.76 pooled adults on Oquirrhs, Utah study area, Stoner et al. 2006).

Road density calculated with a 2.59 km^2 moving window outperformed the 500-m^2 moving window, suggesting that the larger spatial scale better accounted for the relationship between hunter access and roads and that cougars were not necessarily killed near roads. Although some cougars may quickly tree short distances from roads, others are likely treed and killed at distances represented by the 2.59 km^2 moving window because houndsmen release dogs on tracks left from the previous night and a cougar may have traveled far from the road. Although traveling cougars have shown aversion to paved roads during the day, dirt roads and other low vehicle use roads may facilitate cougar movements (Van Dyke et al. 1986, Belden and Hagedorn 1993, Sweanor et al. 2000, Dickson et al. 2005). Cougars that travel snow-compacted roads leave tracks visible to houndsmen driving vehicles or snowmachines. Road access and snow conditions were key factors influencing distribution of hunting pressure and harvest of cougars in western Montana (Murphy 1983).

The possible effect of increased wolf presence on survival was small compared with effects of age, sex, elevation, and density of roads during the hunting season. Wolves caused 15% of adult cougar deaths and all occurred during winter. Our estimates of annual survival were much higher than those reported for cougars approximately 10 years after wolf reestablishment in the North Fork of the Flathead, Montana (0.29 M, 0.65 F, Ruth 2004*a*) where hunting and starvation were the primary sources of mortality and higher than those in Banff National Park during wolf recolonization (0.51 annual rate for pooled sexes, Kortello et al. 2007). Although the influence of increasing wolf use is not clear from our survival modeling, cougars responded to increasing wolf use by concentrating their activities in more topographically complex habitats (Ruth and Buotte 2007). In Banff National Park, Kortello (2007) found that as wolf use increased during winter, cougars shifted to areas with more human development and activity. If cougars in source areas avoid wolves by shifting into or overlapping areas managed as sinks, then source populations could become affected by management outside their boundaries. The direction cougars shift will likely be determined by the availability of complex terrain and other habitat characteristics (e.g., higher human density) that may limit wolf use. Shifts into good quality, occupied cougar habitat could lead to the perception of a growing cougar population and increased quotas, particularly if those areas are managed as sinks. The likelihood of harvest will still depend on the amount of road access in the area of interest. Considering that areas managed for cougar harvest are likely to be managed for wolf harvest as well, competition between the 2 species may be moderated by the effects of hunting.

Kitten Survival

Dependent siblings should not be assumed to have independent fates in survival analyses. Siblings in litters are usually left in a group while their mother hunts. Thus, littermates may equally have an increased risk of mortality from other cougars, wolves, bears, or loss of their mother. Violation of the independence assumption causes sample data to be overdispersed relative to a binomial model, which leads to underestimates of sampling variances (Schwartz et al. 2006, Bishop et al. 2008), a result supported by our analysis of kitten survival.

Estimates of kitten survival in New Mexico (0.59–0.66, Logan and Sweanor 2001) were higher than ours (0.46) in the PW phase and similar to those (0.59) in the DW phase. Kitten survival in a heavily hunted population in Washington (0.57, Lambert et al. 2006) was also similar to our DW survival but higher than kitten survival in the PW phase. The New Mexico and Washington estimates, however, reflect an assumption of independence of survival within litters.

Unlike adult cougars, gender of kittens had little influence on their survival to independence from their mother, similar to findings of Logan and Sweanor (2001) and Laundré et al. (2007). Also similar to findings of Logan and Sweanor (2001), kittens of both sexes had higher mortality at $\leq$4 months of age. Consequently, litters detected at ages >4 months will generally have smaller mean sizes and result in higher estimated rates of survival than those detected at younger ages (Murphy 1998, Ross and Jalkotzy 1992, Logan and Sweanor 2001:119, Quigley and Hornocker 2010).

Our finding that increased density of adult male cougars positively influenced kitten survival is consistent with SSI theory. Although SSI theory proposes that increased removal of adult males can negatively influence kitten survival (Stringham 1980) we suggest the mechanism is not explicitly density of males but rather territorial stability within the adult male social class that may drive SSI in cougars (see Logan and Sweanor 2010). Sustained removal of male cougars does not always result in reduced cougar density, yet can result in high levels of immigration (Robinson et al. 2008) and territorial instability. Thus, in other hunted populations, kitten survival may be inversely related to density. When possible, analyses similar to ours should first evaluate home range stability prior to using density as a covariate and compare it with a temporally changing spatial covariate. A younger age structure is characteristic of heavily hunted populations (Logan and Sweanor 2001, Anderson and Lindzey 2005, Stoner et al. 2006). The high degree of infanticide observed during the PW phase and mostly absent in the DW phase is consistent with an increasing cougar population with frequent annual immigration, younger age structure, and poorly defined male territorial boundaries in the PW phase. However, immigration of new males did not preclude resident males and newly established residents from acting as primary breeders in the PW study (Murphy 1998). In brown bears, both resident and immigrant males may be infanticidal (Miller et al. 2003, Swenson 2003). In 2 of 5 litters during our PW study, infanticidal males were resident breeders. Although breeding opportunities for males are not enhanced unless the whole litter is lost, mothers may defend kittens, resulting in partial loss of litters or the death of mothers and kittens alike (Logan and Sweanor 2001, Miller et al. 2003). Two maternal females were killed by males in the PW study and one litter was killed at the same time as the mother.

There was seasonality to infanticide in our study area; except for one kitten killed in October, all cases of infanticide occurred during winter. Winter density of adult males had a stronger influence on kitten survival, presumably because cougars were condensed on winter ranges, resulting in greater overlap. Infanticide in the PW phase occurred concurrent with newly established males vying for territories (lower density but increasing population) and increased winter overlap, which negatively influenced kitten survival. Conversely, we observed lower rates of infanticide and increased kitten survival in the DW phase when there was greater territorial stability (and higher density) of adult males and females. Breeding also began in January–February and peaked in March–April during both study phases. Males could encounter females unfamiliar to them, or unattended litters, with infanticide a result of males seeking breeding opportunities (Logan and Sweanor 2001).

Whether predation, reduced competition, or individual behavior are motives for some infanticide in cougars and whether infanticide may result in breeding opportunities for infanticidal males remain as questions and may not be consistent across time, within or among areas. We expected but did not observe similar rates of infanticide in the DW study if predation or competition for food resources were strong motives for infanticide. Further, in all 5 cases of infanticide in our PW study, it was unclear whether infanticidal males were sires of litters they killed or of subsequent litters. In New Mexico, infanticidal males were not sires of the litters they killed and they consumed kittens killed during infanticidal events (Logan and Sweanor 2001). On average, the loss of litters accelerated the time for females to breed again by about 5 months (Logan and Sweanor 2001). Other studies documented few cases of infanticide in a population with high male harvest in Wyoming (C. R. Anderson, Jr., Colorado Division of Wildlife, personal communication) and in a reestablishing population in South Dakota (D. Thompson, Wyoming Game and Fish Department, personal communication).

Minimum annual estimates of biomass of elk calves had a strong positive influence on kitten survival. Although the trend in overall elk calf biomass was greater in the PW study, the analyses incorporated year-to-year changes in calf abundance (PW range = 0.9–4.7 metric tons, DW range = 0.8–2.4 metric tons) and functioned in an additive manner to influence kitten survival. Similar to findings of Logan and Sweanor (2001), timing of peak births of kittens coincided with the birth of primary prey, elk calves and deer fawns, in June and July. Abundance and availability of this food source may be essential to supporting litters of offspring to independence. Cougar mothers may forage at greater distances and for longer periods from kittens when calves and fawns are fewer (Laundré and Hernández 2007), potentially exposing kittens to greater risk of predation from male cougars or other carnivores (Logan and Sweanor 2001). Alternatively, Logan and Sweanor (2001) found kitten survival did not appear to be sensitive to the population dynamics of deer and suggested a time lag preceded lower survival in response to a reduced prey base. Laundré et al. (2007) documented a time lag; survival of cougar young declined the year of and 2 years after a mule deer decline, but survival rates returned to predecline levels once cougar numbers adjusted downward to lower abundance of prey.

The effect of wolf presence on survival was small compared with effects of kitten age, season, biomass of elk calves, and seasonal density of adult male cougars. However, kitten deaths due to wolves represented 10–39% of observed average annual kitten production (10.2 kittens/yr over 6 yr) and 7–23% of observed average annual litters (4.3 litters/yr over 6 yr) produced on the GYNR. Although cougars showed spatial avoidance of wolves (Ruth and Buotte 2007, Kortello et al. 2007), the need to access prey may limit avoidance during winter.

Birth pulse did not appear in any of our top models, suggesting this covariate did not have a strong influence on kitten survival. However, models that included the primary birth peak (May–Jul) indicated a positive effect on kitten survival ($\beta = 1.12$, 95%CI = 0.24–2.00 for model = intercept + age + age^2 + bpeak1). Inclusion of the secondary peak (Sep–Oct) with the primary peak did not have a similar outcome; the beta coefficient was negative with a 95% confidence interval that bounded zero for the covariate

Bpeak2. Although there was lack of support for Logan and Sweanor's (2001) hypothesis using the longer birth period, they cautioned that the hypothesis is dependent upon being able to detect kittens born during non-favorable times of the year and being able to quantify their survival. Of the litters we documented, 10% were born outside the 2 birth peaks, which perhaps influenced the lack of relationship to survival. However, betas in models that included only the primary birth peak (which is more pronounced in northern than southern latitudes) had a positive effect on kitten survival indicating support for Logan and Sweanor's (2001) hypothesis.

Our study prior to and after wolf reintroduction provides one of the few long-term telemetry-based studies on cougars in North America. Although our analysis linked factors to interspecific, intraspecific, and hunting-caused mortality, we could not explain all proximate causes of mortality, including disease and accidents, with our analysis. However, Biek et al. (2006) found no evidence that FIV-infected cougars in our study population experienced an increased risk of infection with other feline pathogens and they found no support for an overall reduction in cougar survival caused by chronic FIV infection compared with effects of age, sex, and sampling site. In addition, our study ended prior to determining causes of an apparent decline in the cougar population and whether the decline was sustained. As a consequence, we recommend similar efforts to understand factors influencing cougar survival in ecosystems where wolves are present or expected to reestablish. Such efforts should be long-term (>10 yr) to incorporate variation in cougar, wolf, and prey densities.

Survival Surface and Source-Sink

On the GYNR, low elevations and increasing density of roads, particularly in areas open to hunting, posed greater mortality risk for cougars than in areas of low road density and higher elevations. Our results provide quantitative support to findings of Murphy (1983) for cougars and are consistent with findings for other carnivores (wolves: Person and Russell 2008; grizzly bears: Mattson et al. 1987, McLellan and Shackleton 1988, Schwartz et al. 2010).

Our model provided a good fit between areas predicting low survival and harvest data in Montana and provides the ability to map factors currently influencing cougar survival in the GYNR landscape. Because locations of cougars harvested in Montana were recorded to the nearest section, there was spatial ambiguity as to their exact location with possible error of 1 km (C. Anderson, Jr., unpublished data), which may have influenced the predictive power (ROC AUC) of our model. The predictive power declined slightly as we extended beyond the study area boundary indicating caution in broad application of survival models to large geographic areas or in using our results to establish road density standards in the GYE or other areas (see also Schwartz et al. 2010). In addition, our models highlight covariates that influence survival under current conditions, but they neither predict future conditions (Schwartz et al. 2010) nor indicate which habitats are currently used by cougars. A next step is construction of models that predict cougar habitat use and which are then integrated with our survival models as suggested by Schwartz et al. (2010). Further, Runge et al. (2006) suggest that estimates of emigration are important for delineating source habitats and for evaluating how local populations function with respect to a larger system. Evaluating factors influencing survival and probabilistic classification of source-stable-sink habitats at various local scales, as the landscape changes, and testing across regions could identify different covariates and enhance understanding of where and at what times certain habitats function as sources or sinks.

MANAGEMENT IMPLICATIONS

We recommend that managers take several measures to enhance cougar population management that is based on a source-sink strategy. Managers can identify or create source areas by delineating productive cougar habitats (generally greater than 1,000–2,200 km^2; Beier 1993, Logan and Sweanor 2001) that encompass prey winter ranges and few roads, such as national parks and wilderness areas, or by establishing such areas as refuges with no hunting. The size and function of apparent source populations should be initially verified and then periodically re-verified with any new effects considered as fluctuations in cougar fecundity and survival, changes in road densities, and interactions with competing carnivores may preclude their consistent function in supporting source populations. Because hunting can influence survival of cougars in adjacent untargeted areas, particularly those that are small in size, minimizing road density or limiting road access in critical winter habitats could be applied in an adaptive management approach to enhance protection of certain source populations. Managers should expect highly effective removal of cougars from habitats rendered accessible to sport hunters due to high road density and low elevation and such areas are easily identified and mapped using Geographic Information Systems. We caution that where cougar populations are managed to sustain high annual removal (sinks), immigration from neighboring areas or spatial shifts by adults from adjacent sources may mask actual population declines, leading to the common perception of population growth or stability, and pressure to increase or maintain current harvests (Robinson et al. 2008). Additionally, sinks or areas that experience functional recovery from natural population declines may experience low kitten survival when turnover of males is high or males are newly established. Sink habitats may also already have lower breeding potential due to social instability and can be expected to strongly rely on annual immigration from source populations. At the regional scale, documenting the juxtaposition and connectivity between source and sink populations is critically important to cougar management and conservation planning.

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REVIEW SUMMARY

CLIMATE CHANGE

The broad footprint of climate change from genes to biomes to people

Brett R. Scheffers,* Luc De Meester, Tom C. L. Bridge, Ary A. Hoffmann, John M. Pandolfi, Richard T. Corlett, Stuart H. M. Butchart, Paul Pearce-Kelly, Kit M. Kovacs, David Dudgeon, Michela Pacifici, Carlo Rondinini, Wendy B. Foden, Tara G. Martin, Camilo Mora, David Bickford, James E. M. Watson

BACKGROUND: Climate change impacts have now been documented across every ecosystem on Earth, despite an average warming of only ~1°C so far. Here, we describe the full range and scale of climate change effects on global biodiversity that have been observed in natural systems. To do this, we identify a set of core ecological processes (32 in terrestrial and 31 each in marine and freshwater ecosystems) that underpin ecosystem functioning and support services to people. Of the 94 processes considered, 82% show evidence of impact from climate change in the peer-reviewed literature. Examples of observed impacts from meta-analyses and case studies go beyond well-established shifts in species ranges and changes to phenology and population dynamics to include disruptions that scale from the gene to the ecosystem.

ADVANCES: Species are undergoing evolutionary adaptation to temperature extremes, and climate change has substantial impacts on species physiology that include changes in tolerances to high temperatures, shifts in sex ratios in species with temperature-dependent sex determination, and increased metabolic costs of living in a warmer world. These physiological adjustments have observable impacts on morphology, with many species in both aquatic and terrestrial systems shrinking in body size because large surface-to-volume ratios are generally favored under warmer conditions. Other morphological changes include reductions in melanism to improve thermoregulation, and altered wing and bill length in birds. Broader-scale responses to climate change include changes in the phenology, abundance, and distribution of species. Temperate plants are budding and flowering earlier in spring and later in autumn. Comparable adjustments have been observed in marine and freshwater fish spawning events and in the timing of seasonal migrations of animals worldwide. Changes in the abundance and age structure of populations have also been observed, with widespread evidence of range expansion in warm-adapted species and range contraction in cold-adapted species. As a by-product of species redistributions, novel community interactions have emerged. Tropical and boreal species are increasingly incorporated into temperate and polar communities, respectively, and when possible, lowland species are increasingly assimilating into mountain communities. Multiplicative impacts from gene to community levels scale up to produce ecological regime shifts, in which one ecosystem state shifts to an alternative state.

OUTLOOK: The many observed impacts of climate change at different levels of biological organization point toward an increasingly unpredictable future for humans. Reduced genetic diversity in crops, inconsistent crop yields, decreased productivity in fisheries from reduced body size, and decreased fruit yields from fewer winter chill events threaten food security. Changes in the distribution of disease vectors alongside the emergence of novel pathogens and pests are a direct threat to human health as well as to crops, timber, and livestock resources. Humanity depends on intact, functioning ecosystems for a range of goods and services. Enhanced understanding of the observed impacts of climate change on core ecological processes is an essential first step to adapting to them and mitigating their influence on biodiversity and ecosystem service provision. ■

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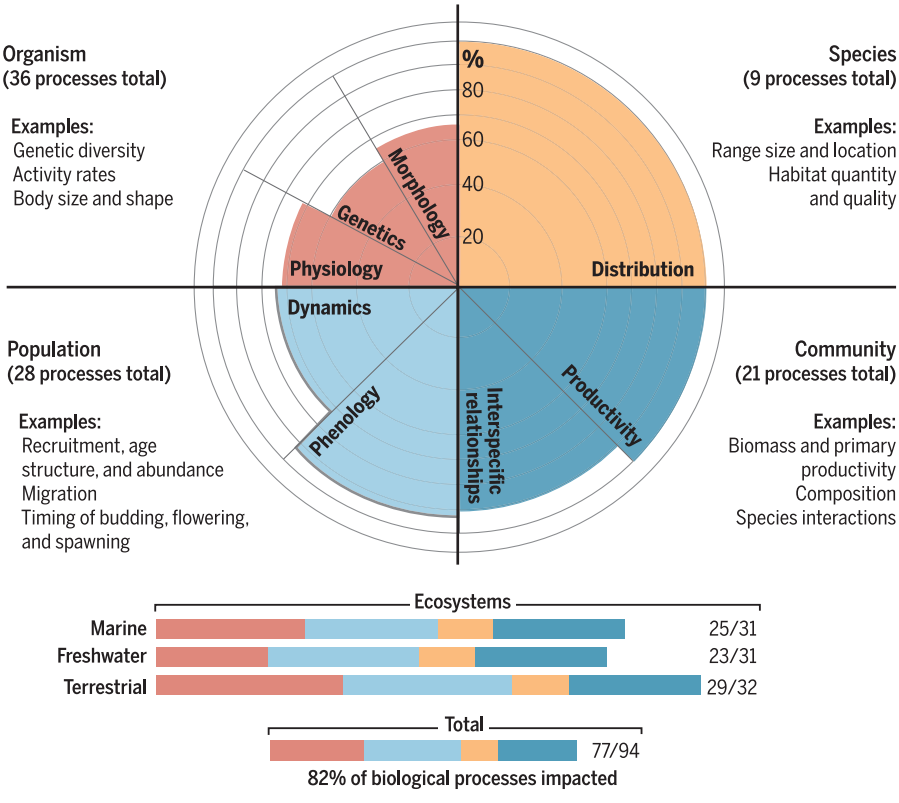

Climate change impacts on ecological processes in marine, freshwater, and terrestrial ecosystems. Impacts can be measured on multiple processes at different levels of biological organization within ecosystems. In total, 82% of 94 ecological processes show evidence of being affected by climate change. Within levels of organization, the percentage of processes impacted varies from 60% for genetics to 100% for species distribution.

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REVIEW

CLIMATE CHANGE

The broad footprint of climate change from genes to biomes to people

Brett R. Scheffers,[1]* Luc De Meester,[2] Tom C. L. Bridge,[3,4] Ary A. Hoffmann,[5] John M. Pandolfi,[6] Richard T. Corlett,[7] Stuart H. M. Butchart,[8,9] Paul Pearce-Kelly,[10] Kit M. Kovacs,[11] David Dudgeon,[12] Michela Pacifici,[13] Carlo Rondinini,[13] Wendy B. Foden,[14] Tara G. Martin,[15] Camilo Mora,[16] David Bickford,[17]† James E. M. Watson[18,19]

Most ecological processes now show responses to anthropogenic climate change. In terrestrial, freshwater, and marine ecosystems, species are changing genetically, physiologically, morphologically, and phenologically and are shifting their distributions, which affects food webs and results in new interactions. Disruptions scale from the gene to the ecosystem and have documented consequences for people, including unpredictable fisheries and crop yields, loss of genetic diversity in wild crop varieties, and increasing impacts of pests and diseases. In addition to the more easily observed changes, such as shifts in flowering phenology, we argue that many hidden dynamics, such as genetic changes, are also taking place. Understanding shifts in ecological processes can guide human adaptation strategies. In addition to reducing greenhouse gases, climate action and policy must therefore focus equally on strategies that safeguard biodiversity and ecosystems.

Atmospheric concentrations of greenhouse gases from burning fossil fuels and deforestation are approaching levels that have not been detected in the past 20 million years (*1*). This has altered the chemical composition of the Earth's atmosphere, oceans, and fresh waters (*2*). As a result, temperatures in the upper ocean and on land are now ~1°C higher than in preindustrial times, and temperature, wind, and precipitation regimes have become more variable and extreme (*3*, *4*). These changes are having clear impacts on planetary biophysical processes, including desalinization and acidification of the world's oceans (*5*) and melting of permafrost, ice sheets, and glaciers (*6*, *7*). Lakes and rivers have increased in temperature, altering seasonal patterns of mixing and flows (*8*).

Changing climate regimes have been an important driver of natural selection in the past (*9*) and, as in the past, species are responding to the current human-induced climate event in various ways. Previous reviews have covered many of the more obvious changes in species ranges, phenologies, and population dynamics (*10*–*15*) but have usually focused on one ecological system at a time. Here, we discuss the full range and scale of climate change effects on biota, including some of the less obvious disruptions observed in natural systems. We present examples of case studies of observed impacts across terrestrial and aquatic biomes and find evidence that climate change is now affecting most biological and ecological processes on Earth—spanning genetics, organismal physiology and life-history, population distributions and dynamics, community structure, and ecosystem functioning (Fig. 1 and table S1). People depend on intact, functioning ecosystems for a range of goods and services, including those associated with climate adaptation (*16*). Understanding the observed impacts of current climate change on core ecological processes is therefore an essential first step in humans planning and adapting to changing ecosystem conditions.

Although inherently different, marine, freshwater, and terrestrial realms share a common hierarchy of levels of biological organization, ranging from genes to organisms, populations, species, communities, and ecosystems. Broadly adapting from Bellard *et al.* (*17*), we screened the literature (supplementary materials) to evaluate evidence that climate change is affecting ecological components across different levels of biological organization, each of which comprises a core set of ecological processes (Fig. 1, fig. S1, and table S1). We identify a set of core ecological processes on Earth (32 in terrestrial and 31 each in marine and freshwater), which together facilitate ecosystem functioning that supports services to people (*17*). These processes include changes in genetic diversity (genetics), metabolic rates (physiology), body size (morphology), timing of migration (phenology), recruitment (population dynamics), range size (distribution), loss of synchronization (interspecific relationships), and biomass (productivity) (*17*). Because our main goal is to assess what processes are affected by climate change, we define "impact" on each process as an observed change in that process linked to climate change. We do not differentiate between "positive" (adaptive, buffering, or mitigating) and "negative" (stress or damage) responses because responses may be positive at one level of biological organization (such as genetic adaptation to climate change) but negative at another (such as reduced genetic variation and capacity to deal with other stressors). We then consider the relevance of the affected ecological processes in human systems and illustrate observed impacts to ecosystem services such as food and resource security (fisheries, agriculture, forestry, and livestock production), human health, and hazard reduction.

Ecological impacts of climate change

Organisms

Genetics

There is now growing evidence that species are undergoing evolutionary adaptation to human-induced climate change. For example, between the 1960s and 2000s the water flea (*Daphnia magna*) evolved to cope with higher thermal extremes in the UK (*18*), and cornflower (*Centaurea cyanus*) life history traits have recently evolved in response to warmer springs across northern France (*19*). Other examples include the evolution of earlier migration timing in anadromous pink salmon (*Oncorhynchus gorbuscha*), with decreased frequency of incidence of a genetic marker that encodes for late migration (*20*). Time-series data that control for physiological acclimatization also show strong evidence for genetic responses to climate change. For example, Bradshaw and Holzapfel showed that genotypic values for the critical day length that induces diapause in the pitcher plant mosquito (*Wyeomyia smithii*) change with latitude, and that the latitudinal relationship has changed over the period from 1972 to 1996 (*21*). Onset of diapause now occurs later, which is consistent with a longer

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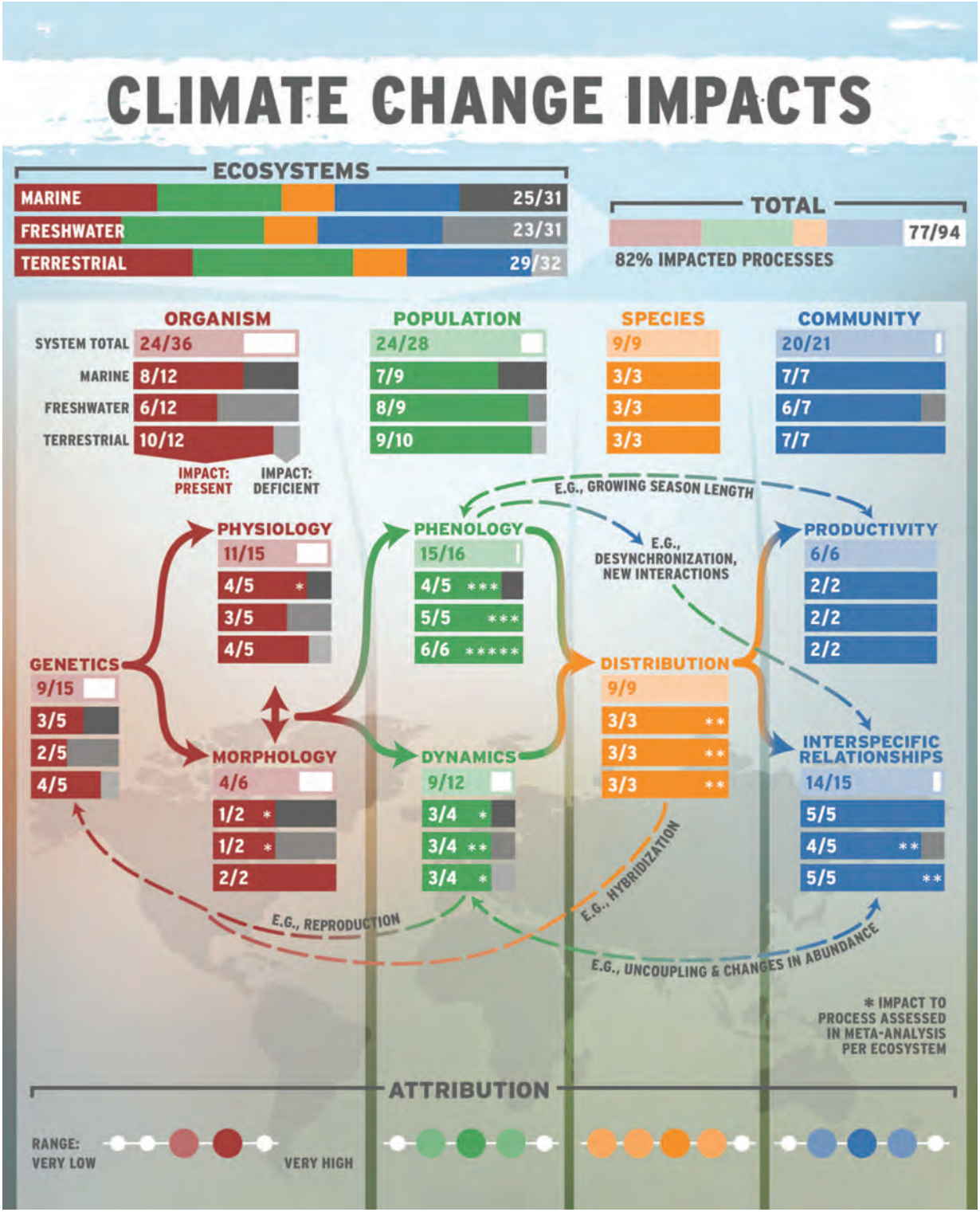

Fig. 1. Climate change impacts on Earth's marine, terrestrial, and freshwater systems. The presence of observed impacts on the different levels of biological organization and its inner components across the Earth's marine, terrestrial, and freshwater ecosystems. The denominator represents the total number of processes that we considered for each group, and the numerator is the number of these processes with evidence of impact (a complete list of processes is provided in fig. S1 and table S1). In total, 82% of all (n = 94) ecological processes that were considered have observed evidence of impact by climate change. Each process has at least one supporting case study. The asterisk indicates whether the affected process was assessed in a meta-analysis in addition to case studies. Thus, double-asterisk indicates that two processes were assessed in at least one meta-analysis. Confidence that the observed impact can be attributed to climate change was assigned for each level of organization and ranges from very low, low, medium, high, to very high; this assessment is based on tables 18-7, 18-8, and 18-11 in (*13*). The darkest circle indicates confidence level with the most literature support.

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growing season under warmer conditions. Oceanic phytoplankton have adapted to a temperature change of +0.73°C associated with 15 years of climate warming in the Gulf of Cariaco, Venezuela, by adjusting their thermal niche by +0.45°C (*22*). Although such evidence from small organisms with short generation times is accumulating, we found little documented evidence of evolutionary change from species with longer generation times such as birds, mammals, and trees (*14*, *23*), although adaptation appears to be possible in some long-lived reef corals (*24*).

Changes in species ranges have altered or created new "hybridization zones" across the planet. For example, in North America, hybrid zones between black-capped (*Poecile atricapillus*) and Carolina chickadees (*P. carolinensis*) are shifting in response to warmer winter temperatures (*25*), and because the southern flying squirrel (*Glaucomys volans*) has expanded its range northward in eastern North America, it is now hybridizing with the northern flying squirrel (*G. sabrinus*) (*26*). In North American rivers and streams, hybridization between invasive rainbow trout (*Oncorhynchus mykiss*) and native cutthroat trout (*O. clarkia*) has increased in frequency as the former expand into warming waters (*27*). Such hybridization events have also been observed in some marine fishes, such as the coastal West Coast dusky cob (*Argyrosomus coronus*), and are expected to increase as species shift their ranges poleward in response to rapidly warming ocean conditions (*28*).

Physiology

Many species display temperature-driven trait plasticity in physiological processes such as thermal optima (*29*). Whereas some responses, such as acclimation to high temperatures, maximize fitness, others can reflect failure to cope with temperature stress and other climate-mediated changes. These responses can occur within a generation or between generations through maternal or epigenetic effects (*30*).

There is some observational evidence that warming has affected temperature-dependent sex determination (TSD) of species in marine and terrestrial systems. Snake pipefish (*Entelurus aequoreus*) in the northeastern Atlantic have altered their operational sex ratios and reproductive rates as a consequence of warmer sea surface temperatures (*31*). Most evidence for impacts on TSD in marine systems, however, is derived from experimental studies, which provide strong support for TSD changes in sea turtles and various fish species (*32*, *33*). In terrestrial and freshwater systems, TSD has been implicated in masculinization and feminization, respectively, of lizard and turtle populations (*34*, *35*).

In marine systems, physiological responses to both climate warming and changing ocean conditions are widespread (*36*, *37*). Matching field and laboratory data for the eelpout (*Zoarces viviparus*) show increased metabolic costs associated with warming in the North and Baltic Seas (*38*). In aquatic systems, warming increases oxygen demand but decreases oxygen content of the water, resulting in substantial metabolic costs (*39*). Although climate change per se does not cause acidification of the oceans, both arise directly from higher atmospheric carbon dioxide, and experimental evidence has raised concerns regarding negative effects of ocean acidification on calcification, growth, development, and survival of calcifying organisms (*12*). For example, acidification has led to extensive shell dissolution in populations of the pteropod *Limacina helicina* in northwest North America and in the Southern Ocean off Antarctica (*40*, *41*).

Morphology

Individuals in some species are becoming smaller with increasing warming because large surface-to-volume ratios are generally favored under warmer conditions (*42*)—a phenomenon that is linked to standard metabolic principles (*43*). In the Appalachian Mountains, six species of *Plethodon* woodland salamander have undergone, on average, an 8% reduction in body size over the past 50 years (*44*). Similarly, three species of passerine birds from the northeast United States show an average 4% decrease in wing length correlated with recent warming (*45*), and the long-distance migrant bird the red knot (*Calidris canutus*) is now producing smaller offspring with smaller bills, which reduces survival in juveniles because of altered foraging success on underground bivalves (*46*). In general, decreasing body size with warming is expected, but evidence from cold, high-altitude habitats suggests that increased primary productivity and longer growing seasons from warming have led to increased body size in some mammal species such as American marten (*Martes americana*) and yellow-bellied marmot (*Marmota flaviventris*) (*47*, *48*). In South Australia, leaf width in soapberry (*Dodonaea viscosa*) has decreased compared with the ancestral condition documented under cooler temperatures 127 years ago (*49*). Other climate change impacts on morphology include color changes in butterflies, dragonflies, and birds (*50*–*53*) and pronounced changes in skull shape in the alpine chipmunk (*Tamias alpinus*) (*54*).

Population

Phenology

For most species, migrations and life-history processes (such as budding and flowering in plants, hatching and fledging in birds, and hibernation in mammals) are closely tied to seasonal and interannual variation in climate, and there is now overwhelming evidence that both have been affected by climate change (*10*, *37*, *55*, *56*). Across marine, freshwater, and terrestrial ecosystems, spring phenologies have advanced by 2.3 to 5.1 days per decade (*10*, *57*). A combination of climate warming and higher atmospheric CO_2 concentrations has extended the growing period of many plant populations (*58*). In a large global analysis, which included 21 phenological metrics such as leaf-off and leaf-on dates and growing-season length, plant phenologies were found to have shifted by more than 2 standard deviations across 54% of Earth's land area during the past three decades (*59*).

In marine and freshwater systems, advances in the timing of annual phytoplankton blooms—the basis for many aquatic food webs—have occurred more rapidly than temporal shifts in terrestrial plants (*37*, *60*). Such changes in plankton phenology have been attributed to increases in water temperatures, reduction in the duration of ice cover, and the alteration of the seasonal duration of thermal stability or stratification of the water column.

Shifts in spawning times have been documented for 43 fish species in the northeast Pacific Ocean from 1951 to 2008, with earlier spawning associated with increased sea surface temperature and later spawning associated with delays in seasonal upwelling of nutrients toward the ocean surface (*61*). Similar impacts on breeding have been observed in terrestrial and marine bird species (*62*).

Changes in the timing of migration events have been extensively documented, including advances in spring arrival dates of long-distance migratory bird species in Europe, North America, and Australia (*63*–*65*). Similarly, long-term data on many amphibians and mammals have shown advancements in spring and delays in autumn migration (*66*–*68*) and altered peak calling periods of male amphibians (*67*–*69*). In the largest meta-analysis to date of phenological drivers and trends among species in the southern hemisphere, 82% of terrestrial data sets and 42% of marine data sets demonstrated an advance in phenology associated with rising temperature (*70*).

Abundance and population dynamics

Acute temperature stress can have severe negative effects on population dynamics such as abundance, recruitment, age structure, and sex ratios. Meta-analyses across thousands of species report that ~80% of communities across terrestrial, freshwater, and marine ecosystems exhibited a response in abundance that was in accordance with climate change predictions (*10*, *70*). In a meta-analysis of marine species, 52% of warm-adapted species increased in abundance, whereas 52% of cold-adapted species decreased (*71*). Temperature spikes may cause mass mortality of key ecosystem engineers in both temperate and tropical oceans. Excessive heat kills canopy-forming macroalgae in temperate marine systems (*72*) and causes bleaching and mass mortality of corals in the tropics (*73*). Reductions in sea ice extent have caused declines in abundances of ice-affiliated species in the Arctic [for example, ivory gulls (*Pagophila eburnea*), ringed seals (*Pusa hispida*), and polar bears (*Ursus maritimus*) (*74*)] whereas in some cases, such as on Beaufort Island in the southern Ross Sea, the loss of ice from receding glaciers resulted in increased abundances of Adélie penguins (*Pygoscelis adeliae*) (*75*). In the United States, the bull trout (*Salvelinus confluentus*) has lost >10% of its spawning grounds in central Idaho over the past 13 years because of increased water temperatures (*76*), while the brown trout (*Salmo*

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trutta) has lost habitat in the Swiss Alps (*77*). In western Canada, reduced survival of adult migrating Fraser River sockeye salmon (*Oncorhynchus nerka*) has been observed with increased water temperatures (*78*), and in eastern Canadian lakes, golden-brown algae dramatically increased in abundance as water temperature increased 1.5°C during the latter part of the 20th century (*79*). Some of the best evidence for climate-change impacts on the abundance of terrestrial species comes from analyses of bird population trends derived from systematic monitoring schemes in Europe, with warm-adapted species having increased in abundance on average since the 1980s and cold-adapted species having declined (*80*).

Climate change can increase the abundance of temperature-sensitive disease vectors, with subsequent effects on disease outbreaks. In the African Serengeti, there is some evidence that a combination of extreme weather, high abundances of ticks carrying *Babesia*-piroplasm, and suppressed immunity to canine distemper virus led to widespread mortality of lions (*Panthera leo*) (*81*). In marine systems, field evidence shows that corals are increasingly susceptible to white band disease at higher temperatures, leading to declines in two of the most important reef-building acroporid (branching) corals in the western Atlantic (*82*).

Species

Distribution

One of the most rapid responses observed for marine, freshwater, and terrestrial species is a shift in their distributions to track optimal habitat conditions (*71*, *83*, *84*). Across land and aquatic ecosystems, species have expanded their leading (cold limit) edge by 19.7 km per decade, with marine species expanding by 72 km per decade compared with 6 km per decade in terrestrial species (*37*). The distributions of many marine taxa have shifted at higher velocities than those of terrestrial taxa (*37*) because areas with rapid changes in climate extend across broader regions of the ocean than on land, and connectivity in marine environments tends to be high (*85*). To illustrate this point, corals around Japan have shifted their range by up to 14 km per year over the past 80 years (*86*), and in waters off the southeast coast of Australia, intertidal invertebrate species have shifted their geographic distributions polewards at an average rate of 29 km per decade (*87*). Where connectivity allows for dispersal, some freshwater fishes are capable of shifting at rates comparable with those of marine and terrestrial taxa (*88*), but mean shifts by river fishes in some regions have been insufficient to compensate for measured temperature rises (*89*).

There has been a consistent overall trend for tropical, warm-adapted species to expand their ranges into environments previously dominated by temperate cold-tolerant species ("tropicalization") (*90*). A similar phenomenon has been documented in the Arctic, where boreal fish communities have responded to warming in the Barents Sea by shifting northward, resulting in a high turnover in Arctic fish communities ("borealization") (*91*). Similarly, on land, increased minimum temperatures have driven rapid changes in the range size (as well as distribution) of Swedish birds, with northern species retracting and southern species expanding northward (*92*).

In addition to latitudinal changes, many observed shifts in species distributions have occured across elevation gradients. In the mountains of New Guinea, birds have shifted their distributions upslope by 95 to 152 m from 1965 to 2013 (*93*). A similar upslope shift was observed in recent decades in mountainous stream-dwelling fish in France (*89*), North American plants (*94*), and Bornean insects (*95*). An analogous response has been the shift to deeper, colder waters among some marine fishes (*91*).

In some cases, species have shown no response or even downhill shifts in their distributions (*96*) or increased frequency of range disjunction rather than poleward or upward range shifts (*97*). Savage and Vellend (*98*) found upward range shifts in North American plant species and an overall trend toward biotic homogenization from 1970 to 2010, but their study also documents considerable time lags between warming and plant responses (*99*, *100*). Delayed community responses to increasing temperature may be in part due to the buffering effects of microhabitats (*101*, *102*) and possibly moisture, which is a critical, but less often studied, driver in the redistribution of species (*103*). For example, Crimmins *et al.* observed downhill movements for North American plants under climate change over an 80-year period, which they attribute to changes in water balance rather than temperature (*104*).

Community

Interspecific relationships

As a by-product of the redistribution of species in response to changing climate, existing interactions among species are being disrupted, and new interactions are emerging (*105*, *106*). These novel biotic interactions can exacerbate the impacts of abiotic climate change (*107*, *108*). Woody plants are invading arctic and alpine herb-dominated communities in response to rapid warming in recent decades, leading to secondary shifts in distribution of other plants and animals (*92*). In the Sierra Nevada Mountains of California, Tingley and Beissinger found high levels of avian community turnover during the past 100 years at the lowest and highest elevations (*109*), and in Greece, Sgardeli *et al.* found similar patterns of temperature-driven turnover in butterfly communities (*110*). There are surprisingly few studies of observed impacts of climate change on competitive interactions (*108*). In one example from Sweden, Wittwer *et al.* found that among four bird species occupying the same ecological guild, resident birds were able to adapt to warmer temperatures and outcompete the sole long-distance migrant, *Ficedula hypoleuca* (*111*).

New interactions among species can also lead to trophic disruptions such as overgrazing. In western Australia, for example, overgrazing of subtropical reefs by the poleward spread of tropical browsing fish has suppressed recovery of seaweeds after temperature-induced mortality (*112*). These types of trophic disruptions are escalating, with range shifts by tropical herbivorous fishes increasing herbivory rates in subtropical and temperate coastal ecosystems where seaweeds are the dominant habitat-forming taxa (*90*).

Phenological mismatches have been observed between butterflies and their annual host plants, with the plants dying before the insect larvae were ready to enter diapause (*113*). Similarly, an analysis of 27 years of predator-prey data from the UK showed asynchronous shifts between the tawny owl (*Strix aluco*) and its principle prey, the field vole (*Microtus agrestis*), which led to reduced owl fledging success (*114*). In Lake Washington, United States, spring diatom blooms advanced by over 20 days since 1962, resulting in predator-prey mismatches with their main grazer, the water flea (*Daphnia pulicaria*), and population declines in the latter (*60*). In Canadian Arctic lakes, asynchronous shifts in diatom blooms resulted in generalist water fleas being replaced by more specialist species (*115*). At higher trophic levels, warming has affected the fry and the juvenile life-history stages of lake char (*Salvelinus umbla*) via direct impacts on their zooplankton and vendace (*Coregonus alba*) food sources (*116*).

Productivity

Changes in productivity are one of the most critical impacts of climate change across aquatic and terrestrial ecosystems (*117*, *118*). In marine systems, climate-mediated changes in chlorophyll-a concentrations as a proxy of phytoplankton biomass have been highly variable (*119*). Depending on location, these include both dramatic increases and decreases in abundance as well as changes in phenology and distribution of phytoplankton over the past several decades. In a global study of phytoplankton since 1899, an ~1% decline in global median phytoplankton per year was strongly correlated with increases in sea surface temperature (*120*), whereas in the Antarctic Peninsula, phytoplankton increased by 66% in southern subregions and decreased by 12% in northern subregions over a 30-year period. These conflicting observations in the Antarctic are in part linked to changes in sea surface temperature but also changes in ice cover, cloudiness, and windiness, which effect water-column mixing (*121*).

In deep tropical freshwater lakes dominated by internal nutrient loading through regular mixing, warmer surface waters confer greater thermal stability, with reduced mixing and return of nutrients to the photic zone, substantially decreasing primary productivity (*122*), phytoplankton growth (*123*), and fish abundance (*122*). In contrast, eutrophication effects are exacerbated by higher temperatures in shallow lakes, resulting in increased productivity and phytoplankton and toxic cyanobacteria blooms (*124*).

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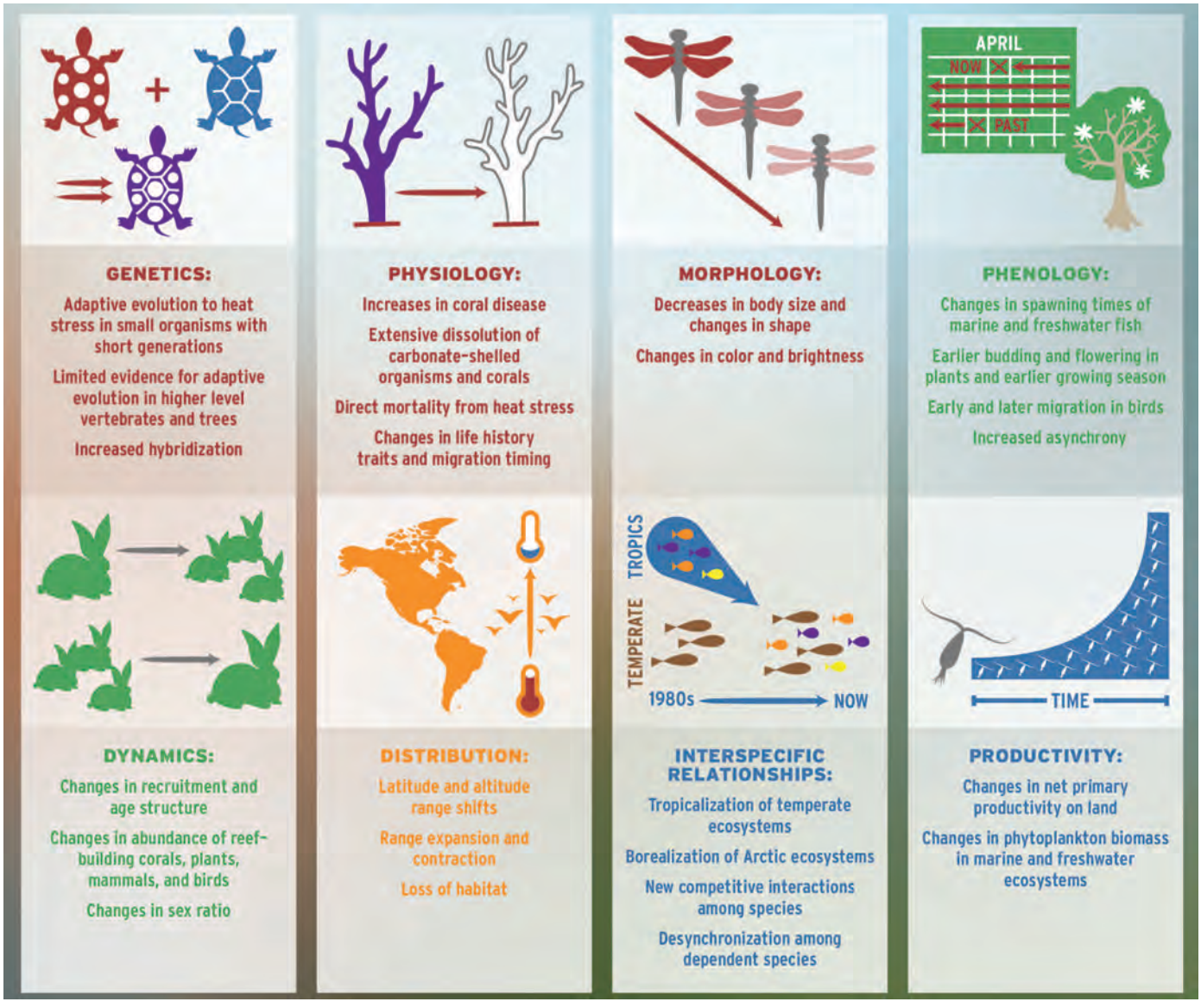

Fig. 2. Climate impacts on ecological processes. Examples of ecological components and processes affected by climate changes across marine, freshwater, and terrestrial ecosystems (fig. S1 and table S1).

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Globally, terrestrial plant growth has increased with increasing temperatures and CO_2 levels. This may in part explain the on average 6% increase in net primary productivity (NPP) from 1982 to 1999 (*125*), although these changes in NPP may also be related to natural variation in El Niño–La Niña cycles (*126*). However, responses are highly variable, and some terrestrial systems are not experiencing increased productivity owing to either extreme temperatures or lack of water. Severe short-term droughts in climatically stable rainforest environments are unusual but in recent years have increased in frequency. These events have led to changes in forest canopy structure in Amazonia (*127*) and decreases in aboveground woody and leaf biomass in the Congo basin (*128*). Across large expanses of the Amazon, there has been an overall reduction in aboveground biomass owing to increased climate variability over the past three decades (*129*).

Impacts across ecosystems

All three biotic realms (terrestrial, freshwater, and marine) are being affected by climate change, and the evidence summarized here reveals that these impacts span the biological hierarchy from genes to communities. Of the 94 processes considered, we found that 82% have evidence of impact by climate change, and this has occurred with just 1°C of average warming globally (Fig. 1). Impacts range from genetic and physiological changes to responses in population abundance and distribution (Fig. 2).

The fact that evidence is missing for some processes is more likely to reflect data deficiencies than the absence of any response to climate change. We only considered field-based case studies that report changes in the processes through time. For many components, such as genetics (*23*) and physiology (*29*), there is strong evidence from experiments on a wide range of species that individuals and populations can and likely will respond to climate change. Thus, even though we found compelling evidence of widespread responses across the biological hierarchy, we still consider our discussion of impacted processes to be conservative. To illustrate this point, Box 1 shows the range of observed responses in the water flea *Daphnia*, which spans the entire hierarchy of biological organization.

Ecosystem state shifts

As ecological systems continue to accumulate stress through compromised ecological processes

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Box 1. A complete hierarchy of climate change impact in one model system: the water flea *Daphnia*. Combining time-series data with experimental approaches can lend insights to the breadth of climate change impacts. For water fleas of the genus *Daphnia*, for instance, there is evidence for responses to temperature at all levels of biological organization. *Daphnia* are important grazers in lakes and ponds (*180*). They adapt to temperature increase through genetic changes in thermal tolerance (*18*), body size, and life history traits (*181*, *182*). In the laboratory, *Daphnia* exhibit phenotypic plasticity in physiology to changing temperatures [for example, hemoglobin quality and quantity (*183*) or metabolic activity (*184*)], behavior [such as swimming activity (*184*)], life history traits (*185*), and body size (*182*). *Daphnia* adjust their phenology (*186*) and abundance (*187*) in response to increases in temperature, which results in mismatches with phytoplankton dynamics (*60*). Warmer, drier weather over two decades can lead to expanded distributions and increased colonization capacity (*188*). Temperature influences interactions of *Daphnia* with predators (*189*) and parasites (*190*), and adaptation to increased temperature influences competitive strength (*185*). In the absence of fish, high abundances of *Daphnia* in +4°C heated mesocosms exert strong top-down control on phytoplankton (*191*).

either directly from climate change or interactively with other forced disturbances (discussion is provided in the supplementary materials), diminished resilience may lead to ecological regime shifts—in which one ecosystem state shifts to an alternative and potentially undesirable stable state. For example, some reefs are transitioning from coral- to algal-dominated states as a consequence of mass coral mortality (*130*), whereas kelp forests are turning into rocky barrens in temperate seas (*90*, *131*, *132*). In lakes, climate change has increased the risk of regime shifts from clear-water to turbid states and increased the occurrence of cyanobacteria blooms (*124*). If sufficient community-based processes are affected at regional scales, wholesale biome shifts can occur such as has been observed in Alaska, where tundra is transitioning to boreal conditions (*133*). These are clear signs of large-scale ecosystem change and disruption, in which disequilibrium rapidly pushes the system into a new state (*134*).

Using ecology to better understand climate change impacts on human well-being

Threats to production

The impacts of climate change on marine fisheries have major consequences for human societies because these currently provide ~17% of the global protein for people (*135*). There is, however, no current consensus on the costs and benefits of the ongoing global redistribution of fisheries because trends are highly variable. In the Arctic, commercially important fish, such as Atlantic cod (*Gadus morhua*) and walleye pollock (*Theragra chalcogramma*), have increased in biomass primarily because of increases in plankton production from reduced sea ice (*136*, *137*), whereas changes in fish biomass in the Southern Ocean are less clear (*138*). In Switzerland, which has experienced twice the average global temperature increase, trout catches have been halved over two decades because of rising temperatures in Alpine streams (*77*).

Changes in total marine productivity are not just attributed to abundance shifts but also morphological shifts. Indeed, some fish species appear to be shrinking, but attributing this solely to ocean warming is difficult because size-dependent responses can be triggered by commercial fishing as well as long-term climate change (*139*). However, long-term trend analyses show convincingly that eight commercial fish species in the North Sea underwent simultaneous reductions in body size over a 40-year period because of ocean warming, resulting in 23% lower yields (*140*). Reduced body size in fish is also being recorded in lakes and rivers throughout Europe and has been linked to increased temperature and climate-induced shifts in nutrient inputs (*141*, *142*).

Impacts on plant genetics and physiology are influencing human agricultural systems. For example, yields in rice, maize, and coffee have declined in response to the combined effects of rising temperatures and increasing precipitation variability over past decades (*143*–*145*). Genetics is being used to counteract decreasing yields in some key crops such as wheat [for which, globally, yields have declined by 6% since the early 1980s (*146*)] through crossing domesticated crops with wild relatives to maintain the evolutionary potential of varieties (*147*). Yet, some important wild strains are also showing signs of impact from climate change. Nevo *et al.* documented high levels of genetic changes in the progenitors of cultivated wheat and barley in Israel over the past 28 years (*148*). These wild cereals exhibited landscape-level changes in flowering time and a loss of genetic diversity in response to increasing temperatures.

Losing genetic resources in nature may undermine future development of novel crop varieties (*149*) and compromise key strategies that humans use to adapt to climate change. One such strategy is to use assisted gene flow, the managed movement of individuals or gametes between populations to mitigate local maladaptation in the short and long term (*150*). Where genetic introgression—the movement of genetic material from one species into the genome of another—can occur from unexploited natural populations to managed or exploited populations that are poorly adapted to warmer or drier conditions, adaptive changes may be facilitated (*147*), as in white spruce (*Picea glauca*), a tree commonly harvested for timber (*151*). Human-assisted evolution may also be a key strategy in maintaining reef-dependent fisheries by accelerating and enhancing the stress tolerance of corals (*152*).

Phenological changes due to milder winters are influencing crop and fruit production (*153*). Climate change has reduced winter chill events in temperate agricultural areas (*154*), which can desynchronize male and female flowers and trigger delayed pollination, delayed foliation, and reduced fruit yield and quality. To counter this, tree crop industries have developed adaptation measures such as low-chill cultivars with dormancy-breaking chemicals. For example, the "UFBest" peach requires four times fewer chill days than cultivars from more temperate climates (*155*). Advances in the timing of budding, flowering, and fruiting of plant species has induced earlier harvesting periods in some countries [such as Japan (*156*)].

Pollination is a key process linked to yields for a large number of crops. The short-lived, highly mobile insect species that provide pollination services to numerous crops have responded rapidly to changing climates by shifting their ranges throughout North America and Europe (*157*). Additionally, over the past 120 years, many plant-pollinator networks have been lost with overall decline in pollination services, which is attributed to a combination of habitat loss, pollution, and climate warming (*158*). Yet, observed changes in the phenology, abundance, and distribution of common pollinators have not been directly linked to declines in yields of animal-pollinated crops. This is likely due to limited data that directly link pollination services to crop yield over time and may, in part, reflect resilience provided by the diversity of insect species that pollinate many crops (*159*, *160*). More specialized pollination systems are expected to be more vulnerable to climate change. Humans have adapted to the declines in native pollinators by transporting domesticated pollinators to crop locations.

Pest and disease threats

Climate-induced ecosystem-level changes, such as forest die-offs, have an obvious impact on

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Table 1. Climate change consequences for humans. Affected ecological processes have direct consequences in food systems and human health.

	Organism	Population	Species	Community
	Genetics, physiology, morphology	**Phenology, dynamics**	**Distribution**	**Interspecific relationships, productivity**
Resource security	Rapid genetic adaptation to climate change in timber species	Increased herbivory on crops and timber by pests	Overall distribution shifts in marine and freshwater fisheries	Decline in plant-pollinator networks and pollination services
	Decreased crop yields in hot climates and increases in cool climates	Decreased genetic diversity and altered flowering time in wild cereals and novel crop varieties	Reduced range size or changes in pollinator abundance	Novel pests and invasive species
	Increased weed-crop competition and parasite-livestock interactions	Reduced fruit yields from fewer winter chill events		
	Decreased yield in fisheries from reduced body size	Reduced productivity in commercial fisheries		
Human health	Decline in reef calcifiers threatens coastal communities; loss of protection from storm surges and loss of food/protein sources	Increased costs and risk to subsistence communities from loss of sea ice and permafrost	Expanding and/or new distributions of disease vectors	Increased human-wildlife conflicts
	Rapid adaptation of disease vectors to new climatic conditions		Redistribution of arable land	Novel disease vectors

people, with a reduction in timber supplies and carbon sequestration, and changes in water quality and watershed volume (*161*–*163*). Several native insect species from North America, with no prior records of severe infestation, have recently emerged as severe pathogens of forest resources because of changes in population dynamics. These include the Aspen leaf miner (*Phyllocnistis populiella*), the leafblotch miner (*Micrurapteryx salicifoliella*), and the Janet's looper (*Nepytia janetae*), which have decimated millions of hectares of aspen, willows, and spruce-fir forests since the early 1990s (*164*). Known pests such as mountain and southern pine beetles (*Dendroctonus frontalis* and *D. ponderosae*, respectively) and spruce beetles (*D. rufipennis*) have recently expanded their distribution and infestation intensity on commercially important pine and spruce trees (*161*, *164*). These outbreaks may increase in the future because hundreds of plant pest and pathogen species have shifted their distributions 2 to 3.5 km year^{-1} poleward since the 1960s (*165*).

An emerging threat to human health under climate change is vector-borne disease (*166*). Vectors that have shifted their ranges and abundance can be found in marine, freshwater, and terrestrial systems. For example, in marine systems, unprecedented warming in the Baltic Sea led to emergence of *Vibrio* infections in Northern Europe (*167*, *168*), a geographic locality that had limited prior occurrence of this waterborne bacterial pathogen. Mosquitoes (e.g., *Aedes japonicus, A. aegypti, A. albopictus*) are extending their distribution into areas that are much warmer than their original habitats. As a result of ecological adaptation, mosquitos have become more competent vectors for spreading diseases such as chikungunya, dengue, and possibly the emerging Zika virus (*169*). Last, in terrestrial systems Levi *et al.* found that the nymph stage of the Lyme disease–carrying blacklegged tick (*Ixodes scapularis*) exhibited an overall advancement in nymph and larvae phenology since 1994, shifting the timing of greatest risk for pathogen transfer to humans to earlier in the year (*170*).

Losing intact ecosystems and their function

Changes in ecological processes might compromise the functionality of ecosystems. This is an important consideration because healthy systems (both terrestrial and marine) sequester substantial amounts of carbon (*171*), regulate local climate regimes (*172*), and reduce risks associated with climate-related hazards such as floods, sea-level rise, and cyclones (*173*). In island and coastal communities, coral reefs can reduce wave energy by an average of 97% (*174*), and coastal ecosystems such as mangroves and tidal marshes buffer storms (*175*), while on land intact native forests are important in reducing the frequency and severity of floods (*176*). In many cases, maintaining functioning systems offers more sustainable, cost-effective, and ecologically sound alternatives than conventional engineering solutions (*16*).

Science and action in a warmer world

The United Nations Framework Convention on Climate Change (UNFCCC) and the recent COP21 agreement in Paris presently offer the best opportunity for decisive action to reduce the current trajectory of climate change. This latter agreement set global warming targets of 1.5 to 2°C above preindustrial levels in order to avoid "dangerous climate change," yet the current 1°C average increase has already had broad and worrying impacts on natural systems, with accumulating consequences for people (Table 1). Minimizing the impacts of climate change on core ecological processes must now be a key policy priority for all nations, given the adoption of the UN Sustainable Development Goals aiming to increase human well-being. This will require continued funding of basic science focused on understanding how ecological processes are interacting with climate change, and of programs aimed at supporting ecosystem-based adaptations that enhance natural defences against climate hazards for people and nature and ensure ongoing provision of natural goods and services (*177*).

We must also recognize the role that intact natural ecosystems, particularly large areas, play in overcoming the challenges that climate change presents, not only as important repositories for carbon but also because of their ability to buffer and regulate local climate regimes and help human populations adapt to climate change (*16*, *173*). These systems are also critical for maintaining global biodiversity because the connectivity provided by large, contiguous areas spanning environmental gradients—such as altitude, depth, or salinity—will maximize the potential for gene flow and genetic adaptation while also allowing species to track shifting climate spatially (*178*).

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The overriding priority of the UNFCCC is to set in motion a sustained global reduction in greenhouse gas emissions. This must be achieved alongside an improvement in our understanding of key ecological processes that form the foundation of biological and human systems, and in tandem with efforts to conserve the natural habitats in which such ecological processes operate.

It is now up to national governments to make good on the promises they made in Paris through regular tightening of emission targets, and also to recognize the importance of healthy ecosystems in times of unprecedented change (*179*). Time is running out for a globally synchronized response to climate change that integrates adequate protection of biodiversity and ecosystem services.

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SUPPLEMENTARY MATERIALS

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Supplementary Text
Fig. S1
Table S1
References (*192*–*310*)

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The broad footprint of climate change from genes to biomes to people

Brett R. Scheffers, Luc De Meester, Tom C. L. Bridge, Ary A. Hoffmann, John M. Pandolfi, Richard T. Corlett, Stuart H. M. Butchart, Paul Pearce-Kelly, Kit M. Kovacs, David Dudgeon, Michela Pacifici, Carlo Rondinini, Wendy B. Foden, Tara G. Martin, Camilo Mora, David Bickford and James E. M. Watson

(November 10, 2016)
Science **354** (6313), . [doi: 10.1126/science.aaf7671]

Editor's Summary

Accumulating impacts

Anthropogenic climate change is now in full swing, our global average temperature already having increased by 1°C from preindustrial levels. Many studies have documented individual impacts of the changing climate that are particular to species or regions, but individual impacts are accumulating and being amplified more broadly. Scheffers *et al.* review the set of impacts that have been observed across genes, species, and ecosystems to reveal a world already undergoing substantial change. Understanding the causes, consequences, and potential mitigation of these changes will be essential as we move forward into a warming world.

Science, this issue p. 10.1126/science.aaf7671

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2019

Impact of Wildlife-Vehicle Conflict on California Drivers and Animals

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8/1/2019

Impact of Wildlife-Vehicle Conflict on California Drivers and Animals

Using observations of reported traffic incidents and carcasses the Road Ecology Center has estimated the **total annual cost** of reported (large) wildlife-vehicle collisions for 2018 in California to be **at least $232 million** and the cost to society over the last 4 years to be **>$1 billion**. The cost is calculated using California Highway Patrol (CHP) reports of crashes with wildlife and US Department of Transportation equivalent values for different types of crashes (e.g., property damage vs. major injury). When including accidents that are claimed to insurance companies but un-reported to police, the estimated cost could be as high as $500 million/year (estimated for 2017). This report provides an overview of wildlife-vehicle conflict (WVC) in general, including collisions with small and large animals and accidents resulting from drivers swerving to avoid colliding with an animal. We highlight WVC hotspots on California highways between 2015 and 2018, inclusive, based on a combination of >26,000 traffic incidents involving wildlife that were recorded by the CHP and >42,000 carcass observations reported to the California Roadkill Observation System (CROS, http://wildlifecrossing.net/california) between 2009 and 2018, inclusive. This report includes **maps of WVC hotspots**, discusses impacts to wildlife and people from WVC, addresses whether mapped "wildlife corridors & linkages" help explain where WVC occurs, and presents new tools to help organizations, state agencies and individuals collect and use this information. Projects to **reduce WVC** can be the most effective of any safety project, with effectiveness often >90%.

For the first time, we **statistically compared the location of WVC** with various computer **predictions of wildlife corridors/linkages** in California. In general, we found no significant correlation between the locations of WVC and these linkages. This may not be surprising because wildlife generally do not follow narrow or predictable paths through their habitat. California agencies have been looking for predictability in wildlife movement to help reduce the **cost of mitigation**. Fortunately, there are ample data available on wildlife movement from WVC databases and studies involving GPS-collared wildlife to identify mitigation locations.

Data Sharing/Collaboration: We receive requests from highway planners, fish and wildlife scientists, academic faculty, students, and non-governmental organizations on a weekly basis. We can typically meet data requests within CA for specific highways, counties, etc., but please keep in mind that this is an unfunded effort of the Road Ecology Center, so give us a few days.

We have developed 2 globally-unique web-tools to collect and to visualize WVC incidents in CA: 1) A re-vamped California Roadkill Observation System to support "one-click" reporting (https://wildlifecrossing.net/california) –take a picture of a roadkilled animal with your smartphone and upload with one click (which automatically creates a database record); and 2) A WVC hotspot tool that shows hotspot areas throughout CA and has a real-time display of WVC events, https://roadecology.ucdavis.edu/hotspots.

Cover photo credit. Female mountain lion killed by a vehicle on a county road near San Luis Obispo, 8/1/2019. Photo taken and provided by Kelly Kephart, wildlife biologist with PGE.

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UC Davis Road Ecology Center: Sixth Annual Special Report on the Impact of Wildlife-Vehicle Conflict (WVC) on California Drivers and Animals

Top 4 Talking Points

1) **We can help the state systematically collect and share data.** The data assembled here from the CHP were not collected with the purpose of studying WVC, the volunteer data were. California agencies should collect and share data about WVC to help inform decision-making about this important conservation and safety problem. Using our extensive datasets and decade of experience collecting and analyzing WVC data, we are open to partnering with Caltrans, California Department of Fish and Wildlife and others to accomplish this.

2) **Legislated support is needed for highway/road projects that that have net WVC benefit.** In the past, WVC-reduction projects (like wildlife crossings) were only occasionally considered and as part of partial mitigation for transportation impacts. There is currently a state program to allow "advance mitigation credit" for WVC-reduction projects where impacts are reduced now, but balanced by doing more harm later. Transportation agency planners and biologists are increasingly discussing wildlife-crossing structures and other projects as stand-alone safety and sustainability projects, providing a net benefit to drivers and wildlife, without the need for the projects to mitigate for further harm later.

3) **Build WVC-reduction projects at known hotspots.** Very few driver safety projects have the overall effectiveness that WVC reduction projects do. There are hundreds of places on state highways and major roads where WVC is a priority. Unfortunately, we can't use "wildlife corridor/linkage" computer models to tell us where these places are. Fortunately, we have the WVC and other wildlife movement data to help show us where to act.

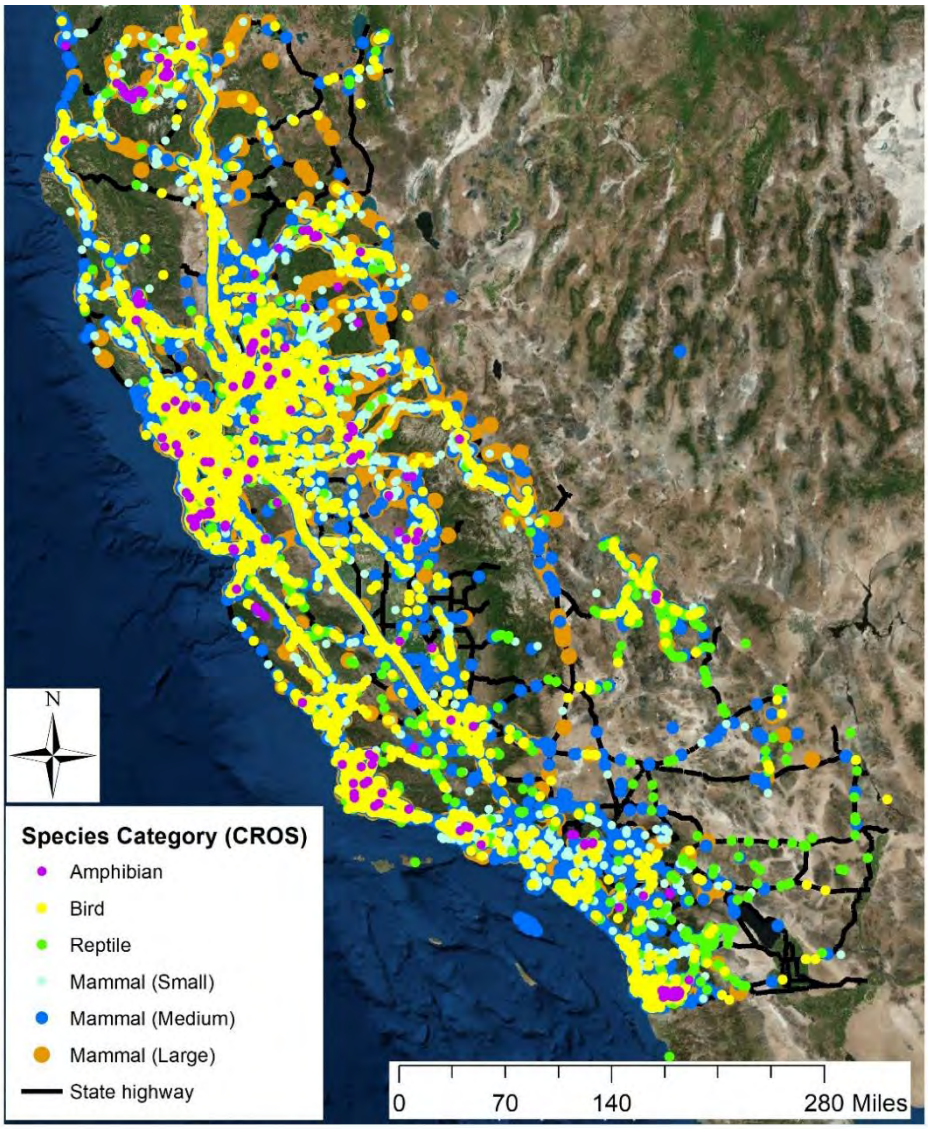
4) **Allocate sufficient funds to build needed WVC-reduction projects.** With the passage of SB1, California voters provided state legislators and transportation agencies with an increase in funding (>$5 billion/year!) to protect driver safety and the environment. We know that doing nothing, or very little to reduce WVC is costly – to drivers and to the environment (~$300 million per year). There are myriad excuses for why "nothing can be done", lack of funding is not one of them.

Introduction to Study

Using California state data on traffic incidents and roadkill observations, the Road Ecology Center has mapped stretches of 15,160 miles of California highways that are likely to be continuing hotspots for wildlife-vehicle conflicts (WVC). Animals entering roadways are often killed and pose a hazard to drivers, who may collide with the animal, or try to avoid the animal

suffering vehicle damage, injury, and even death. Wildlife populations may suffer significant losses from highways with high rates of WVC, which may cause ripple effects into surrounding ecosystems up and down the food chain. In addition, animals are injured during collisions, which is damaging to the animal and traumatic and deadly to drivers.

By identifying stretches of highway where WVC are more likely to occur, the Road Ecology Center is assisting Caltrans and other responsible entities in developing mitigation to protect drivers and wildlife populations. Measures with proven effectiveness include 1) building fencing and over/under-passes along priority highways to allow the safe passage of wildlife across highways and 2) reducing speed limits in protected wildlife habitat. Using CHP data, we have found records of ~7,000 reported accidents per year on California highways involving deer and other large wildlife. We estimate that there are another few thousand with horses, cows, sheep and goats. Data from CROS allow state and local agencies to prioritize stretches of highway for mitigation of conflicts with particular species or groups (e.g., Ha and Shilling, 2017).



Statewide Carcass Observations

Members of the public, agencies, and others made >60,000 observations of animal carcasses on local roads and state highways (Figure 1). These are not the total roadkill that occurred, just the ones that expert observers saw and reported to CROS.

Figure 1. Carcass observations for amphibians, reptiles, birds, and mammals.

Statewide Highway WVC Incidents

There were >2.5 million traffic incidents (of all types) across California reported to the CHP during 2015-2018. Of these, about half were collisions and 26,547 involved wildlife, including 1) reports of animals standing next to, standing in, or running across lanes (potential incidents); 2) collisions with large animals; and 3) swerving to avoid collisions, resulting in a crash (Figure 2).

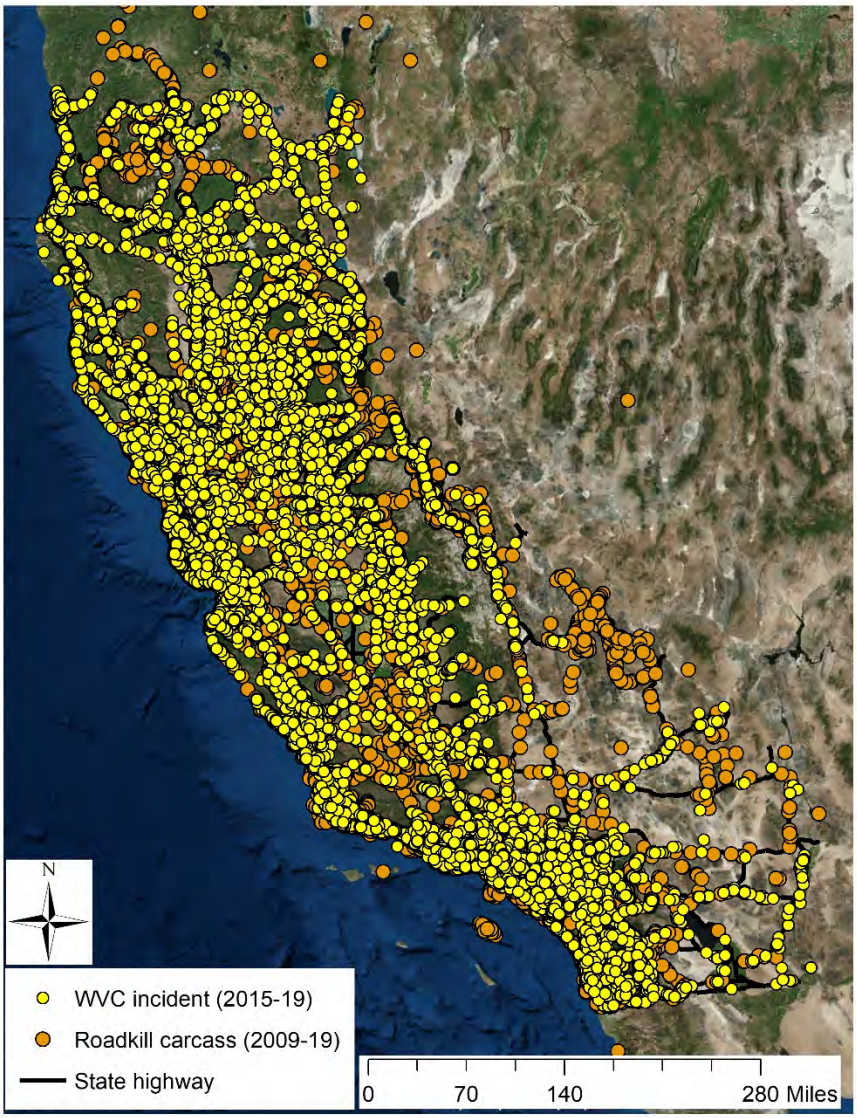


Figure 2. Wildlife-vehicle conflict incidents on highways (2015-2018) and roadkilled animal observations on all roads (2009-2018).

Although WVC occurs on every major road and highway in California, the highest densities were reported in the San Francisco Bay Area (Caltrans District 4), Sierra Nevada Foothills (Caltrans Districts 3 & 10), North Coast (Caltrans District 1), and parts of the Central/South Coast (Caltrans Districts 5, 7, 11 & 12). These high-density areas are most likely where traffic volumes and wildlife populations are greatest, leading to more conflict. The map below shows the high-density clusters of collisions with large wildlife in California (Figure 3). There were 1,584 miles of state highway where ≥4 large animals were involved per mile per year in WVC incidents and 3,138 miles where ≥2 large animals were involved in WVC per year.

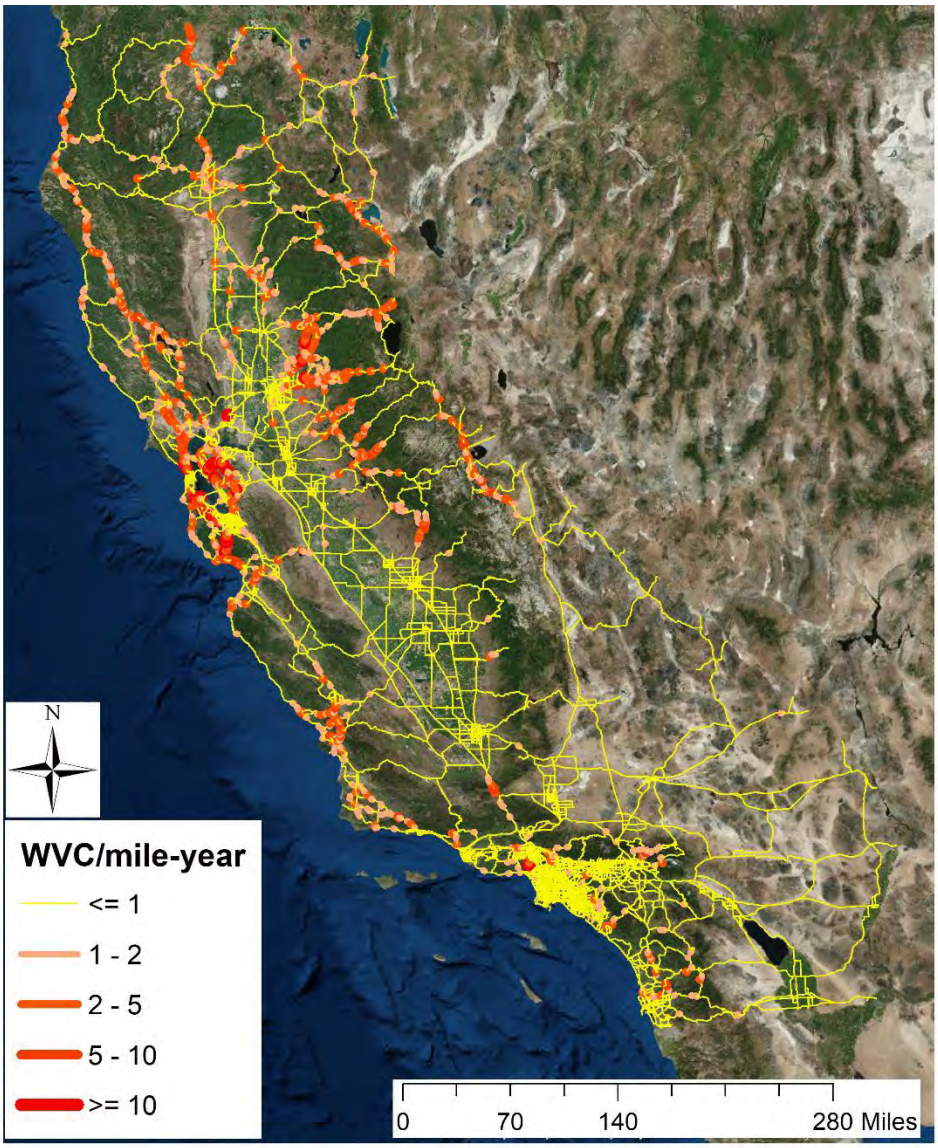


Figure 3. High-density WVC hotspots for 2015 to 2018. Hotspots can vary in length from 1 to several miles. Density is expressed as # incidents per mile per year. Greater than 2 WVC/mile-year is a recognized cost-benefit standard for transportation agencies to start planning for impact mitigation.

Impacts to Specific Wildlife: Mountain Lions

Like most species at the top of the food web, mountain lions are especially vulnerable to WVC because they move around a lot and cross roads and highways. Mountain lions are important ecologically because they are the only large, widespread predator in most California ecosystems. They are also important socially, with great interest in their well-being in Southern California and Bay Area urban regions.

A critical problem for mountain lions in California is that there is no formal program, system or requirement to report when they are killed on roads, which happens frequently. As such, we only know the minimum killed each year on roads, when they are reported to CROS, and have

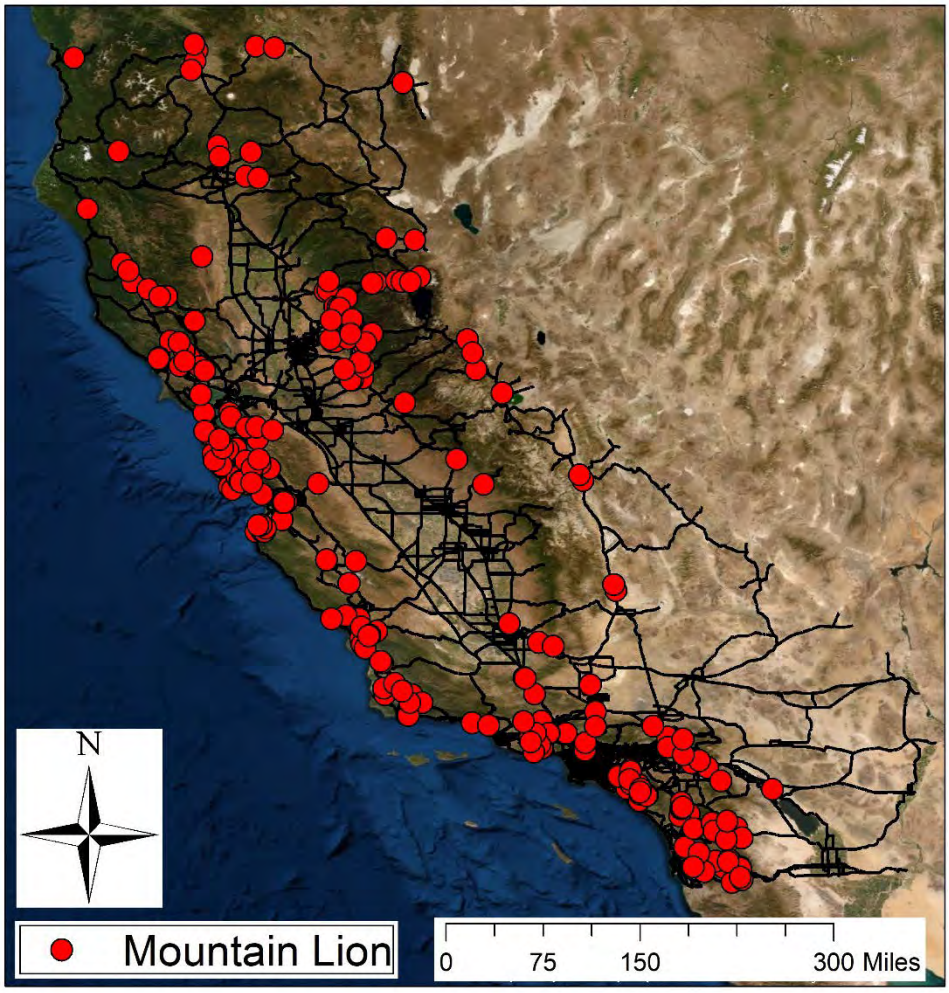


Figure 4. Mountain lions reported killed on roads, or involved in traffic incidents by the California Roadkill observation System, CDFW, CHP, or Winston Vickers and other biologists in Southern California (Vickers et al. 2015, and Vickers unpublished data).

no way of knowing the actual WVC impact to this important and charismatic species. Between 2015 and 2018, inclusive, 299 mountain lions killed on roads (~75/year) were reported by a combination of CROS volunteers, CHP, CDFW, and biologists in Southern California (Figure 4). The cover photograph for this report highlights the problem. It was taken by a wildlife biologist who happened upon the dead animal as part of her work. She reported the finding informally to colleagues in the California Department of Fish and Wildlife, who similarly informally reported the observation to us. This story highlights the need in California for a systematic and legislated approach to reporting wildlife mortality on roadways in order that we can understand the distribution, impacts and risk to wildlife populations and species.

Real-Time, Automated Web-Map of WVC

To provide more current information for California agencies and the driving public, we make our WVC data available in real time, the first tool of its kind in the world. You can see recent WVC events and WVC hotspots here: https://roadecology.ucdavis.edu/hotspots/map. The map was developed with support from the National Center for Sustainable Transportation and can support automatic ingestion by web-systems or driver-assistance programs.

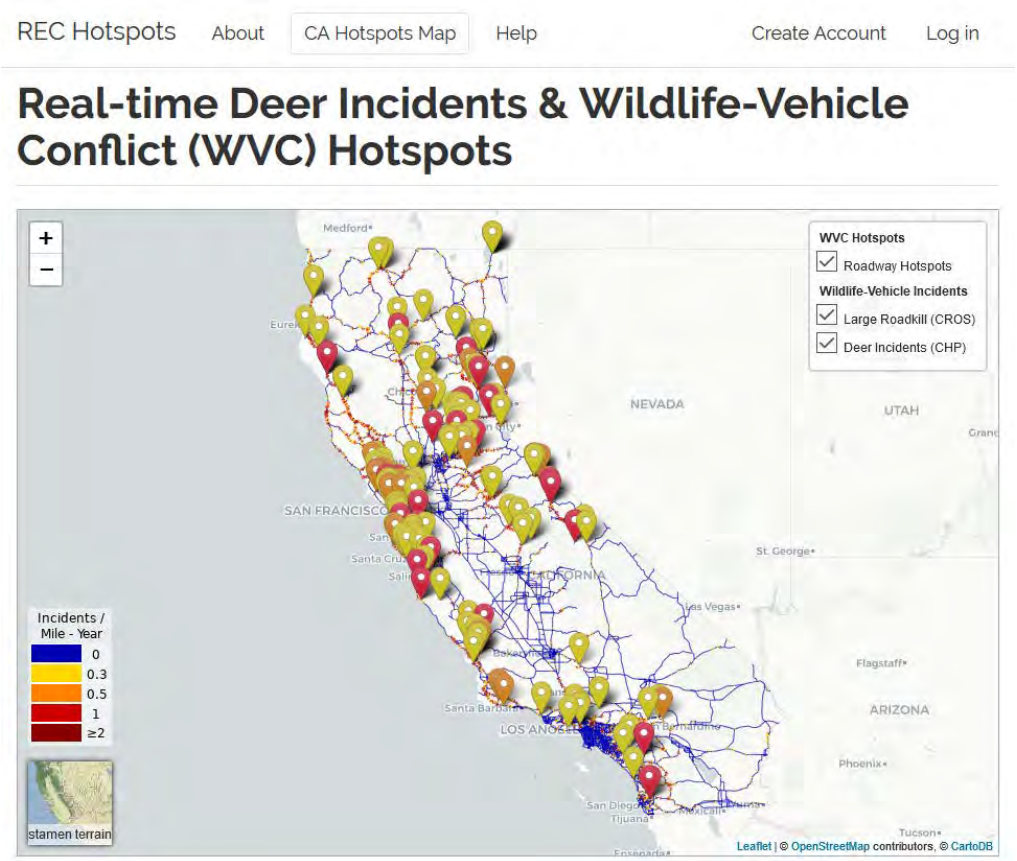


Figure 4. Locations of recent (7/22/2019) WVC incidents and roadkill carcasses (points) overlaying WVC hotspots, defined by annual WVC density (lines). Map available at: https://roadecology.ucdavis.edu/hotspots/map.

Impacts within Assembly & Senate Districts

The ultimate authority for legislating reporting and mitigating impacts to driver and wildlife safety from WVC lies with the state Assembly and Senate. They have the ability to require state agencies to report WVC (e.g., crashes and carcasses), to require analyses (such as the one you are reading), to mitigate impacts at an adequate rate, and to spend available funds (e.g., from the SB1 Fuel Tax). We calculated the total number of WVC with large mammals within Assembly and Senate Districts for the 2015-2018 time period. The total number of WVC varied between a low of 1 for Assembly District 66 (Palos Verde) to 6,466 for Senate District 1 (rural NE California). Because the Districts vary widely in size, we also calculated the density of WVC (#/square-mile). This calculation revealed that the highest-densities of WVC are in Assembly and Senate Districts around the edges of the urban regions of the Bay Area, Sacramento and Southern California (Figure 4). The 10 Assembly Districts with the highest WVC rates were politically-mixed, with 6 represented by Democrats and 4 by Republicans. Our calculations showed that WVC as a conservation and safety problem is not limited to one political party or type of region (rural vs. urban).

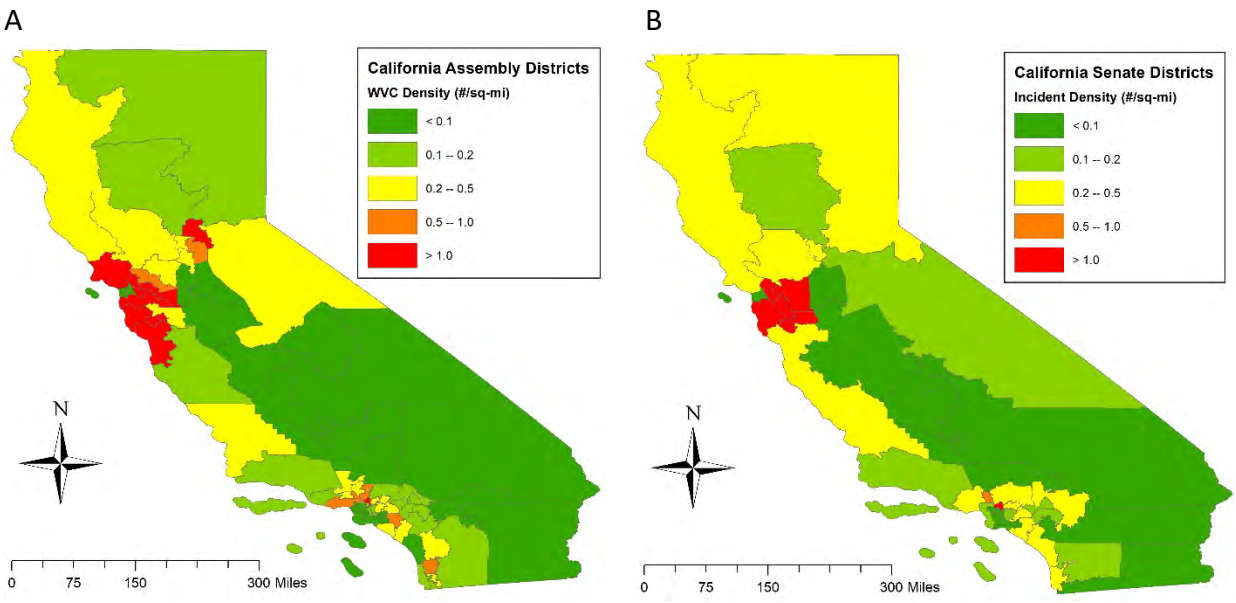


Figure 4. Density of WVC by (A) state Assembly and (B) state Senate districts for 2015-2018, inclusive.

Cost to Society

Any type of collision involves risk and actual damage to drivers and their vehicles. It is no different for collisions involving wildlife, whether the collision is with the animal, or with another object after the driver swerved to avoid hitting the animal. As in previous years, we used cost coefficients from the US Department of Transportation (Harmon et al., 2018, Crash Costs for Highway Safety Analysis. FHWA-SA-17-071) to estimate the total cost to society from collisions involving wildlife. These costs include the expense of vehicle damage, injury treatment and recovery, emergency response, lost work, loss of the wildlife and other costs. We found that the total cost was lower in 2018 than in previous years: ~$232 million in 2018 vs. $307 million in 2017 (Table 1). This was in part due to a lower estimated property damage cost to vehicles and a lower estimated number of fatal collisions, which is only estimated because California does not release these statistics. The total number of collisions did not change very much from year to year.

Table 1. Impact to drivers and estimated cost to society of reported collisions with animals on CA highways and certain major roads in 2018. Equivalent costs for accident types were obtained from Harmon et al. (2018).

Type of Accident	**Coefficient (cost as $/event)**	**Number (2018)**	**Cost (2018)**
Lost animal value (all animals)*			$37,300,000
Collision/Swerve (property damage)	$11,900	6,412	$76,302,800
Injury (minor)	$125,600	271	$34,037,600
Injury (major)	$655,000	43	$28,165,000
Fatality	$11,295,400	5**	$56,477,000
Total			**$232,282,400**

* This value includes both reported and estimated un-reported carcasses, with an estimated 5 times as many total as reported. Others have reported under-reporting rates for carcasses from collisions of 5-10 fold.

** This is an estimate as CA does not release annual rates of fatal collisions with wildlife

Another way to measure costs is according to a California jurisdiction. We totaled all types of injury and non-injury accidents within California Assembly Districts. Except for District 10 (Marin County), the top-5 highest costs were associated with rural Districts (1, 5, 2, 35). District 10 was also among the top-10 districts with the highest number of total WVC and density of WVC, primarily because of US 101. Besides Assembly District 10, other Districts with high total number of WVC, density, and cost were District 16 (San Ramon, I-680, I-580, SR 24) and District 24 (Los Altos, I-280). The total cost over a 4-year period (2015-2018) for the top 10 Assembly Districts was ~$445 million.

Table 2. Estimated number of WVC, injury accidents (from collisions with wildlife) and cost to society of reported WVC between 2015 and 2018, inclusive, for the Assembly Districts with the most WVC impact.

Assembly District	Total Collisions	Injury Accidents	Total Cost ($)
1	4969	226	$105,308,820
5	4395	202	$93,547,800
2	2804	141	$61,660,480
10	1555	60	$31,040,220
35	1505	86	$34,786,980
29	1493	48	$27,098,140
16	1102	36	$20,043,740
24	1039	66	$25,853,820
4	1018	57	$24,364,640
3	1016	51	$21,287,780
			$444,992,420

Corridors, Linkages and Roadkill

Wildlife naturally move around their habitat, meeting daily, seasonal, reproductive, migratory, dispersal, and climate adaptation needs. A common misconception, even among conservation planners, is that wildlife will naturally follow "corridors" or "linkages" when roaming around on landscapes. This idea is related to the hypothesis that most species occupy "patches" of habitat and these patches are connected by corridors/linkages. Except for certain ungulates (e.g., mule deer in certain areas) there is little evidence that most or all of the roughly 180 mammal species in California (or anywhere else) follow predictable paths across landscapes, or only occupy mapped patches of habitat.

We compared densities of roadkilled animals on state highways with different connectivity values in the California Department of Fish and Wildlife's Areas of Conservation Emphasis (ACE) and with the Essential Connectivity Areas in the California Essential Habitat Connectivity (EHC) project (Spencer et al., 2010). We tried all animals together and with different groupings (e.g., mammals). In all cases, we found no statistically significant relationship between location of roadkilled animals and linkage areas, or with connectivity values from ACE maps. Examples of the overlap between WVC/roadkill events and EHC linkage areas are shown in Figure 5. There were a few areas where concentrations of roadkill were associated with modeled linkages, which may indicate that these areas actually are important for wildlife movement. However, there were usually areas outside linkages that also had high concentrations of WVC/roadkill. The simplest explanation for these findings is that, in general, corridor and linkage maps don't predict where animals are primarily moving and should not be used for mitigation planning that leaves out areas where animal movement is also provably occurring.

The importance of this finding is that many people in transportation and conservation planning use these maps as if they were related to wildlife connectivity movement and use the term "data" to describe the maps. In reality they are not data, nor are they based on data for all (or most) wildlife movement. In urban and agricultural regions, the "linkages" were more likely to seem related to locations of WVC, which is probably because these are the only natural habitat areas remaining in these regions. For example, if a stream with a healthy riparian area passes through an urban/residential area, then there tended to be a greater likelihood of predicted connectivity and concentration of WVC. The solution to the problem that our findings highlight is that maps of wildlife connectivity must be based upon where wildlife occur and are moving for them to have utility in wildlife conservation planning. Including additional areas where wildlife may occur after protection and restoration could also be useful.

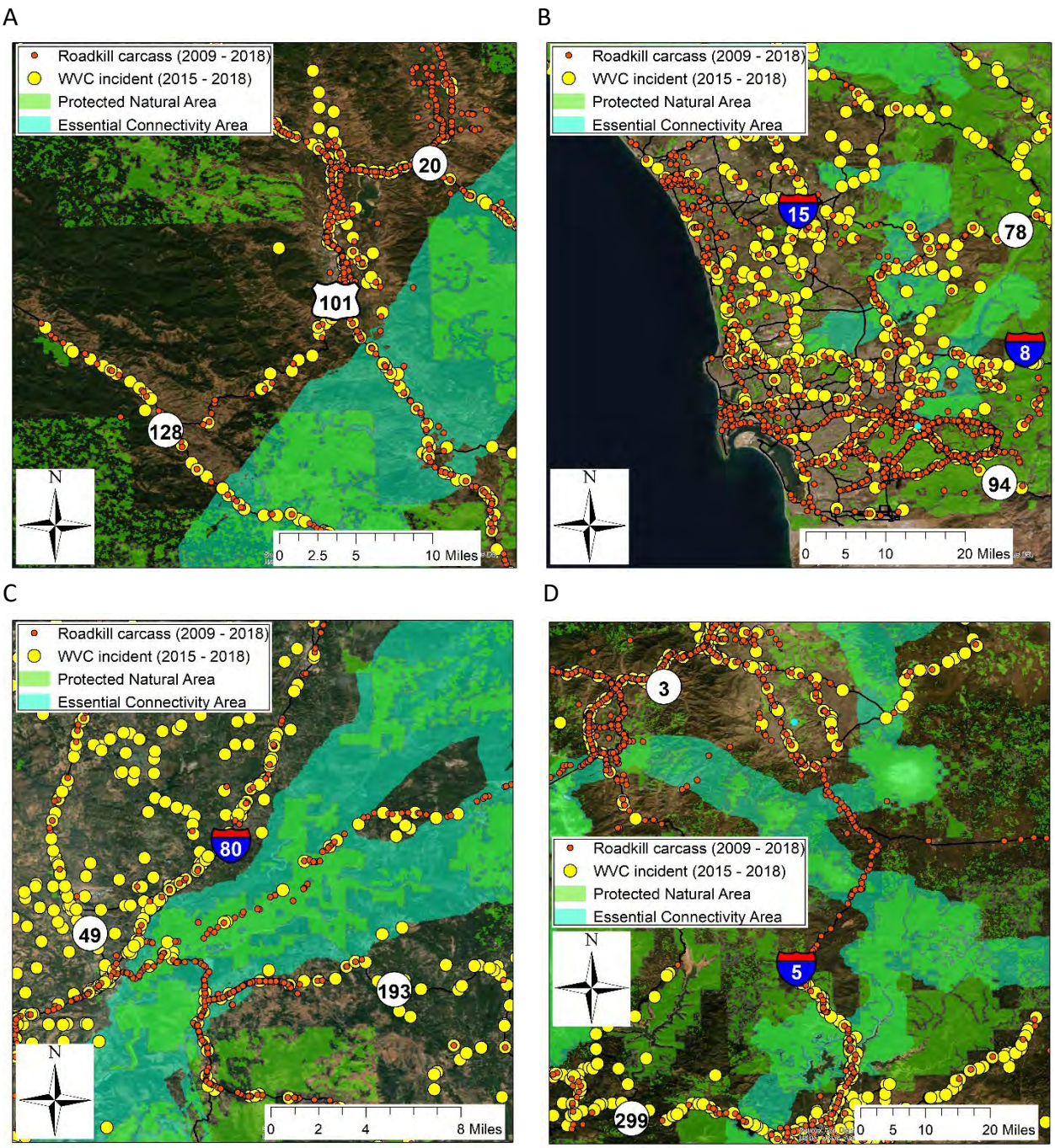


Figure 5. Comparison of WVC/roadkill incidents and maps of essential connectivity areas and natural areas from the California Essential Habitat Connectivity project (Spencer et al., 2010). A) North Bay Area, B) coastal San Diego County, C) American River canyon, and D) Mt Shasta area.

Summary

Monitoring wildlife movement and mortality is critical for improving wildlife connectivity and survival of wildlife species in the face of the combined threats they face, such as transportation systems, climate change, rodenticides, and habitat loss. We reported here on long-term,

successful methods for monitoring WVC in California, an annual (2018) analysis of locations and costs of WVC to wildlife and drivers and society. We provided key recommendations for ways to reduce WVC in California through support for a several-fold increase in mitigation projects with net benefit for wildlife and driver safety. Finally, we suggest that any WVC-reduction and wildlife connectivity mitigation be planned based on evidence-based connectivity design, not the current "linkage" models.

Acknowledgements

We appreciate the support from the National Center for Sustainable Transportation (using USDOT funding) and the Institute of Transportation Studies (CA SB1 funding) for development of the automated wildlife-vehicle conflict hotspot tool and one-click reporting tool California Roadkill Observation System (CROS, https://wildlifecrossing.net/california). This and previous reports and the analyses contained within would not have been possible without the concerted and coordinated efforts of hundreds of volunteer roadkill observers over the last 10 years who contribute to CROS. Through their endeavors, they have so far (7/2019) collected >60,000 observations of >430 species, representing one of the largest and most comprehensive wildlife monitoring programs in California and the US. Their accuracy rate for species identification is >97% and have high locational accuracy (median <±13 meters). For the scientific article describing CROS, see citation below (you can paste the "doi" value below into a browser and access the papers). The report also benefited from the efforts of many unknown law enforcement personnel who described traffic incidents in enough detail that we could use their observations to help plan for reduced wildlife-vehicle conflict. Finally, we have partnered with other similar systems around the world in the Globalroadkill.net project (http://globalroadkill.net).

Citation for CROS: Waetjen DP and Shilling FM (2017) Large Extent Volunteer Roadkill and Wildlife Observation Systems as Sources of Reliable Data. Frontiers in Ecology & Evolution 5:89. doi:10.3389/fevo.2017.00089

Additional CROS citation: Tiedeman, K., R.J. Hijmans, A. Mandel, D.P. Waetjen, F. Shilling (In Press) The quality and contribution of volunteer collected animal vehicle collision data in ecological research. Ecological Indicators. https://doi.org/10.1016/j.ecolind.2019.05.062

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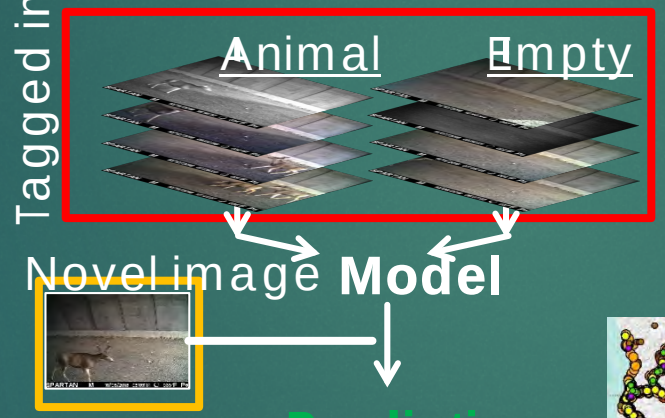
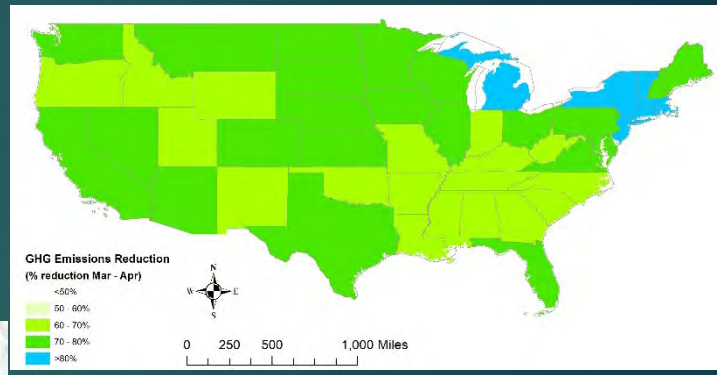
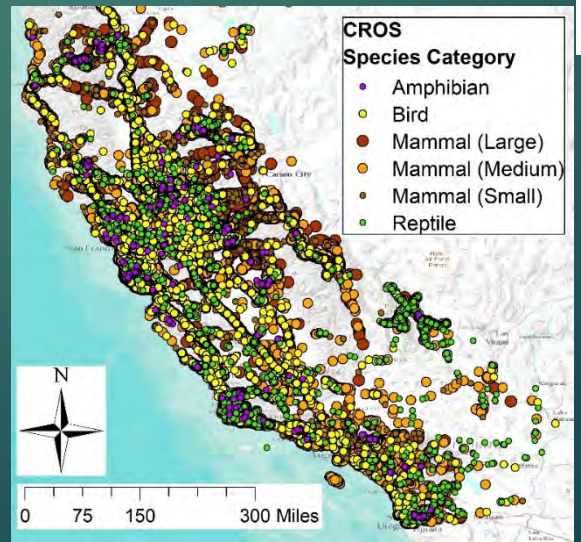
Wildlife Behavior in Response to Traffic Disturbance











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Wildlife Behavior in Response to Traffic Disturbance









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Acknowledgements

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Main Messages and Findings

1) Wildlife are variably sensitive to traffic disturbance, including noise and light from vehicles

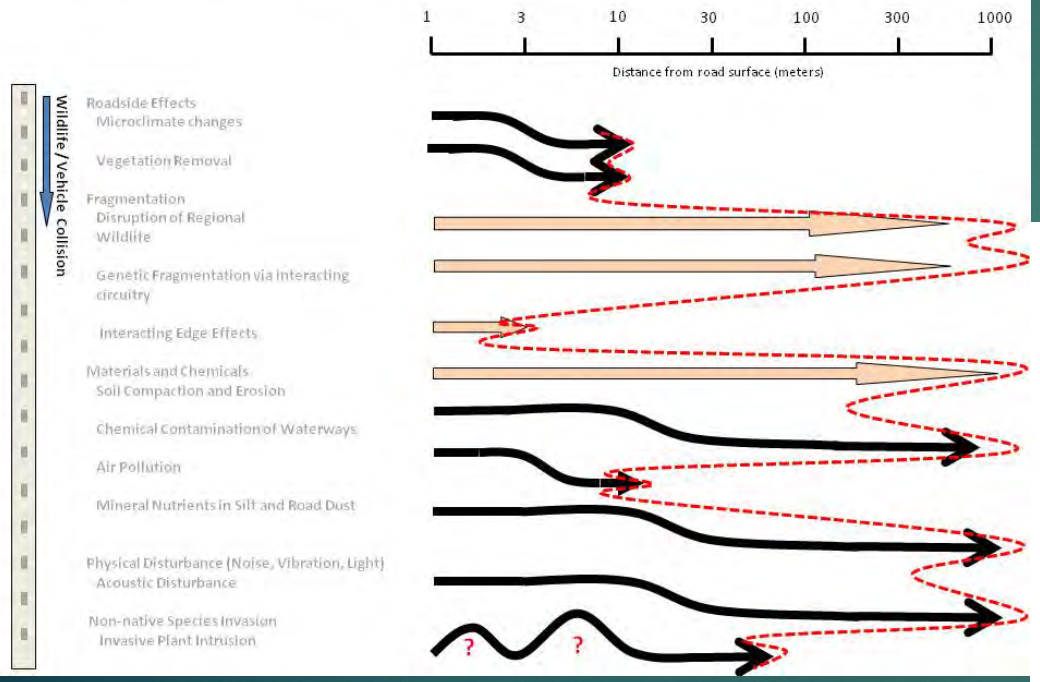
2) This sensitivity will cause different impacts on their distribution and use of crossing structures, which will have environmental impacts (e.g., on predator-prey interactions, juvenile dispersal, resilience to climate change, forage diversity, competitive species interactions, population genetics and recovery, etc.)

3) The mechanism for distribution/visits could be wildlife behavior in response to traffic

4) It is possible that designing the approaches to crossing structures could reduce impacts and improve wildlife use

Background

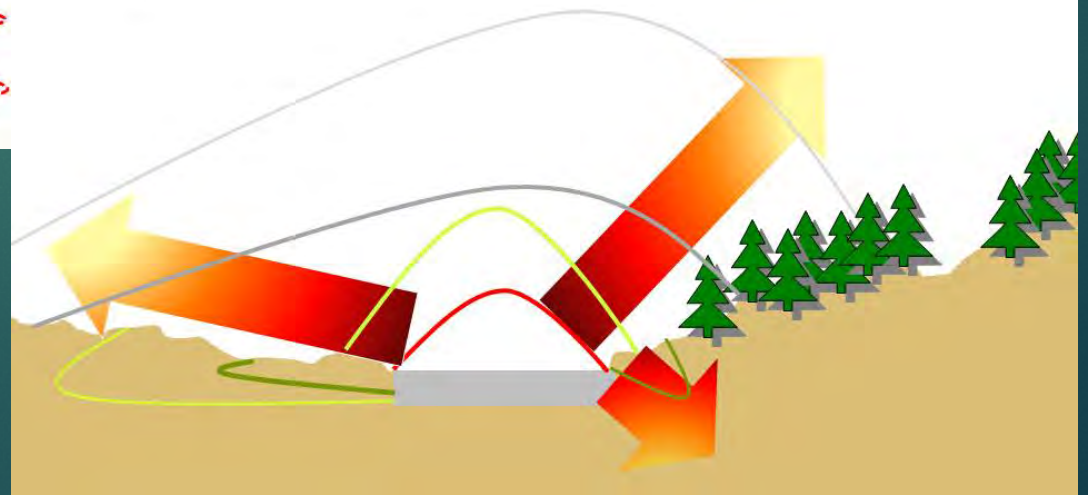
Road-Effect Zone – Geography





3-D Road Effect Zone

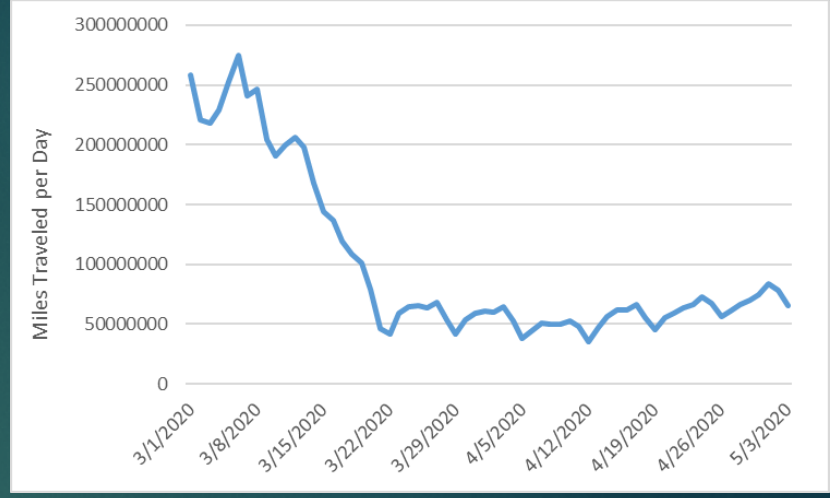
Effects from roads radiate along the surface, through the earth, and into the atmosphere. The extent and severity of radiation depends on the type of effect, the initial intensity of the impact, and the surrounding landscape.

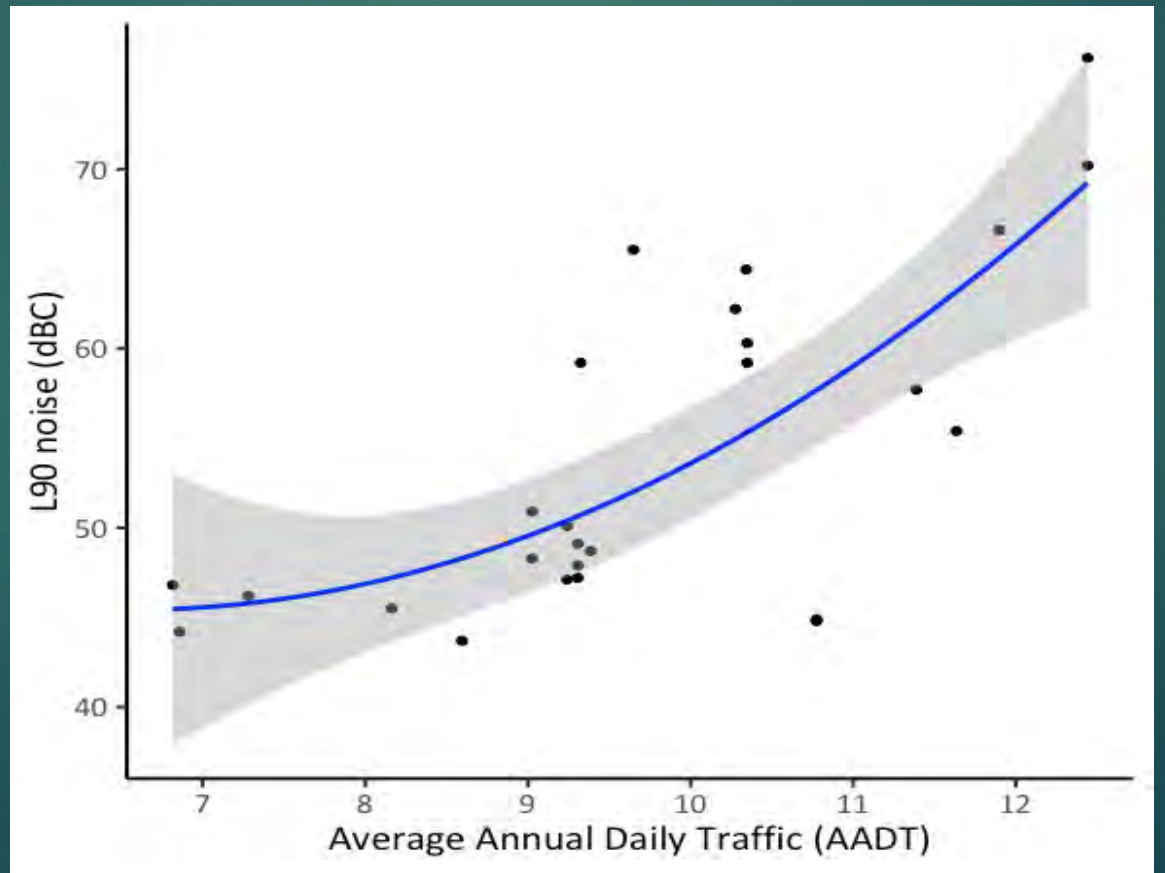


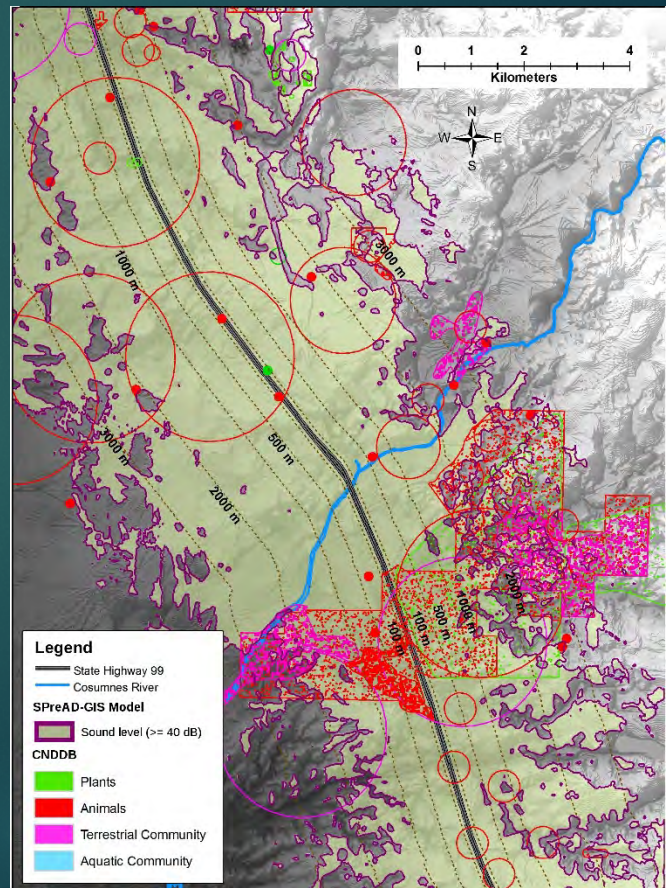
Background

Traffic is loud and variable

Noise can extend hundreds of meters beyond the road

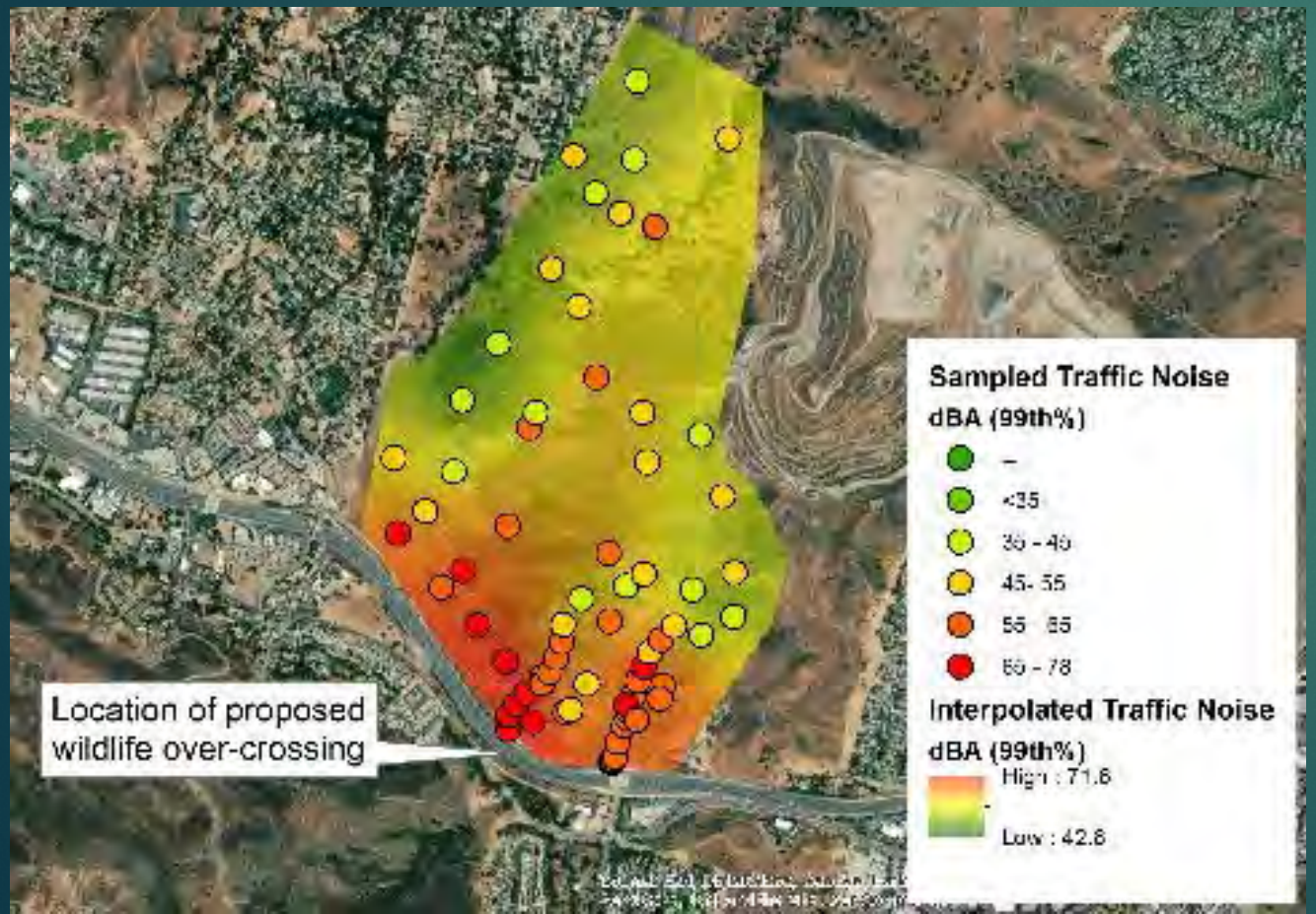


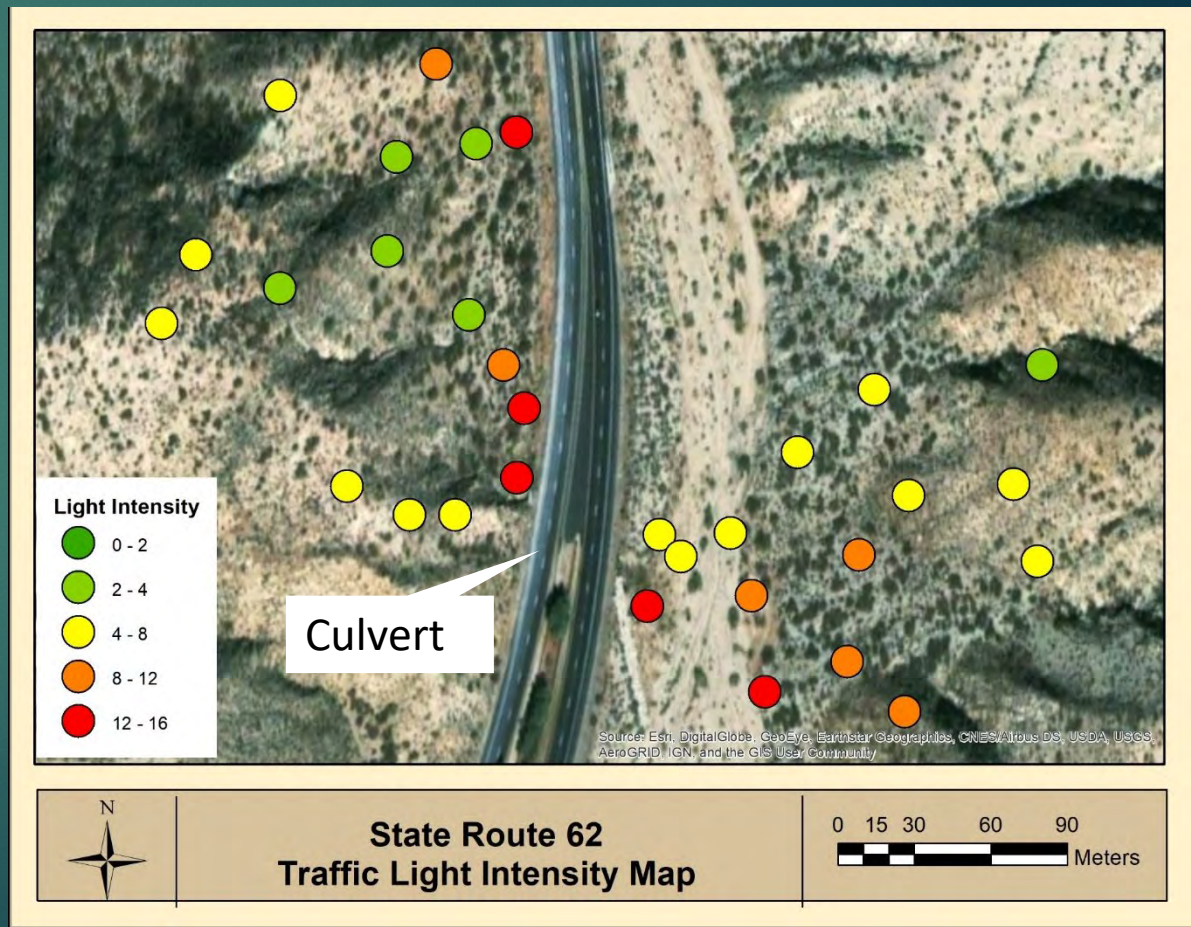




Traffic is loud (and bright)

Noise and light propagation across real landscapes is complex





Are underpasses effective with noise and light disturbance?



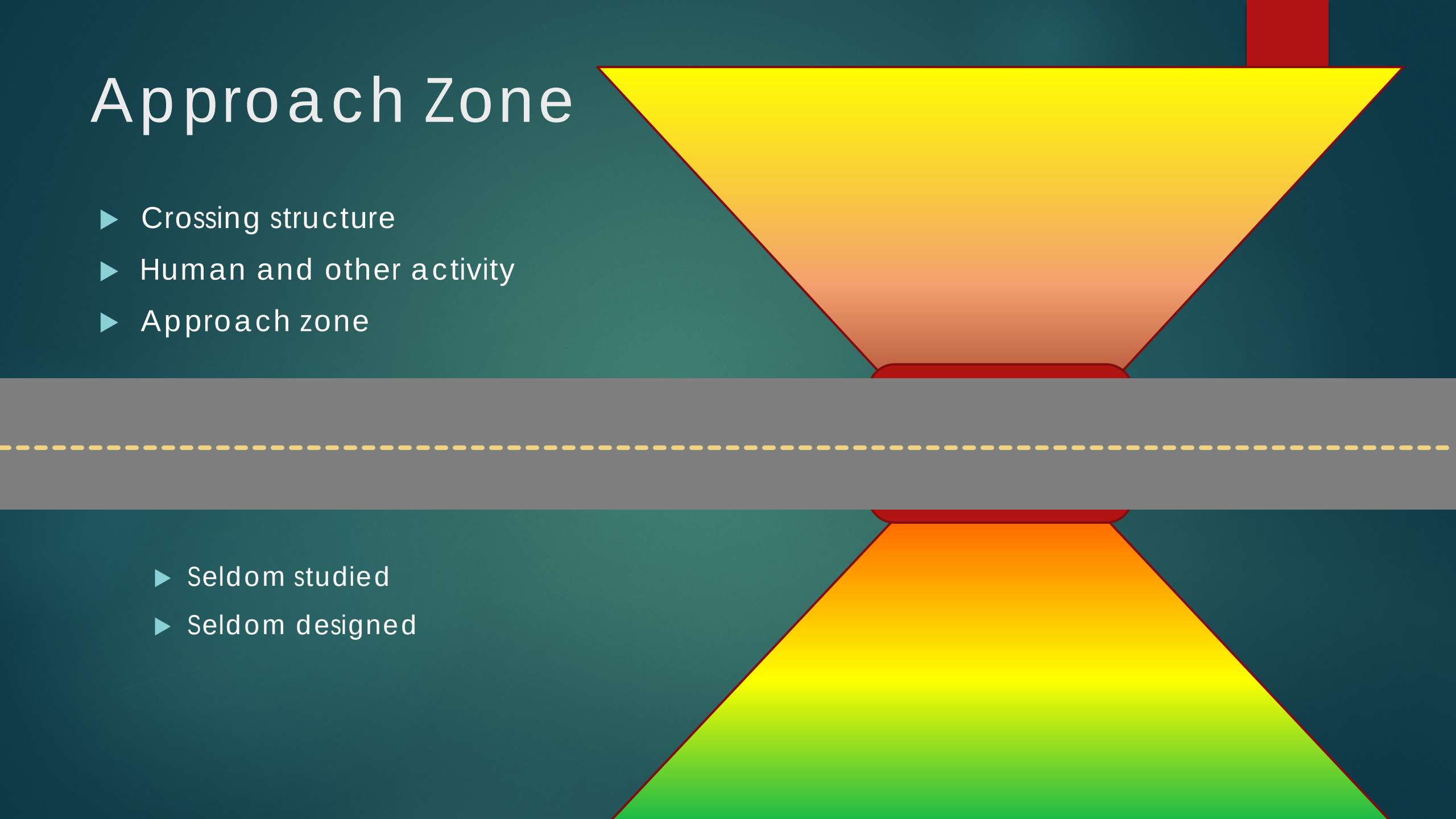






Approach Zone

- Crossing structure
- Human and other activity
- Approach zone



- Seldom studied
- Seldom designed

Workflow

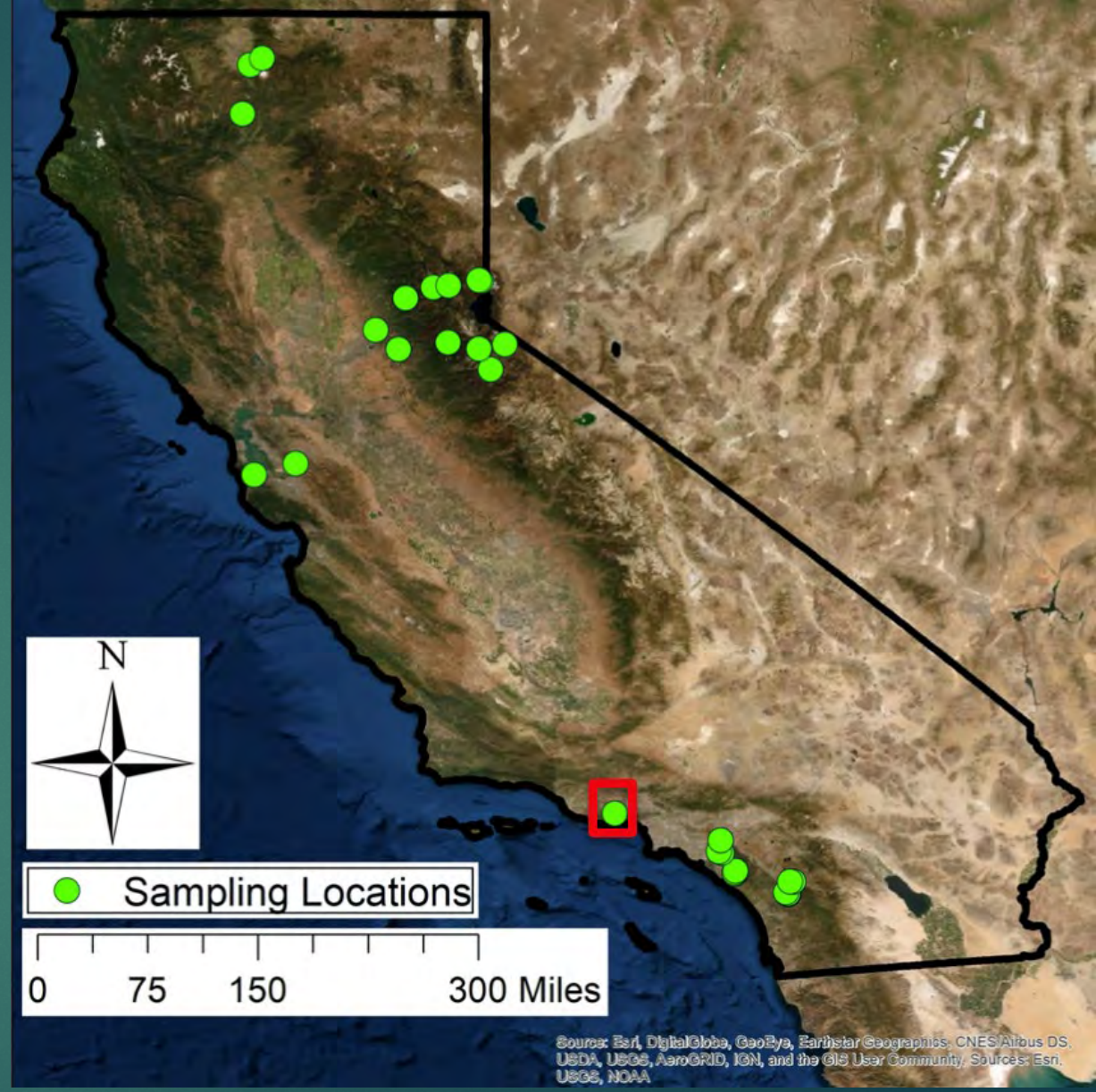
- Field work
- Data processing and management through CamWON (https://wildlifeobserver.net), including removing false positives, counting humans/vehicles, summarizing events/species, events/data etc.
- Wildlife behavior analysis with BORIS (http://www.boris.unito.it/)
- Statistical modeling to find best explanation for data
- Develop “wildlife-responsive design” elements and structures to increase likelihood of structure use

Field work

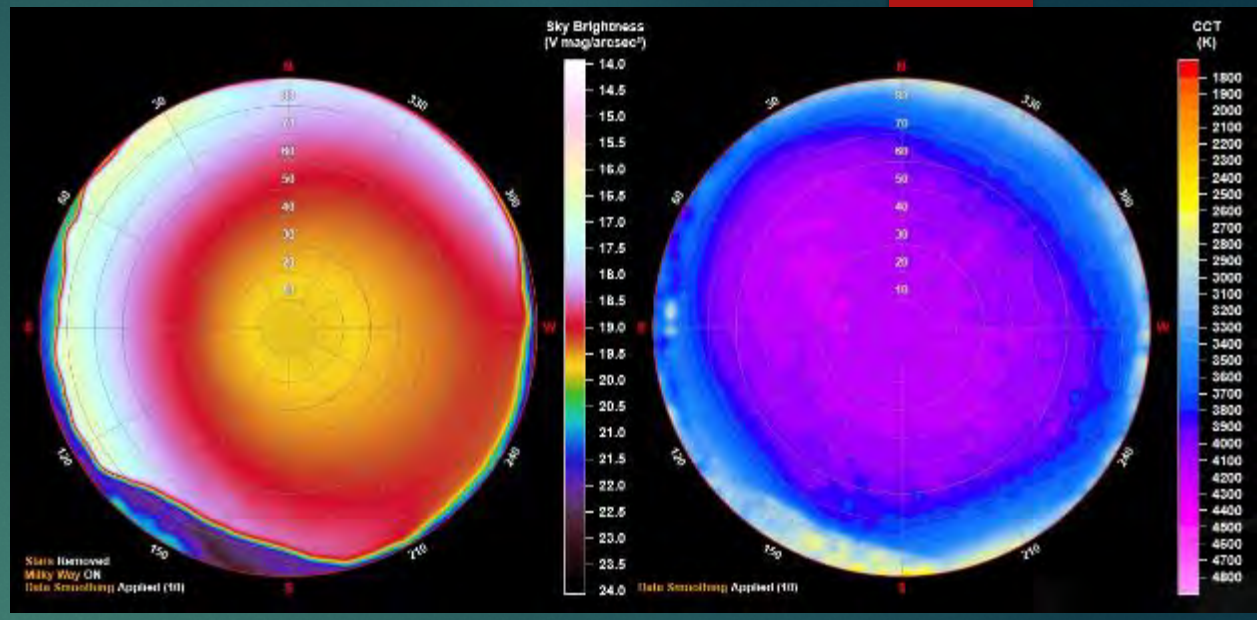
Camera trap, noise (dBA, dBC) & light measurements

- 26 sites in California
- Structures across 1 – 5 lane highways
- 3 years of field study (2016-2019)



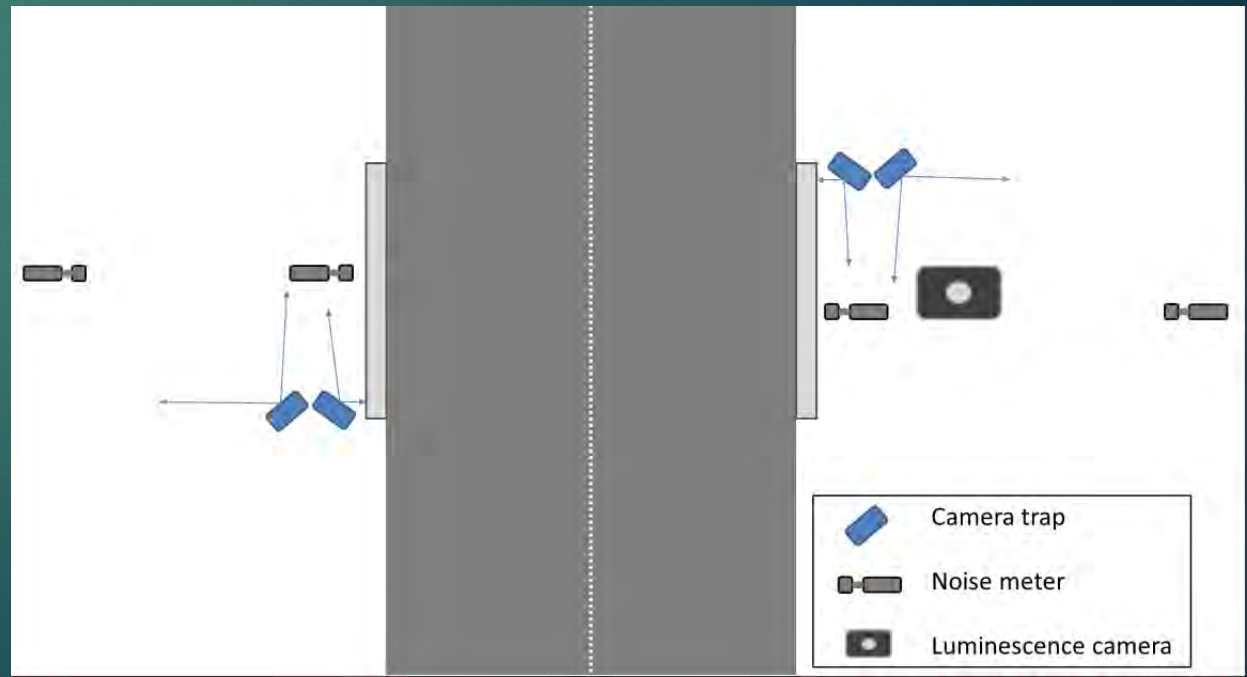


Light and noise









Analysis

Comparison of wildlife distribution in background areas and crossing structures

Analysis of animal activity relative to traffic disturbance, structural and approach zone attributes, human activity, time of day/night

9,360 trap nights

> 28,300 observations!

32 mammal species captured!









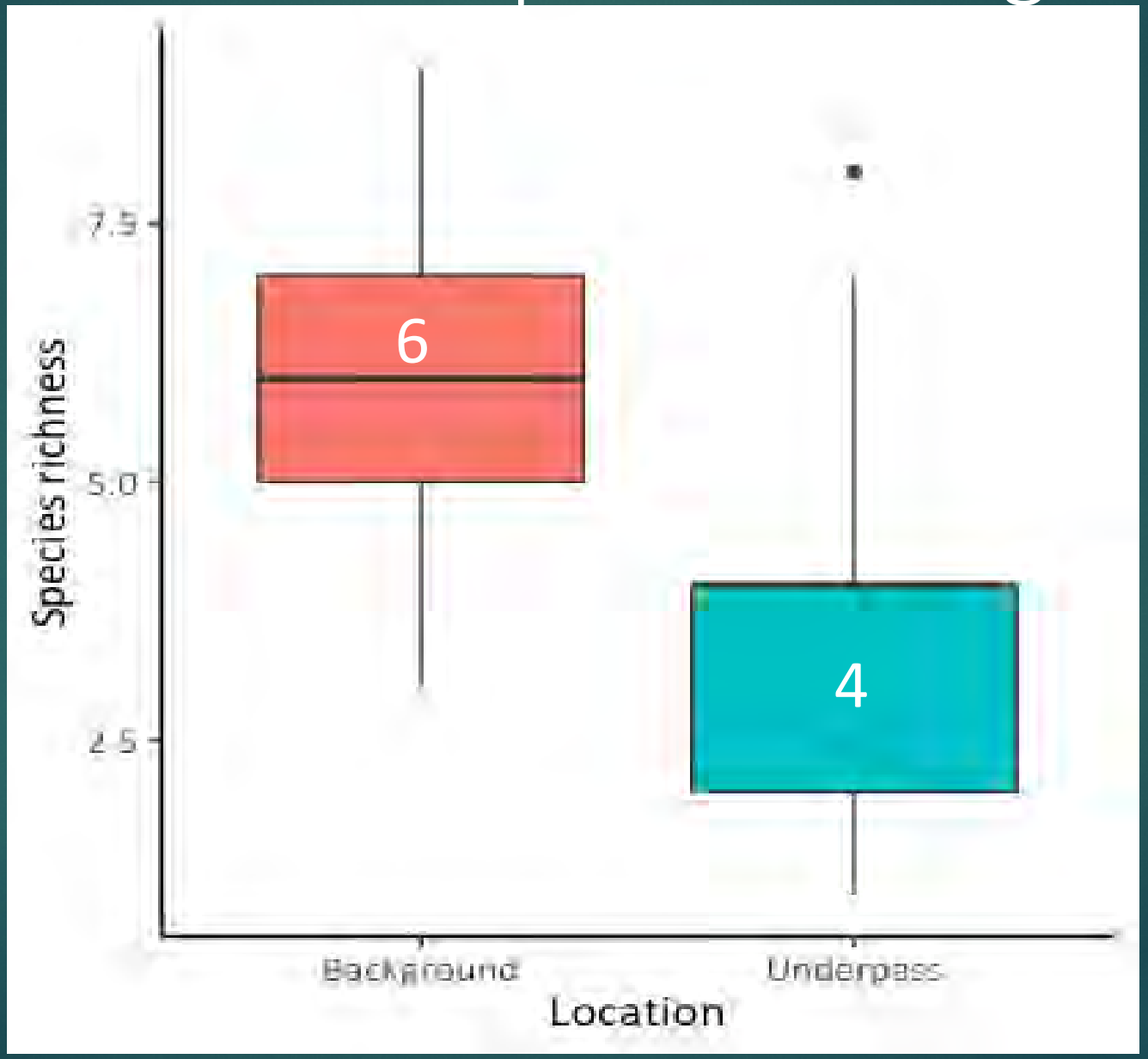




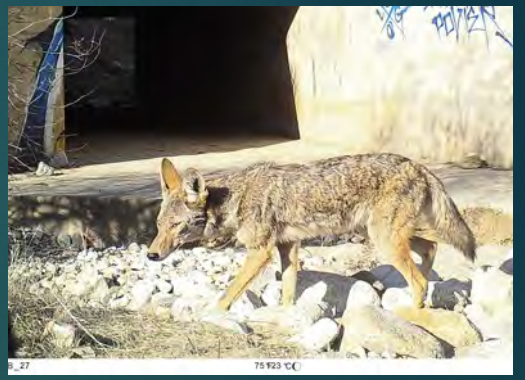
Species richness: underpass vs background













Complete avoidance?

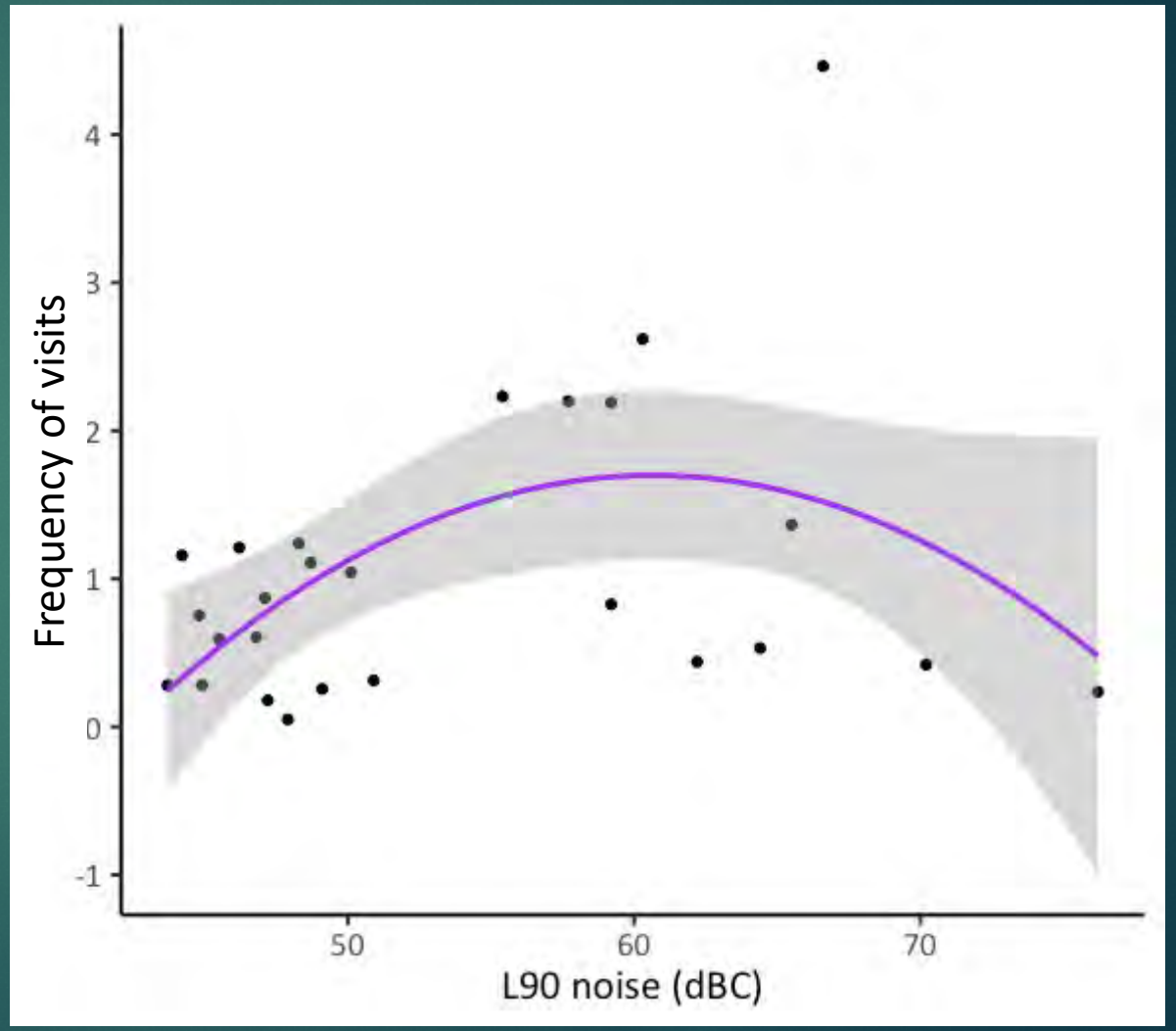
Response variable: Species richness at underpass

- Generalized linear model (environmental characteristics, underpass characteristics, humans, location in CA)
- Best model:

variable	P - value	Relationship to species richness
CA location (south)	0.009 **	-
Elevation	0.02 *	-
1-week minimum noise (dbC)	0.04 *	-
Underpass width	0.09	
Human presence	0.2	

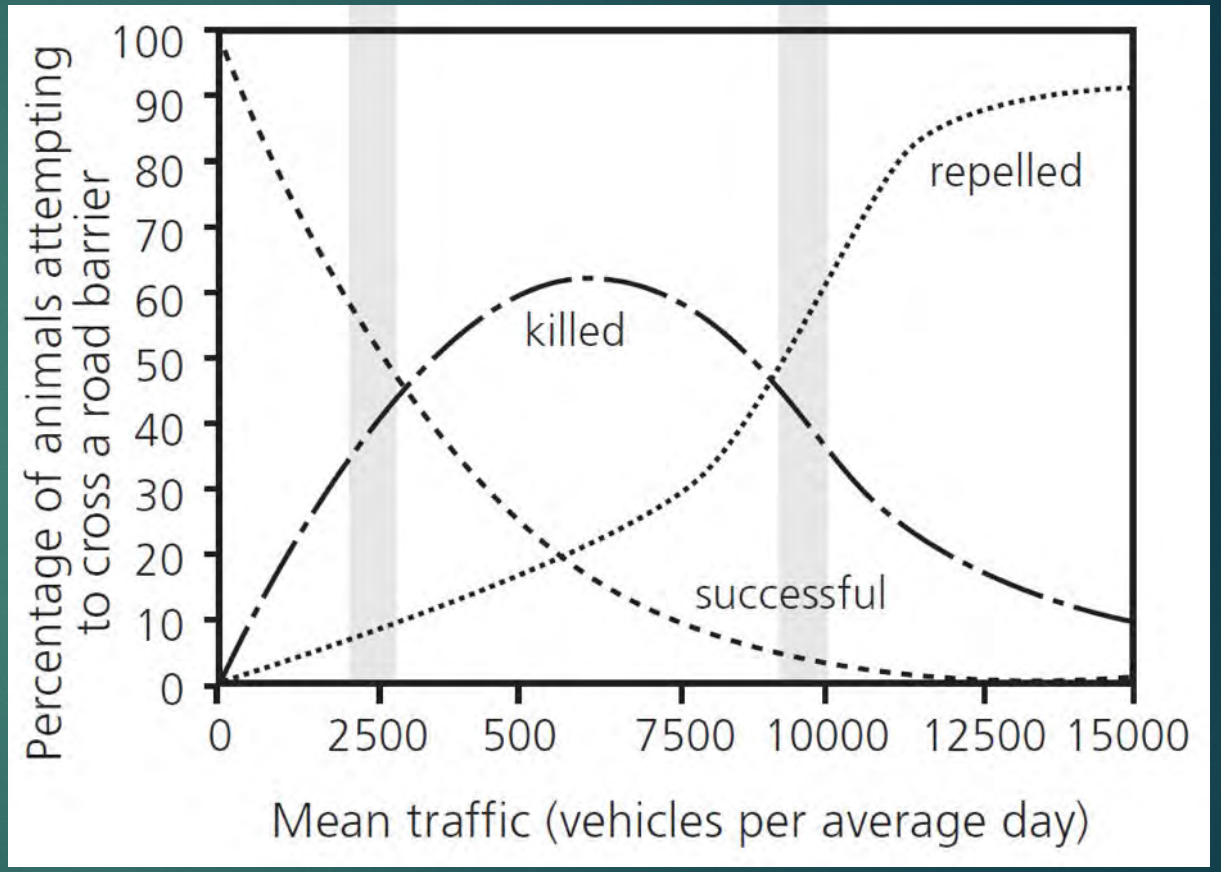
Decreased frequency of visits?

- Response: visits/day
- GLM
- Light had no relationship
- Vehicular noise (1-week) - inverse U



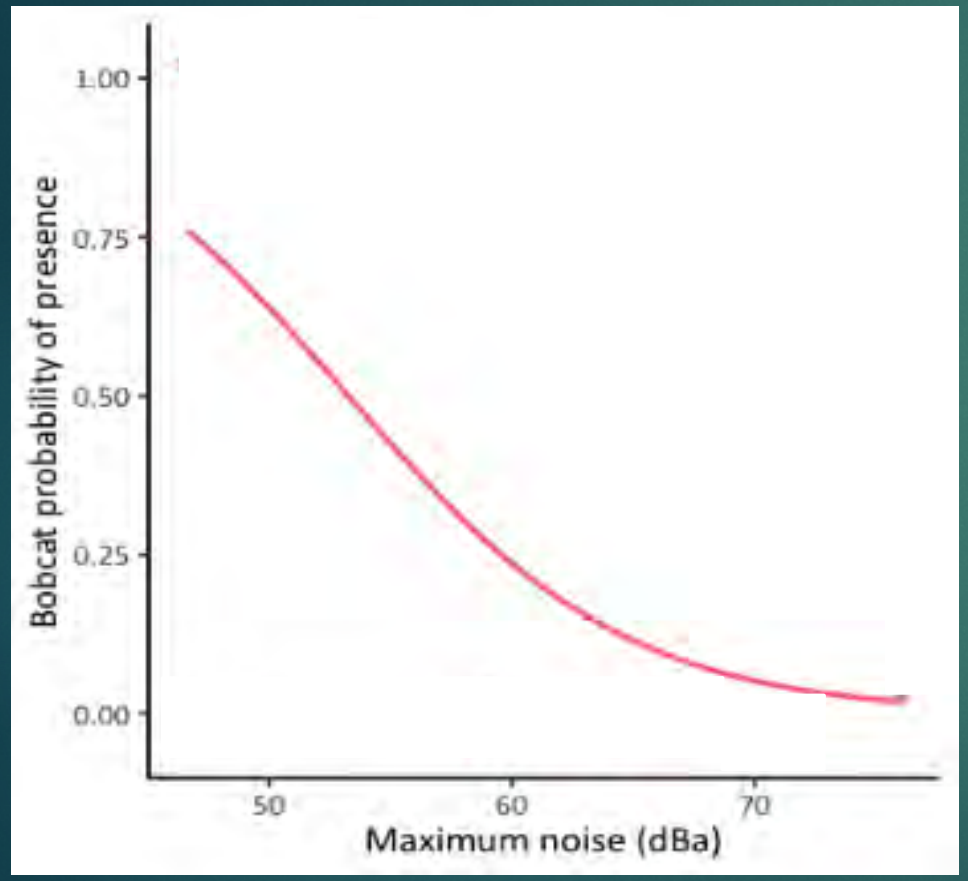
Decreased frequency of visits?

- GLM
- Light had no relationship
- Vehicular noise (1-week) - inverse U
- Similar response roadkill vs AADT



Andreas Seiler, 2003. Effects of infrastructure on Nature

Most wildlife avoid traffic noise



Los Angeles to build world's largest wildlife bridge across 10-lane freeway

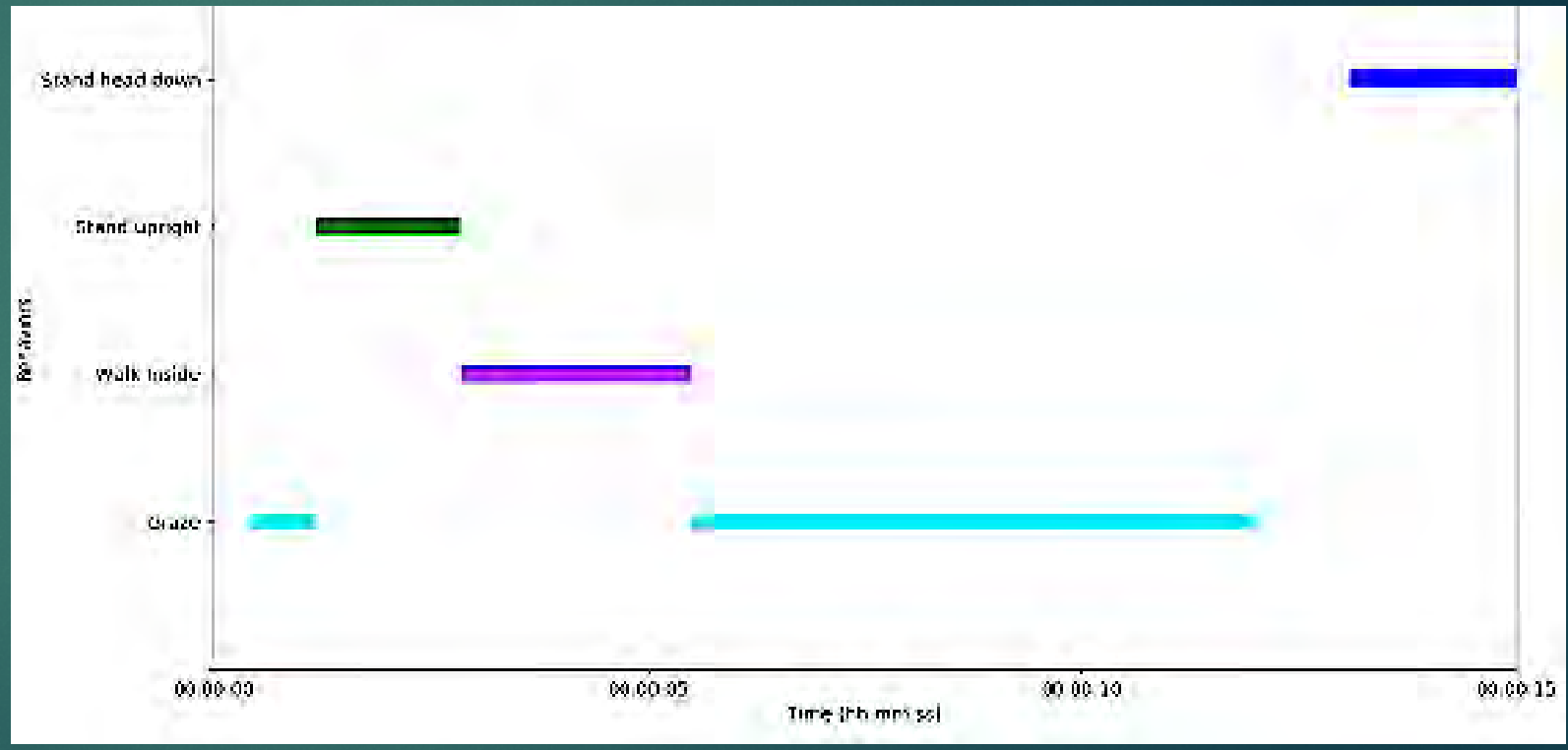
An $87m corridor will extend over Highway 101 to reconnect the ecosystem and possibly save mountain lions from extinction



▲ A wildlife corridor, the biggest in the world, is planned to extend over Highway 101 north-west of Lost Angeles. Photograph: RCD of the Santa Monica Mountains, Clark Stevens (architect), Raymond Garcia (illustrator)

Wildlife behavior with traffic

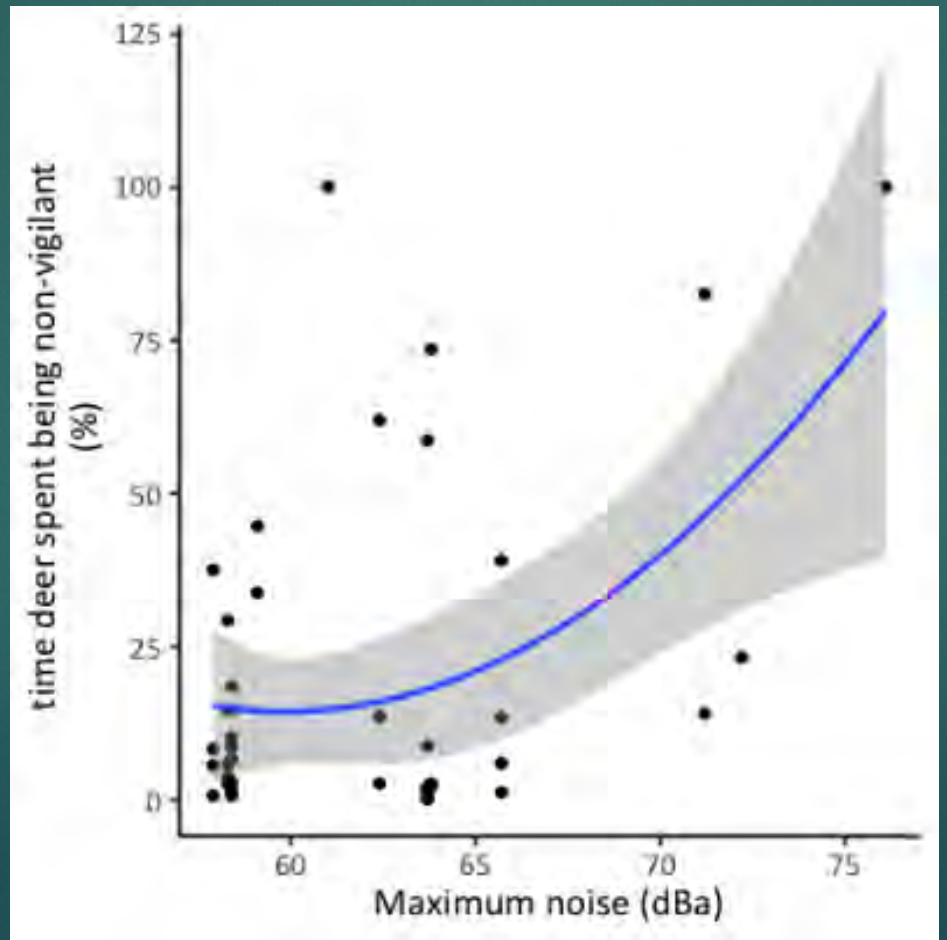
- Behavioral Observation Research Interactive Software
  - User annotates video
  - Indicates time spent on different behaviors

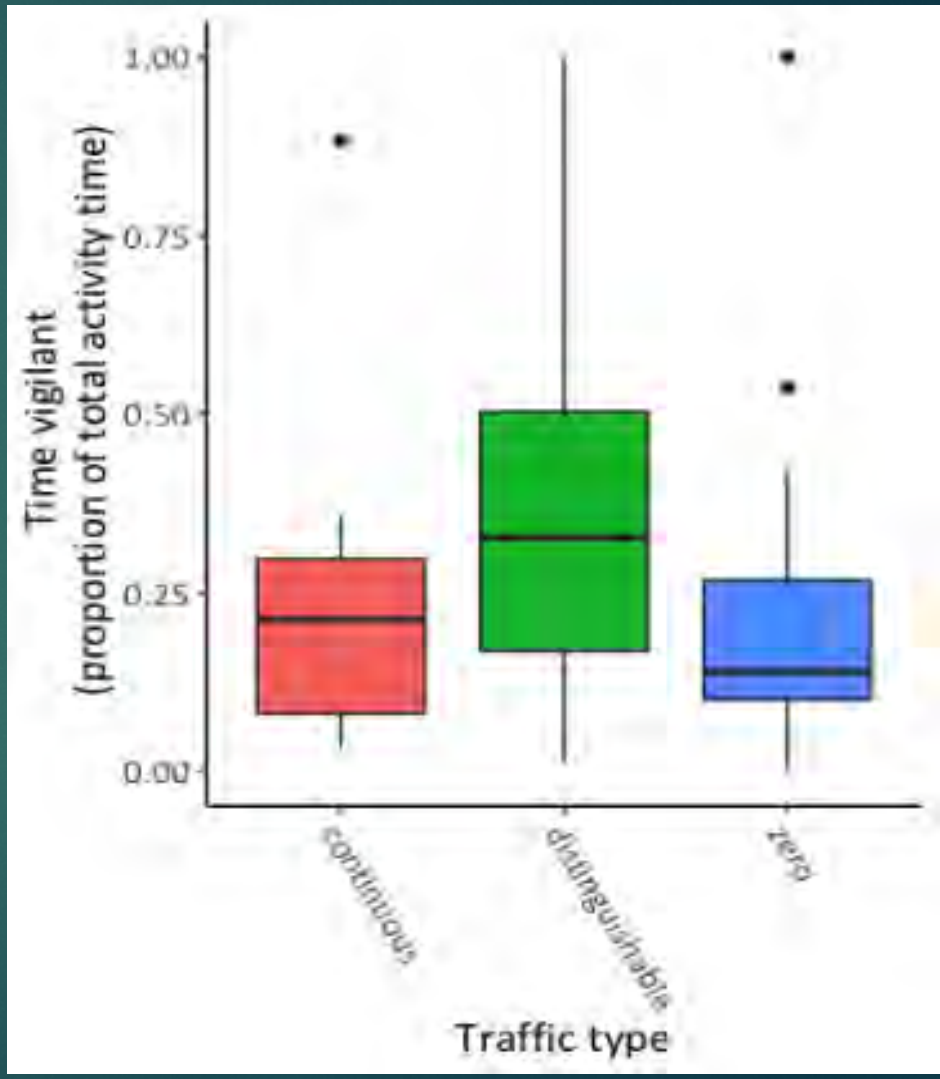


https://wildlifeobserver.net/behaviorid/

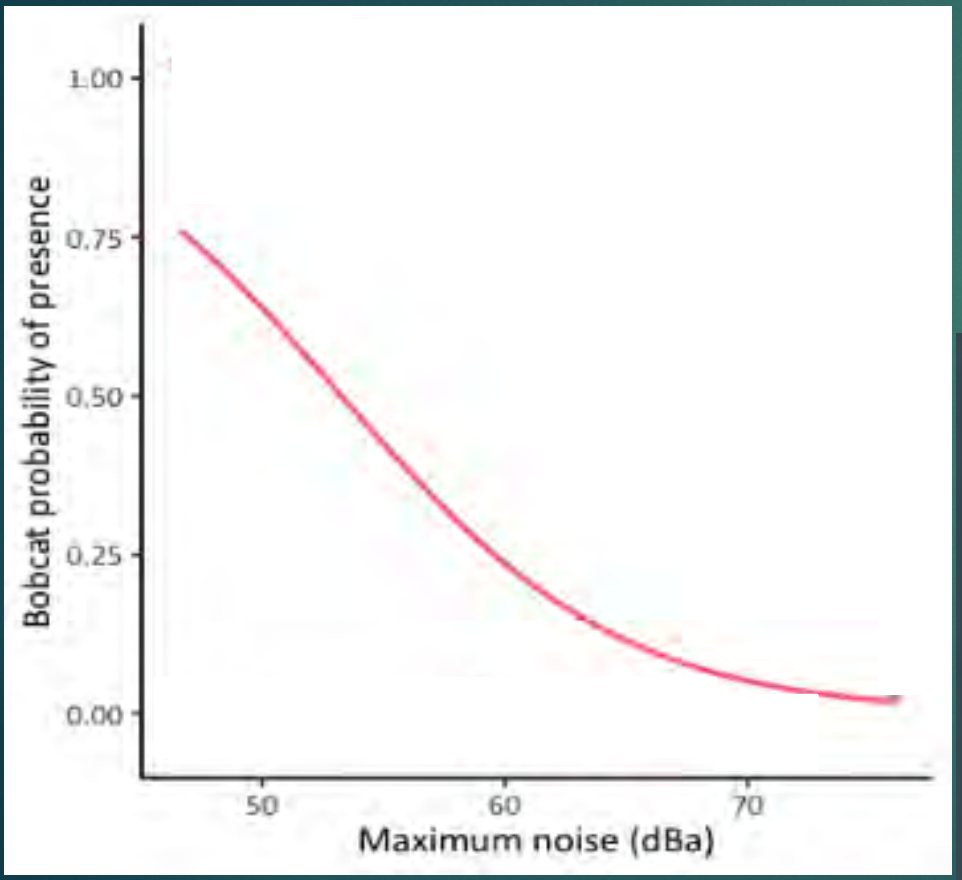
Wildlife behavior with traffic

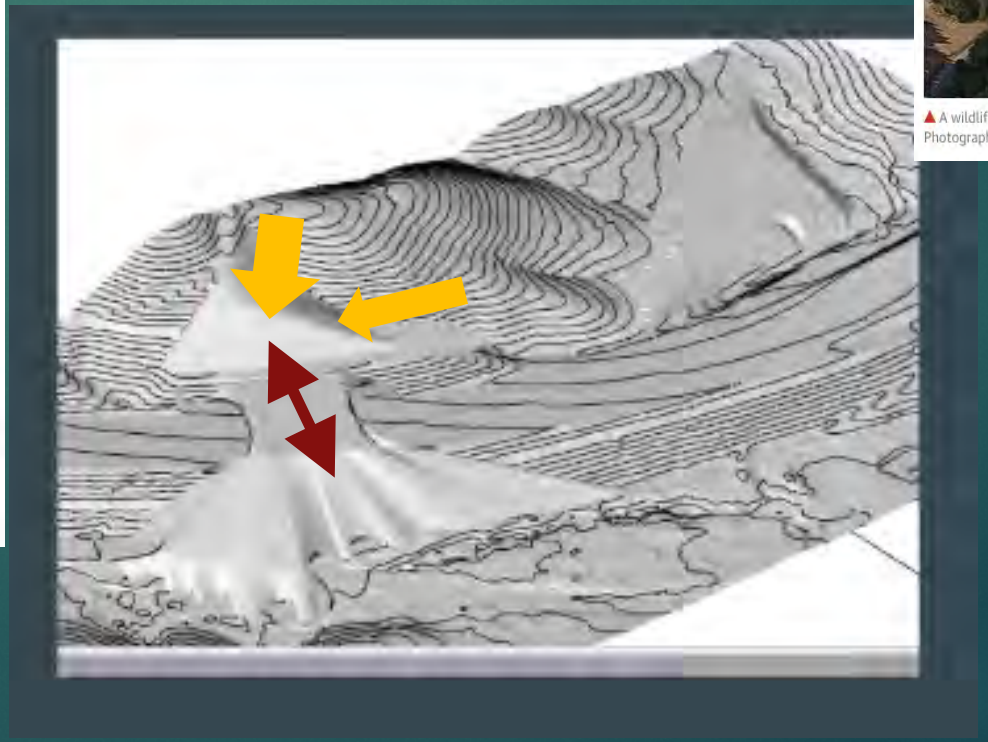
- Mule deer





Most wildlife avoid traffic noise





Los Angeles to build world's largest wildlife bridge across 10-lane freeway

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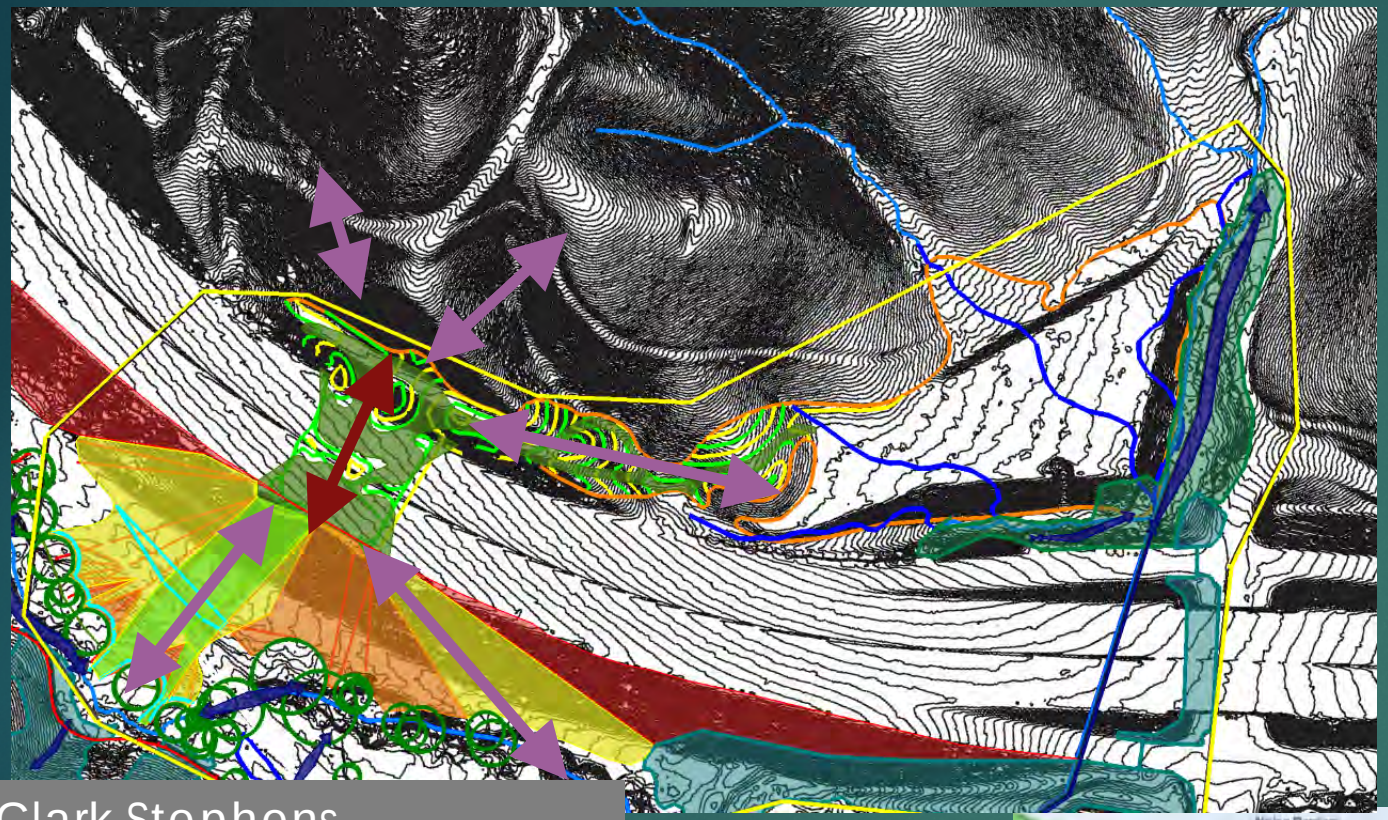
▲ A wildlife corridor, the biggest in the world, is planned to extend over Highway 101 north-west of Lost Angeles. Photograph: RCD of the Santa Monica Mountains, Clark Stevens (architect), Raymond Garcia (illustrator)

Designing for wildlife



Clark Stephens

Los Angeles to build world's largest wildlife bridge across 10-lane freeway

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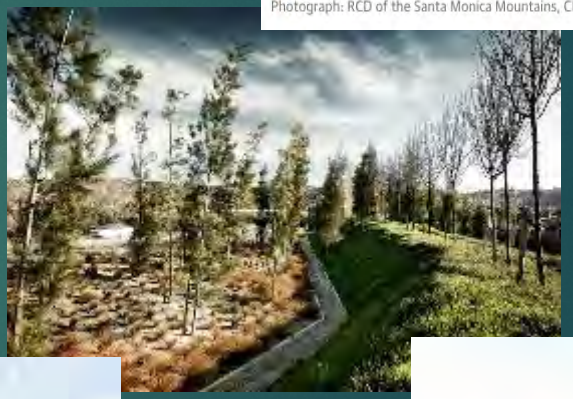






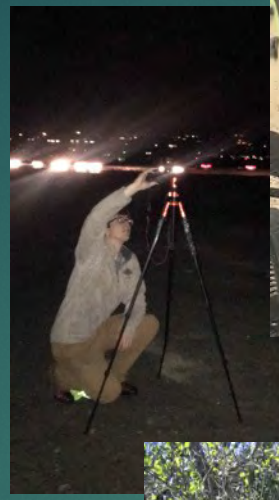

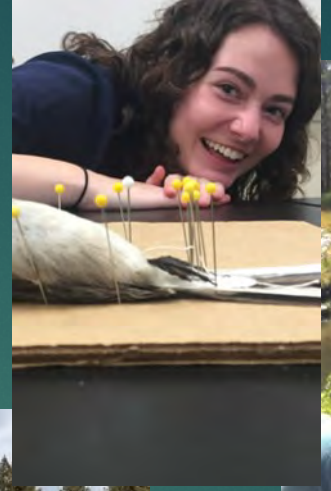

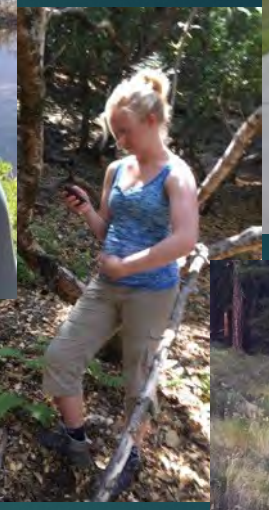

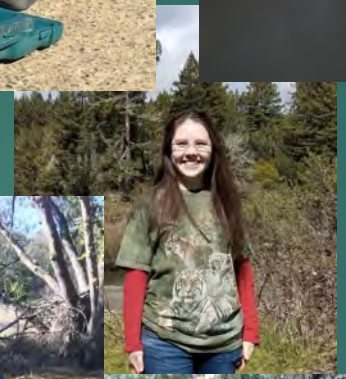









Annabelle Louderback-Valenzuela, Jeff Scott, Mia McNeill, Mia Guarnieri, Parisa Farman, Rachel Alsheikh, Pao Perez, Tricia Nguyen, Vivian lei, Harrison Knapp, Sean McDowell, Adetayo Oke, Jamie Bourdon, Rich Codington, Ben Banet, Collin Raff, Dirk Van Vuren lab, Rahel Sollmann, Catherine Le

Completed Project



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Research

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Top carnivores increase their kill rates on prey as a response to human-induced fear

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The fear induced by predators on their prey is well known to cause behavioural adjustments by prey that can ripple through food webs. Little is known, however, about the analogous impacts of humans as perceived top predators on the foraging behaviour of carnivores. Here, we investigate the influence of human-induced fear on puma foraging behaviour using location and prey consumption data from 30 tagged individuals living along a gradient of human development. We observed strong behavioural responses by female pumas to human development, whereby their fidelity to kill sites and overall consumption time of prey declined with increasing housing density by 36 and 42%, respectively. Females responded to this decline in prey consumption time by increasing the number of deer they killed in high housing density areas by 36% over what they killed in areas with little residential development. The loss of food from declines in prey consumption time paired with increases in energetic costs associated with killing more prey may have consequences for puma populations, particularly with regard to reproductive success. In addition, greater carcass availability is likely to alter community dynamics by augmenting food resources for scavengers. In light of the extensive and growing impact of habitat modification, our study emphasizes that knowledge of the indirect effects of human activity on animal behaviour is a necessary component in understanding anthropogenic impacts on community dynamics and food web function.

1. Introduction

Anthropogenic disturbance can cause shifts in biotic community dynamics, generally through the loss of native species, introduction of novel species or artificially enhanced populations of native generalists [1]. These changes are characterized most often by quantifying the population size or presence of particular species. However, behaviour-mediated interactions are predicted to have equal or greater impacts on animal populations than purely numerical mechanisms [2–4]. Animal behavioural responses to anthropogenic disturbances have the potential to be cryptic but powerful drivers of ecological change in modified habitats [5].

Large carnivores are widely recognized to be sensitive to human disturbances owing to slow life cycles, large space requirements, direct persecution by humans and avoidance of human-dominated areas, often resulting in their decline or extirpation. Reduced large carnivore density and occupancy in some developed areas has resulted in both mesopredator release [6,7] and overpopulation of primary consumers [8,9]. Yet, some large carnivores do persist in modified landscapes, but alter their behaviour to reduce interactions with humans [10,11]. Owing to the strong regulatory influence large carnivores can exert on their competitors and prey, changes in their behaviour are likely to contribute to whole community responses to anthropogenic disturbances [12].

Hunting and foraging are costly behaviours for carnivores, but are often assumed to be optimized so that individuals gain the most energy (or other limiting nutrients) for the least effort [13]. Animals that choose to expend more energy than what is perceived to be optimal may be responding to risks that increase the long-term pay-off of certain energy-expensive behaviours through decreased chance of non-starvation mortality [14]. Hunting in high-risk habitats can therefore create a risk-foraging trade-off in which animals sacrifice efficient foraging to compensate

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for increased vigilance and risk avoidance. Giving-up density studies support that an animal's perceived risk is inversely correlated with food intake, suggesting that time spent consuming a food item reflects the fear experienced by forager [15].

Top carnivores generally kill large-bodied prey species, which require a high initial energetic cost during the hunting stage [16], but provide high energy gain during consumption. However, because carnivores are constrained by gut capacity, solitary carnivores can only maximize their caloric yield by repeatedly returning to feed on a prey carcass. In developed habitats, carnivores can be particularly vulnerable to risk-foraging trade-offs because disturbance-induced carcass abandonment can result in food loss owing to scavenging [17] or decomposition [18]. Prey consumption time can therefore be limited by external forces that reduce carnivore access to a carcass. Anthropogenic disturbances can ultimately reduce the net caloric gain carnivores receive from consuming large prey [19] by displacing carnivores from kill sites and decreasing their prey consumption time at kills. If perceived risk increases with human disturbance, the magnitude of human impact should be a predictor of foraging efficiency and consumption time.

We examined puma (*Puma concolor*) behavioural changes associated with perceived risk at kill sites with increasing housing density levels and investigated the relationship between risk-avoidance behaviours and kill rates in disturbed areas. We hypothesized that disturbance would displace pumas more often in highly developed areas, reducing overall prey consumption time and increasing kill rates. In the long term, we anticipate that more frequent risk-avoidance behaviours will increase puma kill rate and subsequently alter interactions with prey, competitors and scavengers.

2. Material and methods

Our research was conducted in the Santa Cruz Mountains, which lie in the Central Coast region of California. We captured 30 pumas from 2008 to 2013 and fitted them with GPS/radio telemetry collars (IACUC no. WILMC1011 Model GPS Plus 1 or 2 D, Vectronics Aerospace, Berlin, Germany). Collars were programmed to record locations every 4 h, and location data were downloaded remotely via UHF once a month. We used a custom cluster generation algorithm integrated in the Geographical Information Systems program ArcGIS (v. 10; ESRI, 2010) using the programming languages R (v. 2.1.3.1; R Development Core Team, 2010) and Python (v. 2.6; Python Software Foundation, 2010) to identify groups of locations in which each location was within 100 m of the cluster centre and 6 days of another location in the cluster (for full details on the algorithm, see [10]). We field-investigated clusters in reverse chronological order from their time of formation using the most recently downloaded GPS data. Clusters were investigated within 30 days of their first recorded locations. At investigated clusters, we recorded whether a kill was present, and if so, the species, age and sex of the kill (if identifiable).

We constructed a mixed-effects binomial logistic regression model to predict deer kill sites from all generated clusters. We chose to only use deer kills because deer are the preferred prey in our study area. In addition, small prey cannot be predicted accurately from location data in our study area owing to high variability in puma behaviours at small kill sites. The variables used to fit the model were behavioural characteristics associated with clusters, including number of night locations (NIGHT), a binary variable indicating greater than 1 day duration (BINARY), the harmonic mean distance of locations from the cluster centre within the cluster (HMDIST), the proportion of locations occurring at night (P.NIGHT), site fidelity measured by the proportion of points occurring within the cluster over the cluster duration (P.ACTIVE) and the farthest distance travelled during a cluster period (DIST). Total duration of a cluster (DUR) was excluded owing to high correlation ($r > 0.7$) with variables already used in the model. We allowed for random slopes and intercepts for individual pumas when fitting the best model. We also constructed a truncated model without behavioural variables that we expected to correlate with housing density in order to allow inference on behavioural influences on kill rates. This model excluded P.NIGHT, P.ACTIVE and DIST. We compared the truncated model and best-fit model to assess if we could confidently use the truncated model. We constructed receiver operating characteristic curves for both full and truncated models and calculated the area under the curve (AUC) to ensure that both models were similar in their predictive abilities. The AUC for the full model (AUC = 0.818) and the truncated model (AUC = 0.820) were nearly identical, and both support good discriminative ability [20]. We assigned each generated cluster as a deer kill or not a deer kill by applying the truncated model to all generated clusters.

We first investigated puma behavioural responses at the population level at four levels of housing density within 150 m of predicted kill sites: no housing, rural (greater than 0.0 and up to 0.062 houses per hectare), exurban (greater than 0.062 and up to 1.236 houses per hectare) and suburban (greater than 1.236 and up to 9.884 houses ha^{-1}; [21]). Owing to the discrete nature of housing count data, each housing class was rounded up to the nearest number of houses, resulting in housing classes within 150 m of a cluster to be defined as 0 houses for no housing, one house for rural, two to nine houses for exurban and greater than nine houses for suburban. We used the 150 m buffer because this is the scale of development found to most impact puma hunting in our study area [10]. We constrained the response variables to only include behaviours we expected to be associated with risk aversion, which were narrowed down to P.NIGHT, P.ACTIVE, DUR, DIST and a final measure of prey consumption time (P.C.TIME) which was calculated as P.ACTIVE × DUR. We added the prey consumption time measure because it best reflects the energetic gain an animal receives from a kill. We tested the differences in behaviours at all predicted kill sites in different housing density categories using an ANOVA test and examined pairwise comparisons with Tukey's HSD test for all behaviours found to vary significantly with housing density.

To determine kill rates, we calculated the total number of deer predicted to be killed by each puma from the output of the deer kill prediction model using all generated GPS clusters. We divided the predicted number of kills by the total time each puma was actively collecting GPS data to obtain annual deer kill rates. We investigated sex-specific relationships between kill rates and average values for P.NIGHT, P.ACTIVE, DIST, DUR and P.C.TIME for individual pumas using univariate linear regressions owing to high correlation values ($r > 0.7$) among variables.

In order to assess the impact of housing on individual pumas, we calculated housing density within each puma home range. Puma home ranges were obtained using a local convex hull (LOCOH) home range estimator, where the 95% isopleth represented the home range boundary [22,23]. All housing points in the Santa Cruz Mountains were manually digitized from high-resolution satellite imagery. We calculated puma home range housing density as the number of houses per km^2. We tested for the relationship between individual puma kill rates and home range housing densities using univariate linear regression.

3. Results

(a) Behavioural shifts

Of 703 field-investigated clusters, 208 were classified as deer kill sites. The other remaining clusters included 66 non-deer

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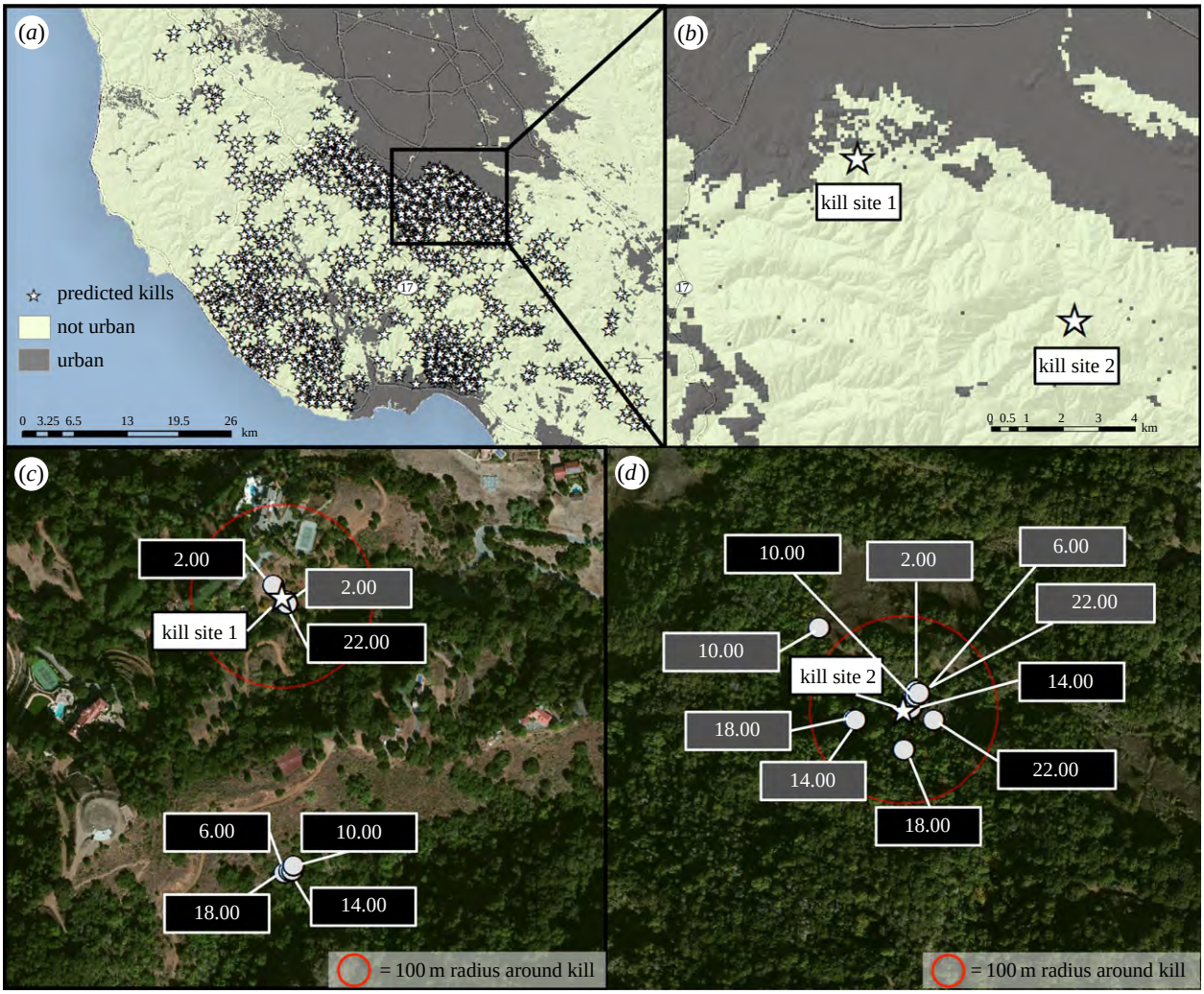

Figure 1. (*a*) Study area and predicted kill sites in relation to housing density. Box shows area (*b*) in which kill site examples (*c*,*d*) are shown. Kill site 1 (*c*) belongs to puma 13F, whose home range is in the top quartile of housing densities among female pumas. Kill site 2 (*d*) belongs to 28F, whose home range in the bottom quartile of housing densities among female pumas. Grey labels depict location times during the first day at the kill site and black labels depict location times during the second day. Note that at kill site 1, the puma has made a kill close to development but spends the majority of time away from the kill, whereas at kill site 2, which has no nearby development, the puma stays within the vicinity of the kill. (Online version in colour.)

kills (e.g. raccoons and house cats) and 429 non-kills (often bed sites). Our best-fit binomial logistic regression model to predict deer kills included NIGHT, BINARY, HMDIST, P.NIGHT and P.ACTIVE. The truncated model included NIGHT, BINARY and HMDIST. Neither the random intercept nor a random slope was included in the best-fit full model or the best-fit truncated model. We used the truncated model to predict 1537 deer kills from 8523 generated clusters (figure 1).

At predicted kill sites, females had lower P.ACTIVE ($F = 67.7$, $p \ll 0.001$), higher DIST ($F = 16.0$, $p < 0.001$) and shorter P.C.TIME ($F = 44.2$, $p \ll 0.001$) as housing density increased (figure 2; example shown in figure 1). In suburban habitat, female P.ACTIVE was 36% lower, DIST was 31% higher and P.C.TIME was 42% lower than in no housing areas. Both males ($F = 19.3$, $p < 0.001$) and females ($F = 144.4$, $p \ll 0.001$) were more nocturnal (higher P.NIGHT) with increasing housing density at kill sites. Males did not show any responses to housing density concerning time spent at kill sites. Identical analyses using only confirmed kills supported each of the reported trends for predicted kills.

(b) Deer kill rates

Male average home range size was 163.0 ± 7.7 s.e. km^2 with 15.6 ± 0.8 s.e. houses km^{-2}. Female average home range size was 53.8 ± 2.1 s.e. km^2 with 25.5 ± 1.3 s.e. houses km^{-2}. Males had an average deer kill rate of 43.7 deer yr^{-1}, whereas females killed on average 67.3 deer yr^{-1}. Male deer kill rates were not correlated with any of our variables of interest (P.ACTIVE, P.NIGHT, DIST, DUR or P.C.TIME), nor with home range housing density ($p = 0.9$, $r^2 = 0.005$; figure 3). Conversely, female deer kill rates showed a strong positive and linear correlation with home range housing density within its observed range ($p = 0.0003$, $r^2 = 0.745$; figure 3). Females with home ranges in the top quartile of housing density killed 36% more deer per year (81.2) than females in the bottom quartile of housing density (59.7). Female kill rates were also negatively correlated with average fidelity to kill sites (P.ACTIVE; $p = 0.05$, $r^2 = 0.322$).

4. Discussion

Our estimate of average male kill rates (43.7 kills yr^{-1}) stayed constant across housing densities and was comparable to previously reported values described by Knopff *et al.* (35 ungulates yr^{-1}, [24]) and Anderson & Lindzey (47 kills yr^{-1}, [25]). However, female kill rates increased positively, strongly and linearly with housing density. Although female kill rates in lower housing density areas (59.7 kills yr^{-1}) were

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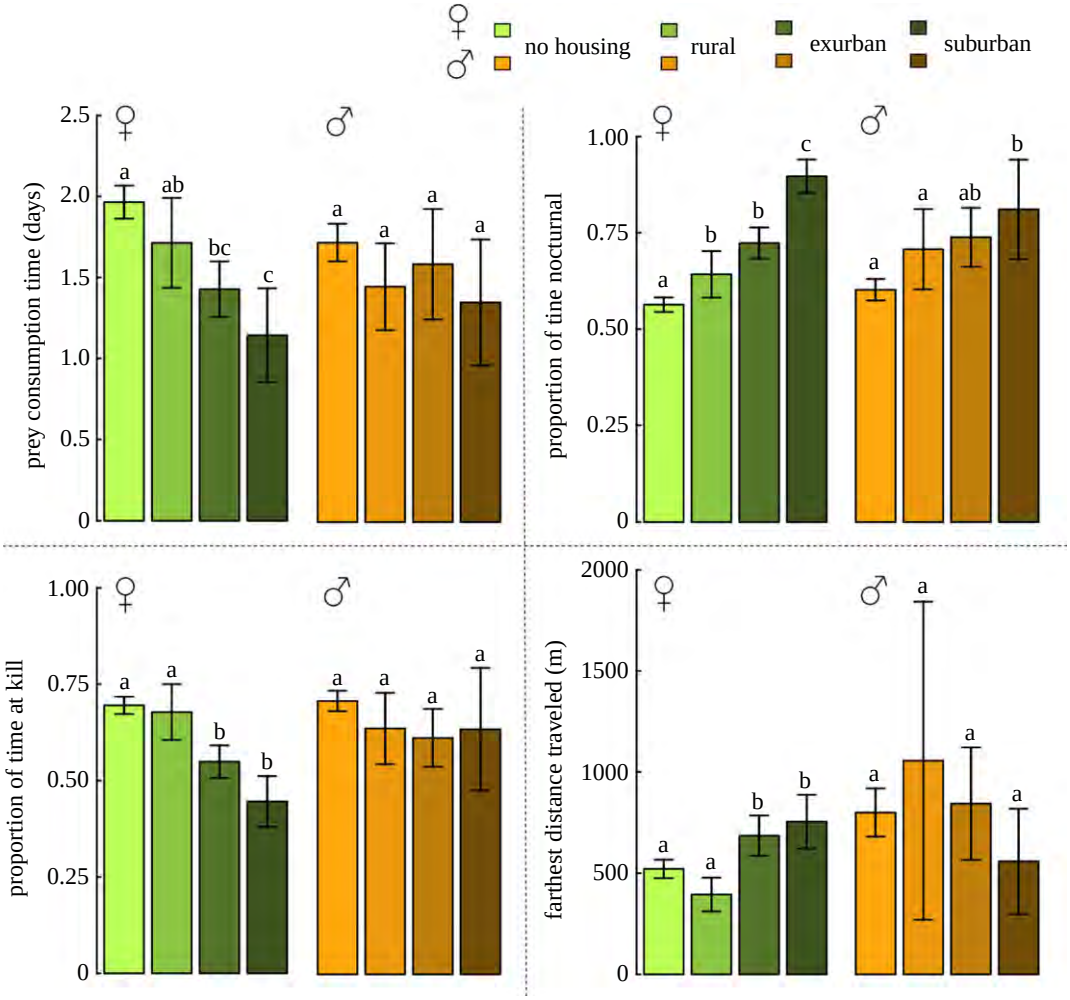

Figure 2. Behaviours that vary with housing density at predicted kill sites. Pairwise comparisons from Tukey's HSD tests reported in superscripts, where different letters represent a statistically significant difference. Error bars represent two standard errors from the mean. Sample sizes of housing classes at female kills are: no housing, 719; rural, 83; exurban, 186; suburban, 71. Sample sizes of housing classes at male kill sites are: no housing, 389; rural, 32; exurban, 42; suburban, 15. (Online version in colour.)

comparable to previously estimated mule deer kill rates for solitary adult females (52.5 kills yr^{-1}, [25]) and females with kittens (62.4 kills yr^{-1}, [26]; 68.1 kills yr^{-1}, [25]; 57.2 kills yr^{-1}, [24]), female kill rates in the highest quartile of home range housing densities were substantially higher (81.2 kills yr^{-1}). This 36% increase in kill rates between the top and bottom quartiles indicates that development may exert a significant energetic cost associated with hunting behaviour.

Hunting deer requires large energetic investments in the stalking, subduing and killing stages for pumas [16]. We have documented a sizable increase in female kill rates that we expect represents higher energetic costs for females in developed landscapes. Although these costs do not appear to influence adult survival (C. C. Wilmers 2014, unpublished data), impacts on reproductive success possibly make development-interface zones sinks for the puma population. Anecdotally, we have observed that the tagged female living in the most developed habitat in our study area has lost at least three litters in the last 3 years, one of which was confirmed as abandonment (C. C. Wilmers 2014, unpublished data). The three other females living in less developed portions of our study area for which we have also documented at least three dens have had the majority of their litters survive. Although there are many stressors in a developed landscape that might influence kitten survival, we expect that higher energetic costs from increased hunting may contribute to this pattern.

Males did not alter their kill rates or prey consumption time at kills with increasing housing density. Because male life histories are constrained by requirements to defend much larger territories [27], this is perhaps not surprising. We found that male pumas have home ranges that are approximately three times as large as female home ranges on average. Male pumas are also known to spend significantly more time performing scent-marking behaviours than females [28]. We found that males have lower DUR at kills than females by 7.2 h on average (males = 2.86 days $\pm$ 0.06 s.e., females = 2.56 days $\pm$ 0.05 s.e.; $t = 3.83$, d.f. = 1000, $p \ll 0.001$), probably owing to their need to patrol and defend their home range boundaries from encroaching males. Therefore, because males already tend to leave their kills early, they may be less influenced by chronic disturbance. In addition, male home ranges are characterized by much lower overall housing densities, indicating that males may exhibit risk-avoidance behaviours at the landscape scale rather than at the kill site scale.

Higher deer kill rates by females in response to increased housing density appear to be driven by a behavioural shift to a lower proportion of time spent at kill sites over the consumption period. Although females did not alter their total duration spent at clusters, their overall prey consumption times declined owing to a lower proportion of time spent at kills, indicating reduced utilization of carcasses at higher housing densities.

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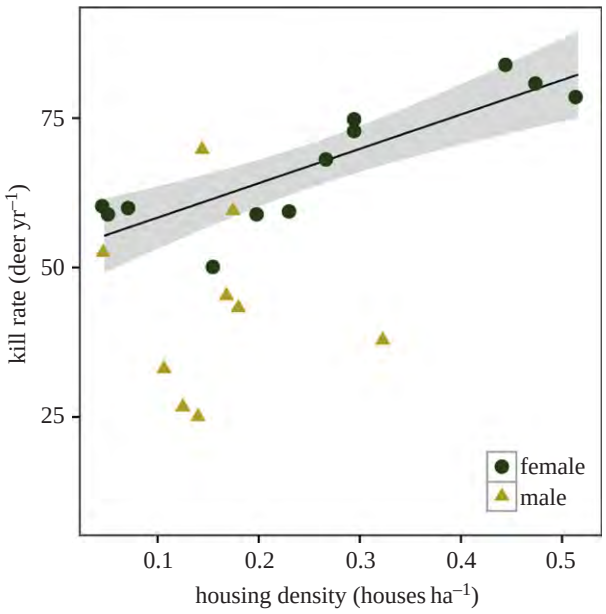

Figure 3. Kill rates of individual male and female pumas in response to housing density per hectare within their 95% LOCOH home range. Regression line and 95% CIs for female kill rates in relation to housing density are shown. Housing density coefficient $\beta_1 = 91.4$. (Online version in colour.)

Other possible explanations for female increase in deer kill rate are not supported by our understanding of puma energetics and reproduction. Deer in our study have lower detection rates in more developed habitats (C. C. Wilmers 2014, unpublished data), therefore variation in deer activity or abundance is unlikely to explain these patterns. In addition, it is unlikely that increased kill rate could be a result of greater reproductive activity in high housing density areas because females in our study area avoid anthropogenic development when denning [10]. We conclude that behavioural risk avoidance is a substantial contributor to female prey consumption time and hence hunting patterns, due to our observation that housing density is associated with decreased prey consumption time. Both food loss and increased movement as a result of these behavioural shifts may contribute to observed increased kill rate in human-modified habitats.

An increase in ungulate carcasses left by female pumas may impact the biotic community by providing additional carrion subsidies to scavengers. By leaving their kills for longer periods of time in more developed areas, female pumas might create greater opportunity for scavenging by mesopredators and birds. Subordinate predators often scavenge kills of apex predators when kills are abandoned or not guarded [29], and carrion can form a large proportion of their diets [30]. Pumas are known to be important sources of food subsidies to mesopredators through carcass abandonment [31]. Our results suggest that mesopredator release may occur not only through the well-documented pathway of apex predator extirpations, but also via behaviour changes in extant apex predators leading to increased food provisioning. The presence of scavengers can exacerbate this pattern by reducing apex predator prey consumption time via food loss [17].

5. Conclusion

The results presented here have bearing on human-modified systems globally. Behavioural responses are often overlooked as ecosystem drivers in modified systems, overshadowed by population declines and extirpations. However, many species are able to persist in developing landscapes, but in an altered behavioural state. Our findings suggest a strong, perceivable impact of observed human-induced behavioural change on species interactions instigated by the presence of development. Risk aversion behaviours that result from anthropogenic disturbances are likely to restructure predator–prey interactions in a variety of contexts, given the large effects risk has been shown to have on foraging across taxa. Behaviour-mediated interactions are powerful forces in biotic systems, often playing an even more impactful role than consumptive interactions. A greater focus on behaviour-mediated effects of habitat alteration can further expand our understanding of community-level processes in human-modified systems.

Ethics statement. The study was carried out under the IACUC approval no. WILMC1011.

Data accessibility. Because pumas are a specially protected species in California, the location data are sensitive and have not been made accessible. However, the data can be available on request by contacting Justine A. Smith at jsmith5@ucsc.edu.

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Author contributions. J.A.S. conceived the study, carried out the data analysis and drafted the manuscript. Y.W. assisted in project development and edited the manuscript. C.C.W. conceived and designed the overall study, supervised data collection, advised on data analysis and edited the manuscript.

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Conflict of interests. We have no competing interests.

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Despite clear risks, Santa Rosa neighborhood that burned down was exempt from state fire regulations

By DOUG SMITH and NINA AGRAWAL
OCT 15, 2017 | SANTA ROSA, CALIF.



An aerial view of the Coffey Park neighborhood in Santa Rosa, where many homes were destroyed in the wildfire. (Marcus Yam / Los Angeles Times)

Coffey Park was built on city streets, not forested country lanes.

The Santa Rosa suburb was a planned development laid out on a typical grid with sidewalks and landscaped yards. The fire hazard zone shown on city and state maps was to the north and east, on the other side of the 101 Freeway.

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Yet when the Tubbs fire swept down the mountain, Coffey Park proved defenseless in its path. In a matter of hours, the neighborhood was almost totally consumed, leaving hundreds of houses burned to the ground and residents in disbelief.

"We live in a subdivision in the middle of freaking Santa Rosa," said Anna Brooner, whose house still stands on the side of Randon Way that didn't burn, facing a scene of rubble and ash oddly punctuated by street trees that still have leaves and a plastic recycling bin that didn't melt.

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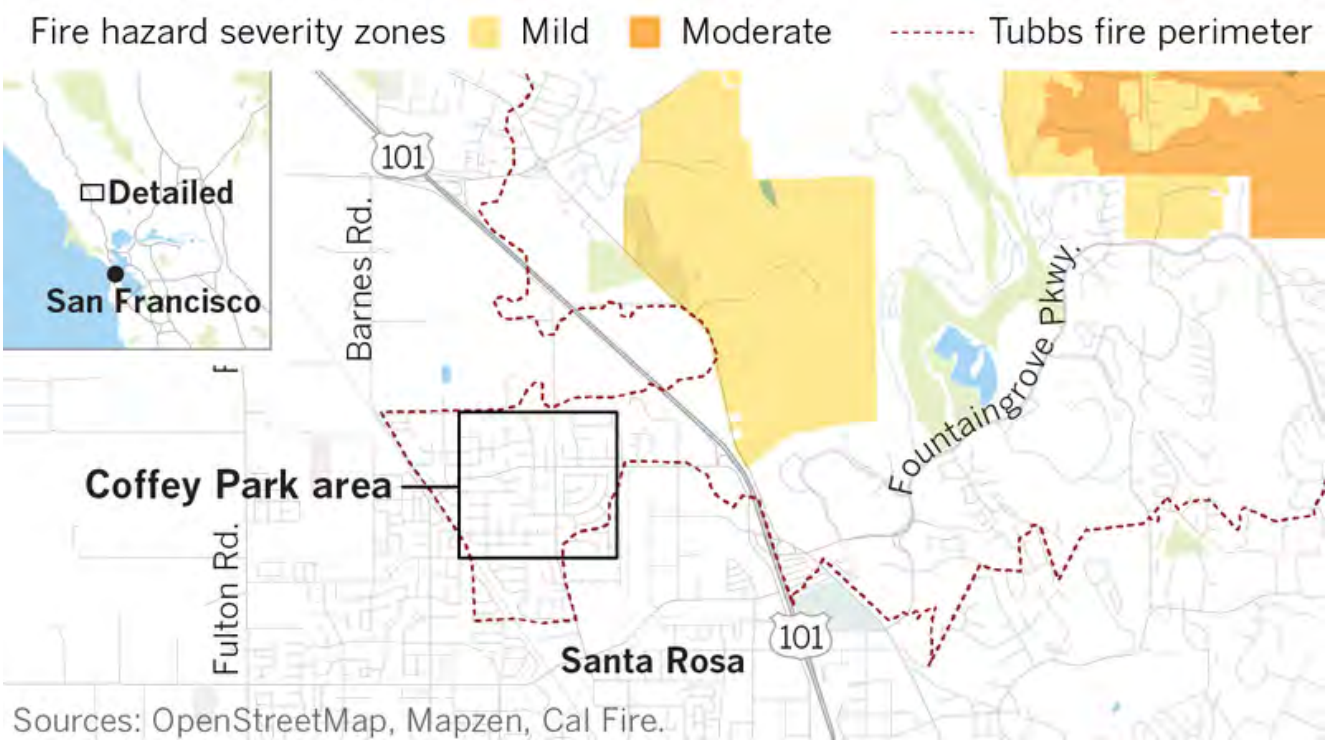
"I could see living on the outskirts of the mountains, you always have the potential of fire," Brooner said. "But you would never expect it in a subdivision of this size."

Surprising as it was to residents, the destruction of Coffey Park wasn't a mystery to fire scientists. They view it as a rare, but predictable, event that has exposed flaws in the way fire risk is measured and mitigated in California. Because it was outside the officially mapped "very severe" hazard zone, more than five miles to the east, Coffey Park was exempt from regulations designed to make buildings fire resistant in high-risk areas.



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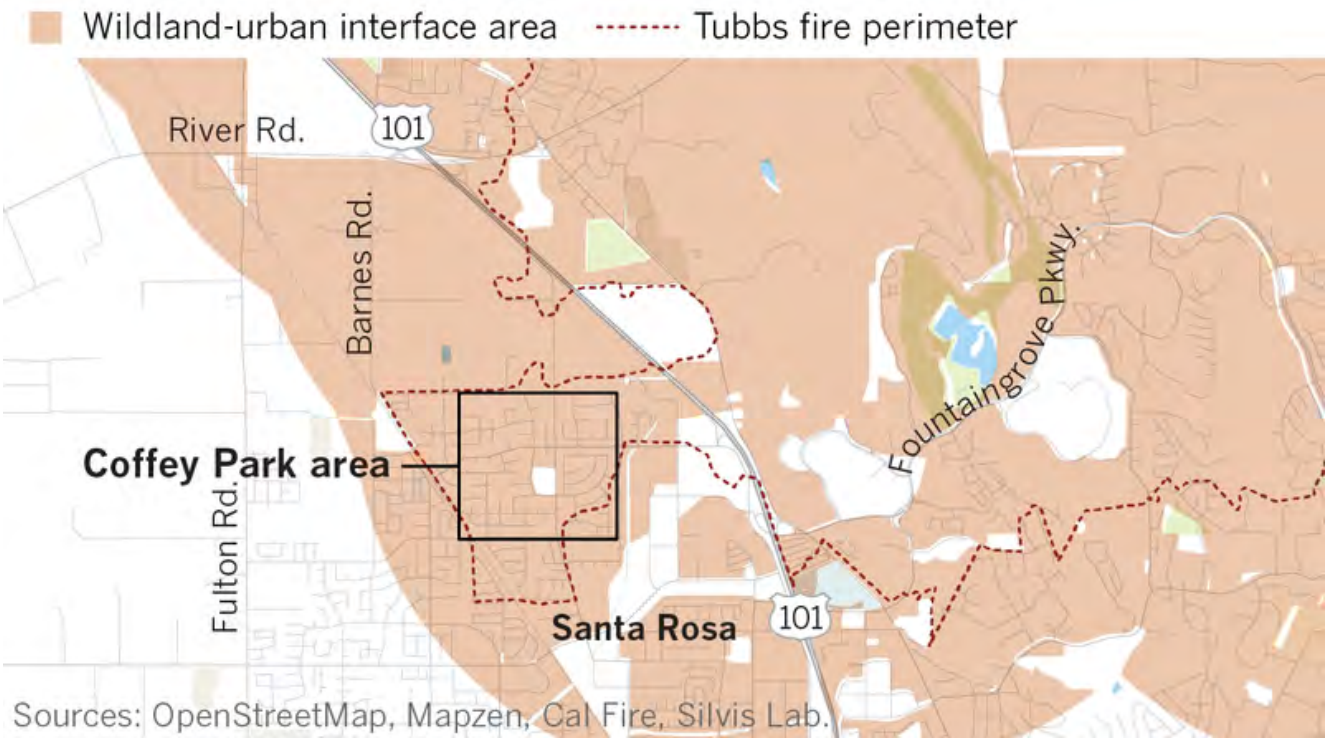

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California fire officials developed hazard maps in the 2000s that for the first time, tied building codes to geographies based on risk. Max Moritz, a fire specialist with the University of California's Cooperative Extension, said the maps were an important step forward in assessing fire danger.

But the Coffey Park catastrophe has shown that the methodology, and the law underlying it, were too narrow.

"With a lot of hazard mapping, once you get into a density of development, it's mapped urban and it's considered unburnable," Moritz said. "From its core, our whole approach to fire behavior modeling, we are not talking about burning in urbanized environments."

The fire hazard zones now need to be recast with more consideration for the impact of wildland fire on developed areas, Moritz said.

Revisions of the hazard maps are in the works and will incorporate lessons from the Tubbs fire, said Dave Sapsis, Research Program Specialist with the state's Fire and Resource Assessment Program, the unit of Cal Fire that maps fire hazard zones.

"I do believe when we remap we are going to be looking at new data that could potentially expand these very high zones into areas that were not mapped." Sapsis said.

Though a forensic examination will be required to understand exactly what happened at Coffey Park, the unburned trees still standing in the neighborhood tell wildland fire experts that the cause was not a giant front of flames sweeping out of the nearby hills and fields.



A charred cooking range sits amid the ruins of a home on Hemlock Street in Santa Rosa. (Brian van der Brug / Los Angeles Times)

Most likely, the fire was touched off by embers blown from a distance. Firebrands capable of igniting a house can travel more than a mile.

"When you've got firebrands going into every crook and cranny, they're going to find somewhere to start combustion," Sapsis said.

Fire experts surmise that most of the damage was caused by fire spreading from house to house, leaving some parkway trees and things like trash cans oddly unscathed.

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"Those houses are like highly concentrated energy packages just waiting to ignite," said Donald Falk, a wildland fire researcher in the University of Arizona School of Natural Resources and the Environment. "In that wind-driven situation, I think the predictions of what's fire-safe and what's not kind of go out the window."

Similar urban conflagrations have been seen before. In 1982, exposed electrical wire touched off a fire that was driven by Santa Ana winds through a four-block area of Anaheim, destroying 40 apartment buildings.

And when the Boles fire tore through the Siskiyou County town of Weed in 2014, more than 150 buildings were destroyed or damaged.

"We are seeing it happen more often," Moritz, the UC researcher, said.

The problem for fire risk management is balancing the huge losses from urban conflagrations with their infrequent occurrence.

The weather events that underlie them — high wind and temperature, low humidity and parched vegetation — are rare in the historical record, said Mark A. Finney, research forester with the U.S. Forest Service's Rocky Mountain Research Station.

"It's not as though this stuff is unprecedented," Finney said. "It's just rare in any one given spot."

To establish the probability of a Tubbs fire destroying a neighborhood 10 miles from its starting point, "you have to incorporate all the uncertainty in ignition locations, uncertainty in weather, uncertainties of terrain. That's a tall order. There are methods. They're relatively new."

A broader measure of risk than Cal Fire's maps is called the wildland-urban interface model. It takes into consideration the proximity of human habitation to wildland areas.

A wildland-urban interface map prepared by the Silvis Lab of Wisconsin encompasses all of Coffey Park and a good deal more of northeast Santa Rosa.



Santa Rosa Mayor Chris Coursey surveys the damage to the Coffey Park neighborhood. (Marcus Yam / Los Angeles Times)

But wildland/interface mapping is also fraught with uncertainty because of the challenge of pinpointing population in wildland areas, Sapsis said.

Although Cal Fire publishes its own wildland-urban interface map, it does not carry any legal consequences, he said.

Another complication is that the legislation underlying hazard mapping only allows Cal Fire to plot "very high severity" zones in areas designated as local jurisdiction, including cities. The hazard zones nearest to Santa Rosa are categorized as "moderate" or "high" and thus would not extend into the city.

"It's likely that if the state had authority to map in local responsibility areas other than very high, much of Santa Rosa would have been included," Sapsis said.

It isn't clear how much the designation of a fire hazard zone would have lessened the damage in Coffey Park. The state law, written in response to the 1991 Tunnel fire that destroyed 2,900 homes in Oakland, applies only to new construction and substantial remodeling.

The designation of a fire hazard zone could, however, ensure that as Coffey Park is rebuilt, there would be mandatory building requirements to better protect it against a future conflagration.

Some experts suggested that the startling losses from the Tubbs fire could spark consideration of more aggressive measures such as mandatory retrofits or at least the canvassing of neighborhoods like Coffey Park to identify vulnerabilities that could be remedied such as ensuring that attic vents, the most common source of firebrand ignition in houses, are screened.

Moritz, the UC scientist, pointed to an analogy with the fire councils that obtain grant money for mitigation programs.

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"They go through to remove vegetation, support fuel break," he said. "Very few of these grant funds ever support mitigating ignition vulnerabilities. It goes to mitigating hazard, not vulnerability."

Experts are reluctant to say that even the most stringent fire proofing would have saved Coffey Park, particularly in light of reports of modern fire-resistant homes and even big-box stores being destroyed in the Tubbs fire.

"It's anybody's guess," Moritz said. "Without a doubt, had that fire come into and hit an interface that was built according to today's standards, you would have much less a chance of getting as far into that neighborhood as it did. It would have made some difference."

Falk, the University of Arizona fire researcher, agreed that the effect of stiffer building codes would be hard to predict, but could only have helped.

And he hopes that officials move quickly.

"The shelf life of an event like this, as devastating as it seems now, eventually will dissipate," Falk said. "Now is the time to have that dialogue."

An aerial view of the Coffey Park neighborhood destroyed by wildfire in Santa Rosa. (Marcus Yam / Los Angeles Times)

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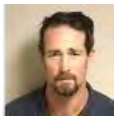

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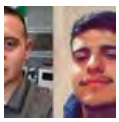

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Global mycorrhizal plant distribution linked to terrestrial carbon stocks

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Vegetation impacts on ecosystem functioning are mediated by mycorrhizas, plant–fungal associations formed by most plant species. Ecosystems dominated by distinct mycorrhizal types differ strongly in their biogeochemistry. Quantitative analyses of mycorrhizal impacts on ecosystem functioning are hindered by the scarcity of information on mycorrhizal distributions. Here we present global, high-resolution maps of vegetation biomass distribution by dominant mycorrhizal associations. Arbuscular, ectomycorrhizal, and ericoid mycorrhizal vegetation store, respectively, 241 ± 15, 100 ± 17, and 7 ± 1.8 GT carbon in aboveground biomass, whereas non-mycorrhizal vegetation stores 29 ± 5.5 GT carbon. Soil carbon stocks in both topsoil and subsoil are positively related to the community-level biomass fraction of ectomycorrhizal plants, though the strength of this relationship varies across biomes. We show that human-induced transformations of Earth's ecosystems have reduced ectomycorrhizal vegetation, with potential ramifications to terrestrial carbon stocks. Our work provides a benchmark for spatially explicit and globally quantitative assessments of mycorrhizal impacts on ecosystem functioning and biogeochemical cycling.

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Mycorrhizas are mutualistic relationships between plants and fungi, in which fungi supply plants with nutrients and plants provide carbon to fungi[1]. Among mycorrhizal types, arbuscular mycorrhiza (AM), ectomycorrhiza (EcM) and ericoid mycorrhiza (ErM) are geographically the most widespread, colonizing over 85% of vascular plants across vegetated terrestrial biomes[1–4]. Due to the facilitation of plant nutrient acquisition[1] and the large biomass of fungal networks in soil[5], the presence and type of mycorrhiza are among the key determinants of ecosystem functioning[6–9] and biogeochemical cycling[10–13]. Thus, the types of mycorrhizal associations present likely also affect the global distribution of soil carbon stocks. There is growing evidence that ecosystems dominated by EcM and ErM vegetation exhibit higher topsoil carbon to nitrogen ratios (C/N) compared with ecosystems dominated by AM plants[11,12,14,15], although in temperate forests the pattern may be reversed in deeper soil layers[16]. The mechanisms driving these differences are heavily debated in current literature, with distinct physiological traits of mycorrhizal fungi most likely playing a critical role[16–20].

Although it can be argued that high abundance of EcM plants is a consequence rather than a driver of high soil C stocks, a large body of recent findings provides evidence that EcM symbionts may be the key drivers of topsoil carbon accumulation through two interacting mechanisms. First, EcM fungi produce greater biomass of more recalcitrant mycelium compared to AM fungi[5]. Second, while EcM fungi are more efficient in taking up N in N-poor soils than AM fungi or roots[10,21], EcM fungi immobilize most of the N in their own biomass. This suppresses saprotrophic decomposition process[22] and reinforces the competitive advantage of EcM and ErM plants via enhanced N limitation[22,23].

A full understanding of global carbon and nitrogen stocks requires quantitative models on the distribution of mycorrhizal types in ecosystems[18]. Despite the existence of regional maps of current[24,25] and past[26] mycorrhizal vegetation, and on the distribution of mycorrhizal fungal species[27,28] we still lack global information on the distribution of biomass of mycorrhizal plants, which is a much better proxy for mycorrhizal impacts on ecosystem functioning than the biodiversity of mycorrhizal symbionts. While current terrestrial biosphere models simulate feedbacks between the carbon cycle and vegetation distribution[29], most models ignore mycorrhizal types and their effects on nutrient cycling. Integration of such information is expected to provide a more realistic simulation of carbon and nutrient fluxes associated with plant nutrition[17,18,21] and soil carbon cycles[15,21]. Quantitative models of the distribution of mycorrhizal vegetation constitute an important missing link between the known effects of mycorrhizas in biogeochemical cycles and their global impacts[30].

Human activities such as forest logging, urbanization and agricultural practices have altered 50–75% of the Earth's terrestrial ecosystems[31], transforming areas with previously natural EcM and ErM vegetation into AM and non-mycorrhizal (NM) vegetation. However, the impact of anthropogenic land use shifts on biogeochemical cycles associated with mycorrhiza have remained poorly known due to the lack of appropriate spatial information.

Based on a comprehensive quantitative evaluation of plant-mycorrhizal associations and the distribution of vascular plant species across biomes and continents, we assembled high-resolution digital maps of the global distribution of biomass fractions of AM, EcM, ErM and NM plants. Building on these maps, we assessed: (i) the amount of aboveground biomass carbon currently stored in each type of mycorrhizal vegetation; (ii) the impact of conversion of natural ecosystems to croplands on the distribution of mycorrhizal types globally; and (iii) the relationships between relative abundance of AM and EcM plants in an ecosystem and soil carbon content in topsoil (0–20 cm), medium (20–60) and deep (60–100 cm) subsoil layers.

Results and Discussion

Assembly of mycorrhizal vegetation maps. To generate global maps of mycorrhizal vegetation, we estimated biomass fractions of AM, EcM, ErM and NM plants within each combination of continent × ecoregion × land cover type. Supplementary Fig. 1 illustrates the data assembly processes for the maps. Ecoregions follow Bailey[32] (Supplementary Data 1), and land cover types were retrieved from the ESA CCI land cover map[33], which specifies cover and biomass fractions of trees, shrubs and herbaceous plants (Supplementary Data 2). For each combination, we determined the dominant species or group of species from 1568 vegetation surveys (Supplementary Data 3). For these species, we determined mycorrhizal type using the FungalRoot database v1.0[34] (see Supplementary Data 4 for data sources). Integrating these data, we obtained mycorrhizal plant biomass fractions of AM, EcM, ErM and NM plants for each combination of Bailey ecoregion, continent, and land cover type (Supplementary Data 5 and 6). These fractions were overlain on a global grid.

Our maps (Fig. 1) provide quantitative estimates of the distribution of aboveground biomass fractions among AM, EcM and ErM plants within areal units of 10 arcmin. The use of a detailed map of ecoregions[32] provides much greater resolution compared with the biome-based patterns of mycorrhizal distributions reported by Read[3] > 25 years ago, whereas the land cover map[33] enabled us to provide accurate spatial positioning of ecosystem boundaries based on satellite-derived data, explicitly taking into account human-driven transformations of vegetation.

We validated the map data using four independent datasets: (i) forest biomass structure for Eurasia[35], (ii) a global dataset of forest biomass structure used for an analysis of mycorrhizal impacts on carbon vs nitrogen dynamics[19], (iii) estimates of mycorrhizal associations in the USA based on satellite remote sensing[36], and (iv) West Australian map of mycorrhizal root abundance[24] (Supplementary Fig. 2). This validation revealed that the vast majority of the data (87% of the AM data points and 89% of the EcM data points) deviate by < 25% from the measurements[19,35,36], when excluding ESA land use classes comprising poorly resolved combinations (i.e. mixed classes of land cover types[33], such as "Tree cover, broadleaved, evergreen, closed to open (>15%)", see Methods for details) that were difficult to couple to our classification scheme. The relationship between the validation data and our estimates is shown in Supplementary Fig. 3.

Our maps of mycorrhizal vegetation were assembled based on multiple published datasets, using a number of conversion factors to obtain per pixel values of mycorrhizal plants biomass fractions. These conversions as well as the fact that the plant species distribution data (Supplementary Data 4) originates from multiple sources constitute important uncertainty sources in our dataset. We examined the uncertainty of our maps based on uncertainties of tree, shrubs and herbaceous plant fractions within the land cover types[37], and the number of data sources used to assess mycorrhizal fractions of plant biomass within each combination of Bailey ecoregion × continent; see Methods for details. Supplementary Fig. 4 shows spatial distribution of uncertainties. The mean uncertainties of AM, EcM, ER and NM maps are 19.6, 17.6, 14.6 and 15.0% at the 90% confidence interval. Overall, tropical areas have the highest uncertainties of the mycorrhizal fraction data, reaching 50% (AM) in the Amazon region. Therefore, our maps should be used with caution for these areas. Future sampling efforts of mycorrhizal vegetation distribution should be more focussed on tropical areas of Asia, Africa and South America.

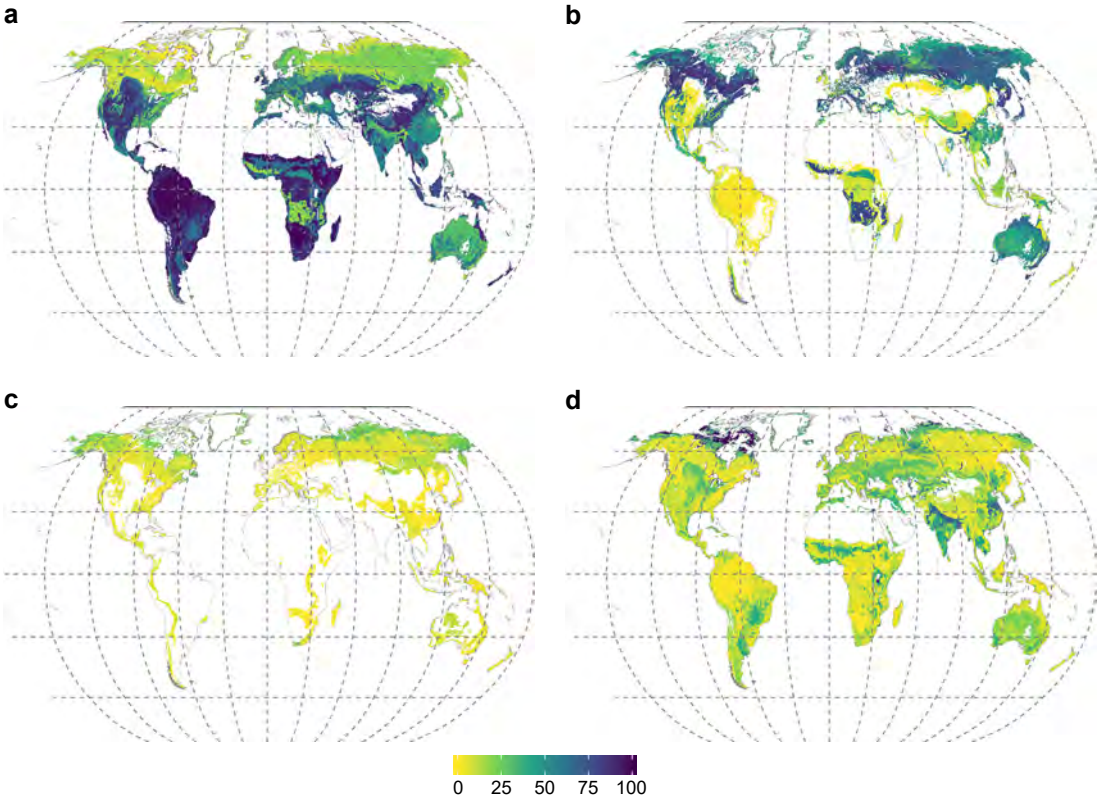

Fig. 1 Percentage of aboveground plant biomass of mycorrhizal vegetation. **a** Arbuscular mycorrhizal plants, **b** ectomycorrhizal plants, **c** ericoid mycorrhizal plants, and **d** non-mycorrhizal plants. The map resolution is 10 arcmin. See Supplementary Fig. 4 for associated uncertainty values. Source data are provided as a Source Data file

Mycorrhizal vegetation and aboveground carbon stocks. By linking our maps of mycorrhizal vegetation to satellite observations of global aboveground biomass carbon[38], we estimated the amount of aboveground biomass carbon stored in arbuscular, ecto-, ericoid and non-mycorrhizal vegetation as 241 ± 15, 100 ± 17, 7 ± 1.8 and 29 ± 5.5 GT (mean values ± uncertainty at 90% confidence interval; Fig. 2). In this analysis, the data were scaled to a resolution of 15 arcmin to match biomass estimates[38]. Most of the aboveground carbon stock stored in arbuscular mycorrhizal vegetation is situated in tropical forests (Fig. 2a). Supplementary Table 1 shows per-biome distribution of the carbon stocks among mycorrhizal types.

Impacts of land transformations on mycorrhizal vegetation. Agricultural practices drive the replacement of natural vegetation by facultatively AM crops[1,39], which could also be de facto non-mycorrhizal due to destruction of hyphal networks by ploughing and excess fertilisation[40,41]. Using past vegetation estimates, Swaty et al.[26] showed that across conterminous USA, agriculture has reduced the relative abundance of ectomycorrhizal plants compared with other mycorrhizal types. However, global quantifications of agricultural impacts on distribution of mycorrhizas have not been possible until now. Based on the current land use data underlying our maps (Supplementary Data 4), we assessed mycorrhizal distributions on Earth in the absence of croplands. For each ecoregion-continent-land cover combination that contained croplands, we replaced current biomass fractions by estimates of per-grid cell biomass fractions in AM, EcM, ErM and NM plants that would be expected at these locations based on natural vegetation types (see Methods for details, and Supplementary Data 7–8 for data). Based on these data, we generated maps presenting potential natural distributions of biomass fraction of AM, EcM, ErM and NM plants in a cropland-free world (Supplementary Figs. 6 and 7). The current biomass fractions of AM plants have increased in Europe, parts of Asia and North America, but declined in Africa, Asia (mostly India) and South America, coinciding with increase in non-mycorrhizal vegetation (Fig. 3, Supplementary Fig. 8). Our analysis suggests that EcM biomass has declined in all continents, primarily due to a replacement of natural forests by agricultural lands, whereas ErM biomass has remained unchanged.

Biomass fractions of mycorrhizal types and soil C stocks. Recent field research in the US temperate forests suggests that soil carbon content increases with increasing EcM abundance in topsoil layers; but, depending on forest type, this relationship may be reversed in deeper soil[16,42]. This is in agreement with the Microbial Efficiency-Matrix Stabilization hypothesis, which predicts that ecosystems with rapid decomposition, such as most AM-dominated forests[19], enhance soil organic matter (SOM) stabilization by accelerating the production and deposition of microbial residues[43–45].

To separate the effects of biome and mycorrhizal type on soil C on a global scale, we modelled the relationships between soil carbon content, biome type[46], and biomass fractions of AM and EcM plants. We did not analyse the relationship between ErM plant cover and soil C content, due to a small proportion of the ErM plant biomass in the majority of ecosystems.

We conducted separate analyses for the topsoil (uppermost 20 cm soil layer) and subsoil (20–60 and 60–100 cm soil layers), as obtained from the ISRIC-WISE Soil Property Databases, at a resolution of 30 arcsec[47]. The data sources used for these analyses are independent: the ecoregion classification, and hence mycorrhizal type distribution, does not account for edaphic parameters,

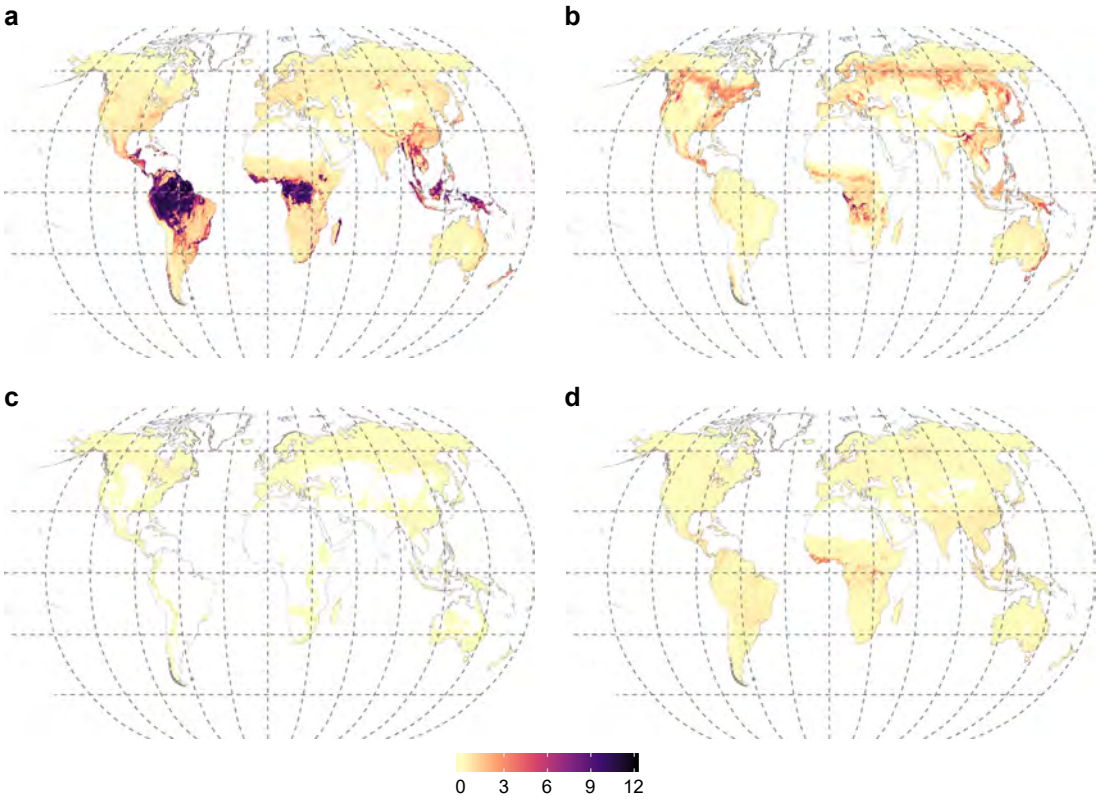

Fig. 2 Amount of carbon stored in plant biomass in vegetation of different mycorrhizal types (Mt C per-grid cell of 15 arcmin). **a** Arbuscular mycorrhizal plants, **b** ectomycorrhizal plants, **c** ericoid mycorrhizal plants, **d** non-mycorrhizal plants. The amount of aboveground biomass carbon stored in arbuscular, ecto-, ericoid and non-mycorrhizal vegetation is 241 ± 15, 100 ± 17, 7 ± 1.8 and 29 ± 5.5 GT (mean values ± uncertainty at 90% confidence interval), respectively

whereas soil C data are unrelated to that of vegetation. Model comparisons were based on the Akaike information criterion (AIC). The relative importance of each predictor was examined using the Lindemann-Merenda-Gold (LMG) metric, providing the fraction of variance explained by each predictor, within the total variance explained by the model.

Our global analysis revealed a moderately strong positive relationship between the biomass fractions of EcM plants and both topsoil and subsoil carbon (Fig. 4, Supplementary Figs. 8 and 9). Consistent with the current paradigm[45], cf. ref. [11], our analysis revealed that biome is the main predictor of soil carbon stocks. Even so, the grid cell biomass fraction of EcM plants still accounted for one third of the explained variation in both topsoil carbon and in subsoil (Table 1). The interaction between biome and EcM biomass fractions was significant ($P < 0.001$) but only marginally important (LMG = 1%), suggesting that the increase in topsoil carbon along with an increase in EcM plant biomass is mostly independent from the environment (Table 1, Fig. 4, Supplementary Figs. 8, 9, Supplementary Table 2). The total aboveground carbon stock stored in the EcM plants was a relatively worse predictor of soil carbon stocks compared with the EcM relative biomass fraction, showing in all cases higher AIC and lower R^2. In contrast to EcM, AM biomass fractions per-grid cell showed negative but inconsistent relationships to soil carbon, with a contrasting positive trend in tundra (Fig. 4, Supplementary Fig. 10). The latter relationship explained only a small amount of variance in tundra soil carbon stocks (12% in top 0–20 cm, 1.7% in 20–60 cm layer and 0.2% in 60–100 cm layer), and could arise from less accurate data of soil C in tundra[47] due to local landscape heterogeneity and prevalence of facultative AM plants with no or low mycorrhizal colonization[48].

Our analysis of the relationships between mycorrhizal type and soil carbon is based on ancillary maps, which feature large uncertainties. Analyses of relationships between ISRIC-WISE predicted soil carbon and the original data that were used to generate the ISRIC soil map yield R^2-values in the range of 0.4–0.6[49,50]. This uncertainty adds ambiguity to our analysis, and reduces the reliability of quantitative estimates of the relationships between EcM plant biomass fractions and soil C. However, these uncertainties equally apply to the analysis of AM vs soil C as well as to that of the EcM vs soil C, due to the fact that the analysis is based on the same geographical data points. Therefore, we consider that the high uncertainty of the ISRIC-WISE soil data is unlikely to affect the qualitative nature of our conclusion that AM and EcM vegetation differently relate to soil C.

Implications. Our work provides the quantitative estimates of the global biomass distribution of arbuscular, ecto-, ericoid and non-mycorrhizal plants, accounting for human-induced transformation of habitats. Previous research has shed light onto the distribution patterns of mycorrhizal plant and fungal species richness[27,28], and onto low-resolution (1 arcdegree) distribution patterns of mycorrhizal trees[51]. In contrast, our maps directly reflect the global distribution of biomass fractions of mycorrhizal plants across all biomes and all main vegetation types. Availability of such data at high resolution of 10 arcmin provides an opportunity for multiple potential analyses aimed at unravelling mycorrhizal impacts on ecosystem functioning at large-geographical scales.

Our maps were derived at spatial resolutions allowing identification of the global patterns of mycorrhizal distributions and are most appropriate for global and large-geographical scale

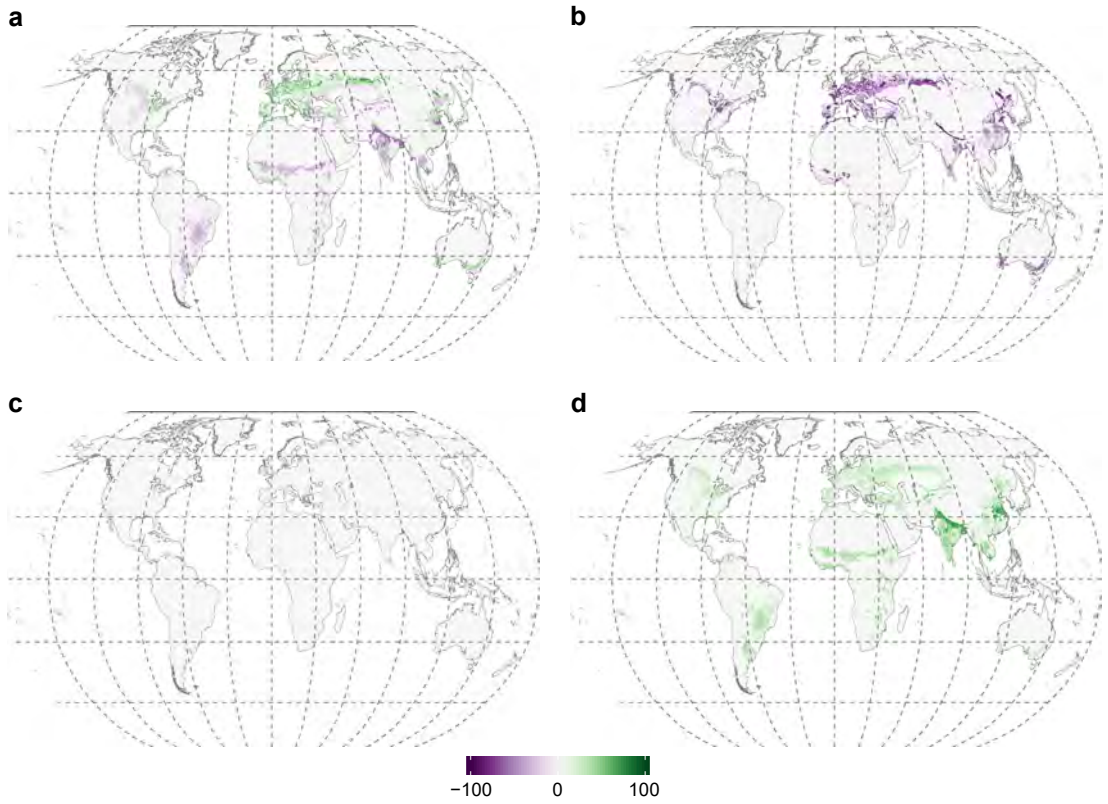

Fig. 3 Changes in biomass fractions of mycorrhizal vegetation induced by crop cultivation and pastures. **a** Arbuscular mycorrhizal plants, **b** ectomycorrhizal plants, **c** ericoid mycorrhizal plants, **d** non-mycorrhizal plants. Purple colours indicate losses, green colours indicate gains. Uncertainties are shown in Supplementary Fig. 7. Source data are provided as a Source Data file

analyses of mycorrhizal impacts on ecosystem functioning and global drivers thereof. Recent estimates suggest that the total soil carbon loss due to agricultural practices accounts for 133 GT, with great acceleration of losses during the past 200 years[52]. Our analyses accounting for pre-agricultural patterns in EcM plant distribution point to large-scale losses of ectomycorrhizal vegetation, with potentially strong effect on the amount of C stored in soils. Analyses of agricultural impacts presented in this paper are based on the assumption that these impacts are limited to shifts in plant species composition, and do not encompass shifts in soil water and nutrient availability, which could affect activity of mycorrhizal fungi, depth distribution of mycorrhizas in the soil, and shifts among mycorrhizal fungal species composition due to the introduction of exotic species. While such simplifications are necessary for the analyses reported in this paper, they should be considered when interpreting our results. Furthermore, our analyses do not address other human impacts that can lead to shifts among AM and EcM vegetation, such as climate change, introduction of invasive species and nitrogen deposition. The latter is known to be an especially important driver of mycorrhizal vegetation shifts[42,53], as it negatively affects abundance of ectomycorrhizal fungi in soil[54]. Given that nitrogen deposition leads to replacement of ectomycorrhizal plants by arbuscular and non-mycorrhizal vegetation, it further enhances agricultural impacts on soil carbon losses.

The question whether increased domination of EcM plants in an ecosystem is associated with higher soil carbon content across both top- and subsoil is heavily debated[11,12,16,18–20,30]. However previous studies have been based on a limited number of observations[11] or regional-scale analyses[11,12,16,53,55]. Our analysis shows that across large geographical scales, higher cover of EcM vegetation is broadly associated with greater soil C stocks in both topsoil and subsoil, while AM vegetation has more variable, weaker and mostly negative relationships. This analysis does not provide evidence of causality of this relationship as multiple environmental variables such as climate, soil nutrients, especially nitrogen availability, and soil texture may affect both soil carbon and mycorrhizal plant distributions. Nonetheless, our study establishes a quantitative framework to test the relation between the dominance of mycorrhizal types and soil C stocks. Complete and directional understanding of the complex nature of the hierarchy of environmental drivers controlling soil carbon patterns requires further detailed (experimental) investigations of the hierarchy of different predictors and importance of local edaphic variables.

Our estimates of the carbon stocks in AM and EcM aboveground biomass together with the quantitative relationships between soil carbon stocks and AM or EcM plant dominance in ecosystems provide qualitative insights into the global carbon cycle, highlighting the substantial role of mycorrhizas therein. Tropical forests, usually dominated by AM symbiosis (Fig. 2), contain 162 GT (44%) of global aboveground biomass[38], whereas the predominately EcM temperate and boreal forests altogether store only 21% of global aboveground biomass carbon[38], indicating that contribution of EcM vegetation to the aboveground biomass carbon is relatively small. In contrast, belowground carbon stocks are positively correlated to the proportion of EcM plant biomass, suggesting that mycorrhizal contribution to large carbon stocks in these regions occurs primarily through the carbon supply to belowground organs and mycorrhizal fungi, which is further emphasized with slowed decomposition processes[22]. Furthermore, our analyses revealed a relatively stronger relationship between soil C and EcM plant biomass fraction (%) than between soil C and the amount of carbon stored

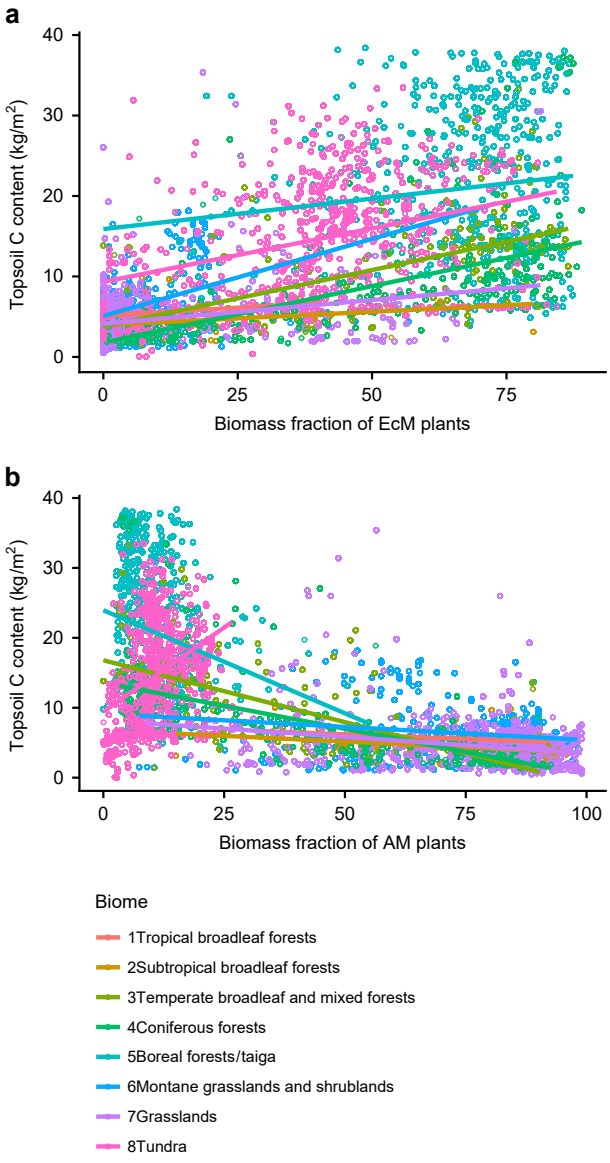

Fig. 4 Quantitative relationships between topsoil (0–20 cm) C and biomass fraction of mycorrhizal vegetation in natural ecosystems. **a** EcM plants and **b** AM plants. The outcomes of individual models are presented in the Supplementary Table 2. Croplands were excluded from the analysis. Per-biome predictions are shown in different colours. Source data are provided as a Source Data file

in EcM plants. These findings suggest that belowground carbon allocation by plants through mycorrhizal pathways is not directly proportional to the aboveground plant biomass, supporting the view of the importance of mutualism-parasitism trade-off in ectomycorrhizal associations[56] across biomes.

Taken together, this study provides a benchmark for relating ecosystem processes to the functioning of distinct types of mycorrhizas on a global scale. So far, quantitative global information about mycorrhizal distribution was virtually absent despite the high demand for such data[12,13,30]. In spite of some uncertainty, our mycorrhizal distribution maps provide an essential source for systematic analyses of mycorrhizal biogeography and environmental drivers. Because our maps are based on field data, and not on a machine-learning model trained with environmental variables, they provide independent data for examining the relationships between mycorrhizal status and ecosystem functioning, without introducing a circular reasoning caused by the use of common environmental variables. Inclusion of mycorrhizal distribution into vegetation models would provide a benchmark for testing hypotheses about mycorrhizal impacts on ecosystem functioning and related ecosystem services. Our maps enable quantifying relationships between mycorrhizal abundances in ecosystems as well as soil and vegetation carbon content in global-scale analyses of biogeochemical cycles. In particular, the results of our study suggest that restoration of native vegetation especially in abandoned agricultural and barren land may help alleviate anthropogenic soil carbon losses and ameliorate increases in atmospheric greenhouse gases.

Methods

Data used for construction of mycorrhizal vegetation maps. To construct the maps of mycorrhizal biomass fraction distribution, we integrated (1) data concerning dominant plant species and their growth forms within each continent × ecoregions × land cover type combination, (2) data describing mycorrhizal type of these species, and (3) data estimating cover and biomass fractions of trees, shrubs and herbaceous plants within individual land cover types. Here we defined a species or a set of species with a similar mycorrhizal strategy and growth form as 'dominant' if it constituted > 20% of vegetation biomass. Supplementary Fig. 1 shows a flowchart of the map assembly process.

We selected the global ecoregion map of Bailey[32] with 98 ecoregions (Supplementary Data 1), provided by the Oak Ridge National Laboratory Distributed Active Archive Center[57] (spatial resolution 10 arcmin), as a basis for mapping of global-scale distribution of mycorrhizal types. This map was preferred over that of biomes provided by Olson and co-workers[46] and others because of higher level of detail for ecoregions and because the boundaries of ecoregions were more strongly related to the distribution of mycorrhizal types. Ecoregions spanning across multiple continents were considered separately for each continent. We used the continent division based upon the FAO Global Administrative Unit Layers (http://www.fao.org/geonetwork/srv/en/).

We determined the land cover types present in each ecoregion using a satellite observation-based map for the year 2015 generated by the European Space Agency[33]. This map includes 38 land cover categories such as croplands, urban areas, grasslands and forests of various types, with a spatial resolution of 300 m (Supplementary Data 2).

Based on vegetation surveys assigned to ecoregions (1568 data sources; Supplementary Data 3) we determined the dominant plant species and their growth form for each continent × ecoregion × land cover type combination. We used relative abundances of plant species averaged across different data points, as available across vegetation surveys, with equal weight to all observations.

We assigned mycorrhizal type (AM, EcM, ErM, NM) to each dominant species using the FungalRoot database[34]. Species with dual EcM-AM and AM-NM categories were allocated to both types equally (50% weight). Mycorrhizal status of species with no empirical records were extrapolated from congeneric and confamilial species. Therefore, all Diapensiaceae and Ericaceae species were considered ErM[58], except for *Enkianthus* (AM), *Arbuteae*, *Pyroleae*, *Monotropeae* and *Pterosporeae* (all subtypes of EcM). Because of multiple incorrect reports and alternative definitions for EcM, we took a conservative approach by considering plants to be EcM only when this was supported by multiple independent studies and the proportion of conflicting reports was < 50%[59]. Although most crop plants are able to form arbuscular mycorrhizas, intensive agricultural practices and breeding may lead to reduction or loss of mycorrhizal infection[40,41]. Therefore, rain fed and flooded croplands were considered to feature partly AM and partly NM vegetation (Supplementary Data 5, 7), unless data indicating dominance of NM vegetation was available. Crop species that belong to *Brassicaceae* family were considered NM.

Combining the prevailing dominant plant species, their growth form and mycorrhizal type, we estimated the biomass proportions of EcM, AM, ErM and NM vegetation in each ecoregion by continent by land cover combination (Supplementary Data 5 and 6). We considered that in forests with a sparse understorey, trees contribute 90–95% of the biomass and the understorey accounts for 5–10% of biomass[36,60–63]. In forests with a dense layer of shrubs, trees, shrubs and herbs/dwarf shrubs contribute 70 ± 15%, 20 ± 10% and 10 ± 5% to plant biomass[36,60–63], respectively. In shrublands, we consider shrubs and herbs to account for 90 ± 5% and 10 ± 5% of biomass, respectively[35,60–63]. We considered that woodlands harbour 30 ± 10% of biomass in trees, 30 ± 10% of biomass in shrubs, and the remaining biomass in herbaceous vegetation[35,60–63]. This resulted in biomass proportions of each mycorrhizal type in continent × ecoregion × land cover type (Supplementary Data 5, 6).

As we focused on the biomass of mycorrhizal plants and not on species diversity; we did not attempt to map the distribution of orchid mycorrhiza. Orchid species are never abundant in ecosystems in terms of biomass, and they are therefore unlikely to play an essential role in biogeochemical cycles at large regional scales.

Table 1 Summary of generalized linear models (glm) predicting soil carbon stocks

Predicted variable	Model	R^2	Predictor	*P*-value	LMG (%)
Topsoil C 0–20 cm	EcM + Biome + EcM × Biome	0.53	EcM	<0.001	42
			Biome	<0.001	57
			EcM × Biome	<0.001	1
Subsoil C 20–60 cm	EcM + Biome + EcM × Biome	0.38	EcM	<0.001	39
			Biome	<0.001	60
			EcM × Biome	<0.001	1
Subsoil C 60–100 cm	EcM + Biome + EcM × Biome	0.33	EcM	<0.001	35
			Biome	<0.001	64
			EcM × Biome	<0.001	1
Topsoil C 0–20 cm	AM + Biome + AM × Biome	0.54	AM	<0.001	38
			Biome	<0.001	56
			AM × Biome	<0.001	6
Subsoil C 20–60 cm	AM + Biome + AM × Biome	0.33	AM	<0.001	29
			Biome	<0.001	67
			AM × Biome	<0.001	2
Subsoil C 60–100 cm	AM + Biome + AM × Biome	0.32	AM	<0.001	31
			Biome	<0.001	67
			AM × Biome	<0.001	2

Predictions are made for C at 0–20, 20–60, and 60–100 cm depth and are based on biome and fraction of EcM or AM plants in vegetation biomass. R^2—Cragg and Uhler's pseudo R^2. LMG—relative importance of individual predictors in a model examined through the Lindemann-Merenda-Gold metric. The LMG shows the percentage of variance explained by each of model predictors within the entire variance explained. The *P* values show the outcome of ANOVA type I models ($n = 78883$ in all models). Source data are provided as a Source Data file

Assembly of raster maps of mycorrhizal vegetation. We generated raster maps based on the proportional mycorrhizal type biomass data. We overlaid the raster map of Bailey ecoregions (10 arcmin resolution)[57] with the raster of ESA CCI land cover data (300 m resolution)[33], which we converted to 10 arcmin using a nearest neighbour approach. The resulting raster was overlain with the polygon map of continents, rasterized at 10 arcmin. To each pixel, we assigned the corresponding mycorrhizal type proportions, considering the prevailing combination of Bailey ecoregion × land cover in each continent. Because some ecoregions covered multiple isolated parts of continents and proportions of mycorrhizal type distribution differed in these regional areas by > 2-fold, we split these ecoregions into two or more subregions using the ArcGIS 10.2.2 Raster Calculator.

Impact of croplands. We estimated the effect of agriculture on mycorrhizal type distribution by substituting the proportions of mycorrhizal types in croplands (land-cover types 10, 11, 12, 20 and 30; see Supplementary Data 2) with estimates of mycorrhizal type proportions from natural land cover types in these ecoregions. For ecoregions naturally harbouring more than one vegetation type (e.g., grasslands, shrublands and forests), we considered that the expected vegetation represents a mixture of these land cover types. This resulted in an additional dataset describing combinations of vegetation as defined by ecoregion × continent × land cover without croplands (Supplementary Data 7 for continent data and Supplementary Data 8 for island data). Maps of potential mycorrhizal type distribution in a cropland-free world (Supplementary Fig. 4) were created based on this dataset, following the aforementioned procedures.

In this analysis, we did not consider forest plantations to be croplands. Therefore, changes in land cover induced by forest restoration through, for instance pine plantations or eucalypt plantations, are not addressed as vegetation changes induced by cropland cultivation. The total area occupied by AM tree plantations exceeds that of EcM tree plantations[64,65] (Supplementary Table 3), suggesting that exclusion of tree plantations leads to conservative estimates of the global reduction of EcM vegetation.

Map validation. The maps of the current distributions of mycorrhizal biomass fractions were validated using the datasets of forest biomass structure for Eurasia[35], global analysis of impacts on mycorrhizas on carbon vs nitrogen dynamics[19], the USA-based analysis of mycorrhizal associations conducted with remote sensing techniques[36], and the map of mycorrhizal root biomass in West Australia by Brundrett[24] (see Supplementary Fig. 2).

The data of forest biomass structure for Eurasia[35] provide information on per-plot tree species abundances for a large number of European sites. As the data contain all records obtained since the 19th century, we used only the data recorded after 1999. Using our database of plant species and associated mycorrhizal types we assigned every tree species with its mycorrhizal type (1344 data points, Supplementary Fig. 2). This provided us with a per-site data of the relative biomass of AM and EcM trees. We used these data as proxies for AM and EcM biomass fractions to compare with the data in our maps. We used the same approach for the data of Lin and co-workers[19], which represent plot-based records of vegetation structure for 100 sites across the globe accompanied with data about plant-mycorrhizal associations.

The dataset of Fisher et al.[36] provides the relative cover of AM and EcM plants from Landsat scenes centred on four sites in USA: Lilly-Dickey Woods (Indiana), long-term research site of Smithsonian Conservation Biology Institute (Virginia), Tyson Research Center Plot (Missouri), and a long-term research site of Wabikon Forest Dynamics (Wisconsin). Given that the dataset comprises forested areas only, we considered areal coverage of AM and EcM plants provides a good estimate of AM and EcM plant biomass. Using this dataset, we directly compared the AM and EcM coverage per pixel with the data of our maps.

In the datasets[19,35,36] biomass and areal fractions of AM and EcM plants are always considered to sum up to 100%. As these datasets do not provide information about non-mycorrhizal and ericoid plants, we estimated these as 5–10% and 0–20%, respectively, depending on the dominant tree association, and accordingly reduced the values of AM and EcM biomass fractions in the validation calculations. While we considered this approach to be acceptable for the validation of AM and EcM data, the data quality is not high enough to validate the NM and ErM maps.

As these three datasets[19,35,36] represent forest data, we evaluated whether all data points or raster cells[36] were indeed located in forest areas. This was done using the ESA land cover categories data[33]. All data points that were located out of the current areas registers by ESA[33] as forests were excluded from the analysis.

The West Australian map of mycorrhizal root abundance[24] provides information about the percentage of total biomass of plant roots featuring AM and EcM root colonization and about the percentage of non-mycorrhizal root biomass. We used this data as a proxy for biomass fractions of AM, EcM and NM plants. In order to quantify the differences between the validation datasets and our maps, we have calculated the Mean Averaged Error (MAE) of the difference between our maps and validation datasets. MAE expresses the deviation between two spatial datasets from the 1:1 line. For AM, EcM and NM vegetation fractions MAE is 18.7%, for EcM it is 13.6%, for NM it is 4.7%, respectively. Due to a virtual absence of information about distribution of solely ErM vegetation, direct validation of the ErM maps was impossible.

To further assess the uncertainties in the maps, we examined which land use classes represent the data points that deviate from the observed data by more than 25% units. Our analysis showed that the large proportion of those deviations (60% for EcM and 40% for AM) fall into those land use classes that represent a poorly described mixture of evergreen or mixed forests and grasslands, i.e. ESA classes described as various forms of "closed to open (>15%) forest" (Supplementary Data 2). Further improvement of the ESA classification data will provide a possibility to improve precision of our maps.

Due to the rarity of datasets on field-examined mycorrhizal vegetation distributions at large special scale we had to validate our datasets used available data on plant species distribution and to accept a number of assumptions and/or recalculations in order to make the data comparable. These adjustments may have affected the quality of the validation dataset and therefore the validation.

Map spatial uncertainty analysis. We quantified the uncertainty in our maps of mycorrhizal vegetation fractions by applying the error propagation rules to the formulas used to calculate the biomass fractions of mycorrhizal plants per-grid cell. For this we used the data provided by refs. [35,60–63] to estimate the uncertainty associated with relative biomass of trees, shrubs, and herbaceous vegetation in each

CCI land cover class. The uncertainty in the proportion of each mycorrhizal type in a given Bailey × continent combination was set to $1/\sqrt{n}$, where $n = b + c/3 + g/20$. In this formula, b is a number of literature sources describing the vegetation composition in a given Bailey ecoregion × continent combination (Supplementary Data 3), while c and g are the numbers of literature sources describing vegetation composition at continent level and global levels, respectively. These latter sources were given less weight, because of their lower spatial explicitness, though these sources were used only if they were providing information relevant for the combination of Bailey ecoregion × continent under consideration. This procedure was applied to the maps of the current distribution of mycorrhizal fractions (Fig. 1) and for the distribution of mycorrhizal fractions in the cropland-free world (Supplementary Fig. 5). The resulting maps of uncertainties are shown in Supplementary Figs. 4 and 6, respectively. We calculated the uncertainties in the estimations of changes in biomass fractions of mycorrhizal vegetation induced by crop cultivation and pastures (Fig. 3) by applying the error propagation rule for the mathematical operation of subtraction. The resulting uncertainty map is shown in Supplementary Fig. 7.

Carbon stocks in the aboveground mycorrhizal biomass. In order to estimate the amount of carbon stored globally in the biomass of plants that belong to different mycorrhizal types, we multiplied the mycorrhizal type biomass fractions by the data of the global distribution of carbon stored in aboveground plant biomass obtained from passive microwave-based satellite observations[38]. As these data have resolution of 15 arcmin, we converted our data of mycorrhizal biomass fractions to this resolution. To calculate the total amount of carbon stored in AM, EcM, ErM and NM plants (illustrated in Fig. 2, and reported per biome in the Supplementary Table 1), we summed the data on carbon stocks per unit area globally and per biome[46].

To assess uncertainty of estimations of carbon storage in mycorrhizal vegetation we used the rule of uncertainty propagation through the operation of multiplication. For this we used the uncertainty of mycorrhizal biomass fraction data and the per biome uncertainty of biomass carbon data, as provided by Liu et al.[38]. Given that the data of carbon stored in vegetation of different mycorrhizal types is a product of two datasets, each featuring a high uncertainty[38], the values of aboveground biomass carbon stored in arbuscular, ecto-, ericoid and non-mycorrhizal vegetation are locally associated with large uncertainties (e.g. Supplementary Table 1). Therefore, we recommend to use these data exclusively for large-scale estimates of biomass carbon storage. However, following the central limit theorem, the uncertainties of the total amount of carbon stored in vegetation of each mycorrhizal type are much lower: 15, 17, 1.8 and 5.5 GT for AM, EcM, ErM and NM vegetation, respectively.

Statistical analysis. We examined whether soil carbon content was related to the biomass fractions of AM and EcM plants, using generalized linear model regressions, with topsoil (0–20 cm) or subsoil (20–60 cm and 60–100 cm) C content per m^2 as a response variable, and biome and ecosystem biomass fraction of AM or EcM plants as predictors. The data for soil carbon content in the top 20 cm of soil were obtained from the ISRIC-WISE Soil Property Databases at a resolution of 30 arcsec[47]. As we were interested in relationships between AM or EcM coverage and soil carbon in natural vegetated environments, we excluded urban and agricultural areas, lakes and "Rock and Ice" areas according to the ESA land cover categories[33], from the analysis. We also excluded wetlands, inundated areas, and extremely dry regions (deserts and Mediterranean areas), because we considered that harsh abiotic conditions instead of biotic interactions are likely to shape biogeochemical cycles in these areas; and we excluded five land cover categories for which our maps showed higher uncertainties, i.e. those where the extent of forest vs grassland cover was unclear. Those land cover categories included "Tree cover, broadleaved, evergreen, closed to open (>15%)", "Tree cover, broadleaved, deciduous, closed to open (>15%)", "Tree cover, needleleaved, evergreen, closed to open (>15%)", "Tree cover, needleleaved, deciduous, closed to open (>15%)" and "Sparse vegetation (tree, shrub, herbaceous cover)".

Data for biome types were obtained from the map of terrestrial biomes[46]. To create a more balanced dataset, we combined all natural grasslands into one single category and all coniferous forests into another single category. To minimize the impacts of imprecise estimations of biome borders we excluded from forest biome areas that we recognized as grasslands according to the ESA land cover data[33]. Similarly, we excluded grassland biome areas that were fully covered by forests and shrubs according to ref. [33]. However, given that AM-EcM-NM interactions are likely to relate to C stocks in the areas featuring forest-grassland and forest-tundra mosaics, we kept such areas in the dataset. As soil carbon content data is known to feature high uncertainties[47], we opted to run the analyses at a resolution of 1 arcdegree, which allow us to grasp large-scale tendencies, while reducing the problem of P-value fallacy[66].

Our models comprised topsoil and subsoil carbon content as a response variable. As predictors, we examined the following combinations of data: (i) biome, biomass fraction of EcM plants, and their interactions, (ii) biome, biomass fraction of AM plants, and their interactions, (iii) biome, amount of carbon stored in the aboveground biomass of EcM plants (product of our EcM map and ref. [38]), and their interactions, and (iv) biome, amount of carbon stored in the aboveground biomass of AM plants (product of our AM map and ref. [38]), and their interactions. All models were examined independently and evaluated based on the Akaike Information Criterion.

In all models, we assessed the total variance explained by the model by R-squared metric and the relative importance of each predictor using the Lindemann, Merenda and Gold (LMG) metric. This metric shows the proportion of variance explained by each of model predictors within the entire variance explained.

Given significant interactions between biome factor and biomass fractions of mycorrhizal plants (Table 1), we fitted generalized linear models with EcM or AM biomass fractions as predictors and topsoil and subsoil C stocks as response variables to the data within individual biomes. The outcome of this analysis is reported in the Supplementary Table 2. As this analysis encompasses considerable errors on both axes of this regression, we have additionally checked if a model II regression would yield qualitatively similar results and confirmed that this was the case (Supplementary Table 4).

Additionally, we examined whether the amount of carbon stored in AM and EcM plants per unit area was a better predictor of soil C stocks than the fractions of AM or EcM biomass per unit area. This analysis was performed in exactly the same manner as the analysis of the impacts of AM and EcM biomass. We assessed the resulting models using the Akaike Information Criterion and R-squared, and detected that these models were worse than the those based on the fractions of AM or EcM biomass per unit area. We also examined how fractions of AM or EcM biomass per unit area, were related to soil C-to-N ratio, and detected that these relationships had a pattern very similar to that of soil C.

Dealing with spatial autocorrelations. The above-described analyses were checked for spatial autocorrelation using a Moran's I metric. These tests revealed a spatial autocorrelation of residuals, which is expected given the nature of our soil and vegetation data with spatial points nested within biomes. We examined how incorporation of a spatial dependence structure affected our models. Accordingly, we ran generalized least square (GLS) models of the same sets of predictors as described in the section "Statistical analysis" of the relationship between soil carbon content and biomass distribution of mycorrhizal types, but included spatial correlation structures. Because calculation of the global spatial autocorrelation matix is computationally intensive, we chose a Monte-Carlo type approach. For each analysis we drew a random sample of 2% of the data points (1624 points) 100 times, taking care that all biomes are included into each sample, and subsequently ran a GLS accounting for autocorrelation structure of the data. For this we used the algorithms proposed by Zuur et al.[67]. The averaged outcomes of these analyses for the relationship between topsoil C, AM, and EcM fractions of vegetation biomass are shown in the Supplementary Table 5. The analyses accounting for autocorrelations yielded the same conclusions as the analyses that did not account for autocorrelations: there is a positive relationship between biomass fraction of EcM plants in vegetation and soil C, and this relationship is biome-independent (non-significant Biome × EcM interaction); in contrast, the relationship between biomass fraction of AM plants in vegetation and soil C was idiosyncratic and biome-dependent.

Including spatial coordinates explicitly in the model, or explicit accounting for autocorrelation matrix, can be problematic to interpret because covariation between spatial coordinates and environmental variables can obscure the interpretation of the relative importance of the predictors[68]. Given that the main goal of our analysis was to detect the global links between AM and EcM dominance and soil C, but not to predict this relationship in new areas or under future climatic scenarios we prioritized the interpretation of the models rather than their predictive power, and therfore report the outcomes of the models that do not account for autocorrelations (Table 1).

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All the authors' data used to create the maps of mycorrhizal vegetation biomass, and all the authors' data underlying figures and tables in the manuscript text and supplementary material are available as Source Date files. All maps presented in this paper have been deposited into the DRYAD Digital Repository at https://doi.org/10.5061/dryad.47d7wm387. All the links to the publicly available datasets used within the process of assembly of the maps of mycorrhizal vegetation, in addition to the authors' data, are provided in the reference list of the paper.

Code availability

All the codes and necessary data files used to the generate maps of mycorrhizal vegetation biomass are available at the GitHub repository at https://github.com/nasoudzilovskaia/Soudzilovskaia_NatureComm_MycoMaps.

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Author contributions

N.A.S. and C.T. generated the idea. N.A.S., P.M.v.B., L.T. and C.T. designed the study, and analysed the data. N.A.S. wrote the paper. N.A.S. and I.M. prepared the figures, with I.M. leading the role. L.T. provided mycorrhizal type assignments to vegetation. C.T., I.M., N.C.d.S. and M.v.Z. performed geoinformatics data processing. M.L.M., J.B.F. and M.C.B. provided data for map validation. All authors contributed to preparation of manuscript drafts.

Competing interests

The authors declare no competing interests.

Additional information

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LETTER

Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice

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Abstract

Apex predators such as large carnivores can have cascading, landscape-scale impacts across wildlife communities, which could result largely from the fear they inspire, although this has yet to be experimentally demonstrated. Humans have supplanted large carnivores as apex predators in many systems, and similarly pervasive impacts may now result from fear of the human 'super predator'. We conducted a landscape-scale playback experiment demonstrating that the sound of humans speaking generates a landscape of fear with pervasive effects across wildlife communities. Large carnivores avoided human voices and moved more cautiously when hearing humans, while medium-sized carnivores became more elusive and reduced foraging. Small mammals evidently benefited, increasing habitat use and foraging. Thus, just the sound of a predator can have landscape-scale effects at multiple trophic levels. Our results indicate that many of the globally observed impacts on wildlife attributed to anthropogenic activity may be explained by fear of humans.

Keywords

Ecology of fear, human impacts, landscape of fear, large-scale field manipulation, playback experiment.

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INTRODUCTION

The fear of predators can itself be powerful enough to drive demographic and community-level changes in wildlife systems, as demonstrated in a growing number of recent experiments (Zanette *et al.* 2011; LaManna & Martin 2016; Suraci *et al.* 2016). The impacts of fear are typically mediated by changes in prey behaviour (Schmitz *et al.* 1997; Brown & Kotler 2004), which may vary spatially with changes in the prey's perception of predation risk across the landscape (Gaynor *et al.* 2019). Anthropogenic activity is reshaping wildlife behaviour across human-dominated landscapes, disrupting movement (Tucker *et al.* 2018), forcing shifts to nocturnality (Gaynor *et al.* 2018) and changing the way predators interact with their prey (Smith *et al.* 2015). Humans are themselves major predators (Darimont *et al.* 2009), killing some species, particularly large and medium-sized carnivores, at many times the rate at which they are killed by non-human predators (Darimont *et al.* 2015), and fear of the human 'super predator' (Darimont *et al.* 2015) may therefore be a significant driver of observed changes in wildlife behaviour (Oriol-Cotterill *et al.* 2015; Suraci *et al.* 2019). Given that humans have evidently superseded large carnivores as apex predators in many ecosystems (Ordiz *et al.* 2013a; Oriol-Cotterill *et al.* 2015; Kuijper *et al.* 2016), our mere presence may be expected to generate landscapes of fear (Gaynor *et al.* 2019) with spatial extents and breadth of trophic impacts equal to or greater than those presently attributed to large carnivores (Laundré *et al.* 2001; Palmer *et al.* 2017). Yet, whether fear of the human 'super predator', or indeed any large apex predator, generates landscapes of fear with impacts across wildlife communities remains to be tested experimentally.

A large number of correlative studies suggest that some wildlife species respond fearfully to human activity (Fernandez-Juricic *et al.* 2005; Stankowich & Blumstein 2005; Bateman & Fleming 2017), but whether such responses are driven by perceived risk from humans as predators or by a generalised response to 'disturbance' (e.g. sudden noises, looming objects) is often unclear (Frid & Dill 2002; Stankowich 2008). Experimentally testing predator-specific responses requires manipulating something the prey is likely to perceive as being specific to that predator (e.g. vocalisations, odours) in conjunction with a non-predator-specific control for the generalised disturbance potentially caused by manipulations. Recently, small-scale ($\leq$ 50 m), short-term ($\leq$ 2 h) controlled experiments on single prey species have demonstrated that wildlife regularly killed by humans exhibit strong fear responses to human vocalisations, just as prey respond fearfully to the vocalisations of any other predator (Hettena *et al.* 2014; McComb *et al.* 2014; Clinchy *et al.* 2016; Smith *et al.* 2017). By isolating human predator-specific responses, such experiments differentiate the impacts of fear of humans as predators from the myriad other aspects of the anthropogenic environment likely to affect wildlife behaviour [e.g. enhanced food resources, habitat fragmentation (Bateman & Fleming 2012; Newsome *et al.* 2015; Tucker *et al.* 2018)]. By scaling up such experiments, we can thus quantify how the fear of humans as predators impacts wildlife at the landscape and community levels.

To experimentally test whether the magnitude of effects caused by fear of an apex predator (in this case humans) can extend to having landscape-scale impacts across wildlife communities, we conducted spatially replicated, landscape-scale manipulations of perceived human presence. We sequentially

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broadcast playbacks of people talking or control sounds for 5 weeks (followed by the opposite treatment for a subsequent 5 weeks) over spatial scales (1 km^2) comparable to those of the largest mammalian predator exclusion experiments (Salo *et al.* 2010), and simultaneously quantified the responses of multiple mammal species across three trophic levels. The study was conducted in the Santa Cruz Mountains of central California. Like an increasingly large proportion of the planet (Venter *et al.* 2016), this region consists of wildlife habitat in close proximity to urban and suburban development, and is thus heavily used by people (Wang *et al.* 2015). The Santa Cruz Mountains support a single native large carnivore, the mountain lion (*Puma concolor*), and several smaller predators (for brevity, referred to as 'medium-sized carnivores') including bobcats (*Lynx rufus*), striped skunks (*Mephitis mephitis*) and Virginia opossums (*Didelphis virginiana*), all of which have been shown to alter their behaviour in response to the gradient of human development that exists across the region (Wilmers *et al.* 2013; Wang *et al.* 2015). Small-scale experiments replicated across this region previously demonstrated that mountain lions here exhibit strong fear responses to hearing human voices, fleeing food caches and feeding less as a consequence (Smith *et al.* 2017). Medium-sized carnivores similarly exhibited fear-induced reductions in feeding and shifts in temporal activity in response to the small-scale experimental presentation of human voices (Clinchy *et al.* 2016). As is true for large and medium-sized carnivores globally (Ordiz *et al.* 2013a; Darimont *et al.* 2015), humans are a major source of mortality for mountain lions in our study area, with legal and illegal shooting accounting for 59.1% of known-cause mortalities of collared animals since 2008 (C. Wilmers, *unpublished data*). Bobcats, skunks and opossums are all common targets of predator control (Conner & Morris 2015), and are all legally hunted in California, with no legal limits on killing skunks and opossums (California Department of Fish & Wildlife 2018). Correlational results from our study area indicate that bobcats are sensitive to risk from humans, decreasing diurnal activity in areas of high human development, but suggest that skunks and opossums may prefer more developed areas (Wang *et al.* 2015). Medium-sized carnivores such as skunks and opossums often rely heavily on human subsidies, including food waste (Bateman & Fleming 2012), and thus could be forced to balance the risk of anthropogenic mortality against the benefits of living near humans.

Given the evidence that carnivores fear humans as predators, both in our study area and in general, our objective was to experimentally test whether such fear leads to landscape-scale impacts across wildlife communities. We quantified the large-scale effects of fear of humans as predators on carnivore movement, activity and foraging behaviour using GPS collars (mountain lions) and camera traps (bobcats, skunks and opossums). Correlational studies suggest that fear-induced suppression of carnivore behaviour by apex predators may cascade to benefit small mammal prey (Brook *et al.* 2012; Gordon *et al.* 2015), although this has yet to be shown experimentally. We therefore additionally tested whether the fear that humans induce in carnivores can have cascading effects on the behaviour of lower trophic level animals, using live trapping and provisioned food patches to document effects on habitat use and foraging by small mammals (deer mice *Peromyscus* spp. and woodrats *Neotoma fuscipes*) known to be preyed upon by several of the carnivores in our study (Azevedo *et al.* 2006; Smith *et al.* 2018).

In a major reclarification of the landscape of fear concept, Gaynor *et al.* (2019) define it as spatial variation in the prey's perception of predation risk, influenced by, but distinct from, both the physical landscape and actual risk of mortality from predators. Here, we use the sequential presentation of human and control vocalisations at each of our 1-km^2 sites to manipulate the perception of predation risk across the same physical landscapes, thus keeping physical characteristics and actual mortality risk constant. We thereby experimentally demonstrate that a landscape of fear, resulting solely from variation in the perception of risk from an apex predator, can have pervasive effects across wildlife communities. That such effects can result from the fear of humans as predators indicates that this may be an important factor underlying many of the globally observed changes in wildlife behaviour associated with anthropogenic activity (Gaynor *et al.* 2018; Tucker *et al.* 2018).

METHODS

Study area

The study was conducted at two 1-km^2 experimental sites (SA and SVR), separated by 26 km (Fig. S1). Both sites were closed to public access, and human presence was therefore low relative to elsewhere in the Santa Cruz Mountains. The presence of humans (including researchers) and vehicles did not differ between experimental sites during the study (Mann–Whitney *U*-test comparing occurrences per camera night on $n = 12$ cameras per site; humans: $P = 0.643$; vehicles: $P = 0.655$). Work was conducted between 29 May and 31 August 2017.

For additional details on the study area and species, see Appendix S1. All procedures described below were approved by the Institutional Animal Care and Use Committee of the University of California, Santa Cruz (Protocol WilmC1612) and the California Department of Fish and Wildlife (Permits SC-11968 and SC-12383).

Playbacks and study design

We manipulated the perceived presence of humans on the landscape using playbacks of human and control vocalisations broadcast sequentially for 5 weeks each at both 1-km^2 experimental sites. Following established protocols (Suraci *et al.* 2016; Smith *et al.* 2017), we compared wildlife responses to human vocalisations with responses to Pacific treefrog (*Pseudacris regilla*) vocalisations. Tree frogs, like humans, can be heard both day and night in our study area, but unlike humans, their perceived presence should be completely benign given that treefrogs are unlikely to be predators, competitors or prey of any study species. As discussed in detail in Appendix S1 (Supplementary Methods – Playback Treatments), there is ample evidence to suggest that wildlife in the

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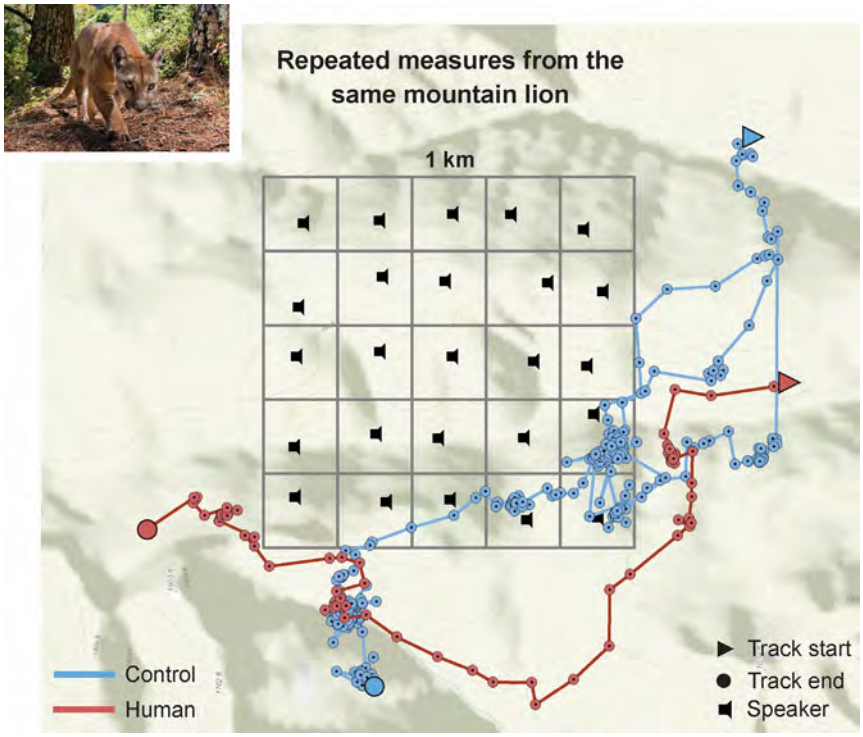

Figure 1 Example of the landscape-scale impacts of fear of humans on mountain lion behaviour, illustrated by repeated-measures movement tracks from a single mountain lion during the control (blue) and human (red) treatments. Points are 5-min GPS fixes, and connecting lines illustrate the approximate movement path. Black speaker icons denote playback speaker locations and the grey grid illustrates the 1-km^2 experimental site. Photo © Sebastian Kennerknecht.

Santa Cruz Mountains will be familiar with both human and tree frog vocalisations.

Playbacks were broadcast from 25 speakers arranged in a 5 × 5 grid at each experimental site (Fig. S1). Each speaker played a randomised playlist of human or frog recordings (n = 10 exemplars of each) interspersed by silence such that each individual speaker was broadcasting 40% of the time and silent 60% of the time. Speakers were thus continuously active, but presentation of cues was random and sporadic across the playback grid. The human treatment thereby mimicked a wildland–urban interface in that human vocalisations were relatively infrequent, but from any location within the playback grid, a human could occasionally be heard at any time. All playbacks were broadcast at a standardised volume of ~ 80 dB at 1 m (human = 78.7 dB ± 1.9 SD; frog = 79.2 dB ± 2.4). Additional details of the playback treatments are provided in Appendix S1.

We employed a repeated-measures design with each experimental site receiving either the human or control treatment for 5 weeks (treatment period 1), followed by the opposite treatment for a subsequent 5 weeks (treatment period 2) with 8 days of silence between the two treatment periods. Thus, both experimental sites received each treatment in opposite order, and as such, detecting consistent responses to playback treatments across sites is critical to concluding that treatments had a significant effect. We therefore included a test for treatment × site interaction in all analyses presented below and only concluded that treatments drove observed changes when no significant interaction was detected (see Tables S1–S8). We also present visualisations of site-level data for all analyses (Figs S2–S7) to illustrate the consistency of treatment effects across sites.

Monitoring mountain lion responses to playbacks

We monitored the responses of seven mountain lions (four females and three males) whose home ranges overlapped one of our two experimental sites. Five individuals (four females and one male) used SVR, while two males used SA. Mountain lions were captured using trailing hounds or cage traps and fitted with GPS collars (GPS Plus, Vectronics Aerospace, Berlin, Germany) with a 5-min fix interval.

We focused mountain lion movement analyses on only those periods when an individual was within audible range of a playback grid (termed an 'encounter' with the playbacks) and used a repeated-measures design to compare responses of individual mountain lions to both playback treatments (Fig. 1). We considered the audible range of the speakers to extend 200 m out from the speaker grid itself (see Appendix S1), and also ran all analyses using a smaller buffer size (150 m), which yielded similar results. Five mountain lions encountered the playbacks on multiple occasions, with subsequent encounters separated by 19.1 days on average (range = 4.6–38.6 days). The median number of encounters per individual was 2 (range = 1–5; total encounters across all individuals = 17).

For all mountain lion GPS locations taken within the 200 m audible range, we determined the distance to the

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nearest playback speaker and the animal's movement speed. For each encounter, we then calculated average distance to the nearest speaker (an estimate of speaker avoidance) and average movement speed across all locations for that encounter. We took the inverse of movement speed as an estimate of 'cautiousness', moving more slowly being considered greater cautiousness. We tested for effects of playback treatment, experimental site and a treatment × site interaction on avoidance and cautiousness using linear mixed-effects models (LMM), with mountain lion ID as a random effect. Cautiousness (movement speed^{-1}) was log-transformed to meet normality assumptions. Unless otherwise noted, we confirmed adequate fit of these and all other frequentist models through visual inspection of residuals and assessed significance of model terms using Type II Wald's chi-squared tests (Table S1). Finally, we confirmed that observed changes in medium-sized carnivore behaviour between treatments (see below) were not due to changes in mountain lion presence by testing for differences in time spent by mountain lions near experimental sites (see Appendix S1 and Table S1 for details).

Medium-sized carnivore responses to playbacks

At each experimental site, we deployed a grid of 12 camera traps, which ran continuously throughout the experiment (camera deployment details in Appendix S1). We scored camera trap images for the presence of three medium-sized carnivore species that occurred at both experimental sites, which prior correlational research in the region indicates are affected by human development (Wang *et al*. 2015): bobcats, striped skunks and Virginia opossums. We considered images of the same species on the same camera to be separate detections if they were separated by > 30 min (Wang *et al*. 2015; Suraci *et al*. 2017). Two other medium-sized carnivore species (raccoons *Procyon lotor* and gray foxes *Urocyon cinereoargenteus*) occasionally occurred on camera traps, but were detected too infrequently to permit statistical analyses, raccoons only occurring on three cameras at one site and foxes only during a subset of treatment periods.

Bobcat temporal activity

Prior research (Wang *et al*. 2015) shows that, whereas bobcats are diurnally active 29.6% of the time, skunks and opossums are almost exclusively nocturnal (94 and 96.6% nocturnality respectively). We therefore tested whether playback treatments affected temporal activity for bobcats, the only species with sufficient diurnal activity to expect an effect. We calculated the overlap between temporal activity during control and human treatments using the kernel density estimation procedure described by Ridout and Linkie (Ridout & Linkie 2009; Linkie & Ridout 2011). We estimated probability density distributions for bobcat occurrences on camera across the 24-h day separately for the control and human treatment periods. We then calculated the coefficient of overlap ($\hat{\Delta}$, range 0–1) between these two activity distributions (Ridout & Linkie 2009), along with 95% CIs (via 10 000 bootstrap replicates (Linkie & Ridout 2011)) using the overlap package in R (Meredith & Ridout 2014). We calculated overlap separately for each experimental site and then with data from both sites pooled. We considered there to be evidence of a change in temporal activity if overlap in activity distributions during control and human treatment was < 0.90.

Bobcats exhibited a consistent shift in temporal overlap between human and control treatments across both experimental sites (Table S2). We therefore quantified the degree to which this temporal shift constituted a reduction in diurnal activity in favour of nocturnality during the human treatment. For each bobcat detection on camera (n = 44 on 12 cameras), we calculated the absolute value of the difference (in hours) between the timestamp of the detection and the middle of the night (the midpoint between sunset and sunrise, averaged across the study period; 01:15) such that detections near midday received the highest values of this diurnal activity metric. We tested for the effects of playback treatment, experimental site and a treatment × site interaction on diurnal activity using LMM with camera site as a random effect.

Modelling medium-sized carnivore occupancy and detection frequency at camera sites

To test whether fear of humans affected medium-sized carnivore behaviour at the landscape scale, we developed a hierarchical model describing (1) use by a given species of individual camera sites within each experimental site and (2) frequency of detections of that species at used camera sites, a proxy for activity level. We based our model on multispecies occupancy models (Burton *et al*. 2012; Broms *et al*. 2016), but with two distinctions: (1) we consider camera site use (rather than occupancy *per se*), as individual carnivores could use more than one camera site, and (2) we modelled the frequency of detections of a given species at a camera site (a Poisson process), rather than the binary estimate of detected/not detected typically used in occupancy models. We treated each week of the experiment as a survey period (Wang *et al*. 2015; Moll *et al*. 2018), yielding five replicate surveys per treatment at each camera site. Three data points were excluded from the analysis when cameras failed to record data for the full week. We formulated our analysis as a zero-inflated negative binomial model (Moll *et al*. 2018), allowing occupancy at a camera site (binomial submodel) to vary between playback treatments, and explicitly modelling detection frequency (negative binomial submodel) as a function of experimental site, playback treatment and their interaction. We analysed the hierarchical detection frequency model in a Bayesian framework using the JAGS language (Plummer 2003) via the R2jags package (Su & Yajima 2015) in R. For a full model description and details on the Bayesian analysis (including JAGS code and model fit), see Appendices S1 and S2. Model results are present in Tables S3 and S4.

The above model indicated a substantial reduction in skunk detection frequency during the human treatment at both sites. To confirm the robustness of this result, we performed a simplified version of the analysis, using a Wilcoxon matched-pairs test to compare total skunk detections during the human and control treatments on each camera.

Medium-sized carnivore foraging trials

We created feeding patches (consisting of a single boiled chicken egg) at each of the 12 camera locations within each

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experimental site. We estimated patch discovery rate (i.e. days required for a medium-sized carnivore to find and consume the egg, determined from camera trap images) as an index of carnivore foraging efficiency. Eggs were set out twice during each treatment period (during weeks 2 and 4), yielding a total of 96 trials. To standardise availability, we consider only those trials in which a medium-sized carnivore ultimately discovered the patch ($n = 36$), as some eggs were taken by other species (e.g. corvids) before being discovered by carnivores. Discovery rate data were log-transformed to satisfy normality assumptions and fit by LMM, using camera site as a random effect. We tested for effects of treatment, experimental site, species, session (first or second deployment during each treatment), and treatment × site interaction. Opossums made the majority of foraging patch discoveries ($n = 20$) and skunks made the remainder ($n = 16$), with no discoveries made by bobcats. We first analysed data from opossums and skunks combined, and then fit species-specific models, using the model terms just mentioned with the exception of species (Table S5).

Deer mouse spatial capture–recapture

We conducted a spatial capture–recapture study using four grids of live traps at each experimental site. Grids were trapped immediately prior to the start of any playbacks, and immediately following each playback treatment period. All captured mice were marked with unique ear tags. See Appendix S1 and Fig. S1 for live trapping details. We analysed live trapping data using spatial capture–recapture (SCR) models (Royle *et al*. 2013), which permit quantification of the amount of space used by individual animals (σ in SCR models; Appendix S1 and (Royle *et al*. 2013)). We modelled spatially explicit capture histories using a zero-inflated binomial model with data augmentation (Royle & Dorazio 2008; Royle *et al*. 2013). Detection probability and/or space use could be affected by playback treatment if mice alter their movements in response to treatment-induced changes in carnivore behaviour. We estimated the effect of playback treatment on detection probability and space use by calculating averages of these parameters (across all trapping grids) for trapping sessions following the control and human treatments. Treatment-level averages were then subtracted to estimate the average difference in parameter values between control and human treatments. If the 95% credible intervals (CrI) of the difference between treatments did not cross zero, we considered there to be evidence of a treatment effect on the parameter of interest (Table S6). Average values (± 95% CrI) of the space use parameter (σ) during each treatment were used to calculate the average area of habitat used during each treatment, following the procedure outlined by Royle *et al*. (2013, pg. 136). For a full description of the deer mouse SCR model and the Bayesian analysis of this model, see Appendices S1 and S2. Model results are presented in Tables S6 and S7.

Small mammal foraging trials

Two small mammal foraging patches, separated by < 3 m, were deployed at each of the 12 camera locations within each experimental site, one under protective cover (shrubs) and one in the open. Each patch consisted of an aluminium tray filled with 10 g of millet seed mixed into 1 l of sifted sand. Patches thus required time to exploit, allowing time for the accumulation of camera trap images and/or small mammal droppings in trays. Patches were deployed twice during each 5-week treatment period (during weeks 2 and 4) and were left in place for two consecutive nights, with millet and sand refreshed after the first night. We focus our analyses on the proportion of available patches visited on a given night and include only those trials in which visitation or lack thereof by small mammals (deer mice or woodrats) could be determined with high confidence based on the presence or absence of camera trap images and/or droppings ($n = 256$). Preliminary analysis indicated that open patches were largely avoided overall (Appendix S1, Table S8). We therefore restricted our analysis to patches under cover.

We coded whether a particular patch was visited (1) or not (0), and analysed these data using a generalised LMM with binomial error distribution, including camera site as a random effect. We tested for effects of treatment, experimental site, night (first or second night of patch deployment), moon illuminance and a treatment × experimental site interaction. Adequate model fit was assessed through inspection of scaled residuals using the DHARMa R package (Harting 2018).

RESULTS

Fear of humans drove significant changes in how mountain lions moved through the same physical landscape (Fig. 1). Mountain lions avoided areas of perceived human presence, encountering the playback grids 30% less often when human sounds were broadcast, and maintaining a 29% greater distance to the nearest speaker during human playbacks relative to controls (Figs. 2a and S2; LMM: Wald's $\chi^2_1 = 6.33$, $P = 0.012$). Mountain lions also moved more cautiously when hearing human playbacks, reducing average movement speed by 34% (Figs 2a and S2; LMM: Wald's $\chi^2_1 = 4.66$, $P = 0.031$).

Fear of humans had an overall suppressive effect on medium-sized carnivore behaviour (Fig. 2b). Bobcats reduced diurnal activity by 31% when hearing humans (Figs. 2b and S3; Table S2; LMM: Wald's $\chi^2_1 = 4.71$, $P = 0.030$), shifting their diel activity patterns towards increased nocturnality [overlap ($\hat{\Delta}$) in activity between treatment and control = 0.68 (95% CI: 0.48–0.86); Fig. S8]. Skunks were the only species to exhibit a reduction in overall activity (Table S4), reducing activity levels by 40% during the human treatment [Figs. 2b and S4; detection frequency model: treatment coefficient = −1.12 (95% CrI: −2.37 to −0.04)], and were therefore detected less frequently on camera traps (Wilcoxon test, $P = 0.007$; $n = 24$). When considering all trials in which a medium-sized carnivore discovered a provisioned food patch, fear of humans had a significant negative effect on food patch discovery rate (Table S5; LMM: Wald's $\chi^2_1 = 5.88$, $P = 0.015$). Species-specific models indicated that this effect was largely driven by opossums. The sound of humans led to a 66% reduction in opossum foraging efficiency (Figs. 2b and S5;

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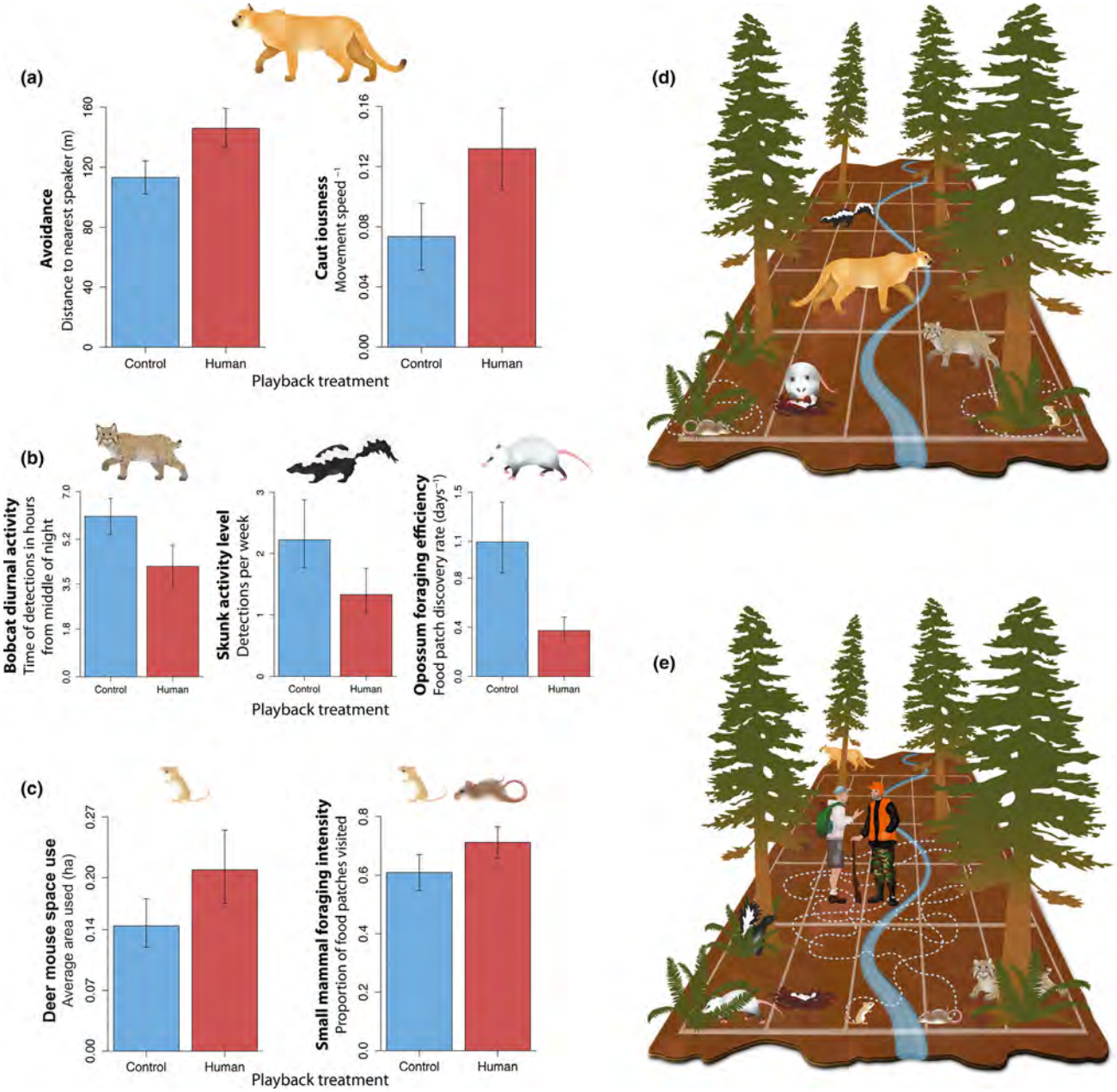

Figure 2 Fear of humans has landscape-scale impacts on wildlife across multiple trophic levels. (a) Fear of humans affects mountain movement behaviour. Mountain lion avoidance behaviour (left panel) is shown as average distance (m) to the nearest playback speaker and cautiousness (right panel) is shown as the inverse of average movement speed (mins/m). Bar plots illustrate means ± SEM. $N = 10$ control and 7 human. (b) Fear of humans suppresses medium-sized carnivore behaviour. Bobcat diurnal activity from camera trap detections (left panel; means ± SEM; $n = 26$ control and 18 human) is shown as time (h) from the middle of the night. Skunk overall activity level (middle panel) is shown as posterior mean and 95% credible intervals for number of detections per week on camera traps. Opossum foraging efficiency (right panel; means ± SEM; $n = 10$ control and 10 human) is shown as rate of discovery (days^{-1}) of provisioned food patches. (c) Suppression of larger predators induced by fear of humans benefits small mammals. Deer mouse space use (left panel) is shown as posterior mean and 95% credible intervals of average area (ha) used. Small mammal (deer mouse and woodrat) foraging intensity (right panel; mean ± SEM; $n = 64$ control and 73 human) is shown as proportion of provisioned food patches visited on a given night. All bar plots illustrate behaviours during control (blue) and human (red) playback treatments. (d) and (e) conceptual illustrations of the landscape-scale effects of fear of humans on wildlife communities. Where the human apex predator is absent or rare (d), large and medium-sized carnivores exhibit greater movement (mountain lion on grid), activity (bobcats and skunks active) and foraging (opossum eating a bird nest), while small mammals exhibit reduced space use (constricted movement paths, shown as dashed lines). Where humans are present (e), fear of humans suppresses the activity, foraging and/or habitat use of large and medium-sized carnivores, while small mammals increase their total space use and foraging intensity. Original artwork by Corlis Schneider.

Table S5; LMM: Wald's $\chi^2_1 = 8.77$, $P = 0.003$) such that opossums took on average 1.8 days longer to discover food patches during the human treatment.

Small mammals benefitted from the apparent presence of humans, increasing both the amount of habitat and number of foraging opportunities exploited. During the human

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treatment, deer mice expanded their space use by 45% relative to controls (Figs. 2c and S6), increasing average area used by 649 m^2 (95% CrI = 116–1209 m^2) while maintaining an overall consistent detection probability across treatments (Tables S6 and S7). Mice and woodrats increased foraging intensity by 17% during the human treatment (Fig. 2c, Table S8; GLMM: Wald's $\chi^2_1 = 4.71$, $P = 0.030$), visiting a significantly higher proportion of provisioned food patches (Figs. S7 and S9).

DISCUSSION

Our results experimentally demonstrate that fear of humans as predators can have pervasive impacts across wildlife communities, suppressing movement and activity of large and medium-sized carnivores, with cascading benefits for small mammals (Fig. 2d and e). Thus, spatial variation in the perception of risk from an apex predator can itself create a landscape of fear (Gaynor *et al*. 2019), manifesting in widespread changes in wildlife behaviour.

Mountain lions significantly altered their movement through the same physical landscape in response to hearing humans (Fig. 1), exhibiting antipredator behaviours comparable to those previously documented in small-scale experiments (Smith *et al*. 2017), but at a substantially larger scale (Fig. 2a). Observational and manipulative studies have similarly found that risk from humans affects large carnivore behaviour across the landscape (Valeix *et al*. 2012; Ordiz *et al*. 2013b, 2019; Oriol-Cotterill *et al*. 2015; Suraci *et al*. 2019), including in our study area, where increased human development is correlated with impacts on mountain lion movement and habitat use (Wilmers *et al*. 2013; Wang *et al*. 2017). Our results confirm that, even in the absence of changes in human infrastructure (e.g. buildings, roads) or habitat fragmentation, increased human presence can impact large carnivore movement by inducing antipredator responses, which, if sustained for long periods, could lead to effective habitat loss for carnivores by limiting hunting and feeding behaviour (Smith *et al*. 2015) or forcing individuals to abandon high risk areas of their home range (Schuette *et al*. 2013).

Fear of humans had suppressive effects on medium-sized carnivore activity across all three study species (Fig. 2b), yet as expected from the diversity of carnivore behaviours, their exact responses differed. Our experimental results confirm previous correlational findings (Wang *et al*. 2015) that bobcats become more nocturnal in response to human presence, demonstrating that fear of humans may contribute to the documented global pattern of increased wildlife nocturnality in disturbed habitats (Gaynor *et al*. 2018). Fear of humans also impacts skunks and opossums, causing reductions in overall activity or foraging behaviour by these often human-associated species. These results highlight the trade-off such species face between the potential benefits of living in an anthropogenic environment [e.g. abundant food subsidies (Bateman & Fleming 2012; Newsome *et al*. 2015)] and the fear-induced costs of sharing habitat with humans (Fig. 2b). Interestingly, none of the three medium-sized carnivores exhibited changes in overall habitat use between treatments (number of camera sites used; Tables S3), potentially reflecting a limited capacity to do so, at least for species (i.e. skunks and opossums) whose relatively small home ranges likely overlapped substantially with our experimental sites (Appendix S1).

Finally, significant increases in small mammal space use and foraging documented during the human playback treatment (Fig. 2c) experimentally demonstrate that the suppression of carnivore behaviour induced by fear of an apex predator (in this case, humans) can have cascading effects on small mammal prey (Brook *et al*. 2012; Gordon *et al*. 2015). These cascading behavioural changes suggest that the presence of people may in some cases act as a 'human shield' (Berger 2007) for small mammals, reducing their perceived risk of predation from carnivores. Human shield effects have been suggested to occur in some large carnivore-ungulate systems, with ungulates preferring areas of high human activity because these areas are avoided by carnivores (Hebblewhite *et al*. 2005; Berger 2007; Muhly *et al*. 2011). If similar human shield effects for small mammals are common where human activity is high, this could ultimately lead to increased small mammal abundance in wildlife areas frequented by people, a potentially undesirable consequence of ecotourism (Geffroy *et al*. 2015).

Our work provides strong evidence that many of the globally observed changes in wildlife behaviour stemming from anthropogenic activity, including changes in large carnivore habitat use (Valeix *et al*. 2012), broader disruptions of animal movement (Tucker *et al*. 2018), and increased nocturnality (Gaynor *et al*. 2018), can be explained in part by the fear of humans as predators. Moreover, if fear of humans triggers substantial sublethal effects comparable to those fear itself has been demonstrated to cause in other predator–prey systems [e.g. increased physiological stress (Zanette *et al*. 2014), reduced reproductive success (Zanette *et al*. 2011; Cherry *et al*. 2016)], this may translate to additional widespread but largely unmeasured impacts of humans on wildlife populations. Given the potential for sublethal effects, apparently 'human-tolerant' species (e.g. medium-sized carnivores using developed areas) could nonetheless experience substantial costs from chronic exposure to perceived risk from humans (Clinchy *et al*. 2016). Pervasive fear of humans may also precipitate widespread community-level changes by disrupting natural predator–prey interactions. Human-induced antipredator behaviour could compromise top-down ecosystem regulation by large carnivores (Kuijper *et al*. 2016) and limit medium-sized carnivore suppression of small mammals (Levi *et al*. 2012). Given continued human encroachment into most wildlife habitats (Venter *et al*. 2016), we suggest that the fear we human 'super predators' inspire, independently of our numerous other impacts on the natural world, may contribute to widespread restructuring of wildlife communities.

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AUTHORSHIP

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DATA AVAILABILITY STATEMENT

Data available from the Figshare Repository: https://doi.org/10.6084/m9.figshare.8315417

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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HUMAN INFLUENCE ON CALIFORNIA FIRE REGIMES

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Abstract. Periodic wildfire maintains the integrity and species composition of many ecosystems, including the mediterranean-climate shrublands of California. However, human activities alter natural fire regimes, which can lead to cascading ecological effects. Increased human ignitions at the wildland–urban interface (WUI) have recently gained attention, but fire activity and risk are typically estimated using only biophysical variables. Our goal was to determine how humans influence fire in California and to examine whether this influence was linear, by relating contemporary (2000) and historic (1960–2000) fire data to both human and biophysical variables. Data for the human variables included fine-resolution maps of the WUI produced using housing density and land cover data. Interface WUI, where development abuts wildland vegetation, was differentiated from intermix WUI, where development intermingles with wildland vegetation. Additional explanatory variables included distance to WUI, population density, road density, vegetation type, and ecoregion. All data were summarized at the county level and analyzed using bivariate and multiple regression methods. We found highly significant relationships between humans and fire on the contemporary landscape, and our models explained fire frequency ($R^2 = 0.72$) better than area burned ($R^2 = 0.50$). Population density, intermix WUI, and distance to WUI explained the most variability in fire frequency, suggesting that the spatial pattern of development may be an important variable to consider when estimating fire risk. We found nonlinear effects such that fire frequency and area burned were highest at intermediate levels of human activity, but declined beyond certain thresholds. Human activities also explained change in fire frequency and area burned (1960–2000), but our models had greater explanatory power during the years 1960–1980, when there was more dramatic change in fire frequency. Understanding wildfire as a function of the spatial arrangement of ignitions and fuels on the landscape, in addition to nonlinear relationships, will be important to fire managers and conservation planners because fire risk may be related to specific levels of housing density that can be accounted for in land use planning. With more fires occurring in close proximity to human infrastructure, there may also be devastating ecological impacts if development continues to grow farther into wildland vegetation.

Key words: California, USA; fire; fire history; housing density; nonlinear effects; regression; wildland–urban interface.

Introduction

Fire is a natural process in many biomes and has played an important role shaping the ecology and evolution of species (Pyne et al. 1996, Bond and Keeley 2005). Periodic wildfire maintains the integrity and species composition of many ecosystems, particularly those in which taxa have developed strategic adaptations to fire (Pyne et al. 1996, Savage et al. 2000, Pausas et al. 2004). Despite the important ecosystem role played by fire, human activities have altered natural fire regimes relative to their historic range of variability. To develop effective conservation and fire management strategies to deal with altered fire regimes, it is necessary to understand the causes underlying altered fire behavior and their human relationships (DellaSalla et al. 2004). Nowhere is this more critical in the United States than in California, which is the most populous state in the nation, with roughly 35×10^6 people. Most of the population lives in lower elevations dominated by hazardous chaparral shrublands susceptible to frequent high-intensity crown fires.

In California, as elsewhere, the two primary mechanisms altering fire regimes are fire suppression, resulting in fire exclusion, and increased anthropogenic ignitions, resulting in abnormally high fire frequencies (Keeley and

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Fotheringham 2003), though climate change, vegetation manipulation, and other indirect factors may also play a role (Lenihan et al. 2003, Sturtevant et al. 2004). For most of the 20th century, fire suppression effectively excluded fire from many western U.S. forest ecosystems, such as ponderosa pine. In these ecosystems, fire exclusion contributed to unnatural fuel accumulation and increased tree density (Veblen et al. 2000, Allen et al. 2002, Gray et al. 2005). Recently, when wildfires have hit many of these forests, hazardous fuel loads have contributed to high-intensity crown fires that are considered outside the historical range of variability (Stephens 1998). While these patterns are widely applicable to many forested landscapes in the western United States, California chaparral shrublands have experienced such substantial human population growth and urban expansion that the increase in ignitions, coupled with the most severe fire weather in the country (Schroeder et al. 1964), have acted to offset the effects of suppression to the point that fire frequency exceeds the historic range of variability (Keeley et al. 1999). Because anthropogenic ignitions tend to be concentrated near human infrastructure, more fires now occur at the urban fringe than in the backcountry (Pyne 2001, Keeley et al. 2004). Profound impacts on land cover condition and community dynamics are possible if a disturbance regime exceeds its natural range of variability, and altered fire regimes can lead to cascading ecological effects (Landres et al. 1999, Dale et al. 2000). For example, too-frequent fire can result in habitat loss and fragmentation, shifting forest composition, reduction of small-mammal populations, and accompanying loss of predator species (Barro and Conard 1991, DellaSalla et al. 2004).

Landscape-level interactions between human activities and natural dynamics tend to be spatially concentrated at the wildland–urban interface (WUI; see Plate 1), which is the contact zone in which human development intermingles with undeveloped vegetation (Radeloff et al. 2005). The WUI has received national attention because housing developments and human lives are vulnerable to fire in these locations and because anthropogenic ignitions are believed to be most common there (Rundel and King 2001, USDA and USDI 2001). The majority of WUI fire research has focused on strategies to protect lives and structures (e.g., Cohen 2000, Winter and Fried 2000, Winter et al. 2002, Shindler and Toman 2003) or on the assessment of fire risk using biophysical or climate variables that influence fire behavior (Bradstock et al. 1998, Fried et al. 1999, Haight et al. 2004). However, it is also important to understand how the WUI itself (or other indicators of human activity) affects fire and to quantify the spatial relationships between human activities and fire (Duncan and Schmalzer 2004).

The influence of proximity to the WUI and other human infrastructure appears to vary markedly with region. In the northern Great Lakes states, areas with higher population density, higher road density, and lower distance to nonforest were positively correlated with fire (Cardille et al. 2001). Also, in southern California, a strong positive correlation between population density and fire frequency was reported (Keeley et al. 1999). However, no relationship between housing count and fire was found in northern Florida counties (Prestemon et al. 2002); population density and unemployment were positively related, and housing density and unemployment were negatively related to fire in a different analysis of Florida counties (Mercer and Prestemon 2005). A negative relationship between housing density and fire was also found in the Sierra Nevada Mountains of California (CAFRAP 2001).

In addition to potential regional differences, it is also difficult to draw general conclusions from these studies because they used different indicators of human activities, their data sets differed in spatial and temporal scale, and they were conducted in small areas where ranges of variability in both fire frequency and level of development were limited. Human–fire relationships may also vary based on factors that were not accounted for, such as pattern of development. Another explanation for the discrepancy is that relationships between human activities and fire may be nonlinear in that humans may affect fire occurrence positively or negatively, depending on the level of influence. These nonlinear effects were apparent in data from a recent study in the San Francisco Bay region, where population growth was positively related to fire frequency over time up to a point, but then fire frequency leveled off as population continued to increase (Keeley 2005).

Whether positive or negative, the significance of the relationships between human activities and fire that were detected in previous studies stresses the importance of further exploring links between anthropogenic and environmental factors and their relative influence on wildfire patterns across space and time. Therefore, our research objective was to quantify relationships between human activities and fire in California counties using temporally and spatially rich data sets and regression models. Although fire regimes encompass multiple characteristics, including seasonality, intensity, severity, and predictability, we restricted our analysis to questions about fire frequency and area burned to determine: (1) what the contemporary relationship between human activities and fire is; (2) how human activities have influenced change in fire over the last 40 years; and (3) whether fire frequency and area burned vary nonlinearly in response to human influence.

Humans are responsible for igniting the fires that burn the majority of area in California (Keeley 1982); therefore, we expected our anthropogenic explanatory variables to significantly explain fire activity on the current landscape and over time. In addition to population density (which simply quantifies the number of people in an area), we expected the spatial pattern of human development (indicated by housing density and

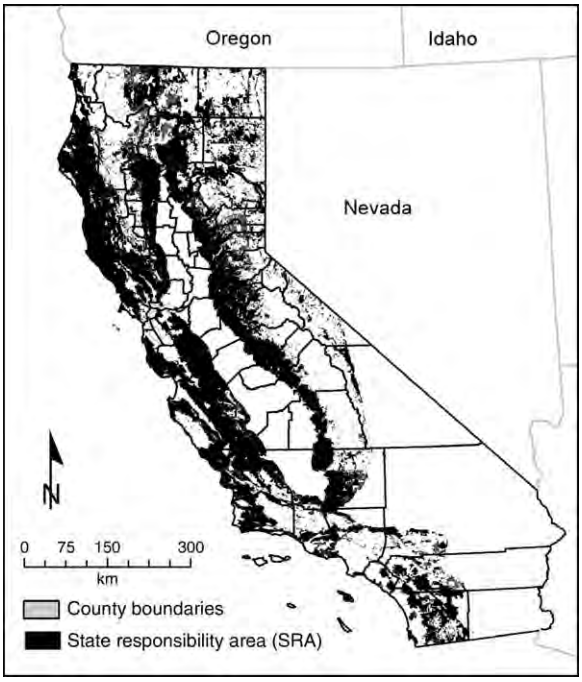

FIG. 1. Map of California Department of Forestry and Fire Protection (CDF) state responsibility areas (SRAs) within county boundaries of California, USA.

land cover combinations and distance variables) to be an important influence on fire because we assumed that anthropogenic ignitions are most likely to occur where human presence is greatest. We also expected that the relationships between human activities and fire would be both positive and negative because humans ignite fires, but development patterns affect fuel continuity and the accessibility of fire suppression resources. Finally, we included several environmental variables in the analysis because we expected the human relationships to be mediated by these other biophysical variables that shape the pattern and frequency of fire (Wells et al. 2004).

METHODS

Study area

California is the second largest state in the continental United States and is the most populous and physically diverse. Most of the state has a mediterranean climate, which, along with a heterogeneous landscape, contributes to tremendous biodiversity (Wilson 1992). Because the state contains a large proportion of the country's endangered species, it is considered a "hotspot" of threatened biodiversity (Dobson et al. 1997). There is extensive spatial variation in human population density: large areas in the north are among the most sparsely populated in the country, but metropolitan regions in the south are growing at unprecedented rates (Landis and Reilly 2004). Much of the landscape is highly fire-prone, but fire regimes vary, and fire management is divided among many institutions. Humans have altered California's fire regimes, and its fire-related financial losses are among the highest in the country (Halsey 2005).

Data

Dependent variables: fire statistics.—We assembled our fire statistics from the California Department of Forestry and Fire Protection (CDF; Sacramento, California, USA) annual printed records, which included information on all fires for which the CDF took action between 1931 and 2004. For all state responsibility areas (SRA; Fig. 1), fire statistics are recorded by county and include numbers by size class, total area burned, vegetation type, and cause. Because the statistics did not include spatially explicit information on individual fires, we weighted the data by the area within the SRA in each county by calculating proportions to use as our dependent variables. These fire statistics were substantially more comprehensive than the readily available electronic Statewide Fire History Database, which excludes most fires <40 ha, which in many counties represents $>90\%$ of the fires. Although both anthropogenic and lightning ignitions would be important to consider for fully understanding fire patterns in other regions (e.g., Marsden 1982), humans were responsible for $\sim 95\%$ of both the number of fires and area burned in California in the last century. We restricted our analysis to these anthropogenic fires because our focus was on human relationships with fire. Although the fire statistics were not spatially explicit, we developed GIS grids at 100-m resolution to derive data for all of the explanatory variables. The data for these explanatory variables were only extracted and averaged from within the SRA boundaries corresponding to the fire data.

Out of the 58 counties in California, we had fire statistics for 54 of them for the year 2000. Therefore, to assess the contemporary relationship between fire and human activities (hereafter referred to as the "contemporary analysis"), we analyzed the data from these counties using the annual number of fires and area burned as our dependent variables (Table 1).

Based on a preliminary exploration of the fire history data (averaged across all counties), we observed two distinct trends during the last 50 years. First, the number of fires substantially increased until 1980 and then decreased until 2000; and second, the average area burned changed inversely to the number of fires, but the differences over time were less dramatic and not statistically significant (Fig. 2). Considering these trends, we broke the historic analysis into two equal time periods (1960–1980 and 1980–2000) to compare the relative influence of the explanatory variables on both the increase (i.e., from 1960 to 1980) and decrease (from 1980 to 2000) in fire activity. The year 1980 is used to compute differences for both time periods because the census data that formed the basis for many of our explanatory variables were only available by decade. We averaged the number of fires and the area burned for 10-

TABLE 1. Variables analyzed in the regression models.

Variable	Source	Processing
2000 data		
Dependent variables		
Number of fires	CDF	proportion in SRA, square-root transformed
Area burned	CDF	proportion in SRA, square-root transformed
Explanatory variables		
Human		
Intermix WUI	SILVIS	proportion in SRA
Interface WUI	SILVIS	proportion in SRA
Low-density housing	SILVIS	proportion in SRA
Distance to intermix WUI	SILVIS	mean Euclidean distance in SRA
Distance to interface WUI	SILVIS	mean Euclidean distance in SRA
Population density	SILVIS	proportion in SRA
Road density	TIGER	mean km/km^2 in SRA
Distance to road	TIGER	mean Euclidean distance in SRA
Biophysical		
Ecoregion	CDF	discrete class
Vegetation type	CDF	area burned in vegetation type/area burned in SRA
Historic data, 1960–1980 and 1980–2000		
Dependent variables		
Change in number of fires	CDF	difference between decadal averages, proportion in SRA, square-root transformed
Change in area burned	CDF	difference between decadal averages, proportion in SRA, square-root transformed
Explanatory variables		
Human		
Change in housing density	SILVIS	difference between decades
Change in distance to low-density housing	SILVIS	difference between mean Euclidean distance in SRA
Initial housing density	SILVIS	mean housing density in either 1960 or 1980
Initial distance to low-density housing	SILVIS	mean Euclidean distance in SRA in either 1960 or 1980
Biophysical		
Ecoregion	CDF	discrete class
Vegetation type	CDF	mean area burned in vegetation type/area burned in SRA over time period

Notes: Key to abbreviations: WUI, wildland–urban interface; SRA, state responsibility area. Sources are as follows: CDF, California Department of Forestry and Fire Protection, Sacramento, California, USA, *unpublished data*; SILVIS, Radeloff et al. (2005); TIGER, U.S. Census Bureau (2000).

year time periods that bracketed the dates of the census data (e.g., 1955–1964 [1960], 1975–1984 [1980], 1995–2004 [2000]) and then calculated the difference in averages from the 1960–1980 and 1980–2000 periods for our dependent variables (Table 1). By averaging the fire data, we smoothed some of the annual variability that may have occurred due to stochastic factors such as weather.

Explanatory variables: housing data.—Data for most of the anthropogenic variables were available through a nationwide mapping project that produced maps of the WUI in the conterminous United States using housing density data from the 1990 and 2000 U.S. Census (U.S. Census Bureau 2002) and land cover data from the USGS National Land Cover Dataset (Radeloff et al. 2005). The maps were produced at the finest demographic spatial scale possible, the 2000 decennial census blocks. The vegetation data were produced at 30-m resolution. These maps delineated two types of WUI in accordance with the Federal Register definition (USDA and USDI 2001). "Intermix WUI" is defined as the intermingling of development with wildland vegetation; the vegetation is continuous and occupies >50% of the area. "Interface WUI" is defined as the situation in which development abuts wildland vegetation; there is <50% vegetation in the WUI, but it is within 2.4 km of an area that has >75% vegetation. In both types of WUI communities, housing must meet or exceed a density of more than one structure per 16 ha (6.17 housing units/km^2). Interface WUI tends to occur in buffers surrounding higher-density housing, whereas intermix WUI is more dispersed across the landscape (Fig. 3A, B).

The WUI data were only produced for 1990 and 2000 due to the lack of historic land cover data, but housing density data were available from 1960 to 2000. Historic housing density distribution was estimated using back-casting methods to allocate historic county-level housing unit counts into partial block groups (as described in Hammer et al. 2004). We used both intermix and interface WUI as explanatory variables (proportions within the county SRAs) in the current analysis to evaluate how these different patterns of vegetation and housing density affected fire activity. We also used low-density housing (housing density $\geq$6.17 housing units/km^2 and <49.42 housing units/km^2) to determine whether it could act as a substitute for WUI as an explanatory variable in the historic analysis (Table 1).

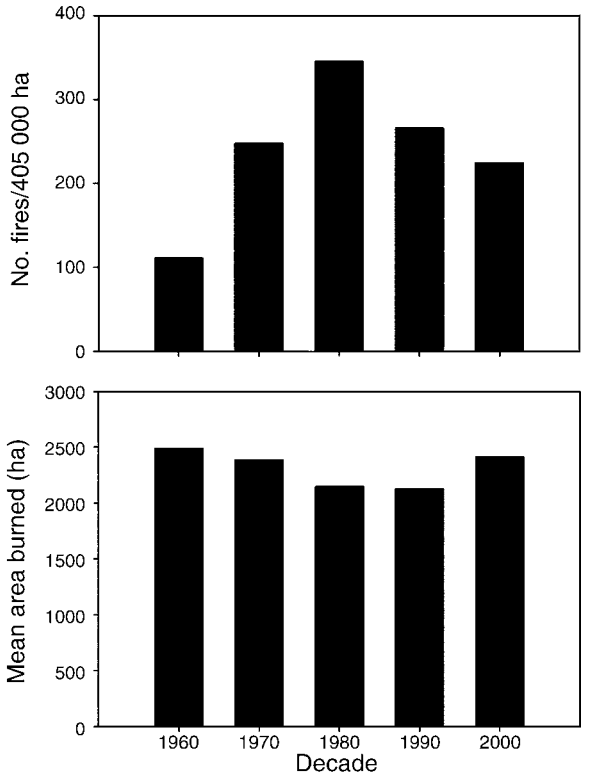

FIG. 2. Trends in number of fires and area burned for all land in the state responsibility areas (SRAs) in California from 1960 to 2000.

Looking at an overlay of fire perimeters from the electronic Statewide Fire History Database (from the last 25 years; *available online*)[7] on the WUI data, it was apparent that many fires occurred close to the WUI, but not necessarily within the WUI (Fig. 3C, D). Therefore, we calculated the mean distance to intermix and interface WUI to evaluate as explanatory variables (Table 1). These means were calculated by iteratively determining the Euclidean distances from every grid cell in the county SRA boundaries and then averaging the distances across all cells to determine means for the counties. We also included population density data from the 2000 Census.

For the historic analysis, we calculated changes in mean housing density and mean distance to low-density housing between the 1960–1980 and 1980–2000 periods to relate to change in the dependent variables. We excluded the proportion of low-density housing from our analysis because it was highly correlated with mean housing density ($r = 0.84$). Unlike the historical fire data that switched in their direction of change over time, housing density continued to increase while the mean distance to low-density housing continued to decline (Fig. 4). We included the initial values of these data (e.g., 1960 and 1980) to account for the fact that the same magnitude of change may have different effects on the dependent variables depending on the starting value of the explanatory variables (Table 1).

Explanatory variables: road data.—The quality of road data can vary according to data source (Hawbaker and Radeloff 2004), so we compared the U.S. Geological Survey digital line graph (DLG; U.S. Geological Survey 2002) and the US TIGER 2000 GIS (U.S. Census Bureau 2000) layers of roads to determine whether there were substantial differences that could affect the interpretation of the results. After calculating and summarizing road density by county, we found a strong positive correlation ($r = 0.97$). Therefore, we used the TIGER data because they were produced in 2000, the same year as the contemporary analysis. The more current TIGER data generally capture new development that might not be included in the DLG data. We evaluated mean road density and mean distance to roads in the current analysis (Table 1), but road data were unavailable for the historic analysis.

Explanatory variables: environmental.—In the absence of human influence, fire behavior is primarily a function of biophysical variables (Pyne et al. 1996, Rollins et al. 2002). These can vary widely across a county, but ecoregions capture broad differences by stratifying landscapes into unique combinations of physical and biological variables (ECOMAP 1993). Our ecoregion data were the geographic subdivisions of California defined for The Jepson Manual (Hickman 1993), designated through broadly defined vegetation types and geologic, topographic, and climatic variation (Fig. 5).

Because vegetation type influences the ignitability of fuel and the rate of fire spread (Bond and van Wilgen 1996, Pyne et al. 1996), we also evaluated the proportion of area burned within three broad vegetation types: shrubland, grassland, and woodland (Fig. 5). Differences in fire regimes between broadly defined vegetation types can be striking, particularly between shrubland and woodland in southern California (Wells et al. 2004). The CDF fire statistics included information on the proportion of area burned in these vegetation types. For the historic analysis, we averaged the proportion of fires burned within different vegetation types over the entire decade (Table 1).

Analytical methods

Diagnostics and data exploration.—Before developing regression models, we examined scatter plots for each variable. Nonlinear trends were apparent (e.g., Fig. 6), suggesting that we needed to include quadratic terms for the explanatory variables in the regressions. Unequal variances in the residual plots prompted us to apply a square-root transformation to the dependent variables. We also plotted semivariograms of the models' residuals (using centroids from the SRA boundaries) and found no evidence of spatial autocorrelation. To check for

[7] ⟨http://frap.cdf.ca.gov/data/frapgisdata/select.asp⟩

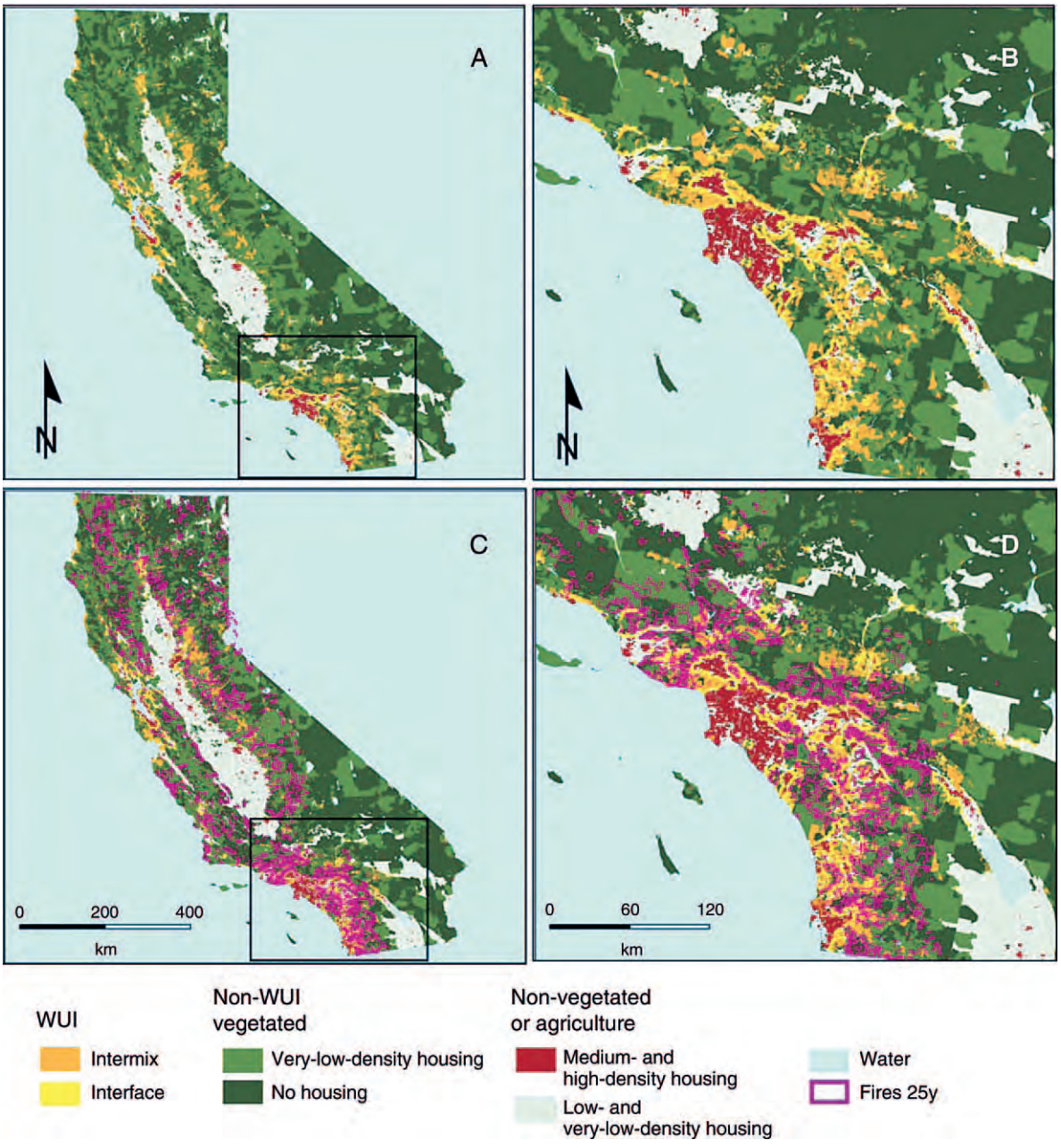

FIG. 3. The wildland–urban interface (WUI) in 2000 with and without fire perimeter overlays (from 1979 to 2004) in (A, C) California and (B, D) southern California. Housing density is defined as follows: very low, >0–6.17 housing units/km^2; low, 6.17–49.42 housing units/km^2; medium, 49.42–741.31 housing units/km^2; and high, >741.31 housing units/km^2 (USDA and USDI 2001). "Fires 25y" refers to 25 years of fire perimeters, from 1980 to 2005.

multicollinearity, we calculated the correlation coefficients between all of the explanatory variables and only included noncorrelated variables ($r \leq 0.7$) in the multiple regression models.

The areas of CDF jurisdiction for each county varied slightly over time. Therefore, we compared separate regressions from the full historic data set ($n = 37$) to a subset of the data excluding counties that experienced a greater than 20% change in area over time ($n = 23$). For both the 1960–1980 regressions and the 1980–2000 regressions, every one of the explanatory variables that was significant in the subset was also significant in the full data set, with very similar R^2 values; therefore, we felt confident proceeding with the full data set for the historic analysis because we had greater power with the larger sample size.

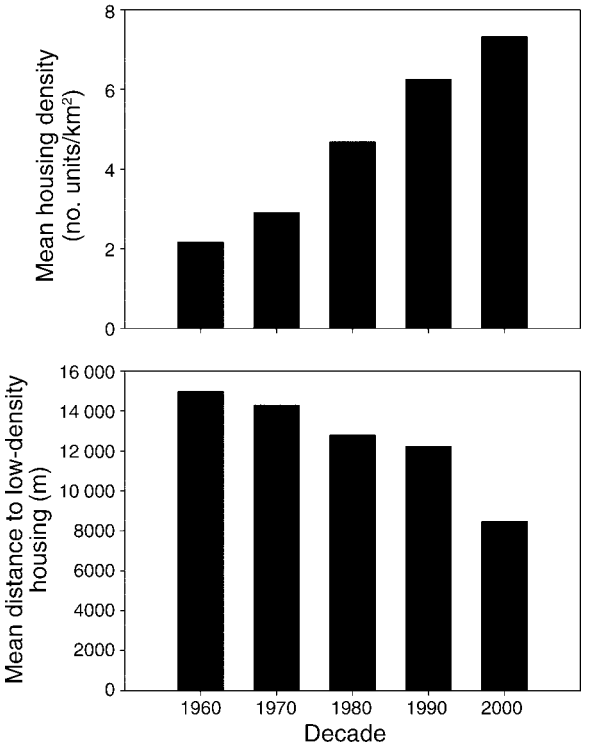

FIG. 4. Trends in housing density and distance to low-density housing (6.17–49.42 housing units/km^2) for all land in the state responsibility areas (SRAs) in California from 1960 to 2000.

Statistical analysis

We used the same regression modeling approach for both the current and historic analyses. First, we developed bivariate regression models for all of the explanatory variables and their quadratic terms so that we could evaluate their independent influence on fire frequency and area burned. To account for the interactions between variables (and their quadratic terms), we also built multiple regression models using the R statistical package (R Development Core Team 2005). For all models, we first conducted a full stepwise selection analysis (both directions) using Akaike Information Criteria to identify the best combination of predictor variables (Burnham and Anderson 2002). Some of the models retained a quadratic term without including the lower-order variable. In these models, we added the lower-order term, rebuilt the model, and then proceeded with a backwards elimination process until all predictor variables in the model were significant with P values ≤ 0.05.

RESULTS

Current analysis

Bivariate regressions.—Many of the anthropogenic variables were highly significant in explaining the number of fires in 2000. The quadratic term for each of these variables was also significant, and the direction of influence was both positive and negative (Fig. 7). Compared to the other variables, population density explained the greatest amount of variability. The proportion of intermix WUI and low-density housing in the counties also explained significant variation in the number of fires; but the proportion of interface WUI was insignificant. The number of fires was significantly related to the mean distance to both types of WUI, but neither of the road variables was significant. All three vegetation types, particularly shrubland, significantly influenced the number of fires, but ecoregion was insignificant.

For the anthropogenic variables, the number of fires was highest at intermediate levels of population density (from ~35 to 45 people/km^2; Fig. 6), proportion of intermix WUI (~20–30% in the county), and proportion of low-density housing (~25–35% in the county). It was also highest at the shortest distances to intermix and interface WUI, but started to level off at ~9–10 km for intermix (Fig. 6) and 14–15 km for interface WUI.

Unlike the number of fires, none of the anthropogenic variables were significantly associated with the area burned in 2000. In fact, shrubland was the only variable that explained significant variation in area burned.

Multiple regression.—When all of the variables were modeled in the multiple regressions, the resulting model for number of fires in 2000 included population density, the proportion of intermix WUI and its quadratic term, grassland and its quadratic term, and shrubland (Table 2). The model was highly significant with an adjusted R^2 value of 0.72.

The multiple regression model for area burned in 2000 included distance to road, shrubland, and woodland, and all three variables had significant positive relationships (no quadratic terms were retained). This model was also highly significant with an adjusted R^2 of 0.50.

Historical analysis 1960–1980

Bivariate regressions.—Change in the number of fires (net increase) from 1960 to 1980 was significantly explained by each of the human-related variables except for change in the mean distance to low-density housing (Fig. 8). The quadratic term was also significant in the separate models, except for the initial distance to low-density housing (in 1960), which had a negative influence on the change in number of fires. Change in number of fires was also significantly related to ecoregion and shrubland vegetation.

The only three variables with significant influence on the change in area burned (net decrease) were the three vegetation types.

Multiple regression.—The explanatory variables that were retained in the multiple regression model for change in the number of fires from 1960 to 1980 included mean housing density in 1960 and its quadratic term, grassland vegetation, and ecoregion (Table 2). The adjusted R^2 value was highly significant at 0.72.

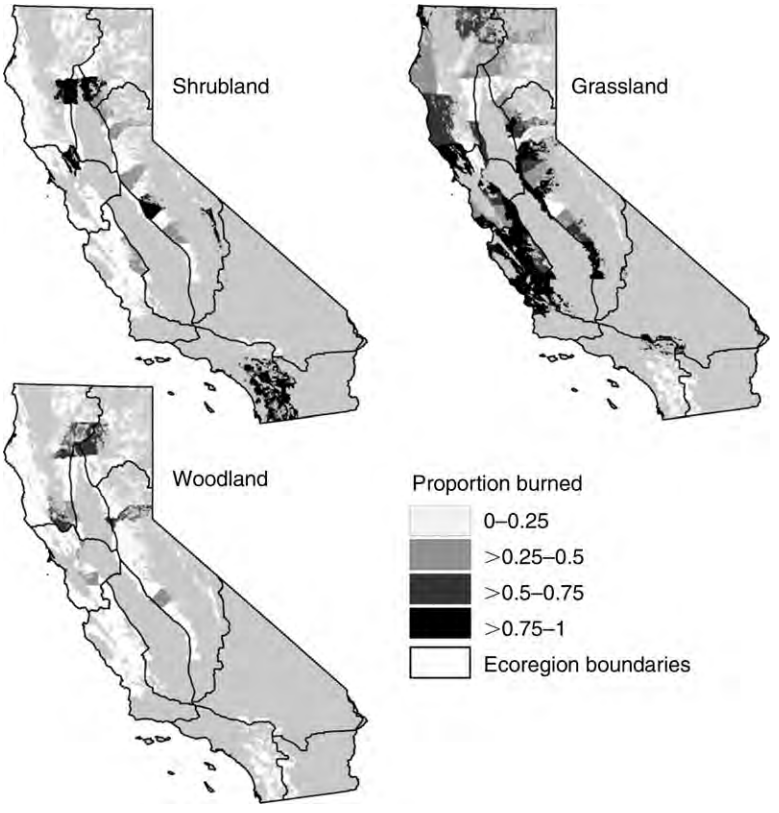

FIG. 5. Maps showing ecoregion boundaries and the proportion of area burned in shrubland, grassland, and woodland in 2000.

Mean housing density in 1960 was positively associated with change in area burned from 1960 to 1980, and the distance to low-density housing had first a positive, then a negative influence because the quadratic term was included. Other variables retained in the multiple regression model included shrubland and its quadratic term, grassland, woodland, and ecoregion.

Historical analysis 1980–2000

Bivariate regressions.—Initial housing density (in 1980) was the only significant explanatory variable explaining change in number of fires (net decrease) from 1980 to 2000 (Fig. 9). Woodland vegetation was the only significant variable out of the separate models explaining change in area burned from 1980 to 2000 (net increase). The quadratic terms were significant for both of these models.

Multiple regression.—The multiple regression model explaining change in number of fires from 1980 to 2000 included change in housing density, initial housing density (in 1980), and woodland vegetation; the quadratic term was also significant for these three variables (Table 2). Although the model was significant, the R^2 was substantially lower than the 1960–1980 model, at 0.26.

The multiple regression model explaining change in area burned included initial housing density (in 1980) and its quadratic term, initial distance to low-density

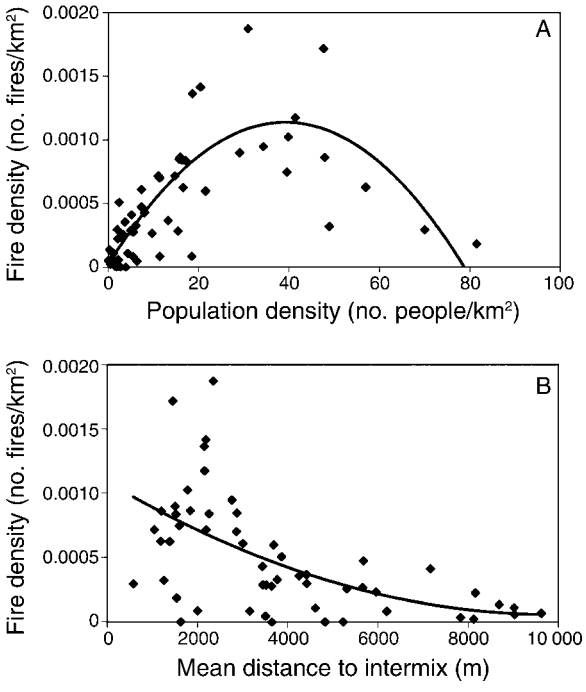

FIG. 6. The relationships between (A) the proportion of the number of fires and population density and (B) the proportion of the number of fires and mean distance to intermix wildland–urban interface (WUI).

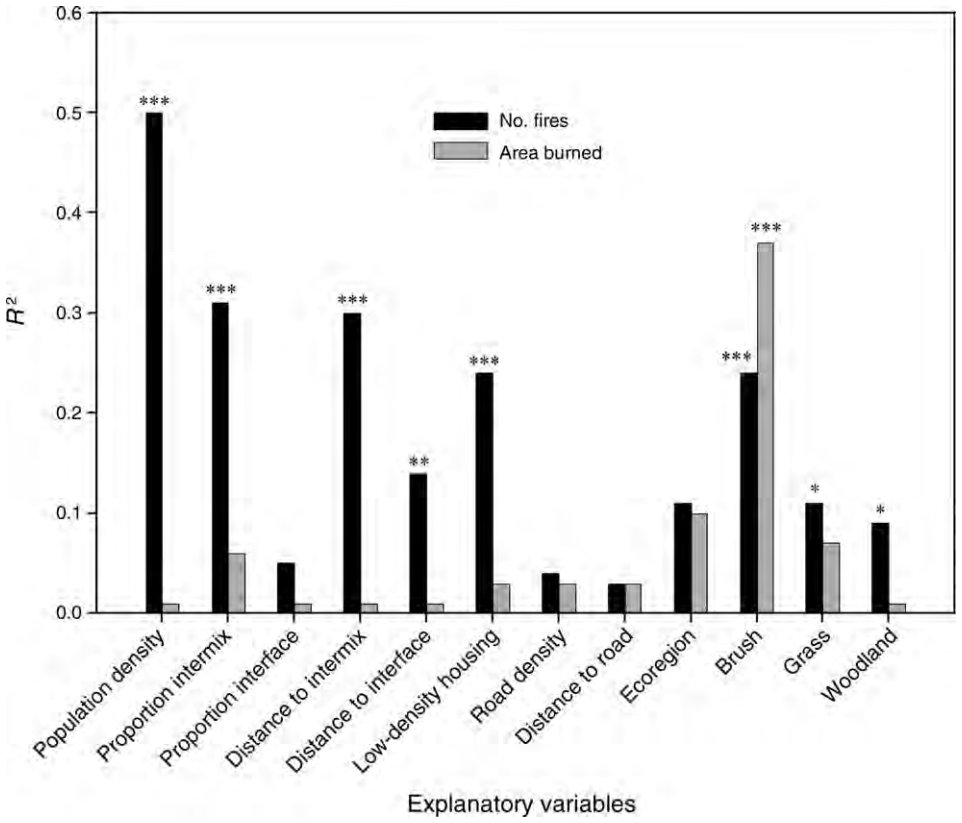

FIG. 7. R^2 values and significance levels for the explanatory variables in the bivariate regression models for number of fires and area burned in 2000.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

housing, woodland vegetation and its quadratic, and ecoregion. This model had better explanatory power than the number of fires model, with an R^2 of 0.41.

DISCUSSION

The expression of fire on a landscape is influenced by a combination of factors that vary across spatial and temporal scales and involve both physical and biological characteristics. Fire behavior has long been viewed as a largely physical phenomenon illustrated by the classic fire environment triangle that places fire as a function of weather, fuels, and topography (Countryman 1972), but clearly the human influence on modern fire regimes must also be understood to meet fire management needs (DellaSalla et al. 2004). We first asked what the current relationship is between human activities and fire in California and found that humans and their spatial distribution explained a tremendous proportion of the variability in the number of fires, but that area burned was more a function of vegetation type. Anthropogenic ignitions are the primary cause of fire in California and were the focus of our analysis, so we were not surprised by the strong human influence. Nevertheless, the high explanatory power of the models underscores the importance of using locally relevant anthropogenic factors as well as biophysical factors in fire risk assessments and mapping. The models also identify which indicators of human activity are most strongly associated with fire in California. For number of fires, the proportion of intermix WUI explained more variation than any other variable except for population density, suggesting that the spatial pattern of housing development and fuel are important risk factors for fire starts.

Human-caused ignitions frequently occur along transportation corridors (Keeley and Fotheringham 2003, Stephens 2005), so it was surprising that neither road density nor average distance to road were significant in explaining fire frequency. Although roads are important in local-scale ignition modeling, detecting their influence on fire ignitions may be difficult at an aggregated, county level since they are narrow, linear features. On the other hand, distance to roads was the only anthropogenic variable associated with area burned, having a positive influence when grassland and shrubland were also accounted for in the multiple regression model, which may reflect the difficulty of fire suppression access contributing to fire size.

Humans influence fire frequency more than area burned because anthropogenic ignitions are responsible

TABLE 2. Variables retained in the multiple regression models for the current and historic analyses.

Analysis and explanatory variable	Coefficient and intercept	*P*
Current		
2000		
No. fires		
Population density	0.0006	<0.01
Proportion intermix	0.0702	<0.01
(Proportion intermix)^2	−0.2629	<0.01
Grassland	0.0496	<0.01
(Grassland)^2	−0.0441	<0.01
Shrubland	0.0093	0.02
Overall model (adjusted R^2: 0.72)	0.0001	<0.01
Area burned		
Distance to road	0.00004	<0.01
Shrubland	0.0833	<0.01
Woodland	0.0559	<0.01
Overall model (adjusted R^2: 0.50)	−0.0052	<0.01
Historic		
1960–1980		
No. fires		
Initial housing	2.7649	<0.01
(Initial housing)^2	−0.1523	<0.01
Grassland	4.6311	0.05
Ecoregion	...†	<0.01
Overall model (adjusted R^2: 0.72)	0.6443	<0.01
Area burned		
Initial housing	0.0188	<0.01
Initial distance	0.00002	<0.01
(Initial distance)^2	-2×10^{-10}	<0.01
Shrubland	−0.3641	0.12
(Shrubland)^2	0.8778	0.01
Grassland	0.0371	<0.01
Woodland	0.0449	0.01
Ecoregion	...†	0.03
Overall model (adjusted R^2: 0.51)	−0.373	<0.01
1980–2000		
No. fires		
Change housing	3.0666	0.01
(Change housing)^2	−0.2661	0.01
Initial housing	−1.8269	0.01
(Initial housing)^2	0.0505	0.03
Woodland	38.1957	0.03
(Woodland)^2	−107.0112	0.02
Overall model (adjusted R^2: 0.26)	−1.894	0.01
Area burned		
Initial housing	−0.0114	0.01
(Initial housing)^2	0.0003	0.05
Initial distance	−0.000003	<0.01
Woodland	0.0292	0.18
(Woodland)^2	−1.2831	0.02
Ecoregion	...†	0.05
Overall model (adjusted R^2: 0.41)	0.0409	<0.01

† Coefficients are not listed for categorical variables.

for fire initiation, but fire spread and behavior is ultimately more a function of fuel availability and type (Bond and van Wilgen 1996, Pyne et al. 1996). Yet humans do have some control over fire size through suppression and, indirectly, through fuel connectivity (Sturtevant et al. 2004), although fires are extremely difficult to suppress in California shrublands under high-wind conditions that typify the most destructive fires (Keeley and Fotheringham 2003). Therefore, human effects on area burned may cancel one another out to some extent because fire suppression can minimize the increase in area burned that would result from increased ignitions, at least at the WUI. Fire suppression resources are more likely to be concentrated on structural protection in developed areas (Calkin et al. 2005), which would explain the positive relationship between area burned and distance to road. Roads can serve as firebreaks and can also provide access routes for firefighters.

The inclusion of vegetation type in the multiple regression models illustrates that, despite the strong influence of humans, fire occurrence remains a function

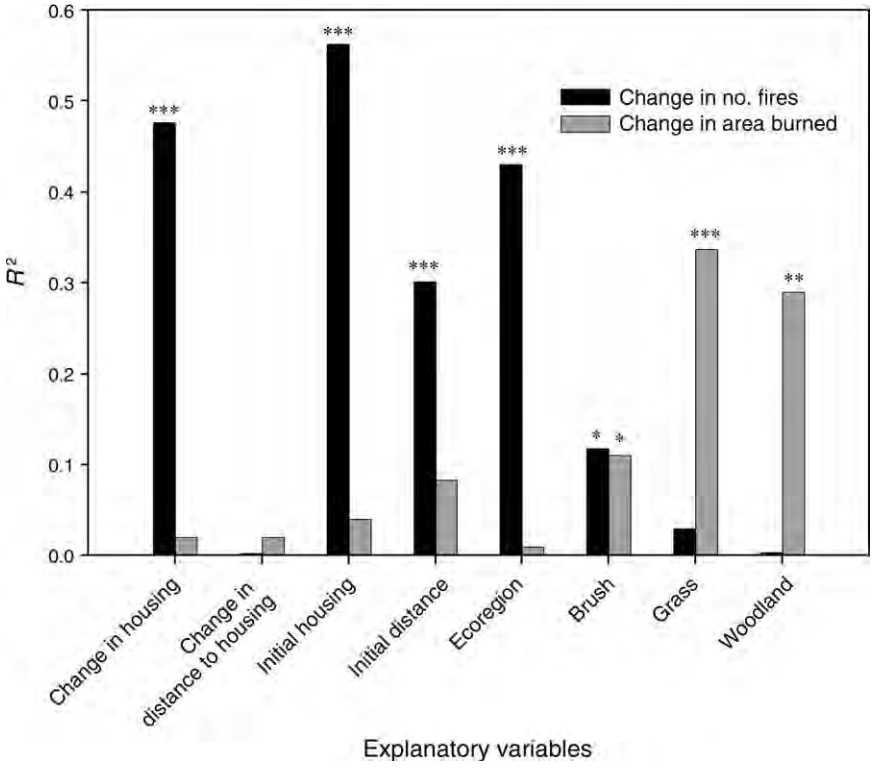

FIG. 8. R^2 values and significance levels for the explanatory variables in the bivariate regression models for number of fires and area burned from 1960 to 1980.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

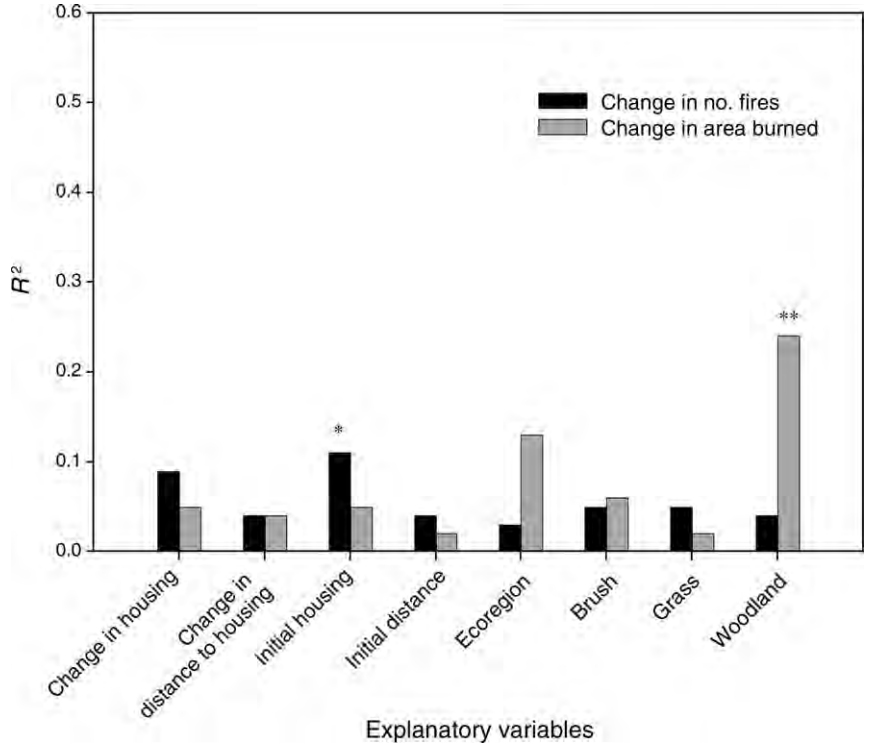

FIG. 9. R^2 values and significance levels for the explanatory variables in the bivariate regression models for number of fires and area burned from 1980 to 2000.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.



PLATE 1. (Left) Wildland–urban interface (WUI) and (right) burned-over fuel break, both at the eastern end of Scripps Ranch (San Diego County, California, USA) after the autumn 2003 Cedar Fire (largest fire in California since the beginning of the 20th century). Photo credits: J. E. Keeley.

of multiple interacting social and environmental variables. For number of fires and area burned, shrubland had the strongest explanatory power of the vegetation types. Chaparral and coastal sage scrub are both extremely fire-prone vegetation types and high human population density tends to be distributed in these types; other studies have shown that they have experienced a higher rate of burning than other vegetation types in the southern part of the state in the last century (Keeley et al. 1999, Keeley 2000, Wells et al. 2004). Increased ignitions in highly flammable vegetation types can lead to very hazardous conditions (Halsey 2005).

The second question we asked was "How do human activities relate to change in fire?" In the last 40 years, the most substantial change was the increase in number of fires from 1960 to 1980. The decrease in number of fires was less dramatic between 1980 and 2000; and the change in area burned was relatively small in both time periods. Housing development patterns were most influential when change was greatest, from 1960 to 1980, and for trends in fire frequency (vs. area burned).

Although anthropogenic influence was partially responsible for the change in area burned, the apparent inverse relationship between change in fire frequency and change in area burned may be spurious. In other words, the explanation for a decrease in number of fires may be independent of the concurrent increase in area burned. Trends in area burned are naturally cyclic due to broad-scale factors such as climate. Recent research has shown that change in climate was a major factor driving fire activity in the western United States in the last several decades (Westerling et al. 2006); however, that research was restricted to large montane fire events on federally owned land above 1370 m. Therefore, while climate change may have played some role in our observed change in area burned, we cannot extend those results to our analysis because we included fires of all sizes under multiple land ownership classes, and historical fire patterns in the lower elevations do not correspond to patterns in montane forests (Halsey 2005).

Fire both constrains and is constrained by the fuel patterns it creates, resulting in cycles of fire activity and temporal autocorrelation in area burned, in part because young fuels are often less likely to burn (Malamud et al. 2005). Temporal autocorrelation effects vary with ecosystem, fuel type, and the area of analysis; but in all vegetation types, temporal dependence diminishes over time due to post-fire recovery. Therefore, we assumed that the effects would be low in our study because we were looking at change over 20-year time periods. Furthermore, the chaparral vegetation that dominates much of California recovers very quickly following fire, meaning that the effect of temporal autocorrelation in this vegetation type would last for only brief periods of time. Also, under extreme weather conditions, young age classes are capable of carrying fires in the southern portions of California (Moritz 1997, Moritz et al. 2004).

In general, the anthropogenic influence on fire frequency and extent was complicated through the combination of positive and negative effects, which helps to answer our third question: "Do fire frequency and area burned vary nonlinearly in response to human influence?" Nonlinear effects were evident in the scatter plots and confirmed by the significance of quadratic terms in most of the models. The regression models indicate that humans were responsible for first increasing and then decreasing fire frequency and area burned. These dual influences may explain why prior studies presented conflicting results, because a positive or negative response was dependent on the level of human presence. Aside from the fact that we intentionally tested hypotheses regarding nonlinear relationships, our data also contained a wide range of human presence due to the large extent and diversity of the state of California.

The scatter plots illustrate how these human–fire relationships occurred. For both the number of fires and area burned, and in the current and historic analyses, the

maximum fire values occurred at intermediate levels of human presence (as in Fig. 6A); and when human activity was either lower or higher, fire activity was lower. Initial increase in fire occurrence with increasing population is reasonable since human presence results in more ignitions. However, it appears that when human population density and development reach a certain threshold density, ignitions decline, and this is likely the result of diminished and highly fragmented open space with fuels insufficient to sustain fire. In addition, above a certain population threshold, fire suppression resources are likely to be more concentrated in the WUI. Inverse relationships were evident in the scatter plots of distance (Fig. 6B). In these, fire frequency and area burned were greatest at short distances to WUI; and at longer distances, the trend lines leveled off. These distance relationships indicate that more fires would be expected in close proximity to settled areas where ignitions are likely to occur.

The inclusion of quadratic terms in the multiple regression models supports the concept that fire frequency and area burned were dependent on the level of human activity. Initial housing density was important in all four historic multiple regression models, and initial distance to low-density housing was important in both of the historic area-burned models. The change in number of fires for both periods was also related to change in housing density, in bivariate regression models for the earlier period and in the multiple regression model for the later period (1980–2000). These results further emphasize that fire activity was a function of a certain level of human presence. In addition to the strong influence of human presence, ecoregion and vegetation types were also highly significant in the multiple regression models, suggesting that the particular level of human activity that was most influential in explaining fire activity was dependent upon biophysical context.

The primary value of the multiple regression models was to identify the most influential variables and their direction of influence when accounting for other factors. While they explained how fire activity varied according to context-dependent interactions, their purpose was not to provide a formula for determining fire risk at a landscape scale. Environmental and social conditions differ from region to region, and processes such as fire and succession are controlled by a hierarchy of factors, with different variables important at different scales (Turner et al. 1997). Nevertheless, these models provide strong evidence about the strength and nature of human–fire relationships. That these relationships are significant across a state as diverse as California suggests that human influence is increasingly overriding the biophysical template; yet, managers must account for the interactions with ecoregion and vegetation type when making management decisions. Determining the conditions (e.g., thresholds) for nonlinear anthropogenic relationships will be important to understand how fire risk is distributed across the landscape.

At the coarse scale of our analysis, we can estimate these thresholds based on the nonlinear relationships in our scatter plots (as in Fig. 6) and suggest that fire frequency is likely to be highest when population density is between 35 and 45 people/km^2, proportion of intermix WUI is ~20–30%, proportion of low-density housing is ~25–35%, the mean distance to intermix WUI is <9 km, and the mean distance to interface WUI is <14 km. Our next step is to more precisely define these relationships at scales finer than the county level (where management decisions often occur) and to understand the conditions under which human activities positively or negatively influence fire.

These results imply that fire managers must consider human influence, together with biophysical characteristics such as those represented in the LANDFIRE database, when making decisions regarding the allocation of suppression and hazard mitigation resources. If human presence is not explicitly included in decision making, inefficiencies may result, because fire occurrence is related to human presence on the landscape. In particular, we identify an intermediate level of housing density and distance from the WUI at which the effects of human presence seem to be especially damaging, i.e., a point at which enough people are present to ignite fires, but development has not yet removed or fragmented the wildland vegetation enough to disrupt fire spread. This intermediate level of development is one that large areas of the lower 48 states, particularly in the West and Southwest, will achieve in the coming decade. Hence, the WUI's location, extent, and dynamics will continue to be essential information for wildland fire management.

Conclusion

In addition to the risk to human lives and structures, changing fire regimes may have substantial ecological impacts, and the results in this analysis support the hypothesis that humans are altering both the spatial and temporal pattern of the fire regime. Although the overall area burned has not changed substantially, the distribution of fires across the landscape is shifting so that the majority of fires are burning closer to developed areas, and more remote forests are no longer burning at their historic range of variability (Pyne 2001). In either case, the ecological impacts may be devastating. Due to lack of dendrochronological information, historic reference conditions are difficult to determine in stand-replacing chaparral shrublands. Although chaparral is adapted to periodic wildfire, there is substantial evidence that fires are burning at unprecedented frequencies, and this repeated burning (at intervals closer than 15–20 years apart) exceeds many species' resilience and has already resulted in numerous extirpations (Zedler et al. 1983, Haidinger and Keeley 1993, Halsey 2005).

If present trends continue in California, the population may increase to 90×10^6 residents in the next 100 years. Recent trends in housing development patterns also indicate that growth in area and number of houses in intermix WUI has far outpaced the growth in interface WUI (Radeloff et al. 2005; Hammer et al., *in press*). Our results showing that fire frequency and area burned tend to be highest at intermediate levels of development (more typical of intermix than interface) suggest that fire risk is a function of the spatial arrangement of housing development and fuels. Therefore, in addition to more people in the region that could ignite fires, future conditions that include continued growth of intermix WUI may also contribute to greater fire risk. Land use planning that encourages compact development has been advocated to lessen the general impacts of growth on natural resources (Landis and Reilly 2004), and we suggest that reducing sprawling development patterns will also be important to the control of wildfires in California.

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fire

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Factors Associated with Structure Loss in the 2013–2018 California Wildfires

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Abstract: Tens of thousands of structures and hundreds of human lives have been lost in recent fire events throughout California. Given the potential for these types of wildfires to continue, the need to understand why and how structures are being destroyed has taken on a new level of urgency. We compiled and analyzed an extensive dataset of building inspectors' reports documenting homeowner mitigation practices for more than 40,000 wildfire-exposed structures from 2013–2018. Comparing homes that survived fires to homes that were destroyed, we investigated the role of defensible space distance, defensive actions, and building structural characteristics, statewide and parsed into three broad regions. Overall, structural characteristics explained more of a difference between survived and destroyed structures than defensible space distance. The most consistently important structural characteristics—having enclosed eaves, vent screens, and multi-pane windows—were those that potentially prevented wind-born ember penetration into structures, although multi-pane windows are also known to protect against radiant heat. In the North-Interior part of the state, active firefighting was the most important reason for structure survival. Overall, the deviance explained for any given variable was relatively low, suggesting that other factors need to be accounted for to understand the full spectrum of structure loss contributors. Furthermore, while destroyed homes were preferentially included in the study, many "fire-safe" structures, having > 30 m defensible space or fire-resistant building materials, were destroyed. Thus, while mitigation may play an important role in structure survival, additional strategies should be considered to reduce future structure loss.

Keywords: defensible space; building construction; homeowner mitigation; firefighting; defensive actions; fire safety

1. Introduction

California has long been recognized for its fire-prone ecosystems and fire-related losses to human lives and property [1]. In the last several years, however, this recognition has turned into bewilderment and terror as tens of thousands of structures and hundreds of human lives have been lost in fire events throughout the state [2]. Deadly and destructive wildfires have been occurring in other regions across the globe as well, such as Portugal [3], Australia [4], and Southern Europe [5]. The increased frequency and magnitude of these fire events have contributed to the recent claim that we are entering a "new normal" phase of wildfires [6]. Most of these catastrophic fires are started by humans, so as populations steadily increase and people are pushed farther into hazardous wildlands, the problem could get even worse. Thus, the need to understand why and how structures are being destroyed during wildfires has taken on a new level of urgency.

Fully understanding why recent California wildfires were so destructive will likely require many years of research focusing on a range of factors at different scales, from fire behavior and climatology to

fire management and land development. Answering questions pertaining to fire behavior will require different data and methodological approaches, compared to answering the questions related to why homes were destroyed, although the actual outcome will be a combination of the two.

In California, there has been a long-standing interest in understanding how local and regional responses are needed to reduce damage from wildfires [7,8]. In terms of understanding why homes are destroyed, there is an emerging literature that includes studies focused on local, property-level factors as well as studies on landscape-scale factors such as vegetation management and fuel characteristics, fire suppression, topography, and housing development patterns (e.g., [9,10]). These studies have significantly advanced our understanding of home safety, but the majority have been conducted through computer simulations and laboratory experiments, and thus, there remains a need for pre- and post-fire empirical data to document and validate what happens under actual wildfire conditions [11]. Recent fire events have generated more data on structure losses, and the number of empirical studies is increasing, particularly relative to understanding spatial patterns of structure loss at a landscape scale [12–15].

In terms of defensible space, the state of California requires fire-exposed homeowners to create a minimum of 30 m (100 ft) of defensible space around structures, and some localities are beginning to require at least 60 m (200 ft) in certain circumstances (e.g., [16]). Of the few studies that have empirically tested the relative benefits of defensible space, the authors demonstrated that up to 30 m (100 ft) of vegetation reduction around a structure can significantly increase the chance of structure survival (e.g., [17–20]). However, in these case studies, the most effective distance of defensible space was much less than regulations require (e.g., [19,21,22]), and other factors, such as housing density, landscape position, proximity of vegetation to the house, irrigation and water bodies, and building construction materials, were equally or more important [20,23,24].

Regarding fire safety in building construction materials, there have been many detailed studies conducted via carefully designed laboratory experiments [25–27]; and recent building codes in California have been designed to reflect these studies. Despite the solid laboratory evidence, few empirical studies have documented building characteristics associated with structure loss in real wildfire situations. In one study, Syphard et al. [23] found several significant relationships among building construction materials and structure loss in San Diego County, CA, USA, with window framing material and number of windowpanes being more protective than roofing or exterior siding material, and year of construction also being a significant proxy for building characteristics. The sample size in this study was somewhat limited, however, and other factors like structure density and vegetation characteristics were found to be equally or more important, depending on the location of the structure.

In addition to knowing whether certain mitigation actions can be statistically significantly associated with structure destruction, it is important to understand how often these homeowner 'best practices' actually translate into structure survival. Statistical significance is not a safety guarantee and does not necessarily translate into probability. While it is important for homeowners to have the best protection available, it is also important for them to understand the extent to which these actions tend to result in a positive outcome. Without large datasets of actual structure losses, it has until now been impossible to know the frequency at which best practices translate into structure survival, and whether those results are generalizable across different landscapes.

As of now, most guidance on homeowner 'best practices' is derived from limited empirical studies and assumptions based on fire behavior, and thus, the relative efficacy of these practices remains largely theoretical. Empirical studies on the effects of local homeowner mitigation practices, including defensible space or building materials, have been mostly in the form of case studies for a selection of wildfires on specific landscapes (e.g., [19,23,28,29]). Although these studies provide insights, we need a broader understanding across multiple fire events, and thus we need a database that captures characteristics of structures exposed to many fires across a variety of ecosystems.

The California Department of Forestry and Fire Protection (Cal Fire) began a statewide building inspection program in the late 1980s that has been continually upgraded and improved over time, and recent large catastrophic wildfires have added enormously to the amount of data available. The Cal Fire Damage INSpection Program (DINS) was founded with the goal to collect data on damaged, destroyed, and unburned structures during and immediately after fire events to assist in the recovery process, to validate defensible space regulations, and to provide local governments and scientists information for analyzing why some structures burned and why some survived [30]. For all fire events in the state that involve the damage or destruction of buildings worth $10,000 or more, a team of trained inspectors visit during and immediately after the wildfire to collect, for all structures exposed to the fire, a range of information including the extent of damage, defensible space before the fire, building characteristics, and other items.

Through a public records request, we acquired DINS data for more than 40,000 structures that survived, were damaged, or were destroyed across all California wildfires from 2013–2018, making this potentially the largest combined dataset of its sort. Our objective was to summarize these data statewide and across three broad California regions (San Francisco Bay Area, Northern Interior forests and foothills, and Southern California) to a develop a more generalized understanding of local-scale factors characterizing and differentiating destroyed or majorly damaged structures ("destroyed") from those that survived or only had minor damage ("survived") during wildfires. Although other studies have shown landscape-scale and other spatial factors such as topography, fuels, and housing arrangement to significantly affect structure loss probability, we focused here exclusively on the homeowner mitigation practices quantified by the building inspectors to answer:

1. How important was the extent of defensible space in distinguishing destroyed and survived structures?
2. What structural characteristics of homes were associated with increased susceptibility to destruction?
3. Did these patterns vary by region?

2. Materials and Methods

2.1. Data and Summary Statistics

The Cal Fire DINS data were collected for all wildfires, of any size, that resulted in structure damage or destruction. Once building inspection teams arrived at a fire, they recorded information on every exposed structure, including damaged, destroyed, and unburned homes, valued at a minimum of $10,000 or greater than 120 square feet (11 square meters), which is the size at which a permit is required for building. The inspection process occurred by dividing active wildfires into geographical zones as the fire was burning, then a designated number of two-person teams of trained inspectors were assigned to the zone and went to the field to record data. Data were collected for surviving structures in addition to damaged and destroyed structures, and the level of structural damage was recorded in different percentage classes.

Given that most recent structure losses in California have occurred in three distinct regions of the state [2], with most losses occurring within single fire events, we divided the dataset into three regions to compare potential regional differences. Thus, we assigned each county with structure loss to either the "Bay Area", which included counties surrounding the San Francisco Bay; the "North-Interior", which included primarily the northern Sierra Nevada but also other northern coastal and interior counties; and "Southern CA", including coastal counties south of San Luis Obispo County (Table 1).

Building inspectors grouped the structures into classes of damage corresponding to unburned; minor (cosmetic or nonstructural damage); moderate (partial to complete failure of structural building elements); and destroyed. The vast majority of structures were in either the minor or destroyed classes (94% in the Bay Area, 99% in the North-Interior, and 95% in Southern CA), so we lumped

unburned with minor and called them "survived," and lumped moderate with destroyed and called those "destroyed."

The types of data collected included features of the property and vegetation, and inspectors also started to use pre-fire ancillary data, such as assessors' parcel information, to add details for badly damaged or destroyed structures. Most data fields were categorical to ensure consistency in recording, and the teams used phone applications and GPS data to enter information in the field. For this study, we summarized data for most categories in the inspection report, including distance of defensible space, roof type, exterior siding, eaves, windowpanes, vent screens, and deck or porch material.

The distance of defensible space around structures was recorded as one of several ordinal categories, including 0; 0–9 m (0–30 ft); 9–18 m (30–60 ft); 9–30 m (30–100 ft); 18–30 m (60–100 ft); and >30 m (100 ft). We therefore labeled defensible space into four classes in which 5 m (15 ft) were added to the lowest number of each class and used as the label. We merged the class 9–30 m (30–100 ft) with the 18–30 m (60–100 ft) class. Therefore, 0 or 0–9 m were labeled as "5 m", 9–18 m was labeled "14 m," 9–30 m or 18–30 m were labeled "22 m," and >30 m was labeled "35 m." We also used these numeric values to calculate average defensible space distances.

In the 2018 fires (including the Camp Fire and Woolsey Fire in the North-Interior and Southern CA regions, respectively), some new variables were added, including defensive action taken and home age. For defensive action, the inspectors recorded whether it was firefighters, civilians, or both who protected the structures during the wildfires, or, they recorded when the information was unknown. For all years, roof type was most frequently recorded as either "combustible" or "resistant" in the Bay Area, but it was broken into different material classes in the other two regions, so for each region we analyzed data according to the most commonly used classification for that variable. Vent screens were also characterized differently for different fires in which the "screened" class was broken into "fine" or "mesh > 1/8" in some cases, and "unscreened" was referred to as "no" or "none" in some cases. We lumped these together into "screened" and "unscreened".

Building data were collected for different occupancy types (e.g., single- and multi-family residences, outbuildings, commercial buildings, and barns), so we conducted an initial sensitivity analysis using the full dataset comparing rankings of proportions using all structures versus single-family residential structures only, and we found similar rankings for most variables. The variables in which the ranking between single-family residential and other buildings was different were those which would likely characterize non-residential structures (e.g., buildings having no windowpanes, vents, or eaves). Therefore, to preserve the integrity of these classes and for a more robust dataset we used all structures for our analyses in the different regions.

For all variables, there were a substantial number of blank fields where no data were recorded, so there are unequal numbers of data points in all data categories (Table S1). Therefore, we summarized and analyzed all data fields based only on the data that were available for those fields. For comparison purposes we calculated two types of proportions for different perspectives. First, we determined the proportion of the category in each burn class (i.e., for both survived and destroyed structures, what proportion belonged to each category of the variable); and second, we determined the proportion of burn class within each category (i.e., for each category in the variable, what proportion survived or were destroyed) (Figures S1–S8).

2.2. Analysis

To assess the relative importance of each variable, we developed simple generalized linear regression models (GLMs) [31] using defensible space or building characteristics as single predictor variables and survived versus destroyed structures as the bivariate dependent variable. For each model, we used a logit link and specified a binomial response, then calculated and compared the deviance explained (D^2), which is analogous to R-squared in linear regression for each variable. For the statewide analyses of defensive action and structure age, we used the combined data for the North-Interior and Southern CA regions only. We did not model roof type statewide (i.e., only ran

models for individual regions) because the classification system varied from region to region. For these regions, we used data from whichever classification was most common in each region (roof type 1 for North-Interior and Southern CA and roof type 2 for the Bay Area, Table 1). Given the large amount of missing data in the different explanatory variables, we did not perform multiple regression, as our objective was to create a relative importance ranking of the variables using only the data available.

Table 1. Number of destroyed and survived structures from 2013–2018 by county and region in California. Dash marks indicate no structure outcomes recorded. The bold totals report the sums of destroyed and survived structures for each region.

Region	County	Number Destroyed	Number Survived
Bay Area	Contra Costa	1	–
	Lake	2588	89
	Mendocino	566	32
	Monterey	88	4
	Napa	1123	587
	Santa Clara	29	700
	Santa Cruz	6	19
	Solano	11	56
	Sonoma	6764	470
	Yolo	24	88
	Total	**11,200**	**2045**
North-Interior	Amador	1	
	Butte	19,061	740
	Calaveras	936	31
	Fresno	10	2
	Humboldt	5	–
	Inyo	2	–
	Lassen	4	1
	Madera	16	4
	Mariposa	142	20
	Mono	58	6
	Nevada	63	4
	Shasta	1889	260
	Siskiyou	339	18
	Tehama	26	4
	Trinity	142	7
	Tuolumne	1	–
	Yuba	274	8
	Total	**22,969**	**1105**
Southern	Kern	398	21
	Kings	1	–
	Los Angeles	1667	339
	Orange	38	43
	Riverside	53	10
	San Diego	246	67
	San Luis Obispo	81	7
	Santa Barbara	110	42
	Ventura	1075	200
	Total	**3669**	**729**

Because defensible space distance classes can be hypothetically considered as progressively protective against harm (i.e., that more defensible space is more protective), we used a calculation common in medical research, the relative risk [32], to compare adjacent pairs of shorter and longer distance classes of defensible space in addition to comparing the protective effect of the shortest versus longest distance classes (0–30 ft vs. >100 ft). Relative risk is a ratio between proportions of classes having a good outcome (here, structure survived wildfire) versus proportions of classes having a bad outcome (here, structure was destroyed) and indicates whether there is either no relationship (a

value of 1) or if the exposed group (structures with shorter distances of defensible space) has either a significantly higher (values >1) or significantly lower (with values <1) risk of surviving the fire given the data available.

We also calculated the relative risk for most of the building inspection variables. For those with more than one independent category, we calculated the relative risk based on the proportion of survived structures in each category relative to the combined proportion of survived structures in all other categories. For variables with binary classes of "combustible" or "resistant", (Table 1), we calculated the relative risk using the combustible class as the exposure group.

3. Results

From 2013 to 2018, building inspectors examined 41,717 structures, with 37,838 (~90%) damaged or destroyed by fires in 36 California counties, with the largest number destroyed in Butte County in the North-Interior Region, followed by the Bay Area, then Southern California (Table 1). Of the total number of structures inspected, 18% (n = 2045) in the Bay Area, 5% (n = 1105) in the North-Interior, and 20% (n = 729) in Southern CA survived the fires.

3.1. Defensible Space and Defensive Actions

The relative importance of defensible space, as quantified by deviance explained in the regression models, was virtually nil statewide, and the only region in which defensible space had a deviance explained of at least 1% was the Bay Area (Figure 1). Statewide, home survival was associated with slightly longer average distances of defensible space, and this distinction was more pronounced for the Bay Area (Figure 2). On the other hand, when averaging mean values of defensible space classes across survived and destroyed homes, there was a slightly higher mean defensible space distance for destroyed structures in the North-Interior, and virtually no difference in Southern CA (Figure 2).

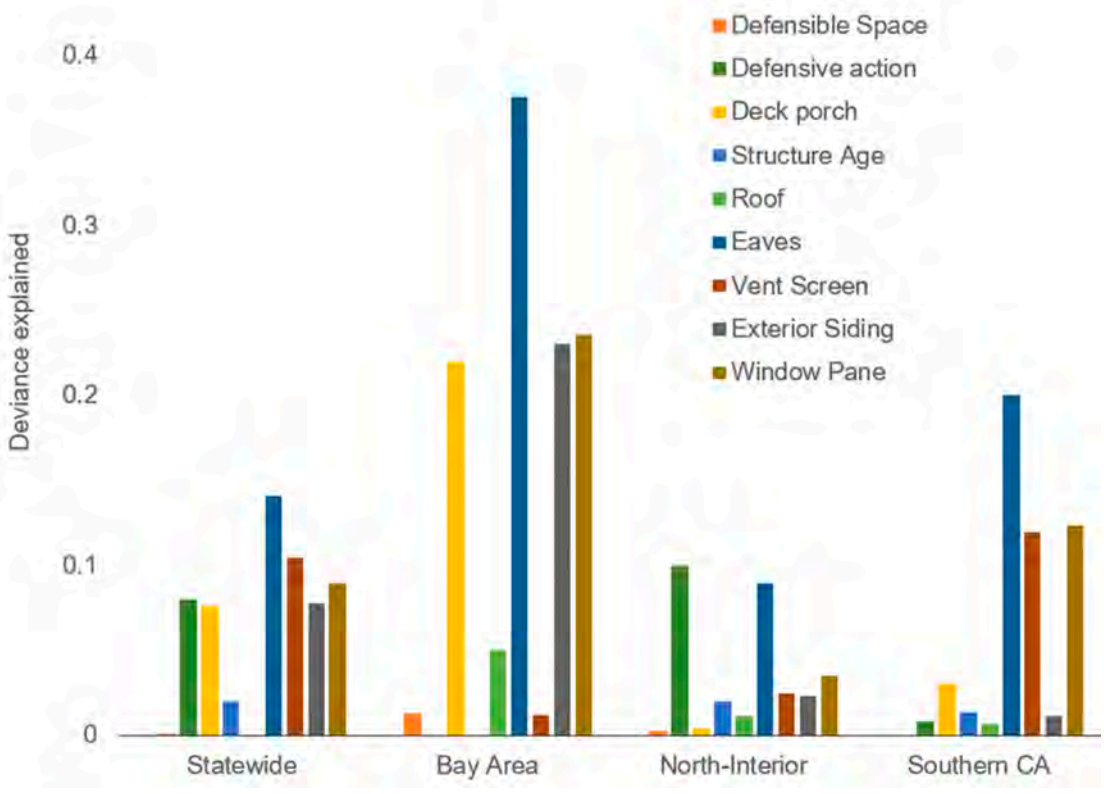

Figure 1. Deviance explained for building inspection variables statewide in three California regions. Defensive action and structure age were only available for North-Interior and Southern CA.

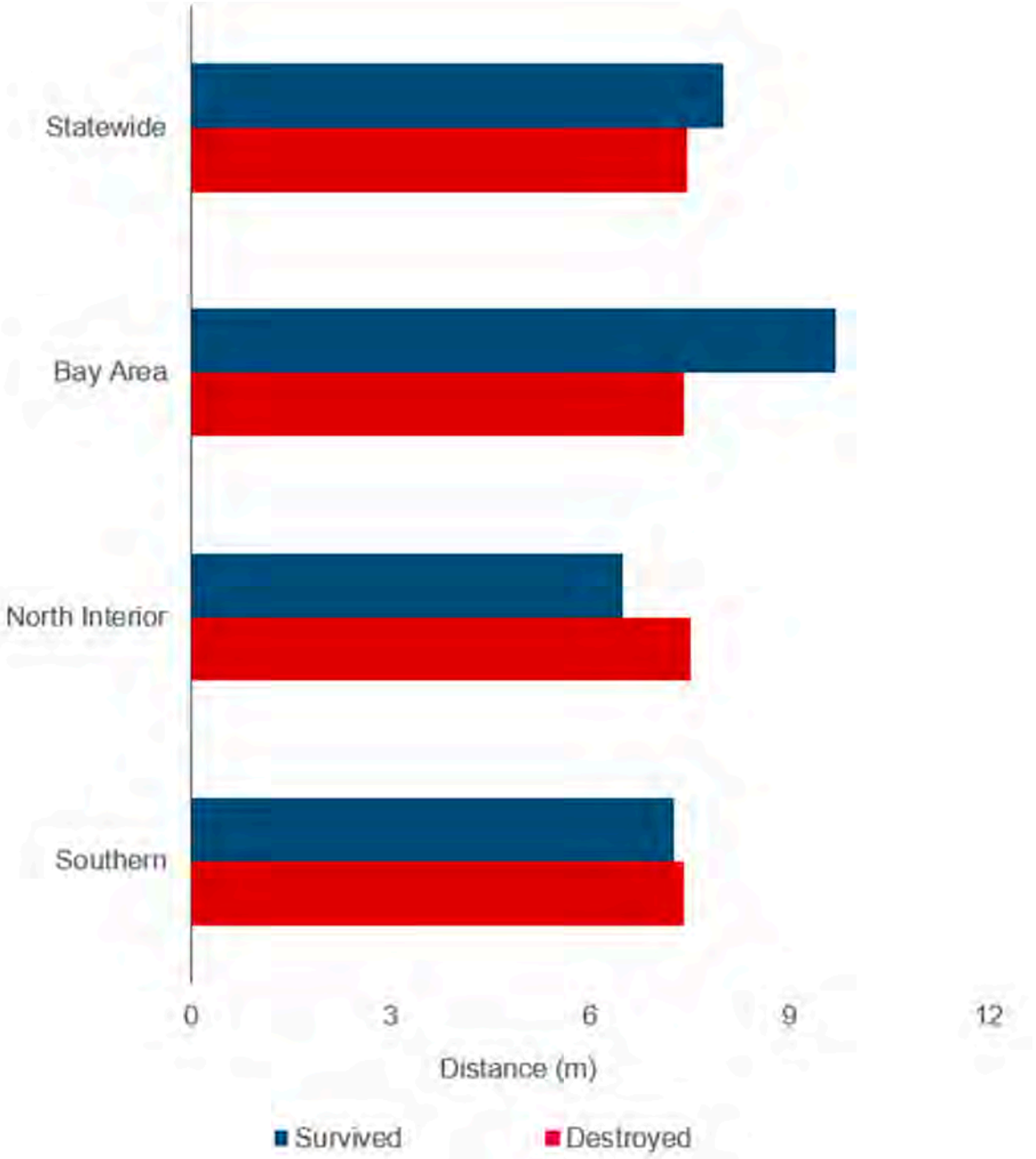

Figure 2. Average distance of defensible space for survived and destroyed structures statewide and in three California regions.

Figure 2. Average distance of defensible space for survived and destroyed structures statewide and in three California regions.

Except for the comparison between 22 m (75 f) vs. 14 m (45 ft) of defensible space statewide, the relative risk ratios for the statewide and Bay Area data showed consistently lower relative risk when comparing classes of longer distance intervals with shorter distance intervals (Table 2). In the North Interior, there was a higher relative risk of destruction with more defensible space when comparing 22 m (75 f) vs. 14 m (45 ft), but there was a significantly lower relative risk when comparing 35 m (115 ft) vs. 22 m (75 ft) (Table 2). There were no significant differences in relative risk among any defensible space distance classes in Southern California (Table 2).

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Although defensive action was only recorded in the 2018 fires in the North Interior and Southern CA regions, it was more important than any other variable for North-Interior, and it was less important in the Southern California data (Figure 1). Statewide (using these two regions and comparing the importance to other variables), it had a medium-high relative importance (Figure 1). The relative risk

Table 2. Relative risk (RR) among building inspection variables statewide and for three California regions. A relative risk of 1 indicates no difference between classes; > 1 means the relative risk of destruction is higher in the first category listed; < 1 means the relative risk of destruction is lower than in the other classes. Dashes indicate where no data were available for certain categories.

ratios for both regions showed that civilian, fire department, and both types of defensive actions were significantly more protective than unknown action (Table 2). In the North-Interior, the fire department providing defensive action provided better protection than civilian actions, but either both or civilian defensive actions provided a slightly better relative risk ratio for Southern CA.

Table 2. Relative risk (RR) among building inspection variables statewide and for three California regions. A relative risk of 1 indicates no difference between classes; >1 means the relative risk of destruction is higher in the first category listed; <1 means the relative risk of destruction is lower than in the other classes. Dashes indicate where no data were available for certain categories.

Variable	Statewide		Bay Area		North-Interior		Southern	
Defensible Space	**RR**	***p*-Value**	**RR**	***p*-Value**	**RR**	***p*-Value**	**RR**	***p*-Value**
14 m (45 ft) vs. 5 m (15 ft)	0.95	0.0001	0.98	0.06	0.97	0.09	0.97	0.24
22 m (75 ft) vs. 14 m (45 ft)	1.08	0.0001	0.98	0.19	1.07	0.003	1.07	0.06
35 m (15 ft) vs. 22 m (75 ft)	0.88	0.0001	0.79	0.0001	0.95	0.0001	0.98	0.61
35 m (15 ft) vs. 5 m (15 ft)	0.91	0.0001	0.76	0.0001	0.98	0.09	1	0.89
Defensive Action								
Both vs. others	0.95	0.0001	–	–	0.68	0.004	0.69	0.04
Civilian vs. others	1.08	0.0001	–	–	0.81	0.0001	0.68	0.04
Fire Department vs. others	0.88	0.0001	–	–	0.44	0.0001	0.81	0.03
Unknown vs. defensive action	0.91	0.0001	–	–	1.02	0.0001	1.01	0.39
Deck, Porch Material								
Composite vs. others	0.85	0.0001	0.93	0.007	0.92	0.03	0.78	0.04
Masonry vs. others	1.002	0.48	1.17	0.0001	0.99	0.03	1	0.78
Wood vs. others	0.98	0.01	1	0.6	1.01	0.002	0.97	0.27
None	1.01	0.10	0.35	0.0001	1	0.24	1.02	0.25
Roof Type								
Asphalt vs. others	1.05	0.0001	–	–	1.03	0.0001	1.02	0.4
Concrete vs. others	0.89	0.0007	–	–	0.94	0.05	0.82	0.04
Metal vs. others	0.97	0.0001	–	–	0.98	0.001	1.04	0.14
Tile vs. others	0.88	0.0001	–	–	0.89	0.0001	0.97	0.25
Wood vs. others	1	0.84			0.99	0.96	1.06	0.38
Combustible vs. resistant	–	–	1	0.75	–	–	–	–
Eaves								
Enclosed vs. others	0.79	0.0001	0.88	0.0001	0.95	0.0001	0.83	0.0001
None vs. others	1.06	0.0001	0.49	0.0001	1.02	0.004	1.35	0.0001
Unenclosed vs. others	1.04	0.0001	1.15	0.0001	1.5	0.0001	0.99	0.86
Vent Screen								
Screened vs. unscreened	0.94	0.0001	0.76	0.0001	0.97	0.0001	0.95	0.23
Exterior Siding								
Combustible vs. resistant	1.05	0.0001	1.03	0.0002	1.04	0.0001	1.07	0.0001
Window Panes								
Multi vs. others	0.94	0.0001	0.94	0.0001	0.97	0.0001	0.74	0.0001
None vs. others	1.01	0.12	0.25	0.0001	0.98	0.04	1.14	0.01
Unenclosed vs. others	1.06	0.0001	1.05	0.0001	1.02	0.0001	1.12	0.0001

3.2. Building Inspection Characteristics

Home construction materials explained a substantial amount of variation in housing losses statewide and across regions (Figure 1). Overall, eaves consistently explained more than any other structural parameters, and having enclosed eaves versus no eaves or unenclosed eaves had a highly significant protective effect as seen in the relative risk ratios (Table 2). The structural variable with the second highest deviance explained across all regions was windowpanes (Figure 1), although statewide this variable was ranked slightly lower than vent screens, and vent screens were also nearly as important as windowpanes in Southern California (Figure 1). The relative risk of having single pane windows was consistently and significantly higher than having multiple pane windows statewide and across all areas (Table 2). Structures that had no windows were not significantly different in relative risk compared to structures with windows statewide, but they had a lower relative risk than structures with windowpanes in the Bay Area and North-Interior, and this was reversed in Southern CA (Table 2). There was a consistent and significantly lower relative risk for structures with screened versus unscreened vents across the state and regions (Table 2).

Aside from eaves, windowpanes, and vent screens, the importance and relative risk of structural parameters associated with structure survival varied across the state and regions. Statewide and in the Bay Area, fire-resistant exterior siding material and deck or porch material were nearly as important as windowpanes (Figure 1), with consistently lower relative risk ratios for fire-resistant siding material (Table 2). In terms of deck or porch material, the most consistently significant effect was the significantly lower relative risk of having composite decking material versus other materials (Table 2). Although roofing material did not explain substantial variation in any of the regions (Figure 1), for the North-Interior and Southern CA regions, where the material types were broken out, concrete and tile both had lower relative risk ratios, although tile was not significant for Southern CA (Table 2). In the North-Interior, metal roofs also had slightly lower significant relative risk (Table 2).

Although structure age, a proxy for all building construction materials, was only recorded for the North-Interior and Southern CA regions, it did not explain substantial variation in structure survival relative to individual building characteristics (Figure 1). On average, however, older homes were consistently more likely to be destroyed than younger homes (Figure 3).

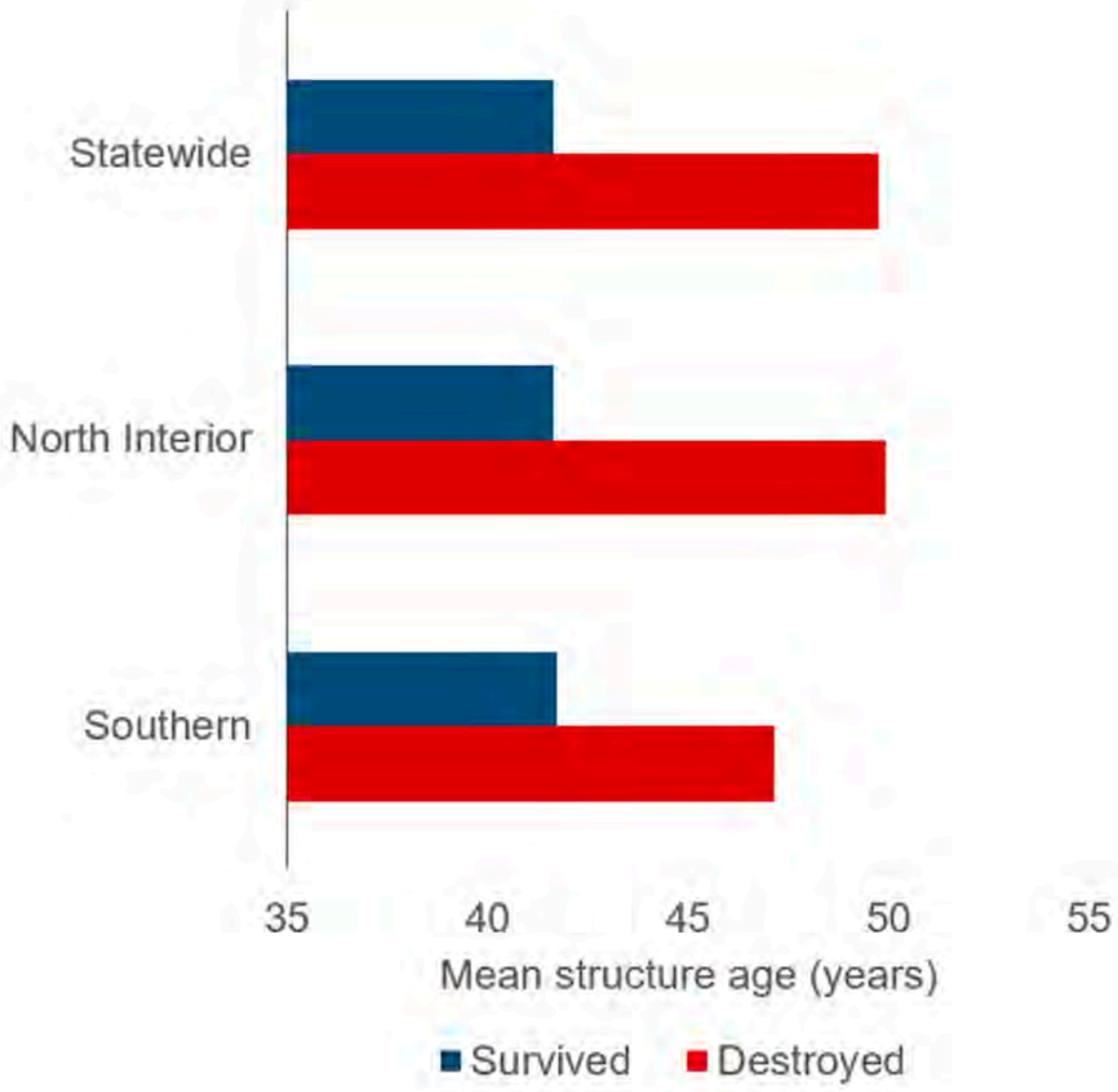

Figure 3. Mean age of structure for survived and destroyed homes in two California regions. The statewide calculations are based on combined totals of both regions (i.e., the Bay Area did not include this variable).

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4. Discussion

In terms of mitigation practices for protecting homes against wildfire, perhaps the most widely recognized and regarded action that homeowners can take is to create defensible space around structures [20,33]. In fact, defensible space and "hardening homes" via building construction

4. Discussion

In terms of mitigation practices for protecting homes against wildfire, perhaps the most widely recognized and regarded action that homeowners can take is to create defensible space around structures [20,33]. In fact, defensible space and "hardening homes" via building construction practices or structure retrofits, collectively referred to as the home ignition zone (HIZ), have often been considered the primary factors that matter in terms of structures surviving wildfire [34,35]. Despite the widespread advocacy of these practices, there has been little empirical study of their effectiveness under actual wildfires, and there is still debate on how much defensible space is critical to home survival despite the regulated distance of 30 m (100 ft).

In this study based on more than 40 k records of structures exposed to wildfires from 2013 to 2018, we found that, overall, defensible space distance explained very little variation in home survival and that structural characteristics were generally more important. Although the relative importance and relative risk ratios of different factors recorded by building inspectors varied slightly from region to region, there were also general similarities, particularly in that structure survival was highest when homes had enclosed or no eaves; multiple-pane windows, and screened vents.

The only region in which defensible space distance explained at least 1% variation in structure survival was the Bay Area, where survived structures had an average of 9.7 m (~32 ft) of defensible space versus 7.4 m (~24 ft) for destroyed structures. Although there were significant differences in relative risk between most pairs of distance classes of defensible space statewide and for the North-Interior, there were some conflicting patterns in the Bay Area and North-Interior, and there was no significant effect of defensible space distance for any comparison in Southern California. The other surprising finding was that, of the structures that did have more than 30 m of defensible space, the vast majority were destroyed in these fires (Figures S1–S8). This of course reflects the large proportion of destroyed structures in the dataset, but it also suggests that structures with greater amounts of defensible space are often still vulnerable.

One potential explanation for the limited importance of defensible space in these data may be that the defensible space distance classes were defined rather broadly, too broad to discern critical details that may have a much bigger impact. Of the few studies quantifying the most effective distance of defensible space for making a significant difference in structure survival probability, Syphard et al. and Miner [19,21] both found the optimum distance to be much shorter than the required 30 m, with the ideal range between 5–22 m. Distances longer than that provided no additional significant protection. Furthermore, these and other studies have shown that more nuanced characteristics of landscaping are most critical for structure protection, including vegetation touching the structure or trees overhanging the roof [36]. The arrangement of vegetation and irrigation are also important factors not accounted for [20]. In fact, despite defensible space traditionally being divided into zones, with the first being from 0–9 m (30 ft) from the structure, newer recommendations are beginning to isolate and focus heavily on the first zone being from 0–1.5 m (5 ft) [37], which may be the most critical zone to account for.

Most structures are lost in wildfires that are burning under severe weather and wind conditions [2], such that burning embers are capable of crossing large, multi-lane freeways and have been reported to blow as far as 1–2 km ahead of a fire front [2,25]. Therefore, one of the primary reasons for the importance of vegetation modification directly adjacent to homes as opposed to longer distances, is that homes are generally not ignited by the fire front but more often by wind-driven embers landing on combustible fuels in or on the house [17,29,38]. Material closest to the house is thus the most likely to cause a proximate spark that can penetrate the structure. To this point, irrigating vegetation and removing dead plant material to reduce ignitability may be as or more important than fuel volume, which is a finding borne out by recent research [24]. While defensible space distances <30 m may be sufficient for increasing structure survival probability, another important reason for requiring 30 m (100 ft) is firefighter safety and providing a zone of protection [39]. Finally, while the inspectors recorded defensible space distances, part of the definition of defensible space in California revolves

around the horizontal and vertical spacing of fuels; thus, if these factors matter as much or more than distance, they could not be accounted for here.

The nature of building loss via ember flow factors such as exterior siding or roof material were much less important than exposed eaves, vents, or windows. This again is likely due to the extreme weather condition characteristics of destructive wildfires. That is, the fire-resistance of materials such as roofs or siding, i.e., preventing them from catching fire, was less important than building characteristics that provided gaps in the structure that could allow penetration of wind-borne burning debris. These results suggest that one of the potentially most effective methods of protecting homes from wildfire destruction would be to perform simple building retrofits, such as placing fine mesh screens over vents and coverings other openings in the structures, such as gaps in roofs, and enclosing structure eaves. Specific recommendations for these types of retrofits are easily found online, e.g., [40], and suggest that improving the fire safety of structures does not necessarily require expensive replacement of construction materials but rather careful attention to structure details.

The previous post-fire study of the role of construction materials in structure survival also found that windows, particularly framing material and panes, were more important than roof or siding material, although the methods and overall suite of variables differed in that study [23]. In the case of windows, they can, like other parts of the structure, provide an easy entry point for firebrands [26]. Additionally, however, they are also vulnerable to radiant heat, and multi-pane windows can withstand much higher levels of thermal exposure than single-pane windows [41]. Although not recorded here, the type of glass used in the window is also important for resistance to cracking [26].

Although individual structural characteristics were highly influential in this study, structure age did not explain a lot by itself, which may mean that, at a broad scale, it does not necessarily serve well as a proxy for the building characteristics most likely to protect homes. On the other hand, Syphard et al. [23] found that structure age did correlate with both building characteristics and structure survival, but that study was only conducted in San Diego County, where building codes had already been updated several times in response to wildfires in the regions. Although the state of California has also recently adopted strict building codes for wildfires [42], those codes only apply to new housing, so the effects may not have been seen yet. Further analysis might be warranted to compare structural characteristics and outcomes as a function of date of code enforcement.

Another consideration is that, despite the importance of structure age in the San Diego study, that study also determined that building location and arrangement were more important in predicting structure loss than structure age, building materials, or defensible space. The effect of structure age was primarily important in higher-density neighborhoods where structure loss was overall less likely. Thus, the role of housing arrangement and location, found to be the most important predictors of structure loss in several California studies [13–15] and nationwide [43] should ultimately be factored into discussions of reducing future fire risk; and this looks to be a challenge given trends of rapid ongoing development in the wildland–urban interface [44].

One of the reasons that housing arrangement and location are such strong predictors of structure loss may be structure accessibility by firefighters, who must divide manpower and resources to reach communities located in dispersed or remote locations [45,46]. The role of defensive actions in determining the extent and location of structure survival has been historically difficult to quantify, mostly because data are sparse, but also because defining suppression effectiveness is an inherently difficult task [47]. In the North-Interior region, defensive action explained more than any other factor in structure survival, although it was less important than building characteristics in Southern California. Even given the high importance of defensive action in the North-Interior, the total number of structures with unknown defensive action was substantial, and the proportion of unknown actions was even larger in Southern California. Thus, while these results suggest that defensive actions may be one of the most important and overlooked factors in structure survival, it remains difficult to make definitive conclusions. Given that building inspectors have just started collecting this information, it is important to recognize this is an on-going process of increasing our knowledge base as more data are collected.

5. Dataset and Limitations

Given the enormous number of structures lost in California in recent years, the dataset compiled for this study may represent the largest existing source of information on homeowner mitigation practices associated with structure loss. Other large databases and studies of house loss have been developed in other countries, however, where wildfires result in substantial losses in structures and human life; much of this work has been conducted in Australia, a country with a long history of destructive wildfires with substantial structure losses [48], and human fatalities [49]. This ongoing data collection process, especially if more exposed but unburned homes are included, will be important for continued understanding of structure loss and identifying the most effective strategies for prevention.

Despite the unprecedented opportunity the DINS data have provided for this broad-scale analysis of structure loss, there are nevertheless uncertainties and limitations within the data, and Cal Fire is working to improve the collection process on an ongoing basis [30].

The primary limitation is, as we discussed previously, that defensible space was presented uni-dimensionally as a function of distance categories and thus excluded other relevant factors such as vegetation spacing, height, type, age, moisture content, or composition. Nevertheless, given the broad scale of the data and similar conclusions for all study areas, these additional vegetation characteristics do not appear to be biased in one direction or the other; thus, our conclusions about distance classes are likely robust.

Another limitation of the dataset is the potential uncertainty inherent in recording building characteristics after a wildfire for homes that have been badly burned with materials largely consumed in the fire. This likely explains the missing data seen throughout the records. Cal Fire is aware of this and is beginning to combine their reports with pre-fire information from county assessors' offices [30]; however, the extent to which pre-fire data may have been incorporated in the reports used for this study is unclear.

Finally, as mentioned previously, this study only focused on the relative importance of the local-scale factors reported by the building inspectors, and full understanding of structure loss will need to include additional factors. Ongoing research will account for a fuller range of landscape-scale factors as well as information on fire behavior and spatial patterns.

6. Conclusions

We have explored the factors correlated with structure loss and survival during a recent five-year period in California. In most regions home structural characteristics are far more important in determining home survival than defensible space. Statewide, the most critical factor was eave construction. Windowpanes were also widely important in the state. Exterior siding was an important structural characteristic in the Bay Area, but vent screens were much more important in southern California. The likely explanation for why structure characteristics play a greater role than defensible space is that most homes burn by embers, which often come from long distances; and the impact of the ember cast is not likely affected by distance of defensible space. Whether or not the embers ignite is largely a function of structure.

Given that the primary role of building inspectors is to assess building damage, most structures in the data were destroyed. As such, one of the striking outcomes of this study is the finding that many of these destroyed structures could be characterized as "fire-safe," such as having >30 m defensible space or fire-resistant building materials. While the number of structures lost in these fire events was unprecedented in California history, structure loss during severe fire-weather and wind conditions similar to some of the fires represented here has occurred for decades in the state [2]. Therefore, it may be safe to assume that these data are broadly representative.

Supplementary Materials: The following are available online at http://www.mdpi.com/2571-6255/2/3/49/s1, Figure S1: Proportion of defensible space distance classes for survived and destroyed structures (a) and proportion of survived and destroyed structures within defensible space distance classes (b) for three California regions, Figure S2: Figure S2: Proportion of defensible action type for survived and destroyed structures (a) and proportion

of survived and destroyed structures within defensive action types (b) for two California regions, Figure S3: Proportion of deck material type for survived and destroyed structures (a) and proportion of survived and destroyed structures within deck material type classes (b) for three California regions, Figure S4: Proportion of roof material type for survived and destroyed structures (a) and proportion of survived and destroyed structures within roof material type classes (b) for two California regions, Figure S5: Proportion of eave type for survived and destroyed structures (a) and proportion of survived and destroyed structures within eave type classes (b) for three California regions, Figure S6: Proportion of Exterior siding classes for survived and destroyed structures (a) and proportion of survived and destroyed structures within exterior siding classes (b) for three California regions, Figure S7: Proportion of vent screen classes for survived and destroyed structures (a) and proportion of survived and destroyed structures within vent screen classes (b) for three California regions, Figure S8: Proportion of windowpane type for survived and destroyed structures (a) and proportion of survived and destroyed structures within windowpane type (b) for three California regions. Table S1: Number or average value of destroyed and survived structures within building inspection classes for three California regions.

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WHY ARE SO MANY STRUCTURES BURNING IN CALIFORNIA?

Alexandra D. Syphard[1] and Jon E. Keeley[2,3]

California has earned a reputation for wildfires that inflict serious damage on human infrastructure, dating back to images of Richard Nixon hosing down the roof of his house in the 1961 Bel-Air fire, and of the famous "fireproof" home of grocery store entrepreneur Fred Roberts burning to the ground in 1982. In recent years, this notoriety has been transformed into public alarm, reflected in the apocalyptic headlines of recent newspaper articles suggesting the "end of California" (*New York Times*, 30 October 2019) and that "California is becoming unlivable" (*The Atlantic,* 30 October 2019). Now the phrase "the new normal" has worked its way into the lexicon, sustained by record-breaking structure loss numbers in 2017 and 2018 despite significantly lower structure losses in 2019.

It remains to be seen whether or not those two recent years were back-to-back one-in-a-hundred-year events, or if the trend has crossed some kind of tipping point, but data do show a long-term trend of significant increase in structures lost to wildfires since the beginning of the 20th century (Fig. 1). What was an average of ~500 homes lost per year in Southern California from about 1950–2000 (CalFire 2000) has recently climbed to ~2700 structures per year statewide from 2000–2018 (Syphard and Keeley 2019). California is not alone in the U.S., or in the world, in suffering increasing impacts from wildfires (e.g., Blanchi et al. 2012, Haynes 2015, Viegas 2018). Impacts so far in the current Australian bushfire season have been record-breaking, with several thousand structures lost, more than 25 fatalities, and unthinkable losses to wildlife. The question that follows, then, is why?

Although trends vary from region to region, one clear reason for increasing wildfire-related losses is the overall

Above: Aerial retardant drop on a chaparral wildfire in coastal southern California, taken July 5, 2008, in the foothills of the Los Padres National Forest. *[Dan Lindsay]*

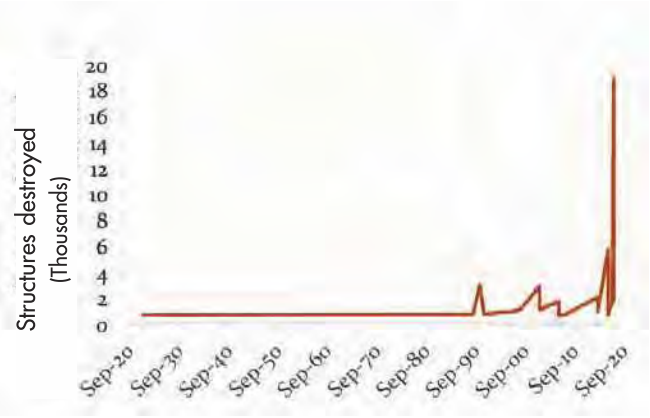

Figure 1. Annual number of structures destroyed in wildfires in California from 1920 to 2018. Source: California Department of Forestry & Fire Protection

increase in wildfire activity. Although, counter to intuition, the number of wildfires has declined in the last several decades, area burned has either remained constant or increased, with substantially higher frequency of large wildfires (Keeley and Syphard 2018), and as discussed further in Keeley and Syphard (this issue). Perhaps an even stronger explanation for increased wildfire-related structure loss is the rapid development of the wildland-urban interface (WUI), which not only exposes more structures to wildland fire, but also increases the likelihood for more human-ignited fires (Radeloff et al. 2018). Despite these trends, however, not all fires result in structure loss, and not all structures are impacted by wildfires they are exposed to. Thus, it is essential to study the factors that are most strongly related to structure exposure and resilience to wildfire, which could then lead to better adaptation and coexistence with wildfire in this era of the "new normal."

In response to this need, a growing number of scientists are conducting empirical research studies to answer the question of why some structures are lost in wildfires and others aren't. Results so far show that the answer to that question is complicated. That is, structure loss results from the confluence of multiple interacting factors across different temporal and spatial scales, which all vary by ecosystem. Given this complexity, misunderstandings and disagreements have arisen over the cause and direction of trends in wildfire activity (Doerr and Santín 2016), fire risk and structure loss (Mccaffrey et al. 2019), and thus, the most effective approach for prioritizing fire management decisions (Moritz et al. 2014). In fact, management techniques appropriate for one region are commonly applied inappropriately to other regions (Noss et al. 2006).

One way that this conflict over priorities can be reduced is through better information and understanding of the similarities and differences that contribute to structure loss among wildfire ecoregions. As data accumulate about the range of conditions under which losses occur, it will be increasingly possible to sort out which risk management techniques are most appropriate for different regions. Wildfire structure losses in the last several decades have already provided a wealth of data for studies comparing factors associated with structures that survived or were destroyed. Most of this work has been done in California (Maranghides and Mell 2009, Syphard et al. 2012a, 2014, 2017, 2019c, Miner 2014, Alexandre et al. 2015, Kramer et al. 2019, Syphard and Keeley 2019) and Australia (Leonard 2009, Blanchi et al. 2010, 2012, Gibbons et al. 2012, 2018, Price and Bradstock 2013, Penman et al. 2019); but some work has also been done in other parts of the continental United States (Alexandre et al. 2016, Kramer et al. 2019).

Combined, the results of this research show clear roles for both local, house-level factors (e.g., structural characteristics of a particular house and property-level landscaping) and broader, landscape-level factors (e.g., housing pattern and location, topography, fuel, and fire characteristics) in explaining why some structures survive wildfires and others don't. This is consistent with the natural hazards literature that theoretically places vulnerability within the intersection of "exposure," that is, potential contact with a hazard; and "sensitivity," or the degree to which the hazard can cause harm (Birkmann 2006). Vulnerability to wildfire is a combination of exposure and sensitivity such that vulnerability results in loss when sensitive characteristics of structures are exposed to hazard events (e.g., the wildfire) (Cutter 1996, Schumann et al. 2019). Thus, exposure is the part of vulnerability related to characteristics of a location, and sensitivity is the risk of loss due to intrinsic physical or social characteristics.

EXPOSURE

Coincidence of fires and houses

A structure's wildfire hazard exposure ultimately lies at the spatial intersection of a wildfire event and the location of the property. The probability of structure

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Caption here. *[Rick Halsey]*

loss thus depends on the relative likelihood that a fire ignition results in a fire within the geographical range of structures in the wildland-urban interface (WUI). In turn, this depends on the location and timing of a fire ignition, which varies depending on cause and biophysical characteristics (Syphard and Keeley 2015) relative to other determinants of fire size, including topographic conditions; fuel amount, moisture, and spatial continuity; and weather (Faivre et al. 2016). Large fires tend to be either primarily fuel-dominated or wind-dominated (Keeley and Syphard 2019), with most damage and economic loss occurring from wind-driven fire events (Jin et al. 2015, Keeley and Syphard this issue).

Large fire probability increases with the co-occurrence of human-caused ignitions and severe wind conditions (Abatzoglou et al. 2018). This means that, as population increases and development further encroaches into wildland vegetation, there is an increased risk that a human-caused ignition will coincide in place and time with hot, dry weather; flammable vegetation; and severe wind conditions. Data show that fires tend to be most frequent at low to intermediate housing and population densities (Syphard et al. 2009, Bistinas et al. 2013). Thus, the rapid increase in the spread of exurban development like that occurring now in California (Radeloff et al. 2018), has the potential to both increase the number of ignitions and decrease the overall distance between wildlands and housing.

As the distance between wildland vegetation and housing development decreases across a landscape, the overall exposure of houses to wildfire increases. This helps to explain research that shows the arrangement and location of housing development to be a top-ranked predictor of whether a structure survives or is destroyed by wildfire (e.g., Syphard et al. 2012b, Alexandre et al. 2016, Kramer et al. 2019). In terms of arrangement, data consistently show that loss to wildfire is highest at relatively low housing density (Kramer et al. 2018, Syphard et al. 2019c) and at the interface between wildlands and development (Kramer et al. 2019), regardless of the geographic region in which a structure is located,.

Other housing patterns, such as the way housing is dispersed, or the size of housing clusters, are also influential, although their relative importance in explaining structure loss varies from region to region (Alexandre et al. 2015, 2016). Topography is an additional exposure-related factor significantly related to structure loss, as fire tends to spread quickly upslope, meaning that houses on ridgetops are particularly vulnerable. An important caveat to the relationship between low structure density and structure loss is that, once a fire reaches a development, structure-to-structure spread is possible if adjacent houses are highly flammable and spaced within at least 50 meters of one another (Price and Bradstock (2013). In these circumstances, high housing density can be a significant risk factor (Maranghides and Mell 2009).

Fire patterns, altered fire regimes, and vegetation management

In addition to housing arrangement, housing location affects the potential exposure of a structure to wildfire because some areas are inherently more fire-prone than others (Syphard et al. 2012b). Certain parts of the landscape tend to burn repeatedly while others do not, and this reflects the wide variation in fire regimes across California (Syphard and Keeley in press). During the last century, fire regimes in California have been altered due to a range of factors including climate change, land use change, and legacies of fire management. However, the cause of fire regime changes, and their relative effects, have been nearly opposite in the northern and southern-coastal parts of the state (Safford and Water 2014). As described in Keeley and Syphard (this issue), a history of successful fire exclusion in dry, mixed-conifer forests contributed to an alteration of what had

been a low-intensity surface fire regime that typically burned back the understory plants without reaching into the canopy and burning the large trees. The subsequent increase in the density of surface litter and the unchecked ingrowth of young trees that serve as ladder fuels now facilitate uncharacteristically severe crown fires. In contrast, in the native shrublands of southern and central coastal California, increased human-caused ignitions have resulted in unnaturally high fire frequency, with increases in wildfire further promoted by ongoing conversion of shrublands to more flammable invasive grasses (Fusco et al. 2019, Syphard et al. 2019b, 2019a).

These differences in the two fire regimes, and how they have been altered, have led to substantial controversy regarding wildfire exposure and the effects and effectiveness of vegetation management (Keeley et al. 2009, Halsey and Syphard 2015). In both northern and southern California, changes in fire regimes could lead to more dangerous or frequent wildfires, thereby increasing structure exposure to hazard. Mechanical treatments and prescribed fire in dry, mixed-conifer forests that reduce the understory and decrease small diameter tree density may help return these forests to a more resilient condition, and thereby potentially reduce exposure of structures to high fire hazard (Knapp et al. 2017).

On the other hand, in the non-forested landscapes that dominate the coastal central and southern parts of the state, vegetation management is primarily focused on reducing the extent of woody vegetation. That is, mechanical treatments are typically designed to remove and reduce the cover of native shrublands and increase the cover of herbaceous vegetation. Prescribed fire in this region *increases* the amount of uncharacteristically frequent fire, putting additional stress on native chaparral and shrublands. Therefore, in non-forested ecosystems vegetation management is inconsistent with ecological integrity and, in addition, has minimal efficacy in the wind-driven fires that result in the most structure loss (Keeley and Syphard this issue).

Access as a risk factor

While vegetation management may control fire behavior by slowing wildfire spread, wildfires during extreme wind conditions typically generate embers and burning debris that can fly kilometers ahead of the fire front. Therefore, fuels management in remote landscapes, even if it does alter fire behavior, has little possibility of preventing wind-driven fires from spreading and expanding if there are no firefighters present to control the fire. This is the likely explanation for why Penman et al. (2014) found that fire size and exposure of property to wildfire in Southern California are primarily controlled by fire weather and characteristics of the built environment, with fuel treatments or fuel load management having minimal influence. Fuel load is less likely to be limiting during wind-driven wildfires and reduction of fuel load in remote areas is unlikely to affect fire outcomes (Keeley et al. 2004, Schoennagel et al. 2004).

On the other hand, strategic placement of fuel breaks near communities may be more effective at reducing exposure because firefighters can use these for safe access to perform suppression activities (Syphard et al. 2011). In addition to strategically placed fuel breaks near communities, the road network surrounding a structure is also important for minimizing exposure from an access perspective. Wide roads and multiple access points can facilitate the transport of firefighting resources to properties within a community; in addition, a good road network provides faster and more efficient evacuation alternatives (Mangan 2000).

SENSITIVITY

Community sensitivity to wildfire, and the capacity to recover from wildfire losses, is related to the social and demographic characteristics of a region (Schumann et al. 2019). In terms of the physical nature of structure loss, however, the primary determinants of sensitivity include defensible space and home structure characteristics as well as firefighter accessibility.

Defensible space

There is certainly a degree of confusion regarding defensible space. A common sentiment is that the larger the defensible space, the better protected the home.

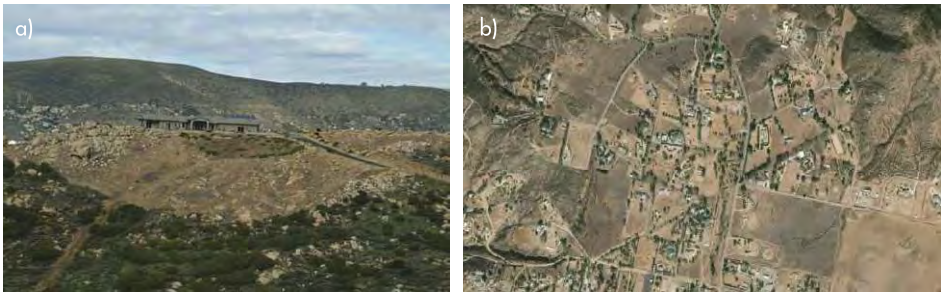

Figure 3. Local (a) and landscape-scale (b) examples of defensible space being performed beyond legal requirements or scientific evidence for protection

Thus, clearance far in excess of legal requirements is increasingly being carried out (Fig. 3a), sometimes at a broad scale (Fig 3b). This is not necessarily helpful or effective. At the same time, many homeowners fail to create sufficient defensible space to improve structure survival.

What does the evidence show about the effectiveness of defensible space? The state of California requires homeowners in state-defined hazardous areas to provide 30 meters (100 feet) of defensible space around their home, which involves the maintenance of specific horizontal and vertical distances of spacing between patches of woody vegetation. Empirical studies in two Southern California areas found that defensible space of approximately 5-20 meters (16-66 feet) provided significant protection, with additional distance providing little or no significant benefit, even on steep slopes (Miner 2014, Syphard et al. 2014). Empirical research looking at structure loss in Australia also found that vegetation reduction and defensible space were most effective at close proximity to the structure (Gibbons et al. 2012, Penman et al. 2019), and that regular irrigation and proper spacing could be as just as effective as clearing woody vegetation (Gibbons et al. 2018).

The largest empirical study of home survival published to date, which included more than 40,000 structures subjected to wildfires over a five year period (Syphard and Keeley 2019), showed that defensible space distance explained little or none of the variance in structure survival. Instead, characteristics of the structure itself were far more significant (Fig. 4). These results should not be interpreted to mean defensible space is not important. But they do suggest that the most important component of defensible space may be the characteristics of vegetation closest to the house. For example, vegetation touching the structure and trees overhanging the roof were highly significant in the two empirical examples from Southern California.

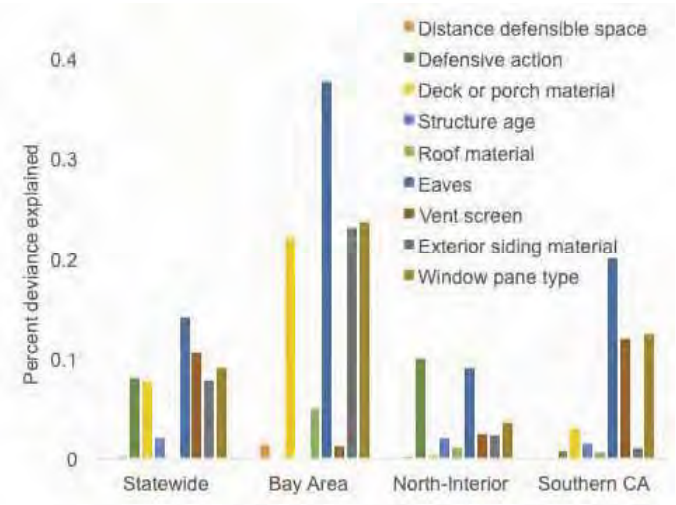

Figure 4. Relative importance (percent deviance explained) of defensible space distance and structural characteristics explaining structure loss to California wildfires from 2013–2018 for the entire state and broken into three broad regions. *Figure modified from Syphard and Keeley (2019).*



Figure 5. Image of flammable debris on a roof that could ignite from wind-blown embers, reflecting how vegetation near or overhanging structures could increase the likelihood of structure loss.

Ember cast

It needs to be appreciated that, particularly during extreme wind-driven fires, most homes do not burn from direct flame contact or from the radiant heat of the fire front, but rather from embers blown from the fire front, even from a kilometer or more away. Thus, the material that embers land on, be it vegetation or the structure itself, is key to whether the structure ignites or not. In some cases, the effect of overhanging trees or nearby vegetation is mostly related to the dead plant material or debris that is close to the structure (Fig.5). Likewise, the structural characteristics found to be most important in this recent study (Syphard and Keeley 2019) were related to the prevention of ember penetration, such as vent screens and eaves. Open eaves (Fig. 6a) are much more vulnerable to fires than closed eves (Fig. 6b). Open eaves have vents that are arranged perpendicular to the ground and thus in direct line of oncoming wind-driven ember cast. Closed eaves have vents facing down towards the ground and perhaps less prone to embers entering the vents.





Figure 6. Images of a) open eave design that may allow ember penetration into the structure more readily than b) closed eave design that has been significantly associated with structure survival in California wildfires.

CONCLUSION

The studies described above illustrate that some structures are destroyed in wildfires and others are not because of multiple, often interacting, factors that variably influence the exposure and sensitivity of a property to wildfire. In an ideal world, strategies to increase community resistance to wildfire would be ranked and prioritized according to their relative potential for success in preventing structure loss in any given ecosystem. Of course, an ideal world would also not have to account for factors such as cost, effort, and feasibility, which add to the complexity of decision-making in the real world.

While most empirical research on structure loss has so far focused on either exposure or sensitivity factors independently, an integrated analysis in Southern California provided a comparison of the relative importance of different exposure-related and sensitivity-related variables (Syphard et al. 2017, Fig. 7) in distinguishing destroyed from surviving structures. Study results suggested that exposure (when measured by structure density) was the most important factor overall that distinguished destroyed from surviving structures. The relative importance of different sensitivity variables (e.g., structure age or landscaping characteristics) varied depending upon whether the structure was highly exposed (i.e., at low housing density) or less exposed (i.e., at high housing density) (Fig. 7).

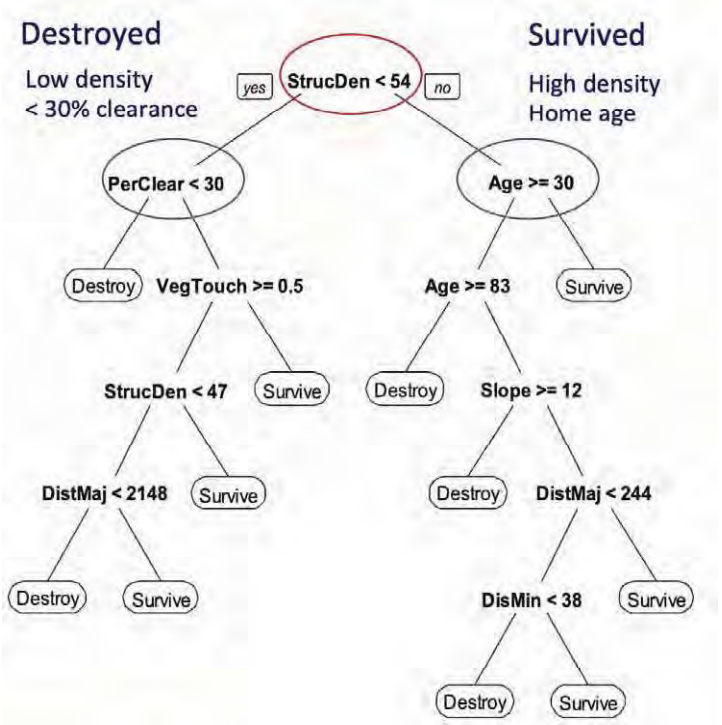

Figure 7. Classification tree showing the hierarchy of factors that best distinguished destroyed from survived structures in Southern California wildfires. Abbreviations are: StrucDen = structure density; PerClear = percentage woody vegetation clearance on property; Age = age of structure; VegTouch = number of sides of structure with vegetation touching; Slope = percentage slope on property; DistMaj = distance in meters to a major road; DisMin = distance in meters to a minor road. *Modified from Syphard et al. 2017.*

These results suggest that, in an ideal world, the most effective strategy at reducing future structure loss would focus on reducing the extent of low-density housing via careful land planning decisions. This conclusion is rather obvious given that reducing exposure reduces the chance that a wildfire could reach a structure in the first place. In the real world, regardless of land use planning decisions for future development, there is extensive existing development that may be exposed to future wildfires. Therefore, strategies like ignition prevention and strategic vegetation management could potentially reduce the exposure of these houses by focusing on the initiation or spread of the wildfire.

Once a fire reaches a property, structure sensitivity then becomes the key determinant for survival. In many areas, effective efforts to minimize sensitivity to wildfire include education and increased awareness of appropriate defensible space practices, development of Firewise Communities (Jakes et al. 2007), and improvement in building codes. Nonetheless, some communities underinvest in defensible space (Taylor et al. 2019), while in others, homeowners create excessive clearance (Fig. 3) that may increase the extent of invasive grass on the property. Conversion of native woody vegetation into grass in the non-forested landscapes of Southern California, for example, could increase the flammability of the property (Fusco et al. 2019), particularly if the grass is not irrigated regularly (Gibbons et al. 2018).

Given the importance of structural characteristics in home survival in recent California wildfires (Syphard and Keeley 2019), the improvement of building codes has been a positive development overall. However, there is already extensive existing residential development in fire-prone areas that was built prior to the adoption of new building codes. Reducing the fire sensitivity of these homes generally entails retrofits and modifications, which can be expensive (Quarles and Pohl 2018). However, some of the most effective actions, such as eave coverings and vent screens, are generally less expensive than replacing roofing or exterior siding, although window replacement can also be expensive (Quarles and Pohl 2018).



The 2017 Thomas Fire. *[Stuart Palley, U.S. Forest Service]*

It would appear, given recent improvements in adapting structures to withstand fire, that the increase in the numbers of houses burned in wildfire is not a matter of increased sensitivity. Instead, the answer lies somewhere in the combination of factors that govern exposure, including changes to wildfire behavior and activity, as well as exurban development that places structures in the path of these wildfires. Climate and vegetation change may increase the probability of large wildfires in some regions, such as the northern parts of California (Syphard et al. 2019c); but in other regions, like Southern California, climate change is likely to manifest differently, most likely indirectly, via factors such as long-term drought and vegetation change.

While the effects of climate change on wildfire vary from region to region, housing pattern variables have consistently been the most important factors explaining structure loss across California and elsewhere. This suggests that much of the increase in structure loss in California may be attributable to increases in this type of exposure—and that planning decisions could have broad-scale benefits in the future. Also consistent across regions is the potential for homeowner mitigation measures to provide significant improvement in structure survival probability. Those measures that focus on reduction of ember impact and penetration are most important.

Despite these overall consistencies, there is variation in the nature and strength of relationships in all of these factors. Wildfire frequency and behavior, and fuel characteristics, vary widely by ecosystem; thus, vegetation management efforts differ greatly in effects and effectiveness and should be implemented appropriately. Regardless of regional variations, everyone, from the individual homeowner, to local planning and permitting officials, to state and federal government authorities, will need to be involved in instituting preventive measures. Management appropriately informed by science and data analysis can reduce future structure losses and minimize ecological impacts to assure a more sustainable future. While these efforts may seem expensive in the present, it is much less expensive than paying for losses in the future.

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Review of Ecological Effects of Roads on Terrestrial and Aquatic Communities

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Abstract: *Roads are a widespread and increasing feature of most landscapes. We reviewed the scientific literature on the ecological effects of roads and found support for the general conclusion that they are associated with negative effects on biotic integrity in both terrestrial and aquatic ecosystems. Roads of all kinds have seven general effects: mortality from road construction, mortality from collision with vehicles, modification of animal behavior, alteration of the physical environment, alteration of the chemical environment, spread of exotics, and increased use of areas by humans. Road construction kills sessile and slow-moving organisms, injures organisms adjacent to a road, and alters physical conditions beneath a road. Vehicle collisions affect the demography of many species, both vertebrates and invertebrates; mitigation measures to reduce roadkill have been only partly successful. Roads alter animal behavior by causing changes in home ranges, movement, reproductive success, escape response, and physiological state. Roads change soil density, temperature, soil water content, light levels, dust, surface waters, patterns of runoff, and sedimentation, as well as adding heavy metals (especially lead), salts, organic molecules, ozone, and nutrients to roadside environments. Roads promote the dispersal of exotic species by altering habitats, stressing native species, and providing movement corridors. Roads also promote increased hunting, fishing, passive harassment of animals, and landscape modifications. Not all species and ecosystems are equally affected by roads, but overall the presence of roads is highly correlated with changes in species composition, population sizes, and hydrologic and geomorphic processes that shape aquatic and riparian systems. More experimental research is needed to complement post-hoc correlative studies. Our review underscores the importance to conservation of avoiding construction of new roads in roadless or sparsely roaded areas and of removal or restoration of existing roads to benefit both terrestrial and aquatic biota.*

Revisión de los Efectos de Carreteras en Comunidades Terrestres y Acuáticas

Resumen: *Las carreteras son una característica predominante y en incremento de la mayoría de los paisajes. Revisamos la literatura científica sobre los efectos ecológicos de las carreteras y encontramos sustento para la conclusión general de que las carreteras están asociadas con efectos negativos en la integridad biótica tanto de ecosistemas terrestres como acuáticos. Las carreteras de cualquier tipo ocasionan siete efectos generales: mortalidad ocasionada por la construcción de la carretera; mortalidad debida a la colisión con vehículos; modificaciones en la conducta animal; alteración del ambiente físico; alteración del ambiente químico; dispersión de especies exóticas e incremento en el uso de áreas por humanos. La construcción de carreteras elimina a organismos sésiles y a organismos de lento movimiento, lesiona a organismos adyacentes a la carretera y altera las condiciones físicas debajo ella misma. Las colisiones con vehículos afectan la demografía de muchas especies tanto de vertebrados como invertebrados; las medidas de mitigación para reducir la pérdida de animales por colisiones con vehículos han sido exitosas solo de manera parcial. Las carreteras alteran la conducta animal al ocasionar cambios en el rango de hogar, movimientos, éxito reproductivo, respuesta de escape y estado fisiológico. Las carreteras cambian la densidad del suelo, temperatura, contenido de agua en el suelo, niveles de luz, polvo, aguas superficiales, patrones de escurrimiento y sedimentación, además de agregar metales pesados (especialmente plomo), sales, moléculas orgánicas, ozono y mutrientes a los ambientes que atraviesan. Las carreteras promueven la dispersión de especies exóticas al alterar los hábi-*

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tats, al estresar a las especies nativas y proveer corredores para movimiento. Las carreteras también promueven el incremento de la caza y la pesca, el hostigamiento pasivo de animales y modificaciones del paisaje. No todas las especies ni todos los ecosistemas son afectados por las carreteras de igual forma, pero en general la presencia de carreteras está altamente correlacionada con cambios en la composición de especies, los tamaños poblacionales y los procesos hidrológicos y geomorfológicos que afectan a la estructura de sistemas acuáticos y reparios. Se necesita más investigación experimental para complementar estudios correlativos post-hoc. Nuestra revisión hace énfasis en que en trabajos de conservación es importante evitar la construcción de nuevas carreteras en áreas carentes de ellas o en áreas con pocas carreteras, además de remover o restaurar carreteras existentes con la finalidad de beneficiar tanto a la biota acuática como la terrestre.

Introduction

Among the most widespread forms of modification of the natural landscape during the past century has been the construction and maintenance of roads (Diamondback 1990; Bennett 1991; Noss & Cooperrider 1994). As conservation biologists seek to understand the forces that influence the viability of populations and the overall health of ecosystems, it is important that we understand the scope of the ecological effects of roads of all types, especially important as conservation biologists are asked to participate in the development and implementation of strategies to protect or restore elements of biological diversity and integrity.

Roads of all kinds affect terrestrial and aquatic ecosystems in seven general ways: (1) increased mortality from road construction, (2) increased mortality from collision with vehicles, (3) modification of animal behavior, (4) alteration of the physical environment, (5) alteration of the chemical environment, (6) spread of exotic species, and (7) increased alteration and use of habitats by humans. These general effects overlap somewhat. In some cases animals modify their behavior and avoid roads because of concentrated human activity along roads. Roads may facilitate the spread of invasive species by disrupting native communities and changing physical habitats. Roads may fragment populations through roadkill and road avoidance. Despite the difficulty of categorizing discretely the causal basis in every example, these seven categories provide a useful framework for assessing what is known and unknown about the ecological effects of roads.

Selective road removal, relocation, or remediation may provide ecological benefits in certain situations. Yet, although roads are commonly identified as important correlates or indicators of loss of ecological health (e.g., Noss & Cooperrider 1994), the specific mechanisms by which biota are affected are often complicated or uncertain. Therefore, mitigation or treatment of specific effects, whether during road design or in post-construction remediation, can be costly and fraught with uncertainty.

Mortality from Road Construction

Road construction kills any sessile or slow-moving organism in the path of the road. The extent to which road construction contributes to direct mortality has not been estimated as has direct mortality from other forms of habitat destruction (e.g., Petranka et al. 1993). The fact that road construction kills individual organisms is obvious, however. The magnitude of such construction is not trivial; the 13,107,812 km of road lanes of all types in the conterminous United States, with an average width of 3.65 m per lane, have destroyed at least 4,784,351 ha of land and water bodies that formerly supported plants, animals, and other organisms (U.S. Department of Transportation 1996). The actual number is likely much higher because this estimate does not include shoulder pavement and land peripheral to the roadbed that is cleared during construction.

Construction may physically injure organisms adjacent to the path of construction. Roads built for extraction of white fir result in damage to trees that is visible up to 30 m from the road (Trafela 1987). Such damage contributes to a decline of up to 30% in forest productivity per rotation, due in part to a decline in growth of damaged trees. Construction also alters the physical conditions of the soil underneath and adjacent to the road. Riley (1984) showed that road construction increases soil compaction up to 200 times relative to undisturbed sites. These changes likely decrease the survival of soil biota that are not killed directly. Direct transfer of sediment and other material to streams and other water bodies at road crossings is an inevitable consequence of road construction (Richardson et al. 1975; Seyedbagheri 1996). High concentrations of suspended sediment may directly kill aquatic organisms and impair aquatic productivity (Newcombe & Jensen 1996).

Mortality from Collision with Vehicles

Mortality of animals from collision with vehicles is well documented. Many reviews of the taxonomic breadth of the victims of vehicle collision have been published (e.g., Groot Bruinderink & Hazebroek 1996). Few if any terrestrial species of animal are immune. Large mammals ranging in size from moose (*Alces alces*) to armadillos (*Dasypus novemcinctus*) are the best-documented roadkills, probably due to interest in their demography and to their size (Bellis & Graves 1971; Puglisi et al. 1974;

Reilly & Green 1974; Holroyd 1979; Wilkins & Schmidly 1980; Bashore et al. 1985; Davies et al. 1987; Bangs et al. 1989; Palomares & Delibes 1992).

Roadkill among many other species includes American Kestrels (*Falco sparverius*; Varland et al. 1993), Barn Owls (*Tyto alba*; Newton et al. 1991), Northern Sawwhet Owls and Eastern Screech Owls (*Aegolius acadicus and Otis asio*; Loos & Kerlinger 1993), tropical forest birds (Novelli et al. 1988), garter snakes (Dalrymple & Reichenbach 1984), granivorous birds (Dhindsa et al. 1988), American crocodile (*Crocodylus acutus*; Kushlan 1988), green iguanas (*Iguana iguana*; Rodda 1990), desert snakes (Rosen & Lowe 1994), toads (van Gelder 1973), plus a wide range of invertebrates, especially insects (H. C. Seibert & Conover 1991).

This form of mortality can have substantial effects on a population's demography. Vehicle collision is the primary cause of death for moose in the Kenai National Wildlife Refuge in Alaska (Bangs et al. 1989) and for Barn Owls in the United Kingdom (Newton et al. 1991), the second highest form of mortality for Iberian lynx (*Felis pardina*) in southwestern Spain (after hunting; Ferreras et al. 1992), and the third highest form for white-tailed deer (*Odocoileus virginianus*) in New York (Sarbello & Jackson 1985) and wolves (*Canis lupus*) in Minnesota (Fuller 1989). Roadkill is a limiting factor in the recovery of the endangered American crocodile in southern Florida (Kushlan 1988) and is contributing to the endangerment of the prairie garter snake (*Thamnophis radix radix*; Dalrymple & Reichenbach 1984). Roadkill is often nonspecific with respect to age, sex, and condition of the individual animal (e.g., Bangs et al. 1989).

Amphibians may be especially vulnerable to roadkill because their life histories often involve migration between wetland and upland habitats, and individuals are inconspicuous and sometimes slow-moving. Roads can be demographic barriers that cause habitat and population fragmentation (Joly & Morand 1997). In the Netherlands, for example, roads with high traffic volume negatively affect occupancy of ponds by moor frogs (*Rana arvilis*; Vos & Chardon 1998). In Ontario, the local abundance of toads and frogs is inversely related to traffic density on adjacent roads, but the incidence of roadkill relative to abundance is higher on highly trafficked roads (Fahrig et al. 1995). Thus, even though populations in high-traffic areas have apparently already been depressed from cumulative road mortality, they continue to suffer higher proportionate rates of roadkill.

Mitigation measures have been employed in different locations with varying degrees of success (e.g., Yanes et al. 1995). For example, underpasses on Interstate 75 have been only partially successful in reducing roadkill of Florida panthers (*Felis concolor coryi*; Foster & Humphrey 1991). Despite mitigation efforts, roads are likely to be a persistent source of mortality for many species. In general, mortality increases with traffic volume (e.g., Rosen & Lowe 1994; Fahrig et al. 1995). Some species are less likely to be killed on high-speed roads than on medium-speed roads because the former usually have vegetation cleared back further from the road's shoulder, creating less attractive habitat and greater visibility for both animals and drivers. Other species, however, are attracted to the modified habitat alongside and in the meridians of high-speed roads (Cowardin et al. 1985), making them population sinks.

Modification of Animal Behavior

The presence of a road may modify an animal's behavior either positively or negatively. This can occur through five mechanisms: home range shifts, altered movement patterns, altered reproductive success, altered escape response, and altered physiological state.

Black bears (*Ursus americanus*) in North Carolina shift their home ranges away from areas with high road densities (Brody & Pelton 1989), as do grizzly bears in the Rocky Mountains (*Ursus horribilis*; McLellan & Shackleton 1988). Elk (*Cervus elaphus*) in Montana prefer spring feeding sites away from visible roads (Grover & Thompson 1986), and both elk and mule deer (*Odocoileus hemionus*) in Colorado in winter prefer areas >200 m from roads (Rost & Bailey 1979). Wolves will not establish themselves in areas with road densities greater than a region-specific critical threshold (Jensen et al. 1986; Thurber et al. 1994), probably as a result of a relationship between road density and hunting pressure. Mountain lion (*Felis concolor*) home ranges are situated in areas with lower densities of improved dirt roads and hard-surface roads (Van Dyke et al. 1986), suggesting that either mountain lions avoid these areas or road construction tends to avoid their prime habitat. Elephants (*Loxodonta africana*) in northeastern Gabon preferentially locate in forests away from both roads and villages (Barnes et al. 1991). Both Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*), on the other hand, preferentially establish home ranges in areas with greater road densities (Coleman & Fraser 1989), probably because of the increase in carrion.

Roads may also alter patterns of animal movement. Caribou (*Rangifer tarandus*) in Alaska preferentially travel along cleared winter roads that lead in the direction of their migration (Banfield 1974). Although the road may enhance caribou movement, it results in increased mortality from vehicle collisions and predation by wolves. After calving, female caribou with calves avoid roads (Klein 1991). The land snail *Arianta arbustorum* avoids crossing roads, even those that are unpaved and as narrow as 3 m (Baur & Baur 1990), and extend their movements along road verges. Reluctance to cross roads is also seen in white-footed mice (*Peromyscus*

leucopus; Merriam et al. 1989) and many other rodent species (Oxley et al. 1974), even when the road is narrow and covered only with gravel. Cotton rats (*Sigmodon hispidus*) and prairie voles (*Microtus ochrogaster*) avoid roads as narrow as 3 m (Swihart & Slade 1984). Black bear almost never cross interstate highways in North Carolina (Brody & Pelton 1989) but will cross roads with less traffic volume. Roads act as barriers to gene flow in the common frog (*Rana temporaria*) in Germany, leading to significant genetic differentiation among populations (Reh & Seitz 1990). Other animals that show a reluctance to cross roads include pronghorn antelope (*Antilocapra americana*; Bruns 1977) and mountain lions (Van Dyke et al. 1986).

Some animals seem unaffected by the presence of roads, at least at some spatial scales. Based on a study of 20 wolverines, Hornocker and Hash (1981) concluded that the sizes and shapes of home ranges of wolverines where they are still found in northwestern Montana are independent of the presence of highways. Similarly, the presence of highways explained none of the allelic differentiation among populations of brown hares (*Lepus europaeus*) in Austria (Hartl et al. 1989).

Roads may affect an animal's reproductive success. Productivity of Bald Eagles (*Haliaeetus leucocephalus*) in Oregon (Anthony & Isaacs 1989) and Illinois (Paruk 1987) declines with proximity to roads, and they preferentially nest away from roads. Golden Eagles (*Aquila chrysaetos*) also prefer to nest away from human disturbances, including roads (Fernandez 1993). The reduced nesting success of eagles in proximity to roads may be more a function of the presence of humans than of the road itself; nesting failure by Golden Eagles in Scotland correlates with how easy it is for people to approach but not with proximity to roads themselves (Watson and Dennis 1992). Relative to habitat availability, Sandhill Cranes (*Grus canadensis*) avoid nesting near paved and gravel public roads (Norling et al. 1992); they do not avoid private roads with low-traffic volume (Norling et al. 1992) and can habituate to roads over time (Dwyer & Tanner 1992). Mallards (*Anas platyrhynchos*) in North Dakota, on the other hand, prefer road rights-of-way for nesting (Cowardin et al. 1985), perhaps because of a lower level of predation there.

Roads can also alter escape responses. Pink-footed Geese (*Anser brachyrhynchus*) in Denmark are more easily disturbed when feeding near roads, flying away when humans approach within 500 m, a greater distance than when feeding in areas without roads (Madsen 1985). Both the Lapwing (*Vanellus vanellus*) and Black-tailed Godwit (*Limosa limosa*) are more easily disturbed near roads and have disturbance distances of 480–2000 m depending on traffic volume (Van der Zande et al. 1980). Less well known is the effect of roads and vehicles on an animal's physiological state. MacArthur et al. (1979) showed that heart rate and therefore metabolic rate and energy expenditure of female bighorn sheep (*Ovis canadensis*) increase near a road independent of any use of the road. Roads contribute to fragmentation of populations through both increased mortality and modification of behavior that makes animals less likely to cross roads. Fragmentation may be accelerated by roads when spatially critical habitat patches (e.g., "stepping stones") become unoccupied as a result of increased local mortality or reduced recolonization.

Disruption of the Physical Environment

A road transforms the physical conditions on and adjacent to it, creating edge effects with consequences that extend beyond the time of the road's construction. At least eight physical characteristics of the environment are altered by roads: soil density, temperature, soil water content, light, dust, surface-water flow, pattern of runoff, and sedimentation.

Long-term use of roads leads to soil compaction that persists even after use is discontinued. Soil density on closed forest roads continues to increase, particularly during winter months (Helvey & Kochenderfer 1990). Increased soil density can persist for decades: logging skid trails in northeastern California over 40 years old have soil that is 20% more compacted than soil in nearby areas that have not been used as trails (Vora 1988).

The reduction of water vapor transport on a road with a hard surface increases the surface temperature of a road compared to bare soil, an effect that increases with thickness of the road surface (Asaeda & Ca 1993). The heat stored on the road surface is released into the atmosphere at night, creating heat islands around roads. Animals respond to these heat islands: small birds (Whitford 1985) and snakes, for example, preferentially aggregate on or near warm roads, increasing their risk of being hit by cars and, at their northern range limits, reducing energetic demands for breeding.

During the dry season, the moisture content of soils under roads declines even if the roads are not in use (Helvey & Kochenderfer 1990), probably in response to changes in soil porosity. Roads through forests also increase the amount of light incident on the forest floor. The amount of increase depends on how much of the original canopy and lower strata remain, which depends in turn on the width of the road and roadside verge. The increase in light increases the density of species that preferentially grow where light levels are high, such as early-successional, disturbance-adapted species such as the North American orchid *Isotria medeoloides* (Mehrhoff 1989).

Road traffic mobilizes and spreads dust, which when settled on plants can block photosynthesis, respiration, and transpiration and can cause physical injuries to plants (Farmer 1993). These effects are sufficient to alter

plant community structure, especially in communities dominated by lichens and mosses (Auerbach et al. 1997). Although most sediment enters water bodies through overland flow or mass failure, dust from highly trafficked roads can serve as a source of fine sediments, nutrients, and contaminants to aquatic ecosystems (Gjessing et al. 1984).

Roads and bridges can alter the development of shorelines, stream channels, floodplains, and wetlands. Because of the energy associated with moving water, physical effects often propagate long distances from the site of a direct road incursion (Richardson et al. 1975). Alteration of hydrodynamics and sediment deposition can result in changes in channels or shorelines many kilometers away, both down- and up-gradient of the road crossing. The nature of such responses to channel and shoreline alteration is not always predictable; it may depend on the sequence of flood and sedimentation events after the alteration is made. Roads on floodplains can redirect water, sediment, and nutrients between streams and wetlands and their riparian ecosystems, to the detriment of water quality and ecosystem health. Roads are among the many human endeavors that impair natural habitat development and woody debris dynamics in forested floodplain rivers (Piégay & Landon 1997).

Road crossings commonly act as barriers to the movement of fishes and other aquatic animals (Furniss et al. 1991). Although many headwater populations of salmonid fishes are naturally migratory, they often persist today as fragmented headwater isolates, largely because of migration barriers created by road crossings and other human developments that fail to provide for fish passage (Kershner et al. 1997; Rieman et al. 1997). Salmonids and other riverine fishes actively move into seasonal floodplain wetlands and small valley-floor tributaries to escape the stresses of main-channel flood flows (Copp 1989), but valley-bottom roads can destroy or block access to these seasonally important habitats (Brown & Hartman 1988). Persistent barriers may encourage local selection for behaviors that do not include natural migration patterns, potentially reducing both the distribution and productivity of a population.

Roads directly change the hydrology of slopes and stream channels, resulting in alteration of surface-water habitats that are often detrimental to native biota. Roads intercept shallow groundwater flow paths, diverting the water along the roadway and routing it efficiently to surface-water systems at stream crossings (Megahan 1972; Wemple et al. 1996). This can cause or contribute to changes in the timing and routing of runoff (King & Tennyson 1984; Jones & Grant 1996; Ziemer & Lisle 1998), the effects of which may be more evident in smaller streams than in larger rivers (Jones & Grant 1996). Hydrologic effects are likely to persist for as long as the road remains a physical feature altering flow routing—often long after abandonment and revegetation of the road surface. By altering surface or subsurface flow, roads can destroy and create wetland habitats.

Changes in the routing of shallow groundwater and surface flow may cause unusually high concentrations of runoff on hillslopes that can trigger erosion through channel downcutting, new gully or channel head initiation, or slumping and debris flows (Megahan 1972; Richardson et al. 1975; Wemple et al. 1996; Seyedbagheri 1996). Once such processes occur, they can adversely affect fishes and other biota far downstream for long periods of time (Hagans et al. 1986; Hicks et al. 1991). Roads have been responsible for the majority of hillslope failures and gully erosion in most steep, forested landscapes subject to logging activity (Furniss et al. 1991; Hagans et al. 1986). Because most of these more catastrophic responses are triggered by the response of roads during infrequent, intense storm events, lag times of many years or decades pass before the full effects of road construction are realized.

Chronic effects also occur, however. The surfaces of unpaved roads can route fine sediments to streams, lakes, and wetlands, increasing the turbidity of the waters (Reid & Dunne 1984), reducing productivity and survival or growth of fishes (Newcombe & Jensen 1996), and otherwise impairing fishing (Buck 1956). Existing problem roads can be remediated to reduce future erosion potential (e.g., Weaver et al. 1987; Harr & Nichols 1993). The consequences of past sediment delivery are long-lasting and cumulative, however, and cannot be effectively mitigated (Hagans et al. 1986).

Alteration of the Chemical Environment

More has been written about the effects of roads on the chemical environment than on all other effects combined. Maintenance and use of roads contribute at least five different general classes of chemicals to the environment: heavy metals, salt, organic molecules, ozone, and nutrients.

A variety of heavy metals derived from gasoline additives and road deicing salts are put into the roadside environment. The most widely documented is lead, but others include aluminum, iron, cadmium, copper, manganese, titanium, nickel, zinc, and boron (Garcia-Miragaya et al. 1981; Clift et al. 1983; Gjessing et al. 1984; Oberts 1986; Araratyan & Zakharyan 1988).

Heavy metal contamination exhibits five patterns. First, the amount of contamination is related to vehicular traffic (Goldsmith et al. 1976; Dale & Freedman 1982; Leharne et al. 1992). Second, contamination of soils, plants, and animals decreases exponentially away from the road (Quarles et al. 1974; Dale & Freedman 1982). Most studies indicate that contamination declines within 20 m but that elevated levels of heavy metals often occur 200 m or more from the road. The pattern of decline is influenced

by prevailing wind patterns (Haqus & Hameed 1986). Once metals reach aquatic environments, transport rates and distances increase substantially (Gjessing et al. 1984).

Third, heavy metals can be localized in the soil, either close to the surface if downward transport has not occurred (Indu & Choudhri 1991) or deep below the surface if pollution levels in the past exceeded those in the present (Byrd et al. 1983). Transportation and localization is largely affected by the physical properties of the soil (Yassoglou et al. 1987). Metals and other persistent chemicals fixed to soils may become remobilized once they are inundated or transported to freshwater environments by wind, water, or gravity.

Fourth, heavy metals accumulate in the tissues of plants (Datta & Ghosh 1985; Beslaneev & Kuchmazokova 1991) and animals (Collins 1984; Birdsall et al. 1986; Grue et al. 1986). As with soil, contamination of plant tissue occurs up to at least 200 m from a road and is greatest for individuals along roads with high traffic volume.

Fifth, heavy metal concentrations in soil decline over time where use of leaded gasoline has been stopped and surface-water flow carries the metal ions away (Byrd et al. 1983; Tong 1990). After they leave the terrestrial environment, however, the mobilized metals may cause additional harm to aquatic biota. Also, some of the processes of metal demobilization may be reversed rapidly if environmental conditions, such as acidity of the soils, sediments, or water, change (Nelson et al. 1991).

Deicing salts, particularly NaCl but also $CaCl_2$, KCl, and $MgCl_2$, contribute ions to the soil, altering pH and the soil's chemical composition (Bogemans et al. 1989). As with lead, discontinuation of the use of deicing salts allows plants damaged by salt stress to recover (Leh 1990). The effects on aquatic biota of temporary surges of salt that often accompany runoff from roads to surface and groundwaters have received little study. Deicing salts on roadways elevate chloride and sodium concentrations in streams (Molles & Gosz 1980; Hoffman et al. 1981; Peters & Turk 1981; Mattson & Godfrey 1994) and in bogs, where road salts can alter patterns of succession in aquatic vegetation (Wilcox 1986). Accumulation of salts from chemicals used for road deicing or dust control can disrupt natural stratification patterns and thus potentially upset the ecological dynamics of meromictic lakes (Hoffman et al. 1981; Kjensmo 1997).

Organic pollutants such as dioxins and polychlorinated biphenyls are present in higher concentrations along roads (Benfenati et al. 1992). Hydrocarbons may accumulate in aquatic ecosystems near roads (Gjessing et al. 1984). In one stream along a British highway, numerous contaminants were present at elevated levels in the water column and sediments, including copper, zinc, and various hydrocarbons, but polycyclic aromatic hydrocarbons associated with stream sediments accounted for most of the observed toxicity to aquatic amphipods (Maltby et al. 1995). Comparatively little research has focused on the questions of the fate and effects of the organic chemicals associated with roads.

Vehicles produce ozone, which increases the concentration of this harmful molecule in the air, especially in areas where vehicle exhaust accumulates (Flueckiger et al. 1984). Roads are also especially important vectors of nutrients and other materials to aquatic ecosystems, because the buffering role normally played by riparian vegetation (Correll et al. 1992) is circumvented through direct runoff of materials in water and sediment where roads abut or cross water bodies. Water moving on and alongside roadways can be charged with high levels of dissolved nitrogen in various forms, and sediment brings a phosphorus subsidy when it reaches surface waters. Road deicing salts are an additional source of phosphorus (Oberts 1986). The degree to which roads directly contribute to eutrophication problems in aquatic ecosystems has been little investigated. Because roads deliver nutrients that originate in the contributing slope area, the nutrient burden is probably largely controlled by surrounding vegetation and land use. An increased density of road crossings of water bodies can be expected to increase delivery of nutrients.

The alteration of the chemical environment by roads results in a number of consequences for living organisms. First, in the terrestrial environment the chemical composition of some woody plants changes in response to pollution. These changes include increased concentrations of chemicals produced by plants, such as terpenoids, which help them resist the toxic effects of pollution (Akimov et al. 1989) and salts (Bogemans et al. 1989), and decreased production of other chemicals, such as soluble protein and chlorophyll *a*, which are necessary for plant function (Banerjee et al. 1983).

Second, organisms may be killed or otherwise displaced as a result of chemical exposure. Virtually all measures of soil biotic diversity and function decline in contaminated soil, including abundance, number of species, species composition, index of species diversity, index of equability, and bulk soil respiration (Muskett & Jones 1981; Guntner & Wilke 1983; Krzysztofiak 1991).

Third, the growth (Petersen et al. 1982) and overall physical health (Flueckiger et al. 1984; Moritz & Breitenstein 1985) of many plants is depressed, even to the point of death (Fleck et al. 1988). The sensitivity of plants to pollutants may change during development; for example, seedlings are more sensitive to salt than are adults (Liem et al. 1984), which influences juvenile recruitment. Pollutants may affect plant health by damaging fine roots, mycorrhizae (Majdi & Persson 1989), and leaves (Simini & Leone 1986) and by changing salt concentrations in plant tissues (Northover 1987). Secondary effects on plant health include decreased resistance to pathogens (Northover 1987), causing further declines. In aquatic environments, plant (and animal) assemblages

may change due to direct and indirect responses to nutrient increases and due to growth suppression or mortality caused by other chemicals introduced by roads.

Fourth, plants (Graham & Kalman 1974; Nasralla & Ali 1985; Dickinson et al. 1987; Guttormsen 1993) and animals (Robel et al. 1981; Collins 1984; Harrison & Dyer 1984; Krzysztofiak 1991; Marino et al. 1992), including those cultivated or raised for agriculture, may accumulate toxins at levels that pose health hazards, including those for humans that consume exposed organisms (Jarosz 1994).

Fifth, increased concentrations near roadsides of some pollutants, particularly salt, attract large mammals, putting them more at risk of being killed by vehicles (Fraser & Thomas 1982). Spills of edible products from trucks and trains also attract wildlife to roadsides. Finally, evolutionary processes may be affected through altered selection pressures that result in local differentiation of populations of both plants (Kiang 1982) and animals (Minoranskii & Kuzina 1984).

Spread of Exotic Species

Roads provide dispersal of exotic species via three mechanisms: providing habitat by altering conditions, making invasion more likely by stressing or removing native species, and allowing easier movement by wild or human vectors. It is often difficult to distinguish among these factors. Soils modified during road construction can facilitate the spread of exotic plants along roadsides (Greenberg et al. 1997). Some exotic plants establish themselves preferentially along roadsides and in other disturbed habitats (Wester & Juvik 1983; Henderson & Wells 1986; Tyser & Worley 1992; Wein et al. 1992). The spread of exotic diseases (Dawson & Weste 1985; Gad et al. 1986) and insects (Pantaleoni 1989; Schedl 1991) is facilitated by increased density of roads and traffic volume. Road construction that alters the canopy structure of forests promotes invasion by exotic understory plants, which affects animal communities (Gaddy & Kohlsaat 1987). Some roadside verges have been invaded by maritime plants because of their ability to tolerate saline soil (Scott & Davison 1982). Feral fruit trees are found preferentially along roadsides, and some populations are maintained solely by seeds in fruit waste thrown from vehicles (Smith 1986).

Exotic species are sometimes introduced along roadsides for the purpose of erosion control (Niordson 1989). Native species are now more widely preferred for this purpose, but Dunlap (1987) argues that in some cases the need for rapid establishment of plant cover requires the use of exotic species.

In another form of deliberate introduction, roads provide easy access to streams and lakes for fishery managers to stock nonnative hatchery fish (Lee et al. 1997), which adversely affect native biota and disrupt aquatic ecosystems in many ways (Allan & Flecker 1993). Unsanctioned, illegal, and unintentional introductions of fishes, mollusks, plants, and other aquatic organisms also occur frequently (Allan & Flecker 1993), and they are facilitated by public road access to water bodies.

The dispersal of a biological agent such as a pathogen along a roadway can affect both terrestrial and aquatic ecosystems far from the road. In northern California and southwest Oregon, for example, vehicle traffic and roadway drainage along logging and mining roads during the wet season disperse spores of an exotic root disease (*Phythoptera lateralis*) that infects the endemic Port Orford cedar (*Chamaecyparis lawsoniana*; Zobel et al. 1985). Transfer of the water-borne spores from forest roads into headwater stream crossings can result in the infection and nearly complete mortality of Port Orford cedars along a much larger network of downstream channel margins and floodplains, even deep inside otherwise roadless areas. The progressive loss of this important conifer species from riparian ecosystems may engender substantial long-term consequences for the integrity of stream biota, including endangered salmon species, for which the Port Orford cedar provides shade, large and long-lasting coarse woody debris, and stabilization of channels and floodplains.

Changes in Human Use of Land and Water

Roads facilitate increased use of an area by humans, who themselves often cause diverse and persistent ecological effects. New roads increase ease of access by humans into formerly remote areas. Perhaps more important, roads often increase the efficiency with which natural resources can be exported. At least three different kinds of human use of the landscape, made increasingly possible by roads, can have major ecological effects: hunting and fishing, recreation, and changes in use of land and water.

Roads open up areas to increased poaching and legal hunting. Hunting reduces population sizes of many game species, including brown bear (*Ursus arctos*; Camarra & Parde 1990), Iberian lynx (Ferreras et al. 1992), wolves (Fuller 1989), black bear (Manville 1983), and Egyptian mongooses (*Herpestes ichneumon*; Palomares & Delibes 1992). Roads also increase both legal and illegal fishing in streams and lakes. Native fish populations in previously inaccessible areas are often vulnerable to even small increases in fishing effort. Increased fishing then often gives rise to public demand for fish stocking as an attempt to artificially compensate for the effects of unsustainable harvest, at the further expense of native fishes and other species (e.g., Gresswell & Varley 1988).

Visitors increase when roads make areas more accessible, leading to increased passive harassment of animals—such as elk on Mount St. Helens in Washington State (Czech 1991) and the Oregon Coast Range (Witmer & DeCalesta 1985), brown bear in Europe (Del Campo et al. 1990), and mountain goats (*Oreamnos americanus*) in Montana (Pedevillano & Wright 1987)—and damage to plant communities (Matlack 1993).

Roads are often built into areas to promote logging, agriculture, mining, and development of homes or industrial or commercial projects. Such changes in land cover and land and water use result in major and persistent adverse effects on the native flora and fauna of terrestrial (Van Dyke et al. 1986; Karnefelt & Mattsson 1989; P. Seibert 1993) and freshwater ecosystems (Schlosser 1991; Allan & Flecker 1993; Roth et al. 1996).

Numerous studies have demonstrated declines in stream health associated with roads. Because the nature and extent of land use within a region tend to be highly correlated with road networks, however, it is often difficult or impossible to separate the direct ecological effects of roads from those of the accompanying land-use activities. For example, Eaglin and Hubert (1993) reported that trout biomass and streambed habitat quality in Wyoming streams declined in relation to the number of road crossings and to the proportion of area logged in the contributing catchment. Findlay and Houlahan (1997) found that herptile species diversity in wetlands declined in relation to the density of roads within 2 km of the perimeter. Among streams in the Pacific Northwest, the status or abundance of bull trout populations has been inversely correlated to road density (Rieman et al. 1997; Baxter et al. 1999); these studies used roads as the best available general proxy of cumulative effects associated with land use and human access. On the other hand, some studies (e.g., Roth et al. 1996) have demonstrated correlations of stream biotic integrity with land-use patterns across large catchments but did not investigate the specific roles that roads might play in mediating the causes and effects.

It appears that roads can serve as useful indicators of the magnitude of land-use changes, but it remains unclear to what degree the associated ecological responses result directly from roads themselves. If roads are largely responsible, effects could be ameliorated through altered road design, placement, remediation, or road removal. Strong interactions between roads and land use are likely, however. Forest roads in Idaho, for example, are less prone to erosion when the surrounding landscape remains in natural forest cover (Seyedbagheri 1996).

Discussion and Conclusions

Roads have diverse and systemic effects on many aspects of terrestrial and aquatic ecosystems. The ecological effects of roads can resonate substantial distances from the road in terrestrial ecosystems, creating habitat fragmentation and facilitating ensuing fragmentation through support of human exploitative activities (Fig. 1a). Habitat deterioration is not widely appreciated as an aspect of ecological fragmentation in aquatic ecosystems. At the scale of an extensive landscape or stream network, however, roads produce a pattern of aquatic habitat loss that differs from the terrestrial pattern yet nevertheless results in the ecological fragmentation of aquatic ecosystems (Fig. 1b). We coin the term *hyperfragmentation* to describe the multidimensional view of ecological fragmentation and habitat loss that emerges when the consequences of roads or any habitat alteration for terrestrial and aquatic ecosystems are considered simultaneously (Fig. 1c). Hyperfragmentation is the result of a spatial footprint of ecological effect that propagates across the landscape differently in freshwater and

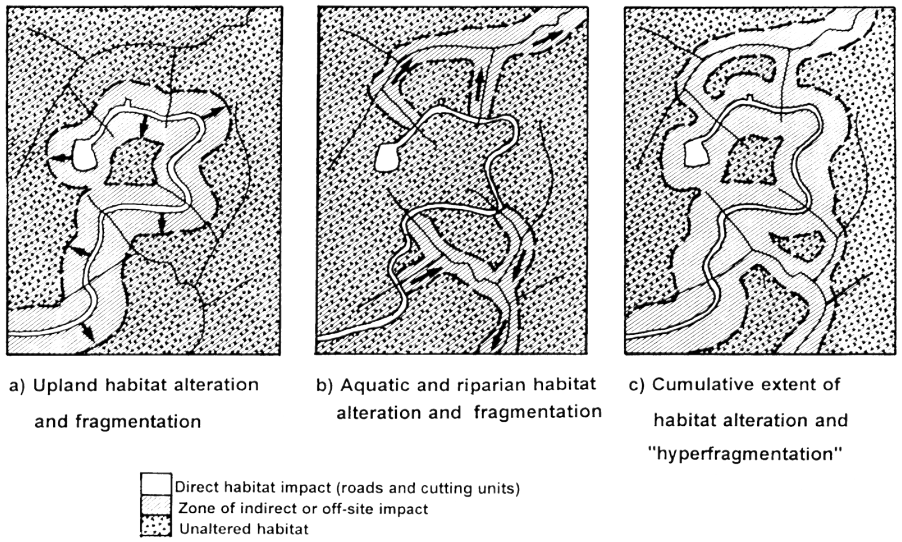

Figure 1. Spatial pattern of direct and indirect habitat alteration caused by human disturbance in a forested watershed: (a) classical forest edge effects contributing to terrestrial habitat fragmentation, (b) downstream-propagating hydrologic and biotic effects leading to large-scale fragmentation of freshwater habitats and populations, (c) combined terrestrial-aquatic view of landscape alteration that we term hyperfragmentation *because it considers multiple ecosystem dimensions on the same landscape. Arrows indicate predominant spatial vector of effects.*

aquatic ecosystems than in terrestrial systems. Even where only a small percentage of the land's surface is directly occupied by roads, few corners of the landscape remain untouched by their off-site ecological effects. The breadth of these effects cannot be appreciated unless one takes a broadly transdisciplinary view of ecosystems and biological communities.

Road design, management, and restoration need to be more carefully tailored to address the full range of ecological processes and terrestrial and aquatic species that may be affected. Deliberate monitoring is necessary to ensure that projects have robust ecological benefits and minimal adverse effects and that they are cost-efficient relative to their actual benefits (e.g., Weaver et al. 1987). Of course, such assessments require time and money that are usually unavailable. Most funds used to remediate problem roads are earmarked for actual field operations and are not available to support such assessment and monitoring. Few of the experts building roads or "restoring" them are trained to recognize and address the full spectrum of ecological issues that we have identified. Moreover, by their nature roads have systemic ecological effects that, even if recognized, cannot be overcome.

If a broad view of the ecological effects of roads reveals a multiplicity of effects, it also suggests that it is unlikely that the consequences of roads will ever be completely mitigated or remediated. Thus, it is critical to retain remaining roadless or near-roadless portions of the landscape in their natural state. Because of the increasing rarity of roadless areas, especially roadless watersheds, conservation efforts cannot rely entirely on protection of existing natural areas. But neither can conservation efforts depend entirely on tenuous and unexamined assumptions about the capability of site- and species-specific mitigation and remediation measures to reduce the ecological consequences of existing and proposed roads.

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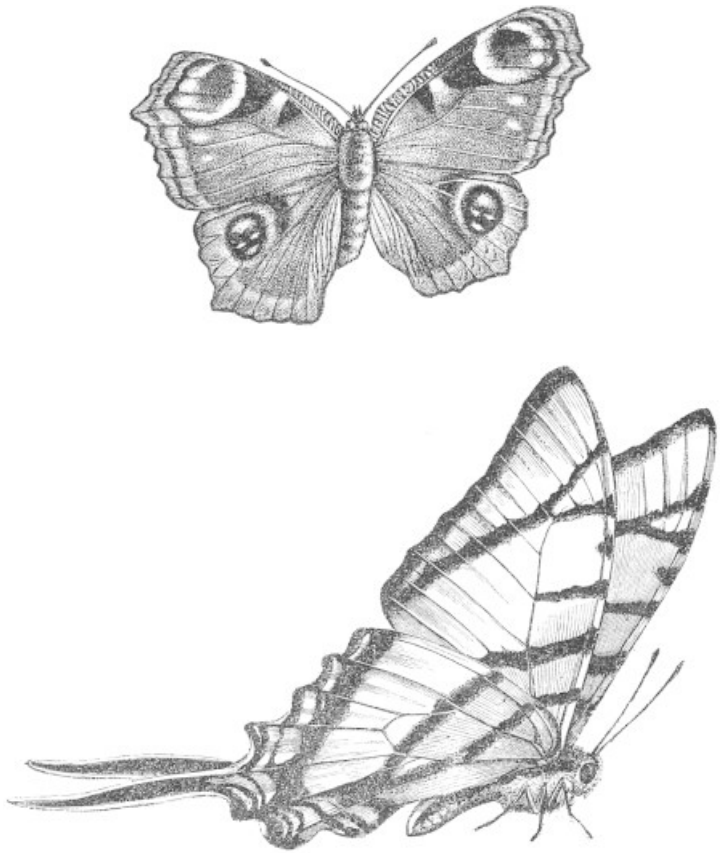

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Guest Editorial, part of a Special Feature on Effects of Roads and Traffic on Wildlife Populations and Landscape Function

Effects of Roads and Traffic on Wildlife Populations and Landscape Function: Road Ecology is Moving toward Larger Scales

Rodney van der Ree [1], *Jochen A. G. Jaeger* [2], *Edgar A. van der Grift* [3], and *Anthony P. Clevenger* [4]

ABSTRACT. Road ecology has developed into a significant branch of ecology with steady growth in the number of refereed journal articles, books, conferences, symposia, and "best practice" guidelines being produced each year. The main objective of this special issue of *Ecology and Society* is to highlight the need for studies that document the population, community, and ecosystem-level effects of roads and traffic by publishing studies that document these effects. It became apparent when compiling this special issue that there is a paucity of studies that explicitly examined higher order effects of roads and traffic. No papers on landscape function or ecosystem-level effects were submitted, despite being highlighted as a priority for publication. The 17 papers in this issue, from Australia, Canada, the Netherlands, and USA, all deal to some extent with either population or community-level effects of roads and traffic. Nevertheless, many higher order effects remain unquantified, and must become the focus of future studies because the complexity and interactions among the effects of roads and traffic are large and potentially unexpected. An analysis of these complex interrelations requires systematic research, and it is necessary to further establish collaborative links between ecologists and transportation agencies. Many road agencies have "environmental sustainability" as one of their goals and the only way to achieve such goals is for them to support and foster long-term and credible scientific research. The current situation, with numerous small-scale projects being undertaken independently of each other, cannot provide the information required to quantify and mitigate the negative effects of roads and traffic on higher levels. The future of road ecology research will be best enhanced when multiple road projects in different states or countries are combined and studied as part of integrated, well-replicated research projects.

Key Words: *animal movement; animal-vehicle collisions; barrier effect; ecological threshold; gene flow; habitat fragmentation; mitigation; population viability analysis; road ecology; road-effect zone; traffic mortality; traffic noise; traffic volume; transportation planning*

INTRODUCTION

Humans are responsible for the current unprecedented rate of biodiversity loss across the globe with climate change, pollution, and the loss, fragmentation, and degradation of habitat being the major drivers of extinction (Vitousek et al. 1997). Roads and other linear infrastructure are a major cause of habitat loss, fragmentation, and degradation and are ubiquitous in most landscapes around the world. Worldwide, there are already an estimated 750 million vehicles travelling on approximately 50 million km of public road (T. Langton, *personal communication*), and the road network and traffic volumes are still increasing, particularly in eastern Europe, China, India, and Latin America.

Linear infrastructure is important for society because it provides connectivity for people. However, linear infrastructure also exerts significant negative effects on adjacent habitats, wildlife populations, communities, and ecosystems. Research about the ecological effects of roads and traffic on the natural environment began in 1925 when Dayton Stoner documented the 225 traffic-killed vertebrates from 29 species that he observed during a 632 mile trip in Iowa, USA (Stoner 1925).

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The term "road ecology" was first used in German ("Straßenökologie") in 1981 (Ellenberg et al.), and was later translated into English by Forman et al. (2003) for their book *Road Ecology: Science and Solutions*. Since the mid 1990s, there has been a rapid increase in the number of studies, publications, and symposia, particularly from Europe, North America, and Australia. These include major national and international reports and best practice guidelines (Iuell et al. 2003, Trocmé et al. 2003, National Research Council 2005, Clevenger and Huijser 2009), regular dedicated conferences such as the biennial International Conference on Ecology and Transportation (ICOET), Infra-Eco Network of Europe (IENE), and symposia and special issues of peer-reviewed journals, e.g., *Biological Conservation* (Mader 1990), *Conservation Biology* (Hourdequin 2000), *GAIA* (Jaeger et al. 2005), and *Naturschutz and Landschaftsplanung* (Roedenbeck and Jaeger 2006).

The overall aim of road ecology research is to quantify the ecological effects of roads, with the ultimate aim of avoiding, minimizing, and compensating for their negative impacts on individuals, populations, communities, and ecosystems. This research has demonstrated the numerous and diverse effects of roads and traffic on plants and animals, with most studies focusing at the level of the individual animal. These effects include the loss and fragmentation of habitat, increased rates of wildlife mortality because of collision with vehicles, alterations to light, moisture and wind regimes due to the creation of edges, pollution from traffic, e.g., light, noise, and chemical, and facilitating the spread and dispersal of weeds and feral animals. Roads also affect the aesthetic and recreational quality of landscapes for humans (Di Giulio and Holderegger 2009). Consequently, roads have been described as the single most destructive element in the process of habitat fragmentation (Noss 1993) and their ecological effects are considered "the sleeping giant of biological conservation" (Forman 2002:viii).

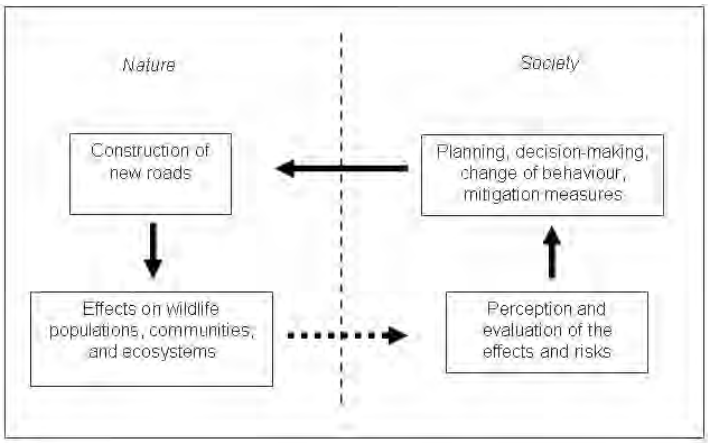
Understanding the impacts of roads and traffic at higher levels is necessary for a number of good reasons. Most governments have agreed that conservation of biodiversity is important and therefore road agencies must endeavor to ensure that they are contributing to achieving this goal. Counting the number of dead animals on the side of the road or measuring the size of the ecological road-effect zone will not, by itself, inform whether roads and vehicles are endangering the existence of populations or species. The important parameter must be the long-term viability of adjacent populations, and this requires data on the sizes of the populations, vital rates, and level of connectivity among subpopulations. Similarly, a critical question when evaluating mitigation works is the extent to which populations have become more viable, and whether they are now sufficiently viable, not simply how many animals pass through an underpass (van der Ree et al. 2007). The extent to which the results from the numerous local studies can be extrapolated to larger spatial and temporal scales is unknown. Therefore, an important next step is to evaluate how the density and configuration of entire road networks affect the functional relationships within and among ecosystems at the landscape scale. Answers to this question will inform cumulative environmental assessments and transportation planning (Roedenbeck et al. 2007). Roads also affect humans in a range of ways but little research on this topic has been completed (Di Giulio and Holderegger 2009).

Reducing the negative effects of roads and traffic will only be possible if more dialogue is achieved between the scientific community and the planners and political decision makers (Fig. 1). The majority of people in the world live in cities and increasingly, their encounters with wildlife involve animals that have died after collision with vehicles. Novel approaches to engage the public, and hence, governments, are required. A recent example was an award-winning exhibition in the Whyte Museum in Banff, Alberta, Canada in 2006 of images of wildlife using the now famous overpasses and underpasses in Banff National Park. A second example was a creative arts competition as part of the IENE 2010 conference for Hungarian school children to portray the conflict, and solutions, between roads and wildlife (Fig. 2).

ABOUT THIS ISSUE: THE EFFECTS OF ROADS AND TRAFFIC ON POPULATIONS, COMMUNITIES, AND ECOSYSTEMS

The two main objectives of this special issue of *Ecology and Society* were to (1) highlight the need for studies that document the population, community, and ecosystem-level effects of roads and traffic, and (2) publish studies that document

Fig. 1. Society's ability to address the negative effects of road networks on wildlife populations and ecosystems depends on the perception of the ecological effects and risks. As the perception of the effects by society has been severely limited (as indicated by the dotted line), alternative approaches may be required that would be based on more indirect indicators of ecological risk and on the precautionary principle.



these effects. The special issue consists of 17 papers from four countries, i.e., Australia, Canada, the Netherlands, and U.S.A., that all deal to some extent with either population or community-level effects of roads and traffic. It became apparent when compiling the special issue that there is a paucity of road ecology studies that explicitly examined higher order effects of roads. No papers on landscape function or ecosystem-level effects were submitted, despite being highlighted as a priority for publication.

The special issue begins with a synthesis paper (Fahrig and Rytwinski 2009) and ends with an insight paper (Simmons et al. 2010). The synthesis is an appropriate first paper because it assesses the widely held assertion that "there are very few studies that assess the population-level effects of roads and traffic." The assertion was found to be partly true and partly false; the authors located 79 studies that provide data on population-level effects (abundance and density) but found that in most cases, the population-level effect was 'hidden' in many of the papers reviewed. Nevertheless, Fahrig and Rytwinski (2009) found that overwhelmingly, roads and traffic had a negative effect on animal abundance, with negative effects outnumbering positive effects by a factor of five. The final paper in the special issue reviews some of the genetic methods used in road ecology and provides an insight into how conservation genetics can be better utilized in future studies. Simmons et al. (2010) argue that conservation genetics is a rapidly evolving field and that many of the widely perceived limitations to the use of genetics are either misconceptions or no longer apply. They conclude with strong recommendations that genetic approaches be combined with field studies to increase the inferential strength of whichever study design is adopted (sensu Roedenbeck et al. 2007).

The road-effect zone is the distance from the edge of the road over which significant ecological effects can be detected (Forman and Alexander 1998). Eigenbrod et al. (2009) quantified threshold effects of a motorway on anuran populations in Canada, and Bissonette and Rosa (2009) investigated the effects of a motorway on the composition and abundance of a small-mammal community in the deserts of Utah, USA. Eigenbrod et al. (2009) were the first to quantify the road-effect zone on the species richness and relative abundance of anurans, and found strong negative effects for four of seven species, extending 250 – 1000 m from the road edge. They conclude that although most anurans are likely to have reduced abundances near motorways, the extent and cause of this relationship will vary among species (Eigenbrod et al. 2009). In contrast, Bissonette and Rosa (2009) found that roadside vegetation in desert environments often provides

Fig. 2. Runner up of the "On Dangerous Roads" Competition organized by Varangy Akciócsoport Egyesület for the 2010 Infra-Eco Network of Europe Conference showing an overpass used by wildlife. An ongoing project in the Netherlands is studying the effectiveness of an overpass for amphibians, in combination with fences along the road. This overpass is equipped with a cascading series of small ponds fed with water pumped into the highest pond in the center of the overpass.



suitable habitat for small mammals. Only 2 of 13 species of small mammals were never captured near roads, and the remaining 11 species' numbers were either similar or more abundant near the road than further away.

Vegetation adjacent to roads often provides habitat (e.g., Bissonette and Rosa 2009), and in some landscapes, even the majority of habitat (van der Ree and Bennett 2003). Wildlife that use this habitat will experience traffic noise and may be affected by it. Anthropogenic noise has the potential to severely disrupt the communication of species by acoustic interference or masking. Three studies in this special issue investigate this effect on frogs and birds. Parris and Schneider (2008) found that the Grey Shrike-thrush (*Colluricincla harmonica*) sang at a higher frequency in areas with traffic noise than the Grey Fantail (*Rhipidura fuliginosa*) and that the probability of detecting either species declined substantially with increasing traffic noise and traffic volume. The effects of traffic noise on frogs were assessed by Parris et al. (2009) in an urban landscape in southeast Australia and by Hoskin and Goosem (2010) in tropical rainforest in northeastern Australia. One species of urban frog in and around Melbourne called at a higher pitch in traffic noise, while the second species studied may also call at a higher pitch, but more data is required to be sure (Parris et al. 2009). *Litoria rheocola* in tropical rainforest also called at a higher pitch when closer to the road, as well as calling at a higher rate when near roads (Hoskin and Goosem 2010). The abundance of some species of rainforest frogs was also lower near roads.

A significant proportion of the road ecology literature is focused on evaluating the use and effectiveness of mitigation measures that aim to restore connectivity for wildlife or reduce rates of animal-vehicle collisions. A review presented at the ICOET conference in 2007 concluded that most studies in the scientific and grey literature had focused almost exclusively on documenting rates of use of wildlife passages, and that few had explicitly evaluated the effectiveness of mitigation measures

at enhancing population viability (van der Ree et al. 2007). In this special issue, five papers have addressed the topic of mitigation of road effects on wildlife in differing perspectives. Thorne et al. (2009) highlight the importance of landscape-scale planning to better integrate the needs of wildlife into regional transportation plans. Using two examples from California, USA, they show how road projects can benefit financially and ecologically when road agencies and conservation groups collaborate early in the planning stages. Approximately 1 – 2 million mammal-vehicle collisions occur annually in North America, causing in excess of 200 human fatalities and over one billion U.S. dollars in property damage each year (references in Huijser et al. 2009). Huijser et al. (2009) reviewed the effectiveness and cost of 13 measures considered effective at reducing collisions with large ungulates and found that for many sections of road, the effectiveness, measured as money saved, exceeds the costs to install the mitigation. The results of their cost-benefit model suggests that there must be many locations in North America where the mitigation measures are cost-effective, and thereby would save society money and improve road safety for humans and wildlife if implemented more often. At a smaller spatial scale, Grosman et al. (2009) combined real data on the movement of moose (*Alces alces*) with agent-based computer simulations to investigate if the removal of salt pools or their relocation from adjacent to the highway to 100 – 1500 m away from the road would result in fewer moose-vehicle collisions. Their model predicted that the removal of salt pools from near the edge of the highway would result in an almost 50% reduction in moose-vehicle collisions (Grosman et al. 2009).

The viability of populations adjacent to wildlife crossing structures is one of the fundamental measures of success of mitigation (van der Ree et al. 2007). Two papers in this special issue explicitly investigated the increase in the viability of a population of wildlife after mitigation (Taylor and Goldingay 2009, van der Ree et al. 2009). Taylor and Goldingay (2009) used population modeling to assess the viability of the Greater Glider (*Petauroides volans*) in Brisbane, a rapidly urbanizing area of Australia. They concluded that even a relatively low rate of dispersal across the road was sufficient to substantially reduce the risk of extinction of the smaller subpopulation isolated by the road. Similarly, van der Ree et al. (2009) used population viability modeling to assess the effectiveness of under-road tunnels installed in 1985 to restore connectivity for the critically endangered Mountain Pygmy-possum (*Burramys parvus*; Mansergh and Scotts 1989). They found that the tunnels reduced, but did not completely eliminate the negative effect of the road, with the density of the population affected by the road still 15% lower than a comparable undivided population nearby (van der Ree et al. 2009).

The majority of studies that assess the use of wildlife crossing structures have utilized two primary methods to detect and record wildlife passage, namely remotely triggered cameras, and/or the detection of tracks in a suitable substrate (van der Ree et al. 2007). Clevenger and Sawaya (2010) have used the suggestions of Simmons et al. (2010) and tested the feasibility of a noninvasive genetic sampling approach to identify the species as well as the sex, individual, and relatedness of different individuals using the crossing structure. The technique, if successful, would be applied at a larger scale to determine the level of genetic fragmentation and natural and anthropogenic factors influencing gene flow. They tested their approach on Black Bears (*Ursus americanus*) and Grizzly Bears (*U. arctos*) at two underpasses in Banff National Park. Hair was collected from 90% of crossing events (determined from cameras), and 70% of hair samples had sufficient DNA for extraction, resulting in the identification of five individual bears at each underpass, and highlighting the potential of this method for population-level analysis of the efficacy of wildlife crossing structures (Clevenger and Sawaya 2010).

There is still a paucity of data on the behavior and movement of animals near roads. Bouchard et al. (2009) evaluated the behavioral response of the Northern Leopard Frog (*Rana pipiens*), a species known to be negatively affected by roads and traffic. They studied the movement of frogs during their spring migration and also undertook short distance translocations of migrating frogs and found frogs near roads with more traffic took longer to move and tended to deviate more from straight-line movements when released near roads (Bouchard et al. 2009). The combination of the Northern Leopard Frog's apparent inability to avoid roads and their slow rate of movement make them highly vulnerable to road mortality. The second study in this special issue on the movement behavior of wildlife near roads was for the Squirrel Glider (*Petaurus norfolcensis*) in southeast Australia (van der Ree et al. 2010). The authors found that the size

of the gap in the canopy was the primary determinant of the rate of crossing in their study, with similar rates of crossing across the dual-roadway with tall trees in the median and across single-lane roads. In this study, traffic volume, i.e., approximately 5000 vehicles per day per roadway of which about 25% occurs at night when the gliders are active, did not appear to greatly influence crossing rates.

The traffic volume on minor roads is expected to continue to increase in areas with high human population densities because existing motorways are nearing capacity and the minor roads are expected to accommodate the excess flows (references in van Langevelde and Jaarsma 2009). Traffic calming is a regional planning approach to concentrate these flows onto a few roads, and ensure low-volume and low-speed roads are maintained. The conclusions of population viability modeling suggest that the results are species specific and depend upon the size of the traffic-calmed area as well as the area and quality of habitat (van Langevelde and Jaarsma 2009).

ROAD ECOLOGY: THE ROAD AHEAD

The research presented in this special feature shows that road ecology is moving toward larger scales. However, it also became evident while compiling this special issue that many higher order, e.g., population, community, ecosystem, or landscape-level, effects remain unquantified. These higher order effects must become the focus of future studies because the complexity and interactions among the effects of roads and traffic are large and potentially unexpected. An analysis of these complex interrelations requires systematic research. Therefore, a promising avenue to further develop the field of road ecology is to establish collaborative links with road and transportation agencies. Experience shows that the level of engagement with each local, state, or national road agency depends largely on the presence of interested people, rather than an institutionalized approach to environmental matters. However, institutional mandates are important as they are often a precondition for interested people to spend their efforts during work hours on these issues. Many road agencies have "environmental sustainability" as one of their goals and the only way to achieve such goals is for them to support and foster long-term and credible scientific research. Every road project is essentially an experiment and when combined with other road projects, they become replicated. The challenge we face as researchers is to (1) use good scientific approaches to design studies that are scientifically robust and maximize the individual value of each road project within a larger experimental scope; (2) ensure our research is applied and has tangible value for road agencies and for ecological outcomes; (3) address the higher order effects of roads, traffic, and mitigation measures.

This special feature demonstrates that the emerging field of road ecology is confronted with many important unanswered questions. Research needs to address large spatial and temporal scales that are not compatible within most postgraduate programs, i.e., single MSc or PhD theses, or short-term research contracts. The synergistic effects of roads and other factors that operate simultaneously, e.g., agricultural intensification and increased urbanization, have rarely been investigated. However, empirical studies are limited by the delayed response of wildlife to many environmental changes, i.e., there is an extinction debt such that wildlife populations will continue to decline for many years, in the order of decades, before they will reach a new equilibrium (Tilman et al. 1994, Findlay and Bourdages 2000). This lack of knowledge is often used as a justification to build more roads by arguing that not enough is known and more research is needed before road construction may slow down. This constitutes a "fragmentation spiral" (Jaeger 2002), because research has been unable to catch up with the ecological effects of the rapid increase in road densities. This situation is contrary to the precautionary principle and flies in the face of the principles of sustainability. The use of computer models may help overcome these limitations. For example, simulation models have demonstrated that there are thresholds in the effects of road density on the viability of wildlife populations above which populations are prone to extinction (Jaeger and Holderegger 2005, Frair et al. 2008). In addition, a research approach is required that will address the remaining uncertainties that to a large degree are irreducible, e.g., through building on the precautionary principle (e.g., Jaeger 2002). This would open up promising new lines of action for landscape management. For example, the German Federal Environment Agency recently suggested that region-specific limits to control landscape fragmentation should be introduced (Penn-Bressel 2005).

With this issue, we hope to contribute to the field of road ecology and to highlight both its appealing theoretical insights and its high practical relevance. Most importantly, we hope that this special issue will inspire further research in road ecology at the scale of populations, communities, and ecosystems. We are looking forward to these exciting research studies to come.

Responses to this article can be read online at: http://www.ecologyandsociety.org/vol16/iss1/art48/responses/

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Response of vegetation to drought time-scales across global land biomes

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We evaluated the response of the Earth land biomes to drought by correlating a drought index with three global indicators of vegetation activity and growth: vegetation indices from satellite imagery, tree-ring growth series, and Aboveground Net Primary Production (ANPP) records. Arid and humid biomes are both affected by drought, and we suggest that the persistence of the water deficit (i.e., the drought time-scale) could be playing a key role in determining the sensitivity of land biomes to drought. We found that arid biomes respond to drought at short time-scales; that is, there is a rapid vegetation reaction as soon as water deficits below normal conditions occur. This may be due to the fact that plant species of arid regions have mechanisms allowing them to rapidly adapt to changing water availability. Humid biomes also respond to drought at short time-scales, but in this case the physiological mechanisms likely differ from those operating in arid biomes, as plants usually have a poor adaptability to water shortage. On the contrary, semiarid and subhumid biomes respond to drought at long time-scales, probably because plants are able to withstand water deficits, but they lack the rapid response of arid biomes to drought. These results are consistent among three vegetation parameters analyzed and across different land biomes, showing that the response of vegetation to drought depends on characteristic drought time-scales for each biome. Understanding the dominant time-scales at which drought most influences vegetation might help assessing the resistance and resilience of vegetation and improving our knowledge of vegetation vulnerability to climate change.

drought impacts | NDVI | drought adaptation | Standardized Precipitation Evapotranspiration Index | drought index

Drought is a natural phenomenon that occurs when water availability is significantly below normal levels over a long period and the supply cannot meet the existing demand. Drought is one of the main drivers of the reduction in Aboveground Net Primary Production (ANPP) (1), although land ecosystems differ in their sensitivity to drought (2). However, a general theory of the effects of drought on land vegetation is lacking and the subject of scientific debate (2–4).

Understanding the response of land vegetation to drought is a crucial challenge, as growth and CO_2 uptake by plants are constrained to a large extent by drought (5). Its study is hindered by difficulties for drought quantification (6) and by the synergistic effects of temperature rise and drought on vegetation (7, 8). Differences in the physiological response of plant species to drought determine different levels of resistance and resilience to water deficits (9, 10) and ultimately influence the type of impact of a drought, differentiating those that slow growth (11) or reduce greenness (12), those that lead to loss of biomass (5), and those that result in plant mortality (8, 13).

The quantification of drought is a difficult task, as we usually identify a drought by its effects on different systems (agriculture, water resources, ecosystem), but there is not a unique physical variable we can measure to quantify drought intensity. Droughts are difficult to pinpoint in time and space, and it is very difficult to quantify their duration, magnitude, and spatial extent with a single variable or metric. Furthermore, the intrinsic multiscalar nature of drought introduces another element of uncertainty. In recent years the concept of drought time-scale has been widely used in drought studies (6, 14). The term refers to the time lag that typically exists between the starting of a water shortage and the identification of its consequences, for example by a decrease of the ANPP or an increase of tree mortality. Thus, the time-scales at which different plant species respond to drought may differ noticeably (11, 12, 15).

The response to water deficit among vegetation types is a crucial issue underlying geographic patterns of vegetation and a central concept to understanding the structure and dynamic of terrestrial ecosystems (2, 16). Nevertheless, the way by which the temporal variability of drought determines vegetation activity across the world biomes remains largely unknown because vegetation types have different characteristic response times (11, 15) and vulnerability (9, 10) to drought. Moreover, most studies considered the response of vegetation to climate by means of the simple anomaly of precipitation with respect to the average conditions. Such approach neglects the role of temperature and the drought time-scale at which the response of vegetation is highest. Both elements are essential to identify the response to climate variability and to understand the sensitivity of vegetation to drought.

In this study we focus on the analysis of drought impacts on vegetation by means of three vegetation parameters: (*i*) vegetation activity and greenness, (*ii*) tree radial growth, and (*iii*) ANPP. We stress the importance of considering the drought time-scale to understand drought impacts on a variety of vegetation types and biomes. For this purpose, we used the Standardized Precipitation Evapotranspiration Index (SPEI) (17), which is a site-specific drought indicator of deviations from the average water balance (precipitation minus potential evapotranspiration) (*SI Appendix*). Different SPEIs are obtained for different time-scales representing the cumulative water balance over the previous n months. The SPEI includes the role of temperature on drought severity by means of its influence on the atmospheric evaporative demand, hence improving the performance of previous drought indices based on precipitation data alone when determining the drought impacts on different hydrological and ecological systems (6, 18).

Results and Discussion

Considering an annual summary of the analysis of the Global Inventory Modeling and Mapping Studies–Normalized Difference Vegetation Index (GIMMS-NDVI) dataset, the vegetation activity

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correlates with drought in large areas of the world (Fig. 1*A*), although drought influence on NDVI changed markedly with season and among regions (*SI Appendix*, Figs. S1 and S2). Correlation between the SPEI and the GIMMS-NDVI data are particularly strong throughout large regions (e.g., eastern North America, the Mediterranean Basin, the Sahel). Overall, 72% of the vegetated land areas show significant correlation between the GIMMS-NDVI and the SPEI (*SI Appendix*, Fig. S3 and Table S2).

Tree-ring width data come predominantly from sites corresponding to mountain areas, temperate regions, and high latitudes of the Northern Hemisphere. Therefore, several forest types are not sampled, mainly in tropical and subtropical areas in which tree growth is not subject to seasonal variation and tree-rings are rarely formed, thereby limiting global spatial comparisons. Nevertheless, the high density of tree-ring series in North America, covering humid (mean annual water balance higher than 500 mm per year), subhumid (between 0 and 500 mm), semiarid (between 0 and –500 mm), and arid (lower than –500 mm) sites, shows that forests located in the semiarid and arid areas of central and southwest United States and Mexico have the highest correlations between the SPEI and tree-ring width (*SI Appendix*, Fig. S4). The same pattern is observed with the NDVI and the ANPP datasets, as the influence of the SPEI is lower in humid regions (including tropical rainforests and cool temperate areas of the northern hemisphere) than in semiarid and arid ones (*SI Appendix*, Fig. S5). This is consistent with other studies based on ANPP data (2, 19), as humid regions are characterized by a positive water balance and by vegetation having low water use efficiency (16, 19). Nevertheless, although vegetation activity in humid areas is less determined by drought than in arid ones, drought events also cause a marked reduction of vegetation activity and ANPP (16), as has been observed in the Amazon basin, particularly during the droughts of 2005 (20) and 2010 (21). Accordingly, the GIMMS-NDVI analysis showed that 78% of tropical and subtropical rainforests are

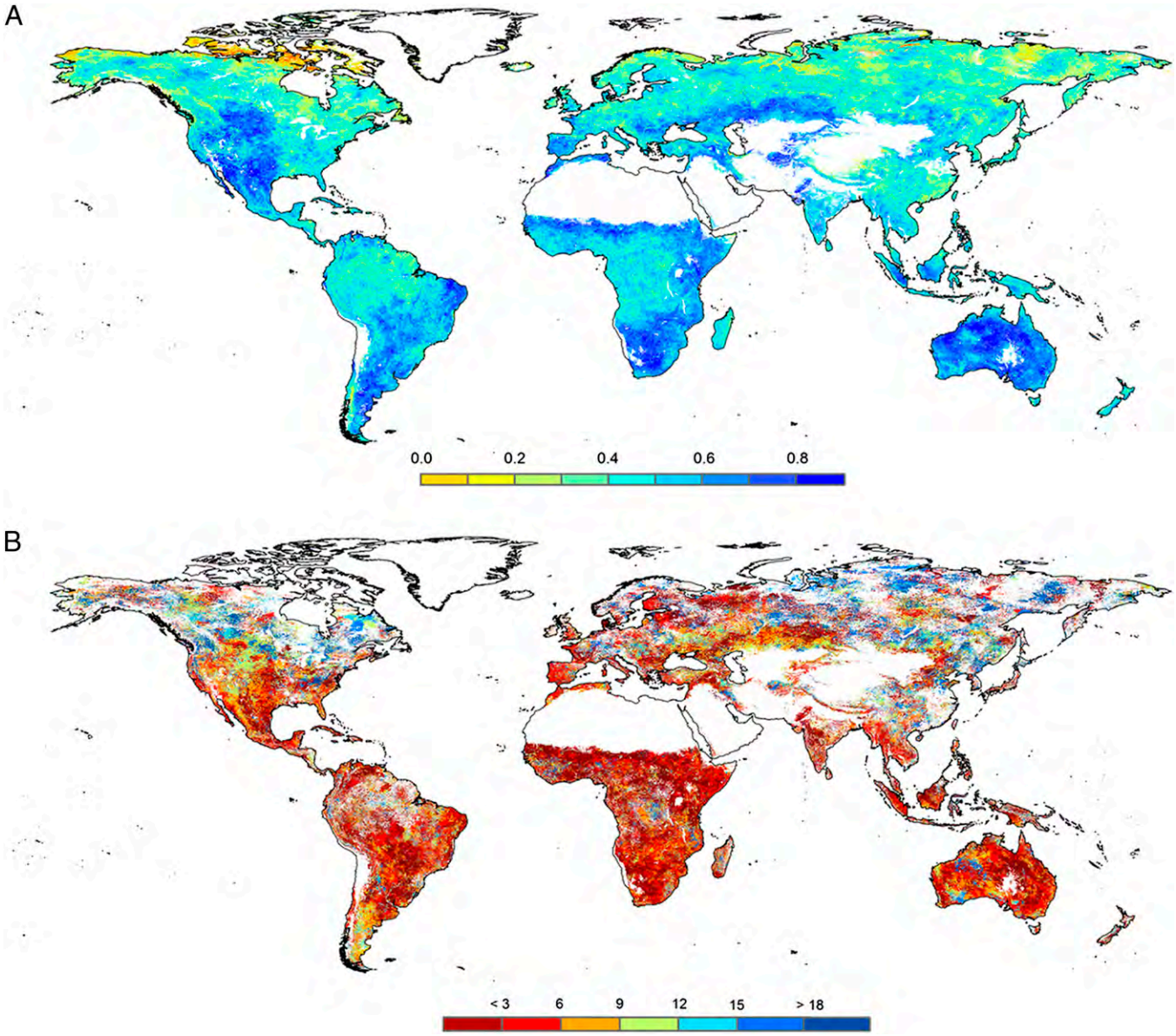

Fig. 1. Geographical patterns of the association observed between drought and vegetation activity. (*A*) Spatial distribution of the correlations (Pearson coefficient, *r*) between SPEI and GIMMS-NDVI for the period 1981–2006. The values represent the maximum correlation recorded for each pixel, independently of the month of the year and the SPEI time-scale. (*B*) SPEI time-scales at which the maximum correlation between SPEI and GIMMS-NDVI is found. Areas with no significant correlations are depicted in white. Desert and ice areas are masked and not included in the analyses.

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characterized by significant correlation with the SPEI. This percentage was found to be even higher for the Moderate Resolution Imaging Spectroradiometer (MODIS) images obtained for the period 2001–2009 [90.7% for the Enhanced Vegetation Index (EVI), and 90.9% for the NDVI]. The percentage of surface area showing significant correlations was also high for boreal forests, cool temperate moist forests and rainforests (65.6% for the GIMMS-NDVI, and 85.5% and 84.4% for the MODIS-EVI and MODIS-NDVI datasets, respectively).

One of the main climate drivers of the geographical distribution of vegetation types is the water balance—that is, the difference between the annual precipitation and the atmospheric water demand (22). The water balance determines forest gradients and variations of forest biomass (23), but also the resistance of vegetation to drought explains the spatial distribution of vegetation in both humid (24) and dry environments (25). It is a reasonable hypothesis to think that not only the average water balance but also the characteristics related to the temporal variability (i.e., the frequency, severity, and duration of drought episodes) may play an important role in explaining the spatial distribution of vegetation types. Following the classification of world biomes by Holdridge (*SI Appendix*, Fig. S6), we found a relationship between the mean water balance in each biome and the average influence of droughts on the interannual variability of NDVI (Fig. 2*A*), tree growth (Fig. 2*B*), and ANPP (Fig. 2*C*). The drought influence was quantified by means of correlations between the SPEI series and the series of the three vegetation parameters. Thus, wet and moist forests of each region are always located in areas with a positive water balance, where the control of vegetation activity by drought is low, as indicated by low correlation with the SPEI. In cold regions, where temperature but not precipitation is the major constraint on plant development, there is little influence of drought on vegetation activity, resulting in low correlations too. In temperate, subtropical, and tropical regions, there are clear gradients of drought influence on vegetation activity as a function of the annual water balance, as revealed by large differences in the correlation with the SPEI. These areas contain dry biomes (including dry forests, scrublands, steppes) with very low ANPP (1, 2), which show the highest correlations with the SPEI.

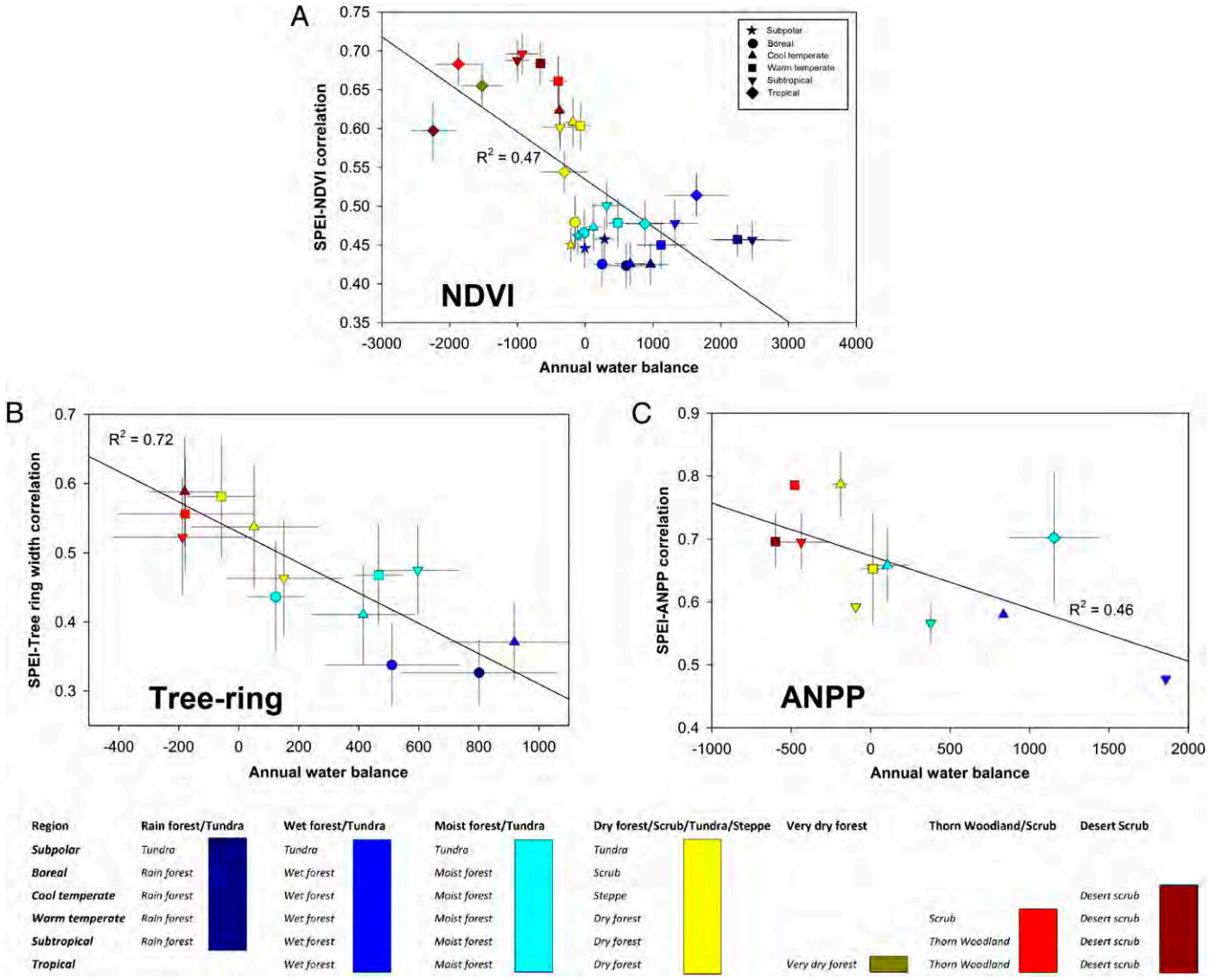

Fig. 2. (*A*) Relationships between the average SPEI/GIMMS-NDVI maximum Pearson correlation coefficients and the average annual water balance (in mm) across the world biomes. (*B*) Relationships between the average SPEI/tree-ring width correlations and the average annual water balance across the world biomes. (*C*) Relationships between the average SPEI/ANPP correlations and the average annual water balance across the world biomes. The biomes are grouped according to six eco-regions: subpolar, boreal, cool temperate, warm temperate, subtropical, and tropical. Colors represent the different biomes of each one of the six eco-regions in the *A*, *B*, and *C* plots. The symbols represent the different eco-regions in plots *A*, *B*, and *C*. Error bars represent ±1/2 SDs. The linear fits and their coefficients of determination are also shown in all graphs.

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The time-scales at which droughts affect vegetation provide useful information to understand how biomes respond to drought. From analysis of the SPEI time-scales at which the maximum correlations are recorded, we found that vegetation activity responds predominantly to short drought time-scales (e.g., 2–4 mo; *SI Appendix*, Fig. S7), although spatial variability is high (Fig. 1*B*). Nevertheless, it is possible to identify general patterns, as the NDVI, for example, tends to respond to shorter drought time-scales in arid areas than in humid ones. This pattern is particularly evident in regions that include the most arid biomes. In warm temperate, subtropical, and tropical regions, the most arid biomes tend to respond at shorter time-scales than the humid ones (Fig. 3). This could be related to different mechanisms, which allow plants to reduce the damage caused by water deficits in arid areas (9). Generally, arid ecosystems respond in a highly plastic way to water availability (26), as plant species are adapted to water shortage (27) thanks to physiological, anatomical, and functional strategies that reduce water loss, respiration costs, photosynthetic activity, and growth rate

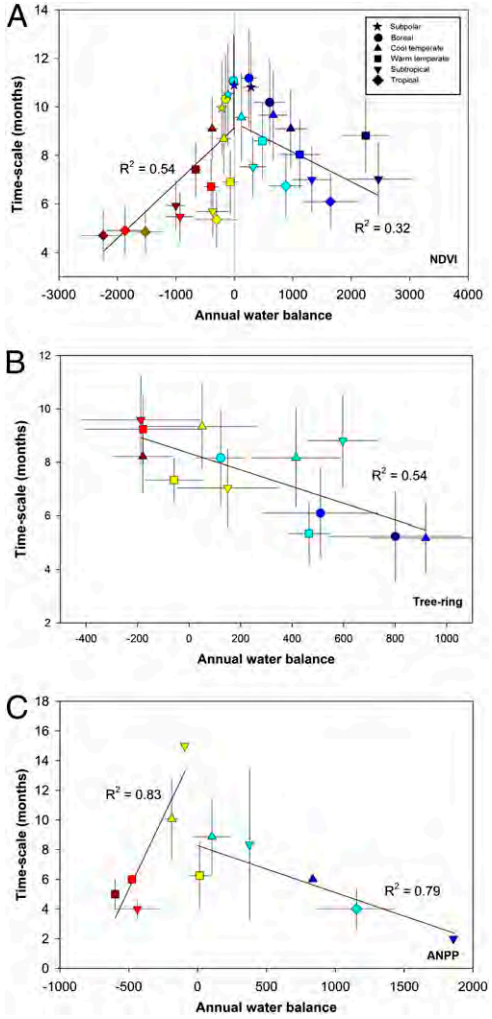

Fig. 3. (*A*) Relationships between the average SPEI time-scales at which the maximum SPEI/GIMMS-NDVI correlation is found and the average annual water balance across eco-regions considering separately negative and positive water balances. (*B*) Relationship between the average SPEI time-scale at which maximum SPEI/tree-ring correlation is found and the average annual water balance across eco-regions. (*C*) Relationship between the average SPEI time-scale at which maximum SPEI/ANPP correlation is found and the average annual water balance across eco-regions for negative and positive water balances. Error bars represent ±1/2 SDs. The linear fits and the coefficients of determination are also shown in all graphs. See corresponding colors in the legend of Fig. 2.

(9). When areas with positive water balance are analyzed independently, it is found that correlations between SPEI and NDVI (Fig. 4*A*, blue), ANPP (Fig. 4*B*, blue), and tree growth (Fig. 4*C*) tend to occur at shorter time-scales as the average water balance increases. This suggests that the influence of drought time-scales is relevant to explain the temporal variability of vegetation parameters also in humid biomes.

In contrast with arid and humid regions, vegetation in semiarid and subhumid regions tends to respond to drought at longer time-scales. Vegetation of these regions is adapted to tolerate regularly periods of water deficit and has physiological mechanisms to cope with these conditions (9). Therefore, it is a reasonable hypothesis to consider that these plant communities must be exposed to sustained water deficits—that is, those registered by long time-scales of the SPEI—to be negatively affected by drought. Thus, in areas with water balance approaching zero, the highest correlations between SPEI and NDVI, tree-ring width, and ANPP occur at time-scales between 8–10 mo, but in the areas with the most positive water balance, the highest correlations between SPEI and vegetation parameters are found at shorter time-scales than in subhumid regions. There are relatively few tree-ring records available for wet tropical rainforests. However, the available data for humid boreal and cool temperate forests show a dominant response to drought at shorter time-scales than is generally recorded for semiarid and subhumid forests (Fig. 3). Boreal and cool temperate moist forests are thus highly sensitive to drought (28), an indicator that tree species dominating these forests do not tolerate water deficits (29). This may explain why droughts predominantly affect tree growth in these areas at short time-scales, as even a short period of water deficit could have negative consequences in vegetation activity and plant growth. Although tree-ring data are not available for the most humid areas of the world such as the tropical rainforests, the results derived from the NDVI suggest a similar pattern: a predominant effect of short-term droughts on vegetation activity (Fig. 3 and *SI Appendix*, Fig. S8). Previous studies identified a lagged response between drought, declining plant growth (30), and forest mortality (31) in similar humid forests. Using various drought time-scales, we have shown that this lag might be usually short, as demonstrated by the response of vegetation activity, forest growth, and the ANPP to very short drought time-scales.

Knowledge of the dominant time-scales at which drought influences vegetation could be critical for the early detection of vegetation damage, but it may also be useful for identifying response patterns that determine the resistance of diverse vegetation types and biomes to drought. Drought vulnerability, however, is related not only to the resistance of vegetation to water stress but also to how fast it recovers after the episode has ended—that is, by its resilience. Drought resilience depends on a variety of factors including the severity and duration of the water deficit, but also the vegetation type (32), the type and magnitude of the damage (33), the plant growth rates and competition between species (34), and even variations in environmental conditions recorded at small spatial scales (35). Although our analysis did not focus on the recovery times of vegetation after drought disturbance, the concept of drought time-scales also seems to constitute a promising tool for analyzing vegetation resilience to drought.

It is noteworthy that the highest influence of drought on vegetation identified in arid areas does not imply necessarily that plant communities from those areas are more vulnerable to drought than those dominant in humid biomes (3, 10). Thus, the short drought time-scales that mostly affect both arid and humid biomes are probably indicative of different types of impacts and different biophysical mechanisms. In arid and semiarid regions, drought impacts usually result in decreased vegetation activity (15) and plant growth (11), but rarely cause plant mortality or long-term damage, as plant communities commonly exhibit a strong resistance to water stress (36), as they contain species that are well adapted to water shortage through different mechanisms (9). This is in agreement with studies analyzing long-term trends of vegetation greenness in arid ecosystems that demonstrated the capacity of such ecosystems to recover the initial greenness values after

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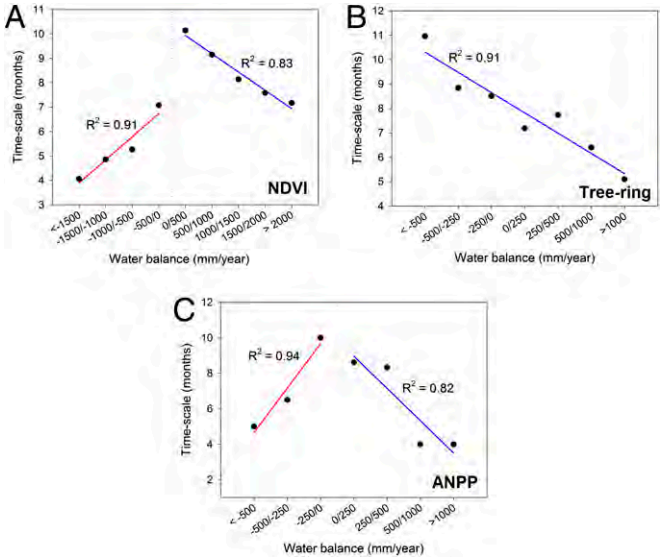

Fig. 4. Average values of the time-scales (in months) at which the GIMMS-NDVI/SPEI (*A*), the tree-ring width/SPEI (*B*), and the ANPP/SPEI (*C*) maximum correlations are recorded, summarized for different ranges of the annual water balance. The linear fits and the corresponding coefficients of determination for negative and positive water balances are also shown.

severe and long-lasting droughts as soon as water is available (37). Nevertheless, although vegetation in arid regions is usually highly resistant to drought (3), when strong damages (e.g., tree mortality) occur during very extreme droughts, the recovery rates after the event has passed may be slow, as arid woody species have generally slow growth rates (38). Thus, unusual severe droughts, which correspond to long SPEI time-scales, can cause plant mortality (34) and even trigger desertification processes (35) in arid environments. Moreover, recurrent droughts can produce a progressive loss of resilience that affects negatively the ability of recovering the initial state (39), often leading to vegetation change.

In general, drought vulnerability is much larger in humid biomes than in arid ones (3, 24), although we found a lower response to drought in the former. This might be explained by the more complex relationship between drought and vegetation activity and plant growth in humid areas because they are characterized by water surplus. Consequently a negative SPEI there does not necessarily imply a water deficit because the water balance may still be positive, albeit lower than usual. Moreover, in humid sites other factors including phenological aspects such as the period of active leaf flushing and vapor pressure deficit may influence the effect of drought on plants (40). In humid regions, drought impacts are most probably linked to damages to plant tissues that result in loss of foliar biomass (29, 31), given the general poor tolerance of plants to water stress (3, 10), but the fast growth rates characteristic of plants of humid regions could allow vegetation to recover its prior state in a short period as soon as the drought has ended. However, in humid areas, long-lasting or recurrent droughts may also be too intense to allow for a fast vegetation recovery, and this could help explain some recent plant mortality episodes in humid forests around the world after severe drought events (7, 20, 29).

Our results concerning the time-scales of drought are similar irrespective of the data sources used: NDVI from National Oceanic and Atmospheric Administration-Advanced Very High Resolution Radiometer and MODIS images, EVI from MODIS images, a vast dataset of tree-ring growth series, and ANPP series across the world. Therefore, our results should be considered robust and unlikely to be explained by alternative causes, such as (*i*) possible residual noise in the GIMMS dataset, (*ii*) the saturation of the NDVI at high values of leaf area index, (*iii*) the low temporal coverage of the MODIS dataset, (*iv*) the low spatial representativeness of the available ANPP series, and (*v*) the lack of adequate coverage of dry and very humid regions by the tree-ring growth dataset. Despite the uncertainties present in each dataset, all of them point toward the same conclusions, and taking into account their complementary nature, this further enhances the robustness of our findings.

Overall, our results provide extensive evaluation of the impact of droughts on global vegetation activity and plant growth. They are particularly relevant within the changing climate framework because the degree to which ecosystems respond to limited water indicates how responsive they may be to future changes in precipitation and temperature. Therefore, the assessment of drought impacts on vegetation parameters may improve the accuracy of projections of vegetation shifts under global change scenarios. Global warming will almost certainly continue in the future (41), which would imply more land areas vulnerable to drought stress, including humid areas such as temperate, mountain, boreal, and wet tropical forests. Vegetation in these areas is already subject to increased drought stress leading to local and regional die-off events because of warming-induced drought stress (7, 29, 31). Although with increased aridity a reduction in vegetation activity might be partially compensated for by rising atmospheric CO_2 concentrations, this mechanism will not enhance production under drought conditions because plant physiological processes are highly constrained by water deficits, independently of the atmospheric CO_2 concentration (42). Increasing drought severity in humid areas may have unpredictable consequences for the biosphere and the global carbon cycle, because the main terrestrial carbon pool is stored in the humid world biomes (43).

In conclusion, we show that vegetation responds to drought at different characteristic time-scales across regions and biomes. Vegetation of both arid and humid biomes respond mostly at short drought time-scales (i.e., a fast reaction of several vegetation parameters is found as soon as relative water deficit occurs), but the mechanisms that drive this response are most likely very different. These mechanisms affect the resistance and resilience of vegetation to drought stress, conditioning their vulnerability to drought. Understanding the relationship between these mechanisms and the characteristics of droughts (for example, as determined by the drought time-scale) is crucial for improving our knowledge of vegetation vulnerability to climate fluctuations and climate change. As expected from current climate change scenarios, the water balance will become more negative in most areas of the world as a consequence of warming processes, which will probably reinforce drought severity worldwide (44).

Methods

To quantify drought severity we used monthly data of the SPEI at a spatial resolution of 0.5° and time-scales ranging from 1 to 24 mo obtained from the SPEIbase (45) (http://sac.csic.es/spei/download.html, *SI Appendix*). We used three different datasets of vegetation parameters, which provide information on ANPP, leaf photosynthetic activity, and tree radial growth across the world. First, we collected long-term ANPP series from the scientific literature using the published tabular data or by digitizing figures. A total set of 40 series that contain a minimum of 10 y were collected (*SI Appendix*, Table S1). The series cover different biomes and vegetation types. The second dataset was based on annual tree-ring width data, obtained from the International Tree-Ring Data Bank (www.ncdc.noaa.gov/paleo/treering.html). From the entire dataset, we selected the tree-ring width series with at least 25 y of data within the period 1945–2009. A total number of 1,846 site chronologies were selected and analyzed (*SI Appendix*). Finally, we included time series of vegetation indices obtained from long-term satellite imagery. We used the NOAA GIMMS-NDVI (46) from July 1981 to December 2006, at a resolution of 0.1°, available from the Global Land Cover Facility (www.glcf.umd.edu/data/gimms). Vegetation indices from the MODIS were also used to replicate the GIMMS-NDVI for the period 2001–2009. Monthly composites of the EVI (47) and the NDVI at a spatial resolution of 5.6 km from the MOD13A2 dataset were obtained from NASA (https://lpdaac.usgs.gov). To characterize the spatial distribution of the world biomes, we used the Holdridge classification (48) from the United Nations Environment Program–Division of Early Warning and Assessment/Global Resource Information Database–Geneva (www.grid.unep.ch) at a spatial resolution of 0.5°. The Global Land Cover Map (http://ionia1.esrin.esa.int/) was used with the purpose of masking the urban areas and irrigated lands.

The 0.5° SPEI data series were interpolated to 8 km for 1981–2006 to match the spatial resolution of the GIMMS-NDVI and to 5.6 km for the

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2001–2009 to match the MODIS vegetation indices. The biweekly GIMMS-NDVI series were monthly composited according to the maximum monthly value to avoid different sources of noise. Taking into account the Gaussian shape of the monthly NDVI distributions (49), the 1981–2006 GIMMS-NDVI and the 2001–2009 MODIS EVI and NDVI series were standardized, according to the average and the SDs of the monthly series obtained for each NDVI pixel. In addition, annual ANPP and tree-ring growth series were also standardized before applying the analysis.

The impact of the SPEI interannual variability on vegetation activity, tree growth, and ANPP was assessed by means of parametric correlations using the Pearson coefficient for the entire period of available data, and considering a significance threshold of $\alpha < 0.05$. Twelve series of the GIMMS-NDVI (one per month) were obtained per pixel, and each one was correlated (Pearson coefficient) to the monthly 1- to 24-mo SPEI series of the pixel for the period 1981–2006. For each grid cell, we obtained 288 correlation values (24 for each month of the year). To eliminate the influence of phenology on the results, the monthly correlations were summarized seasonally and annually. For this purpose, the highest correlation found in each season was retained and also the SPEI time-scale at which the maximum seasonal correlation was obtained. After that, seasonal results were summarized annually following the same approach. The same methodology was applied to the MODIS datasets, ANPP, and tree-ring series (*SI Appendix*).

Maximum annual and seasonal correlations between the GIMMS and MODIS vegetation indices and the SPEI as well as maximum annual correlations between tree-ring width and ANPP records and the SPEI were summarized according to the Holdridge classification by means of the calculation of the average correlation and average maximum SPEI time-scale for the different biomes. For this purpose, the average aridity conditions in each biome were quantified using precipitation and potential evapotranspiration data taken from the CRU TS3.0 dataset (*SI Appendix*).

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RESEARCH ARTICLE

Survival and Mortality of Pumas (*Puma concolor*) in a Fragmented, Urbanizing Landscape

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Abstract

Wide-ranging large carnivores pose myriad challenges for conservation, especially in highly fragmented landscapes. Over a 13-year period, we combined monitoring of radio collared pumas (*Puma concolor*) with complementary multi-generational genetic analyses to inform puma conservation in southern California, USA. Our goals were to generate survivorship estimates, determine causes of mortality, identify barriers to movement, and determine the genetic and demographic challenges to puma persistence among >20,000,000 people and extensive urban, suburban, and exurban development. Despite protection from hunting, annual survival for radio collared pumas was surprisingly low (55.8%), and humans caused the majority of puma deaths. The most common sources of mortality were vehicle collisions (28% of deaths), and mortalities resulting from depredation permits issued after pumas killed domestic animals (17% of deaths). Other human-caused mortalities included illegal shootings, public safety removals, and human-caused wildfire. An interstate highway (I-15) bisecting this study area, and associated development, have created a nearly impermeable barrier to puma movements, resulting in severe genetic restriction and demographic isolation of the small puma population (n ~ 17–27 adults) in the Santa Ana Mountains west of I-15. Highways that bisect habitat or divide remaining "conserved" habitat, and associated ongoing development, threaten to further subdivide this already fragmented puma population and increase threats to survival. This study highlights the importance of combining demographic and genetic analyses, and illustrates that in the absence of effective measures to reduce mortality and enhance safe movement across highways, translocation of pumas, such as was done with the endangered Florida panther (*P. c. coryi*), may ultimately be necessary to prevent further genetic decline and ensure persistence of the Santa Ana Mountains population.

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Introduction

Many large carnivores have been extirpated from substantial portions of their historic range, and extant populations are threatened by habitat loss and fragmentation, and conflict with humans [1]. Human population growth expected over the next century exacerbates these threats [2–5], and exurban development will have substantial impacts on habitat that today is still relatively intact [6]. Because large carnivores pose myriad challenges for conservation in urbanizing landscapes, we began a long-term study of pumas (*Puma concolor*) in 2001 in southern California, USA, to provide quantitative insights and guidance for conservation of pumas and other large carnivores in human-dominated habitats.

Pumas, also known as mountain lions, cougars, or panthers, are wide-ranging carnivores that historically occurred throughout the Americas. Humans have extirpated or greatly reduced puma numbers in much of their former range in the past 200 years [2]. The only documented breeding population of pumas remaining in the eastern United States is in Florida, where a small population of federally endangered pumas (Florida panthers–*Puma concolor coryi*) persists, largely because their endangered status spurred intensive management including translocation and genetic introgression [7, 8]. In the western United States, pumas are hunted for sport in several states, but there is considerable controversy and uncertainty about the long-term consequences of hunting on population persistence. For example, a recent study of heavily-hunted and semi-protected puma populations in Utah [9] did not detect a compensatory decrease in natural mortality in response to heavy hunting pressure, and concluded that uncertainties in the functional relationship between natural and anthropogenic mortality could lead to biased conclusions and mismanagement.

In California, pumas are considered a "specially protected mammal" and hunting is prohibited [10]. Despite these protections, recent genetic studies of pumas in southern California show that the genetic viability and long-term persistence of some populations are in jeopardy [11, 12]. The threats facing pumas in southern California—habitat loss, increased conflict with humans, demographic isolation, and genetic restriction [11–15]—mirror the challenges facing large carnivores in urbanizing landscapes around the world [3], and long-term studies intended to guide conservation and management in these settings are difficult and expensive to conduct. We addressed this information gap by conducting a 13-year study of pumas in the California south coast ecoregion, USA, a biodiversity hotspot [16, 17] with a growing population of >20,000,000 people [18].

Sandwiched between the sprawling metropolitan areas of greater Los Angeles and San Diego, much of the available puma habitat in our study area is not protected from new highways and development, and is subject to ongoing habitat loss and fragmentation [15]. Our goals for this study were to generate survivorship estimates and cause-specific mortality data for pumas in this region, and identify options for improving survivorship and facilitating movement within and among conserved and non-conserved areas. This demographic study builds upon and complements our recent genetic analysis [11], and provides the essential ecological context for understanding the causes and potential solutions to the genetic restriction we found in pumas in the Santa Ana Mountains.

Materials and Methods

Statement

We operated under Protocol 10950/PHS, Animal Welfare Assurance number A3433-01, with capture and sampling procedures approved in Protocol number 17233 by the Animal Care and Use Committee at the University of California, Davis, and Memoranda of Understanding and

Scientific Collecting Permits from the California Department of Fish and Wildlife (CDFW). Permits and permissions for access to conserved lands where captures and monitoring were conducted were obtained from CDFW, California Department of Parks and Recreation, The Nature Conservancy, United States (U.S.) Fish and Wildlife Service, U.S. Forest Service, U.S. Bureau of Land Management, U.S. Navy / Marine Corps, U. S. Fish and Wildlife Service, Orange County Parks Department, San Diego County Parks Department, Riverside County Parks Department, San Diego State University, University of California—Riverside, Audubon Starr Ranch, Vista Irrigation District, Rancho Mission Viejo / San Juan Company, Sweetwater Authority, California Department of Transportation, the City of San Diego Water Department and Parks Department, and the Irvine Ranch Conservancy. Anesthetic drug combinations used in capture procedures were either teletamine / zolazapam (Telazol) or medetomidine / ketamine at dosages prescribed in the scientific literature.

Study Area and Population

The study area encompassed the Santa Ana Mountains (a portion of the Peninsular Ranges) and the remainder of the Peninsular Mountain Ranges and surrounding foothills to the east (hereafter referred to as the eastern Peninsular Range). These areas constitute the majority of occupied puma habitat in southern California south of greater Los Angeles (Fig 1). Pumas are the primary large carnivore remaining in the study area since grizzly bears (*Ursus arctos californicus)* were extirpated in the early 1900s [19, 20].

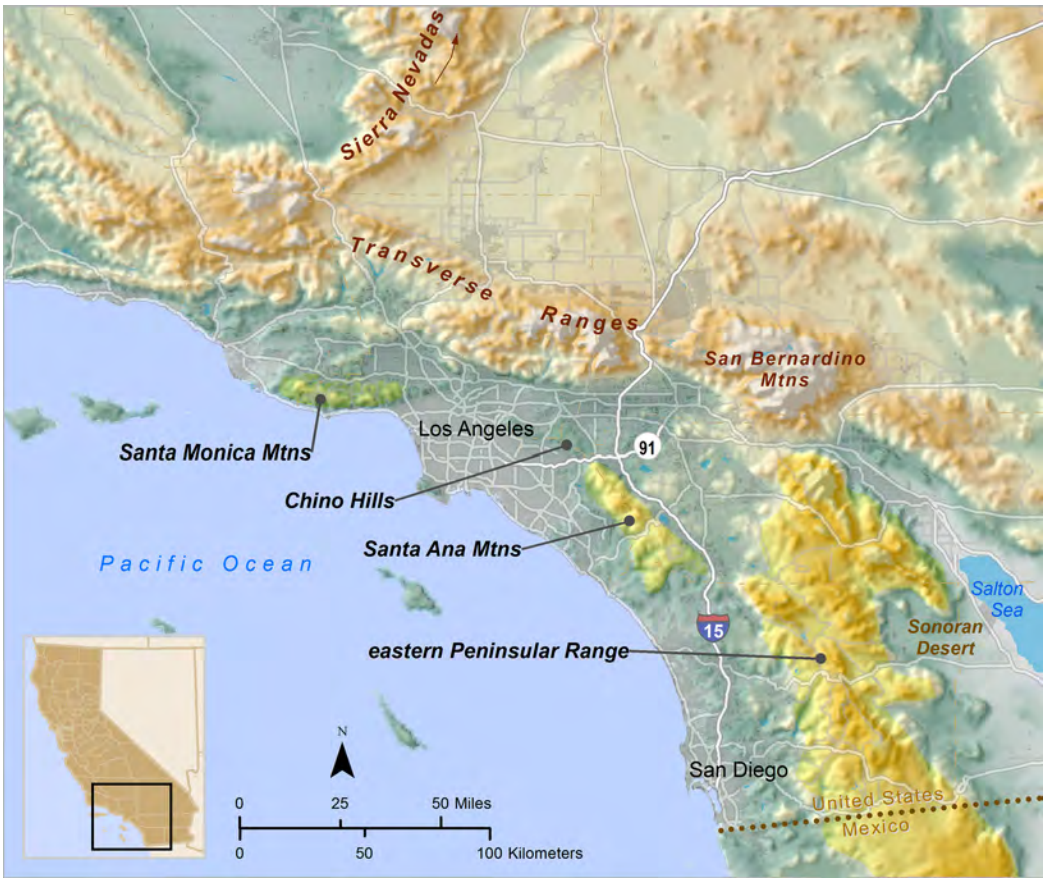

Fig 1. Puma study area in southern California, USA, and regional context. The focal area of this study includes the Santa Ana Mountains and the eastern Peninsular Range. Inset shows location within California.

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An extensive and growing network of roads, some carrying more than 250,000 vehicles per day, encircles and fragments the study area [21] (Fig 1). Interstate highway 15 (I-15) connects the greater Los Angeles, Riverside, and San Diego metropolitan areas, and the highway and associated development have been hypothesized to be a barrier to puma movement between the Santa Ana Mountains in the west and the eastern Peninsular Ranges [11, 13, 22, 23]. Therefore, we assigned pumas that were captured or found dead west of I-15 to a putative "Santa Ana Mountains" source population, and those east of I-15 to a putative "eastern Peninsular Range" source population.

Land use varies considerably across the study area, with the eastern Peninsular Ranges generally having less intensive development and more rural, undeveloped, and protected lands. Burdett et al. [15] classified land use and urbanization in the study area into five categories: protected public lands (55% of the study area), private undeveloped (9.5%), rural (14.4%; >16.18 ha per housing unit), exurban (15.7%; 0.68–16.18 ha per housing unit), and suburban/urban (5.4%; <0.68 ha per housing unit). The Santa Ana Mountains have substantial protected public lands, but new highway construction, development, and land use practices tend to be much more intensive immediately adjacent to remaining high quality puma habitat [15].

Capture and Monitoring Methods

We captured, marked, and monitored radio collared pumas from 2001 through 2013. Pumas were captured primarily using baited cage traps [24], and to a lesser extent using hounds or foothold snares [25, 26]. Each captured animal was tattooed in one ear with a unique numerical identifier ("marked") and a numbered tag was placed in the opposite ear. Age was determined from dental characteristics and body morphometrics as described in Ashman et al. [27] and Laundre et al. [28, 29]. We classified pumas <18 months as kittens, 18–30 months as subadults, and >30 months as adults [30]. We applied Very High Frequency ("VHF"; MOD500 Telonics, Mesa, AZ), and/or Global Positioning System ("GPS"; Simplex P-1D, Televilt, Lindesberg, Sweden; TGW 3580, Telonics, Mesa, AZ; GPS4400S, GPS3300S, and GlobalstarTrack S, Lotek, Ontario, Canada) radio collars to pumas if their body weight exceeded 22.7 kg. GPS locations were collected at varying time intervals from every 5 minutes to every 6 hours depending on specific study objectives.

Puma Movements

We hypothesized that the Pacific Ocean, Sonoran Desert, major highways, and urban centers would form barriers that constrained pumas in our study area into one or more discrete populations. To test this hypothesis, we examined movements of radio collared pumas from 2001–2013 to determine the degree of interchange within and between the Santa Ana Mountains and eastern Peninsular Range populations, and whether monitored pumas emigrated out of the entire study area. We were particularly interested in determining if ongoing habitat fragmentation had created or hardened existing barriers, and in evaluating puma movements relative to corridors or linkages identified through previous modeling efforts. These included: 1) the east-west "Santa Ana—Palomar Mountains Linkage" across I-15 that connects the Santa Ana Mountains and eastern Peninsular Range puma populations [31]; 2) the "Coal Canyon Corridor" under California State Route 91 (SR-91) linking the Santa Ana Mountains and the Chino Hills to the north [17, 32]; and 3) the "Parque-to-Park Linkage" connecting California and Baja California, Mexico to the south [33].

Mortality and Survival Analyses

The distribution of radio collared pumas in the populations west and east of the I-15 freeway were compared using the Fisher exact test to determine if they differed by sex or age class,

and a two-sample t-test was used to determine if they differed by average age at entry or exit to the study (in months), or the average number of days monitored (STATA IC 13.0, STATA-Corp, College Station, Texas, USA). A P value of ≤ 0.05 was used as the cutoff for significance for all analyses.

Deaths of radio collared pumas from 2001–2013 were detected when VHF or GPS data indicated a lack of movement, and the cause of death was determined by field investigation and necropsy. In addition, we combined mortality data for our marked (n = 36) pumas with "unmarked" (n = 218) pumas that were confirmed to have died in the study area from 1981–2013 based on CDFW records. Age determination was less precise for unmarked animals due to conditions of carcasses at discovery or variable experience of reporting parties in the aging of pumas. Therefore, we classified unmarked pumas as either subadults ($\leq$30 months) or adults (>30 months) [30].

We compared long-term trends in the number of pumas being killed under depredation permits in our dataset to the total number of puma mortalities across all of California during the same time period, as reported by CDFW [34], by plotting 5-year simple moving averages for each dataset. For each calendar year, the number of puma mortalities was averaged for the current year and previous 4 years. This allowed us to smooth short-term fluctuations and visualize long-term trends in the data.

Radio collared pumas entered the study on the date they were first captured, and exited on the date of mortality or the last date of detection by radiotelemetry. The number of days each animal was monitored was calculated as the time between entry and exit dates. Cause of death was determined at necropsy for both marked and unmarked animals unless the state of carcass decomposition precluded definitive diagnosis. In those cases, cause of death was classified as "unknown". Because numbers of at-risk individuals varied across the course of the study, a formal cause-specific mortality analysis was not possible [35]. However, source population, sex, and age class (at time of mortality) were evaluated in both marked and unmarked populations for associations with the various causes of mortality using the Fisher exact test (STATA IC 13.0, STATACorp, College Station, Texas, USA).

We estimated survival using the known-fate model in Program MARK (Version 7.1) [36]. We chose a set of 8 models a priori for analysis that included combinations of population, sex, and age class (at the time of collaring) as parameters. Support for each model was assessed using Akaike's Information Criterion (AIC), corrected for small sample size (AIC_c). The *sin* link function was used to run all models. If no model was clearly superior to all others (AICc weight >90% andΔAIC >2) [36–38], we performed model averaging to reduce the uncertainty in our parameter estimates.

We used a Cox proportional hazards model (STATA IC 13.0) to evaluate the relationship of biologically important covariates (source population, sex, age, and year of mortality) to the length of time pumas survived during the study. Adult age class (>30 months old) and mortality years 2007 and 2008 were used as reference categories in the models. Staggered entry into the study was addressed by including the Andersen-Gill formulation [39, 40]. The Breslow approximation method was used to address tied failure times [41], and Schoenfeld residuals were used to test the proportional hazards assumption that relative risk for each variable of interest was the same for the duration of the study.

Results

Puma Monitoring and Movements

Our analyses included 74 pumas that were captured, marked, and radio collared between March 2001 and December 2013 (Table 1). The distribution of these marked pumas in the

Table 1. Demographic characteristics of radio collared pumas in southern California, USA from 2001–2013.

Variable	Number of pumas		
	Total	Santa Ana Mountains	Eastern Peninsular Ranges
Sex			
Females	37	17	20
Males	37	14	23
Outcome			
Survived	38	18	20
Died	36	13	23
Age class at entry			
<18 months	19	6	13
18 to 30 months	19	9	10
>30 months	36	16	20
Age class at exit			
<18 months	2	0	2
18 to 30 months	16	7	9
>30 months	56	24	32

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eastern Peninsular Range (n = 43) and Santa Ana Mountains (n = 31) did not differ significantly by sex, age class, average age at entry or exit to the study, or the average number of days monitored.

We detected numerous long distance (>80 km) movements by radio collared pumas from 2001–2013, but only one radio collared puma moved out of the overall study area. In 2009, a young adult male (M53) traveled approximately 150 km south from his capture site in the eastern Peninsular Range, utilizing the Parque-to-Park Linkage to cross the U.S.-Mexico border (Fig 2). He reached a point 70 km south of the border before returning to his original location in the U.S. Several other radio collared pumas were detected near, but not across, the U.S.-Mexico border (Fig 2).

Radio collared puma movements between the eastern Peninsular Range and Santa Ana Mountains were limited, indicating the pumas in these regions formed relatively discrete populations. In 2010, a dispersing sub-adult male (M56) crossed I-15 from west to east several miles south of the proposed Santa Ana Mountains—Palomar Mountains Linkage (Fig 2), but he was killed 25 days later for depredating domestic sheep.

None of the radio collared pumas used the Coal Canyon undercrossing beneath SR-91 at the northern tip of the Santa Ana Mountains to move into the Chino Hills to the north (Fig 2). However, two unmarked pumas were killed from 2001–2013 while attempting to cross this major freeway within 3 km of the Coal Canyon undercrossing.

Puma Mortality

The number of pumas alive (n = 38) vs. dead (n = 36) by the end of the study did not differ between source populations, sexes, or age class at entrance or exit (Table 1). Though time-at-risk and sample size constraints prevented a formal cause-specific mortality analysis, we report here proportional mortality of both marked and unmarked pumas over the entire study period. Over the course of the entire study period, proportional mortality due to vehicle collisions and depredation permits was greater than for all other causes of mortality. Other known sources of mortality included disease, illegal shooting, arson-caused wildfire, public safety removal, and intraspecific aggression (Table 2). Proportional mortality due to vehicle strikes and

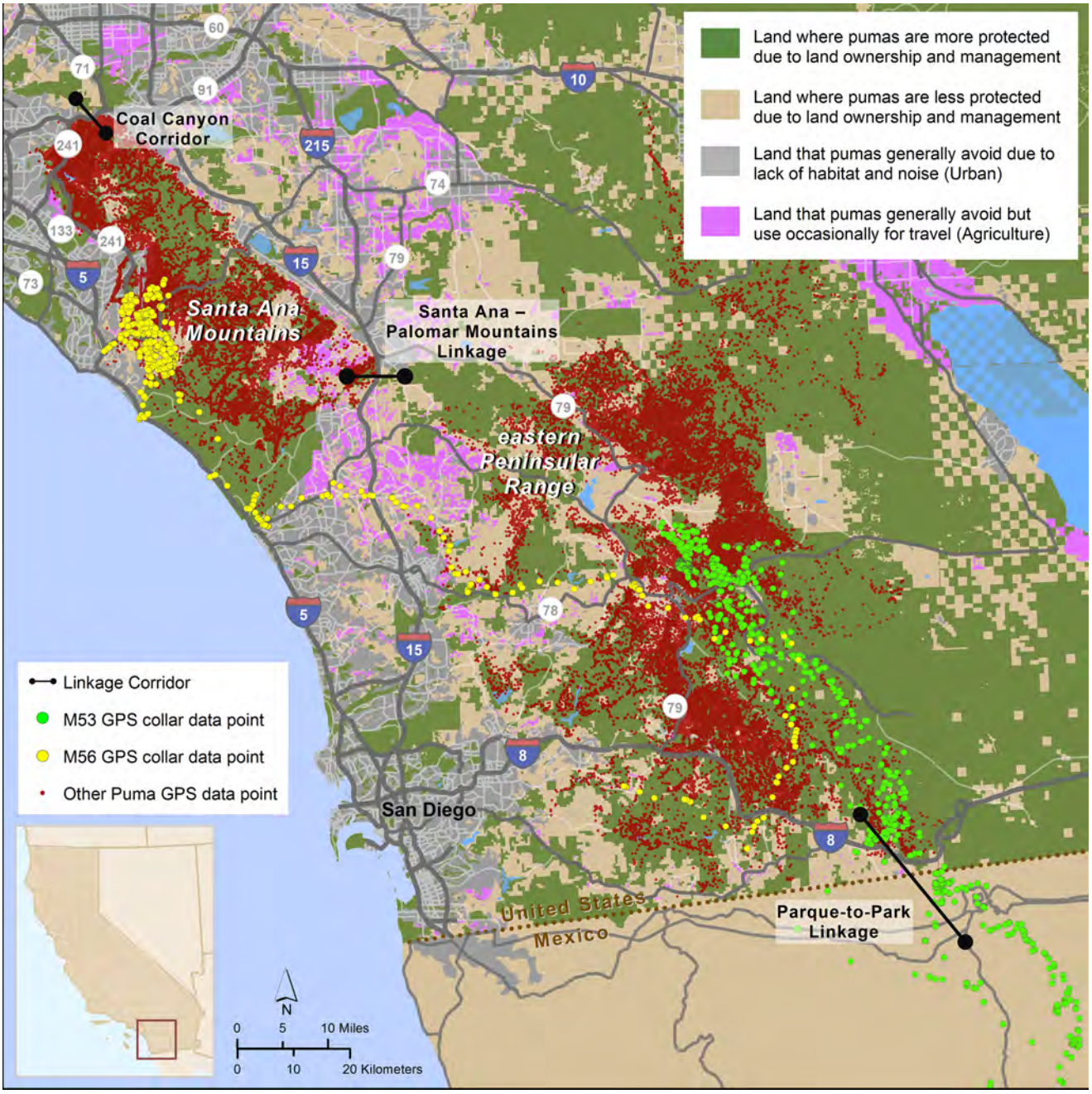

Fig 2. Puma GPS collar data points collected from 2001–2013 in southern California, USA. GPS collar data points are overlaid on lands classified (by color) based on their relative levels of puma protection and typical usage. Primary linkages within the study area are noted and GPS collar data points from pumas M53 and M56 are highlighted. Inset shows location within California.

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depredation permits differed between pumas from the eastern Peninsular Range and Santa Ana Mountains populations ($P = 0.034$), but did not differ by sex or age class. In fact, all mortalities of marked pumas due to depredation permits occurred in the eastern Peninsular Range, while 60% of mortalities due to vehicle collisions were in the Santa Ana Mountains (Table 2; Figs 3 and 4). With the exception of vehicle strikes and depredation, the data were too sparse to evaluate relationships between specific causes of mortality and various risk factors.

Table 2. Proportions and numbers of radio collared pumas that died from different causes in Southern California study areas from 2001–2013.

Cause of mortality	Total	Santa Ana Mountains	Eastern Peninsular Ranges
Vehicle Strike[a]	0.28 (10)	0.46 (6)	0.17 (4)
Depredation Permit[a]	0.17 (6)	0.00 (0)	0.26 (6)
Killed illegally	0.11 (4)	0.23 (3)	0.04 (1)
Disease suspected	0.11 (4)	0.08 (1)	0.13 (3)
Disease confirmed	0.06 (2)	0.00 (0)	0.09 (2)
Fire	0.06 (2)	0.08 (1)	0.04 (1)
Public safety	0.03 (1)	0.00 (0)	0.04 (1)
Killed by other puma	0.03 (1)	0.00 (0)	0.04 (1)
Capture related	0.03 (1)	0.00 (0)	0.04 (1)
Unknown	0.14 (5)	0.15 (2)	0.13 (3)
Total	36	13	23

[a] Mortalities secondary to depredation permits and vehicle strikes differed between the two populations (P = 0.034; Fisher's exact test).

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In the combined dataset (marked and unmarked pumas; n = 254), proportional mortality due to depredation permits was approximately 3.4 times higher for males than females (54M:16F; $P = 0.001$), while proportional mortality due to vehicle collisions was equal for both sexes (45M:45F). In the combined dataset, proportional mortality varied between the eastern Peninsular Range and Santa Ana Mountains populations ($P < 0.001$). There were more mortalities due to depredation permits in the eastern Peninsular Range (n = 62, compared to n = 11 in the Santa Ana Mountains), and almost equal numbers of mortalities due to vehicle collisions in the two populations (n = 46 in the eastern Peninsular Range, compared to n = 50 in the Santa Ana Mountains; Fig 5). Mortality varied substantially year by year in the combined dataset, but the trend for mortalities due to depredation permits tended to increase from 1981 to 2004 and then began to decline, before trending upward again through 2013 (Fig 6), a pattern generally similar to that seen in CDFW's graph of statewide depredation data (http://www.dfg.ca.gov/wildlife/lion/depredation.html). In contrast, the trend for deaths due to vehicle collisions increased steadily through 2013, with no decline or downward trend detected after 2004 (Fig 6). Vehicle mortalities occurred throughout the study area (Figs 3 and 4), however the majority of vehicle-related mortalities in the Santa Ana Mountains occurred on California State Highway 241 (SR-241) and SR-74, two highways that traverse puma habitat, and I-15 in the Santa Ana Mountains to Palomar Mountains Linkage area (Fig 3).

Puma Survival

Survival estimates were calculated using data from the 74 radio collared pumas that were monitored from 2001–2013 for a total of 29,578 puma days (mean = 400, SE = 38 days per animal). Using the known-fate model within Program MARK, the estimated mean annual survival rate was 55.8%, (95% CI = 44.5–65.6%). In the most parsimonious model survival was constant across populations, sexes, and ages ("S(.)"; Table 3). Two models had ΔAIC values <2: model "S(Sex)" which included sex as a parameter (model likelihood = 0.43), and model "S(Population)" which included population as a parameter (model likelihood = 0.37; Table 3). These models yielded annual survival estimates of 58.6% for females and 52.5% for males across the entire study area, and 56.5% for the Santa Ana Mountains population and 55.4% for the eastern Peninsular Range population across all sexes and age groups (Table 3). Due to the distribution of AICc weights among the top models (Table 3), we performed model averaging of similarly

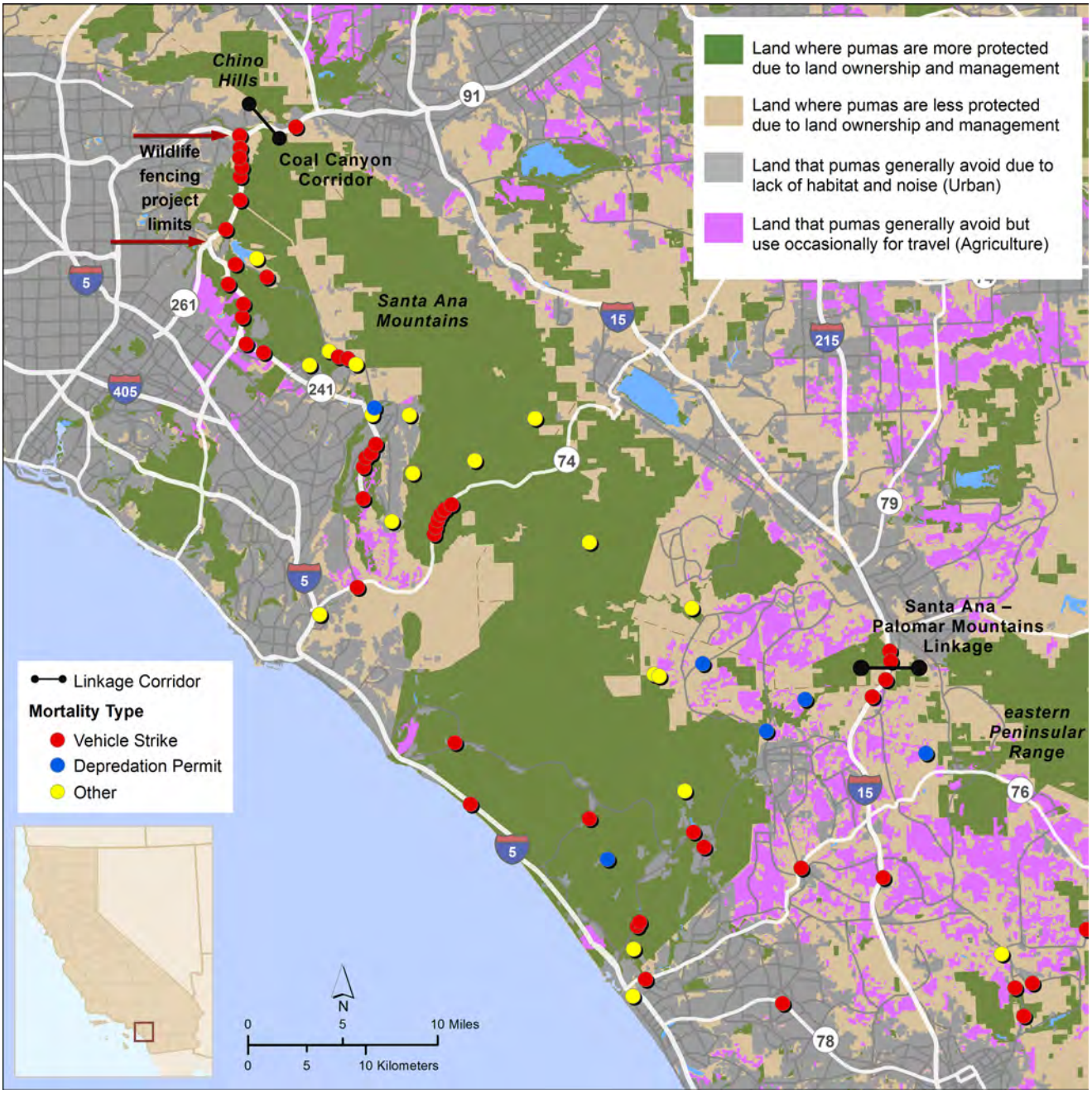

Fig 3. Sites and causes of puma mortalities in the Santa Ana Mountains, 1981–2013. The Coal Canyon Corridor and Santa Ana—Palomar Mountains Linkage are noted, as well as the limits of a wildlife fencing project on SR 241. Inset shows location within California.

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parameterized models but did not detect any differences among groups (95% CI of survival estimates overlapped).

Survival rates varied widely among years, and the Cox proportional hazards model identified calendar years 2001, 2003 2005, 2006, and 2009 as having significantly higher hazard ratios compared to years 2007 and 2008 (Table 4). All other covariates, including source population, sex, and age at entry were not significantly associated with time to death. Evaluation of the proportional hazards assumption for the final model based on a test of Schoenfeld residuals

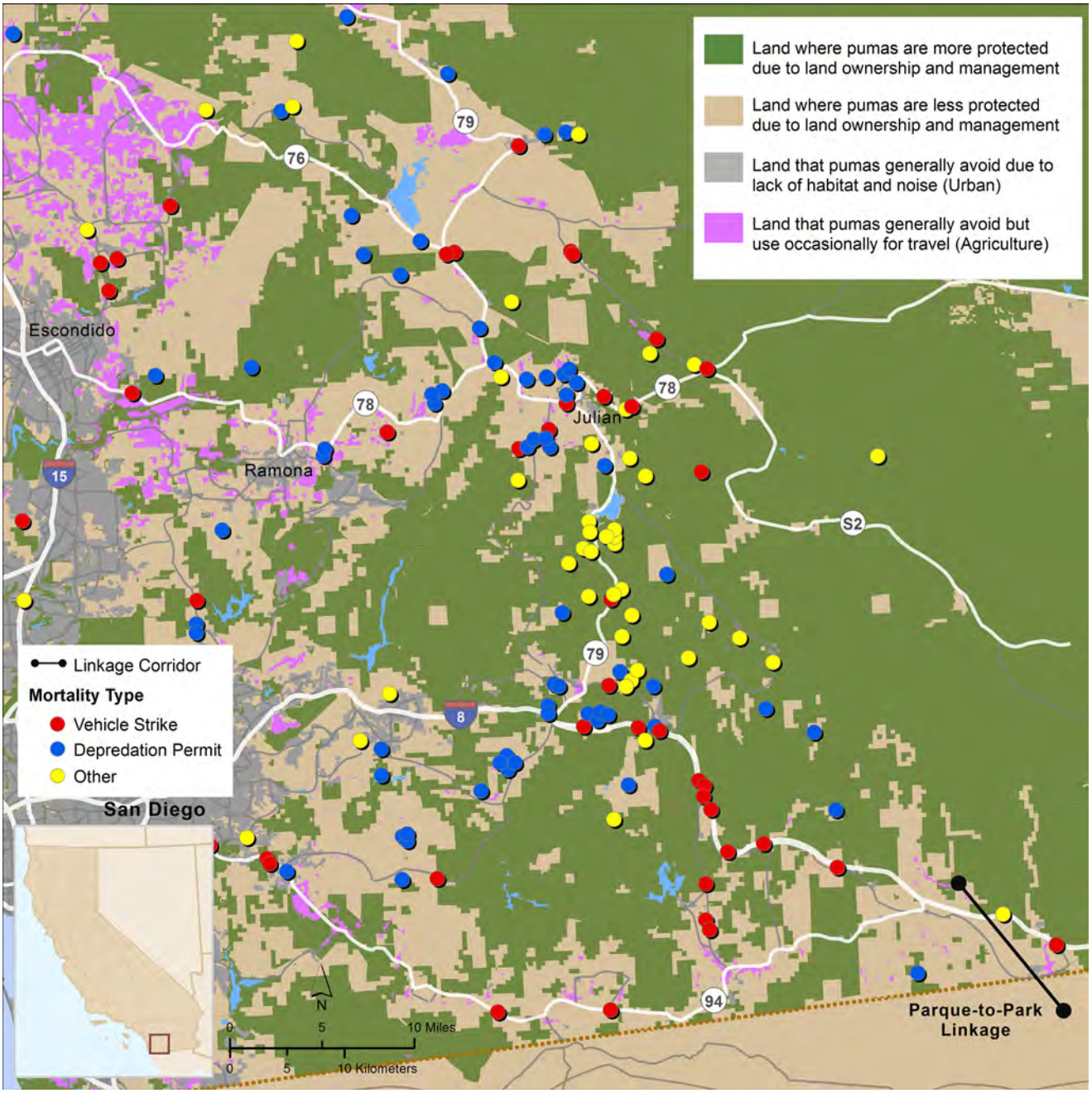

Fig 4. Sites and causes of puma mortalities in the eastern Peninsular Range, 1981–2013. Area depicted is generally east of Interstate 15, with the Parque to Park linkage noted. Inset shows location within California.

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indicated that the relative risk for each variable of interest, after including year as a variable in the model, did not differ for the duration of the study ($P = 0.99$).

Discussion

This 13-year study demonstrates the high risk of mortality for pumas associated with fragmentation and urbanization, and coupled with our genetic analyses [12], we conclude that puma

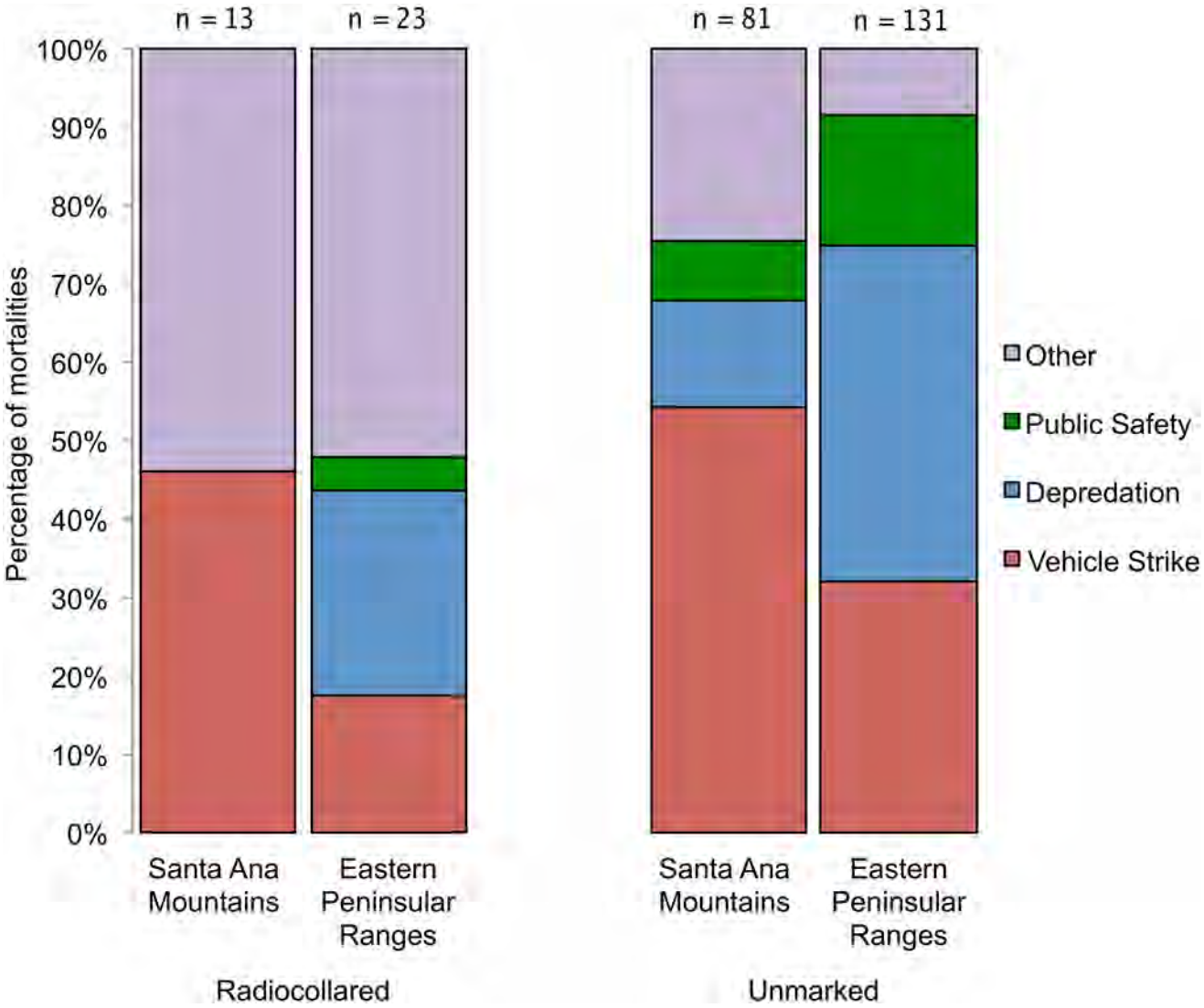

Fig 5. Percentages of pumas dying from different causes of mortality in southern California, USA. Mortalities of radiocollared (n = 36; 2001–2013) and unmarked (n = 212; 1981–2013) pumas were assigned to the Santa Ana Mountains or the eastern Peninsular Ranges subpopulation. Six unmarked pumas were not included in this figure because they were found on the I-15 freeway and could not be assigned to a population.

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persistence in this human-dominated landscape is threatened [42–46]. Annual puma survival rates for radio collared pumas in the Santa Ana Mountains (56.5%) and eastern Peninsular Range (55.4%) were very low from 2001–2013, and were similar to those in heavily hunted populations [2, 9, 43]. Indeed, annual survival rates for our study population were lower than rates for pumas in the peri-urban Santa Monica Mountains population northwest of Los Angeles (>75%) [12], and are within the range that is considered a threat to persistence of puma populations [13].

Our movement data (this paper) and our genetic findings [11] support the hypothesis that pumas in the Santa Ana Mountains and eastern Peninsular Range effectively form two subpopulations, bisected by an interstate highway and neighboring development. Our data demonstrate that both subpopulations had low survival; and though proportional mortality is a crude measure of causes of death in a population, the major causes of puma proportional mortality

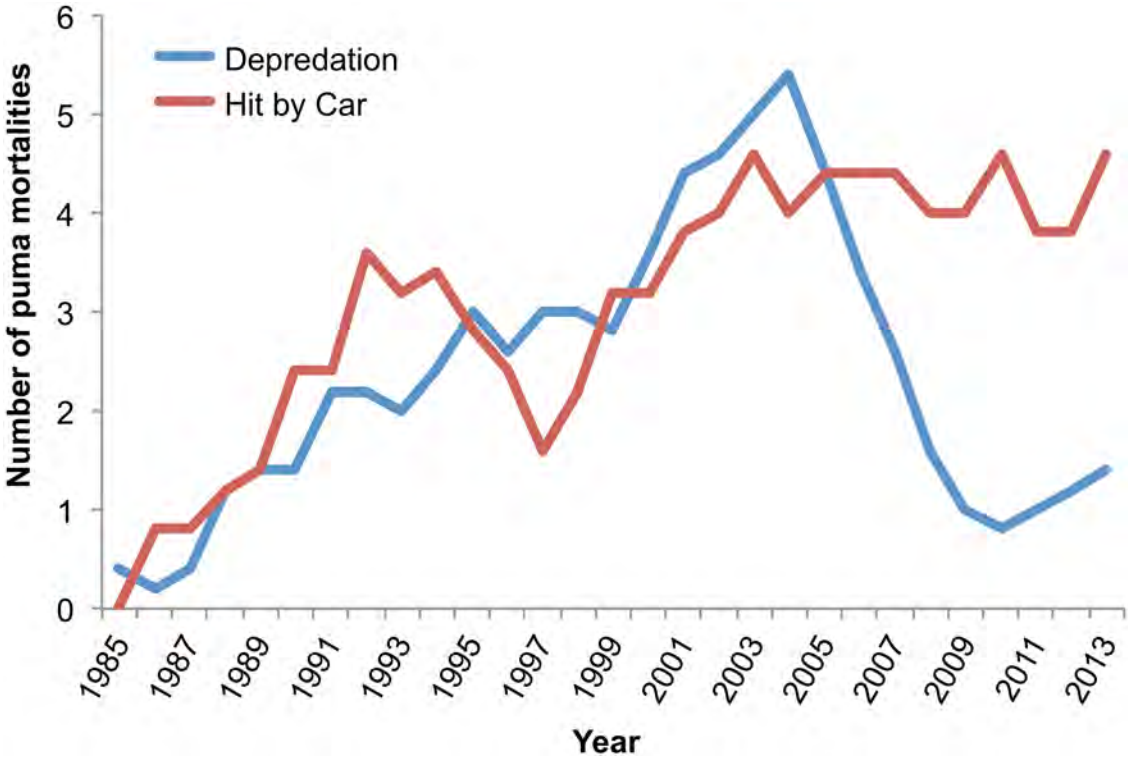

Fig 6. Pumas killed secondary to vehicle collisions or depredation permits from 1981–2013 in southern California, USA. Five year moving average of pumas killed secondary to vehicle collisions or depredation permits (n = 174) in the Santa Ana Mountains and eastern Peninsular Ranges.

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differed between these areas. Depredation permits were the most common proportional mortality factor in the eastern Peninsular Range and primarily affected males, whereas vehicle strikes were the main source of proportional mortality in the Santa Ana Mountains, affecting males and females equally. Conservation biologists have long expressed concern about demographic and genetic isolation of pumas in the Santa Ana Mountains [11, 13], and this study, coupled with our companion genetic study [11], provides a comprehensive view of the fractured demographic and genetic connectivity among pumas in this region.

Ernest et al. [11] concluded that Santa Ana Mountains pumas monitored in this study "had high average pairwise relatedness, high individual internal relatedness, a low estimated effective population size, and strong evidence of a bottleneck and isolation from other populations in California." Genetic restriction and isolation were pronounced even though limited gene flow

Table 3. Results of the known-fate model (Program MARK) for survival (S) for radio collared pumas in southern California, USA.

Model	AICc	ΔAICc	AICc Weights	Model Likelihood	Number Parameters	Deviance
S(.)	397.21	0.00	0.4668	1.00	1	327.25
S(Sex)	398.89	1.68	0.2012	0.43	2	326.93
S(Population)	399.20	1.99	0.1724	0.37	2	327.24
S(Age)	400.24	3.03	0.1026	0.22	3	326.27
S(Population*Sex)	402.69	5.48	0.0301	0.06	4	326.72
S(Population*Age)	403.68	6.48	0.0183	0.04	6	323.70
S(Sex*Age)	405.22	8.01	0.0085	0.02	6	325.24
S(Population*Sex*Age)	414.57	17.37	0.0001	0.00	12	322.52

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Table 4. Variables related to time to death in the Cox proportional hazards model of survival of radio collared pumas in southern California, USA.

Covariate[a]	Hazard Ratio	SE	Z	P>|z|	95% CI
Age at Entry[b]					
<18 months	0.53	0.28	-1.21	0.23	0.19–1.48
18–30 months	1.56	0.75	0.93	0.35	0.61–3.99
Year at Exit[c]					
2001*	149.20	209.78	3.56	0.00	9.48–2347.27
2002	5.16	6.85	1.24	0.22	0.38–69.63
2003*	9.86	8.34	2.71	0.01	1.88–51.73
2004	5.41	6.98	1.31	0.19	0.43–67.91
2005*	12.75	11.51	2.82	0.01	2.18–74.76
2006*	7.10	6.82	2.04	0.04	1.08–46.64
2009*	8.02	7.79	2.14	0.03	1.20–53.77
2010	1.70	1.71	0.53	0.60	0.24–12.16
2011	3.03	4.03	0.84	0.40	0.23–40.89
2012	6.16	6.14	1.82	0.07	0.87–43.44
2013	3.55	3.48	1.29	0.20	0.52–24.23

*Covariates significant at $P \leq 0.05$.

[a]The final model controlled for population and sex which were not significantly associated with time to mortality

[b]Oldest age class (>30 months old) designated as reference category.

[c]Years 2007 and 2008 designated as reference category

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did occur from the eastern Peninsular Ranges into the Santa Ana Mountains. Genetic analysis showed that a male puma (M86) captured in the Santa Ana Mountains was likely born in the eastern Peninsular Ranges, and successfully migrated into the Santa Ana Mountains during our study. This male, and two females (F61 and F89) captured in the Santa Ana Mountains, were the likely parents of four pumas born in the Santa Ana Mountains in 2010–2011 (M91, F92, M93, and M97) [11]. However, this is the only evidence of successful genetic interchange between the two populations during the study period other than an 8 month old kitten (F102) [11] killed by a car in the Santa Ana Mountains in August 2003. In 13 years, none of the pumas radio collared in the eastern Peninsular Range were observed to move west into the Santa Ana Mountains, and the single radio collared male that did move from the Santa Ana Mountains into the eastern Peninsular Range was killed for depredating domestic sheep within weeks of crossing I-15. This suggests that the estimated 17–27 adult pumas in the Santa Ana Mountains [13] have become an insular population, much like the small population of pumas located in the Santa Monica Mountains [12]. The combination of small population size, limited potential for immigration of new individuals (male and female) into the area, female mortality rates that are similar to males, and negative effects of genetic restriction [11], collectively put the Santa Ana Mountains population at risk for demographic collapse [13, 22, 47].

Southern California has been the focus of multiple regional-scale conservation planning efforts aimed at protecting a network of natural habitats, among extensive urban, suburban, and exurban development and a burgeoning population of >20,000,000 people [48]. Pumas have been a focal species for these efforts because of their ecological value, their inherent value to humans, and their utility as surrogates for other wide-ranging taxa in conservation planning [13, 22, 42, 49–52]. Despite some concerted conservation efforts (e.g. [14]), this study shows that pumas are currently subject to high levels of human-caused mortality, and that wildlife corridors that facilitate safe movement through the landscape are lacking or insufficient. These

threats will only grow worse without further action. For example, additional urban development is underway or proposed on both the east and west sides of I-15 in the Santa Ana–Palomar Mountains Linkage (Figs 2 and 3) [53, 54], and 14,000 new homes and associated highways will be constructed at the south end of SR-241 in the center of puma habitat in the Santa Ana Mountains [55].

Conserving core habitat areas and functional wildlife corridors has been the main focus of conservation efforts for pumas in southern California [15, 31, 32, 56, 57] and coordinated regional action in the form of targeted investment in habitat protection is especially urgent to maintain viability of the Santa Ana Mountains population. However, our analysis highlights that land protection alone will not be sufficient to ensure puma persistence in the region. Also important will be directed focus on improving road infrastructure to facilitate safe wildlife crossings, and reducing depredation conflicts that precipitate puma deaths. Options for enhancing movements across I-15 and other highways include protection of additional lands on both sides of the highway, improving or adding large culverts, adding exclusionary fencing [58] such as that currently being constructed on SR 241 (Fig 3) [59], and possibly constructing vegetated overpasses for wildlife use [60, 61]. Strategies to reduce mortalities stemming from depredation permits include education activities to promote wider use of predator-proof enclosures for their domestic animals during the crepuscular periods and at night [62–65]. A focus on land protection, roadway and wildlife crossing design, and landowner outreach will be critical for persistence of puma in southern California, and may well be a formula for conserving large carnivores in highly populated and fragmented landscapes generally.

The combination of long term field monitoring of radio collared animals coupled with genetic analyses was critical for understanding puma biology and providing directions for conservation efforts in southern California. The movement of puma M86 across I-15 from the eastern Peninsular Ranges may aid in the genetic rescue of the Santa Ana population, but only if his offspring survive and reproduce. To date, only one of his four known offspring are still alive in the wild—a female with two dispersal-age offspring, and evidence points towards pumas being less likely to successfully navigate this human-dominated landscape in the future. In the absence of effective measures to reduce mortality and enhance safe movement across highways, translocation of pumas, such as was done with the Florida panther [66], may ultimately be necessary to prevent further genetic decline and assure persistence of the Santa Ana Mountains population.

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Author Contributions

Conceived and designed the experiments: TWV WMB RB SAM PRH TS HBE. Performed the experiments: TWV WMB RB HBE JNS. Analyzed the data: TWV WMB JNS CKJ BSC HBE PRH RB. Contributed reagents/materials/analysis tools: JNS CKJ HBE SAM BSC. Wrote the paper: TWV JNS CKJ SAM RB TS BSC PRH HBE WMB.

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66. Johnson WE, Onorato DP, Roelke ME, Land ED, Cunningham M, Belden RC, et al. Genetic restoration of the Florida panther. Science. 2010; 329(5999): 1641–5. doi: 10.1126/science.1192891 PMID: 20929847.

Project Title: Santa Ana Mountains to eastern Peninsular Range Conservation Connectivity Infrastructure Planning Project for Interstate 15 and Closely Associated Roadways



Collaborators

- **Winston Vickers, UC Davis Karen C. Drayer Wildlife Health Center**
- **Trish Smith, The Nature Conservancy**
- **Brian Cohen, The Nature Conservancy**
-
- **California Polytechnic University, Pomona**
- **Senior Students led by team leaders Elena Pierce and Ali Moetazed Monajjemi**
- **Civil Engineering Faculty leading and advising student teams were:**
- **Wen Cheng, Xudong Jia, and Lourdes Abellara**

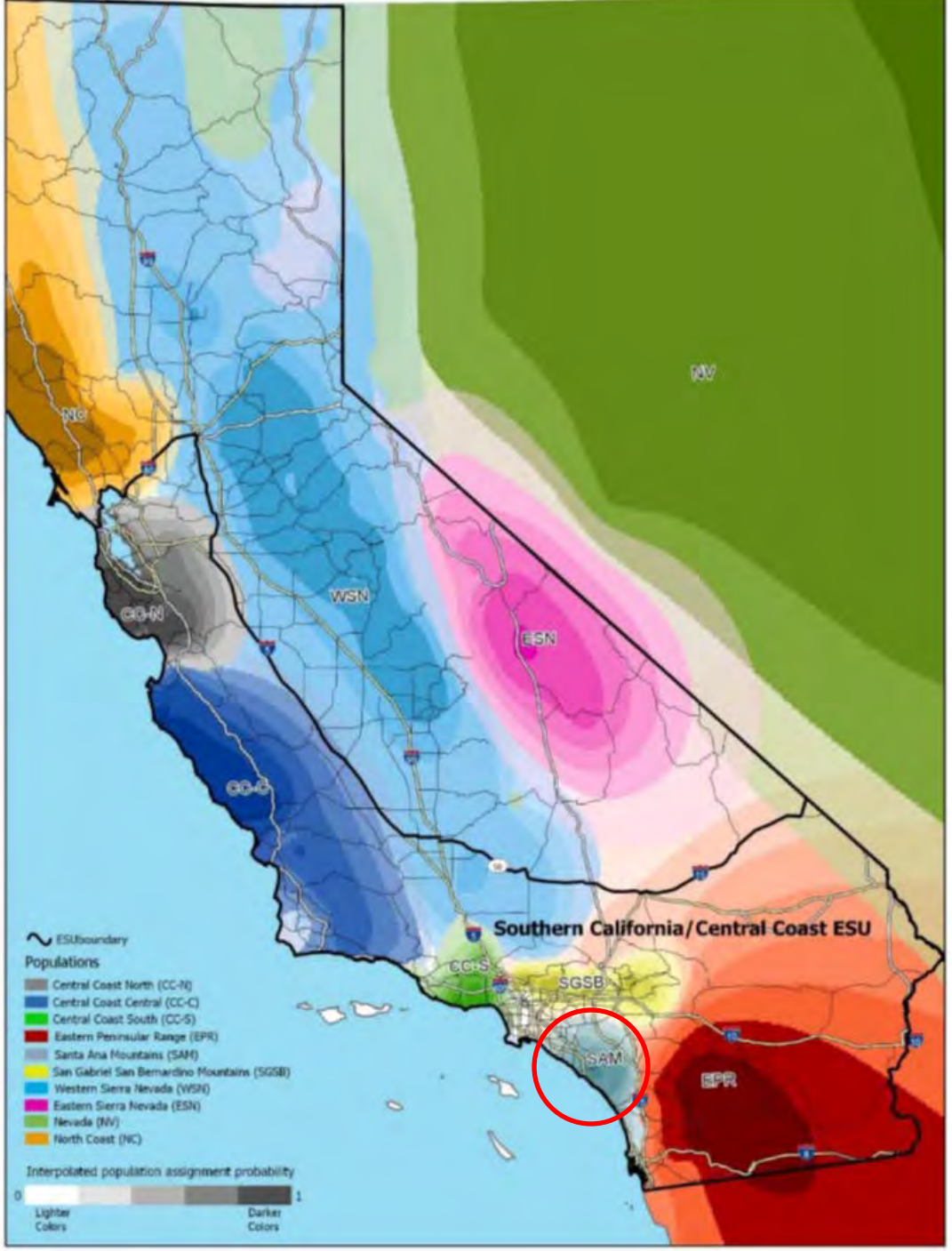
- **Amy Collins and Fraser Shilling - UC Davis Road Ecology Center**
- **Travis Longcore – USC**

- **Kathy Zeller – U. Mass**
- **Justin Dellinger – CDFW**
- **Jessica Sanchez - UCD**

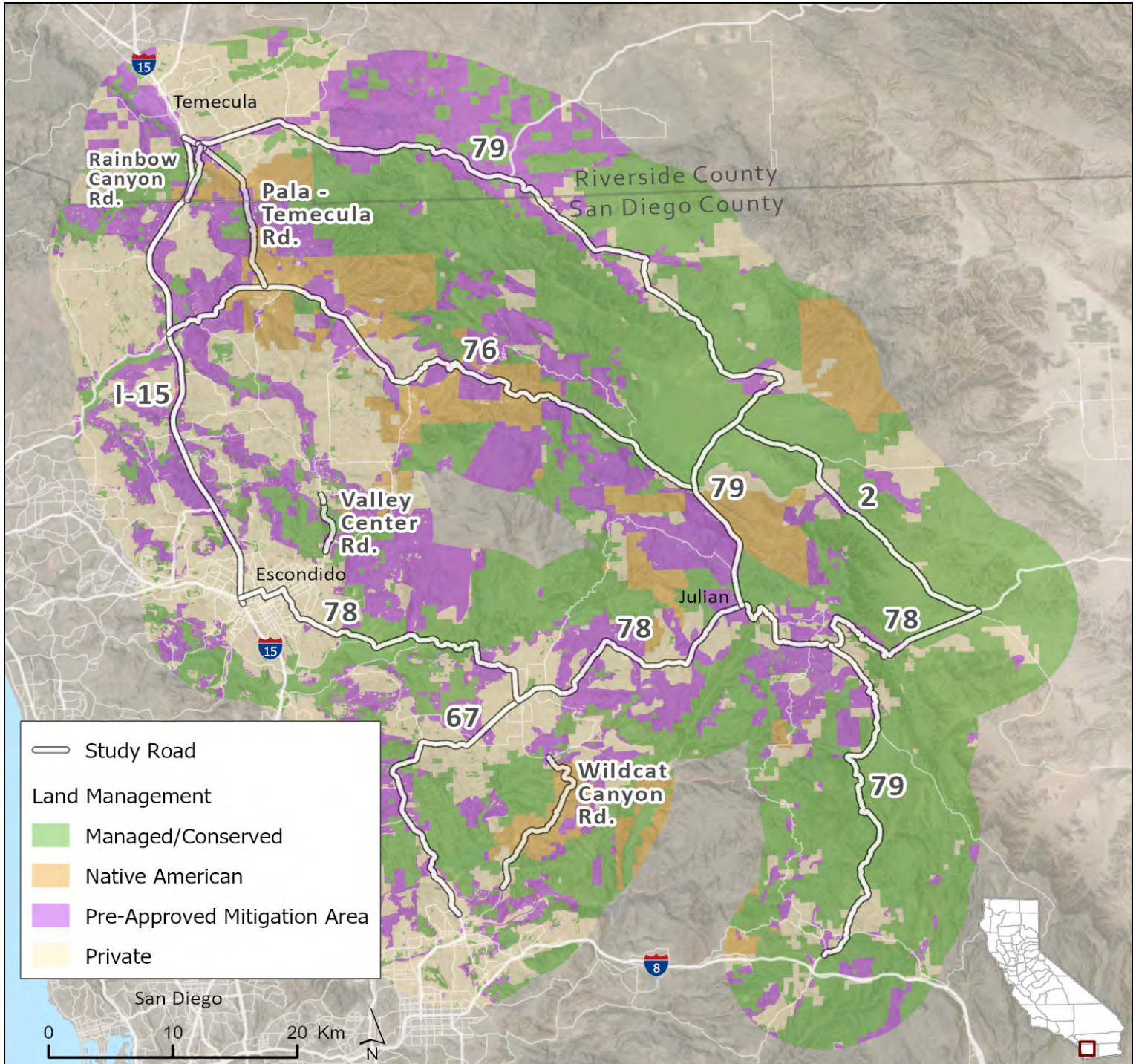
- **UCD Field Crew – Jamie Bourdon and Rich Codington**

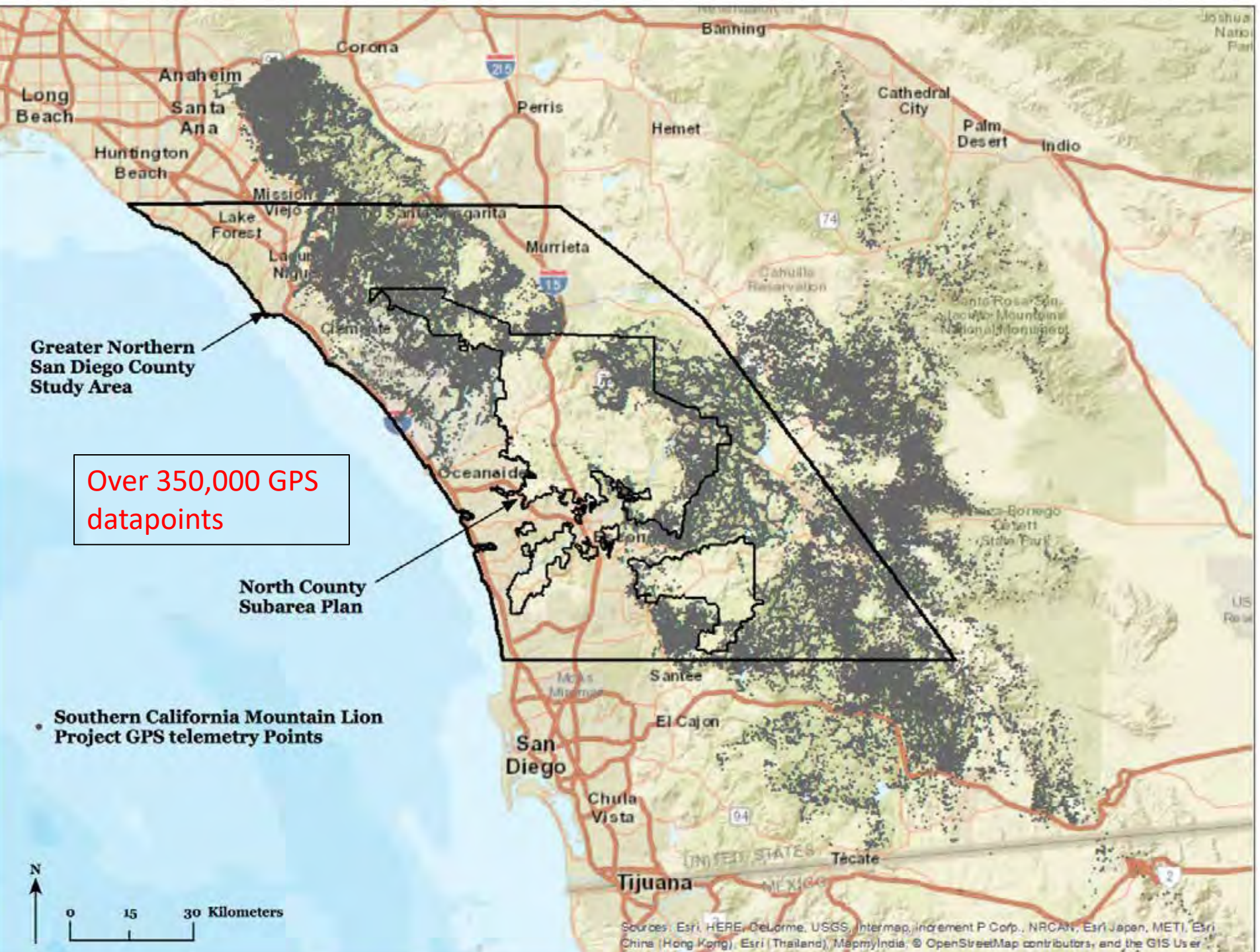
From CESA 2019 petition to list 6 southern and coastal populations as threatened or endangered. Map adapted from Gustafson et al. 2018

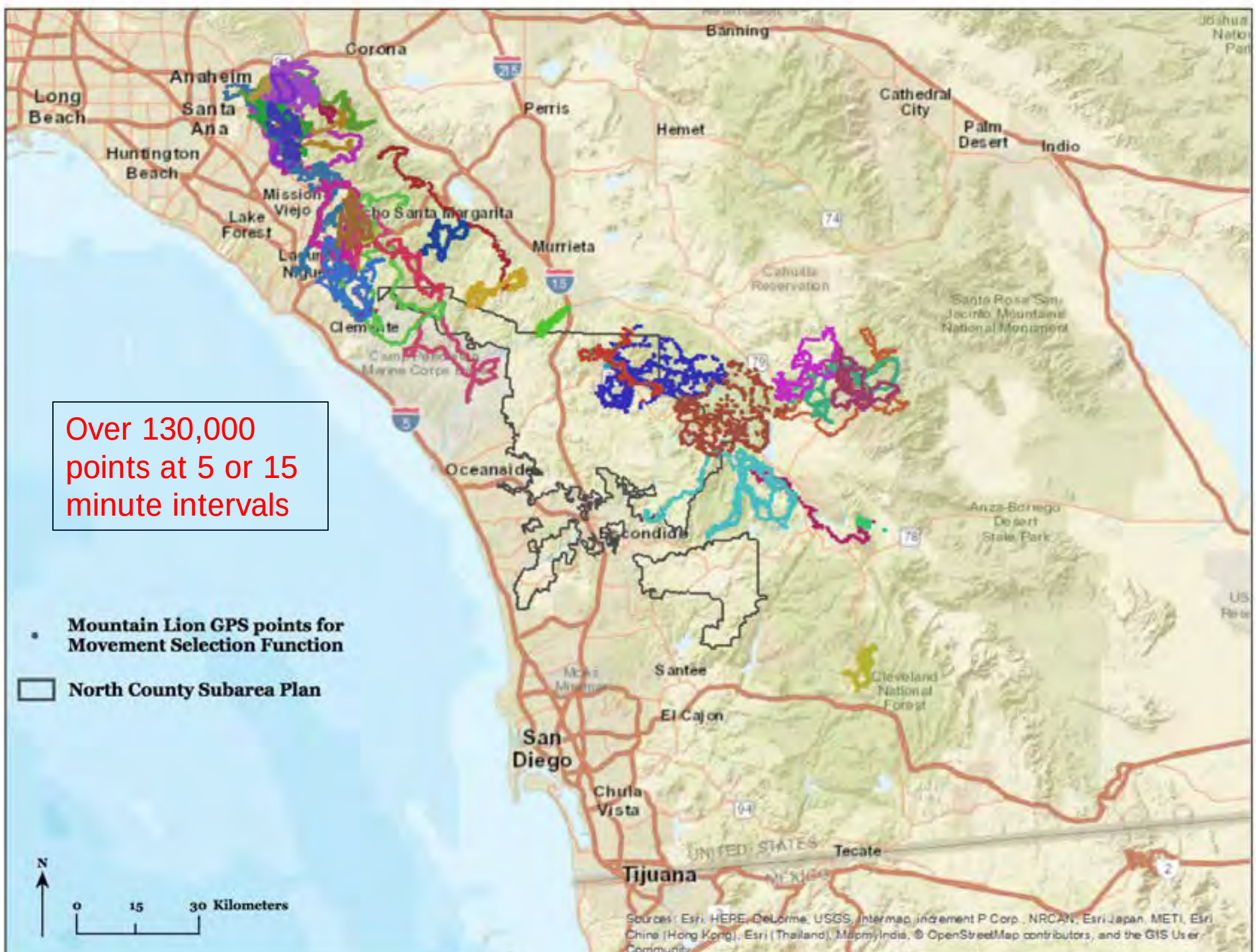
Santa Ana Mountains circled

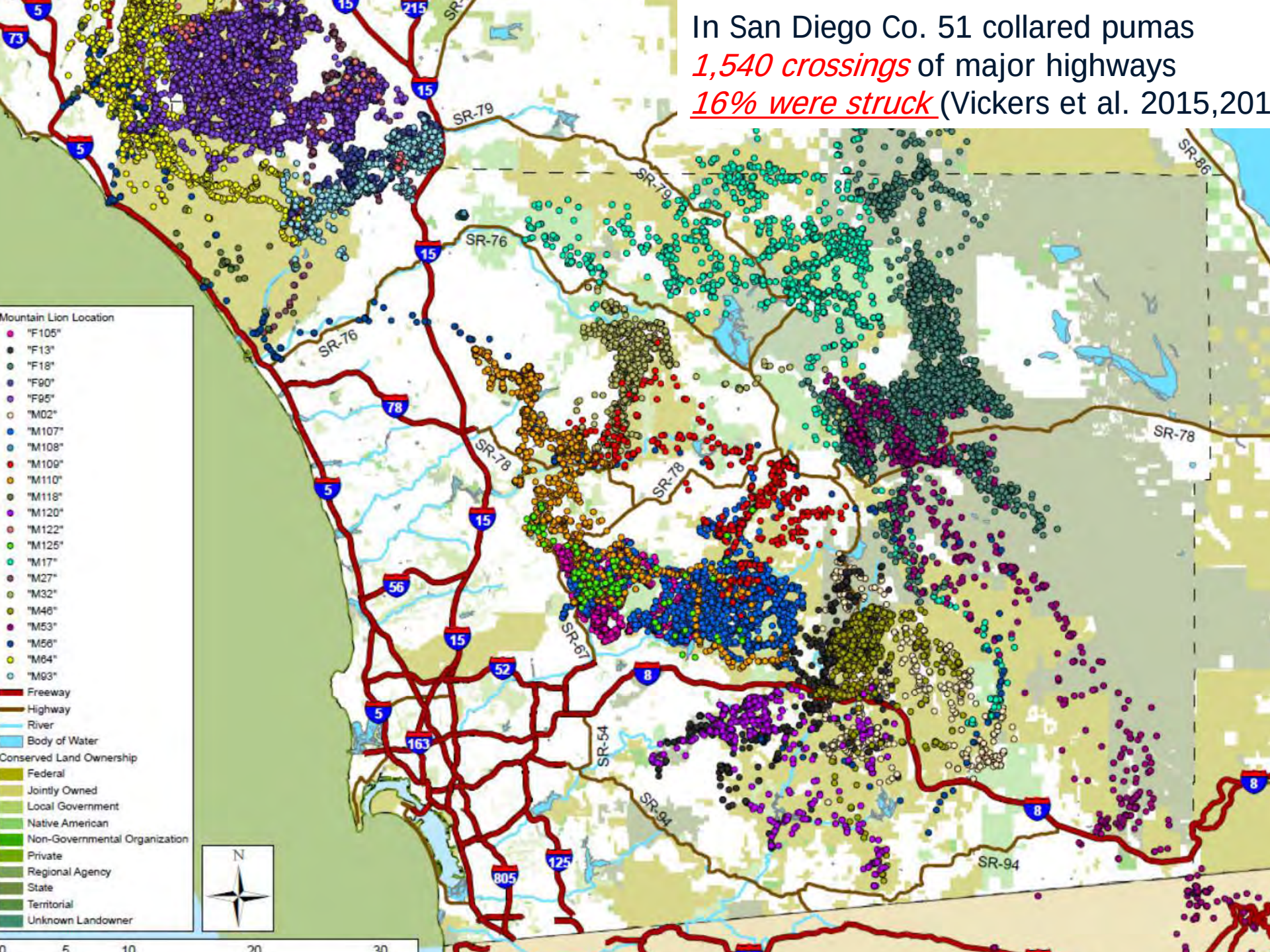


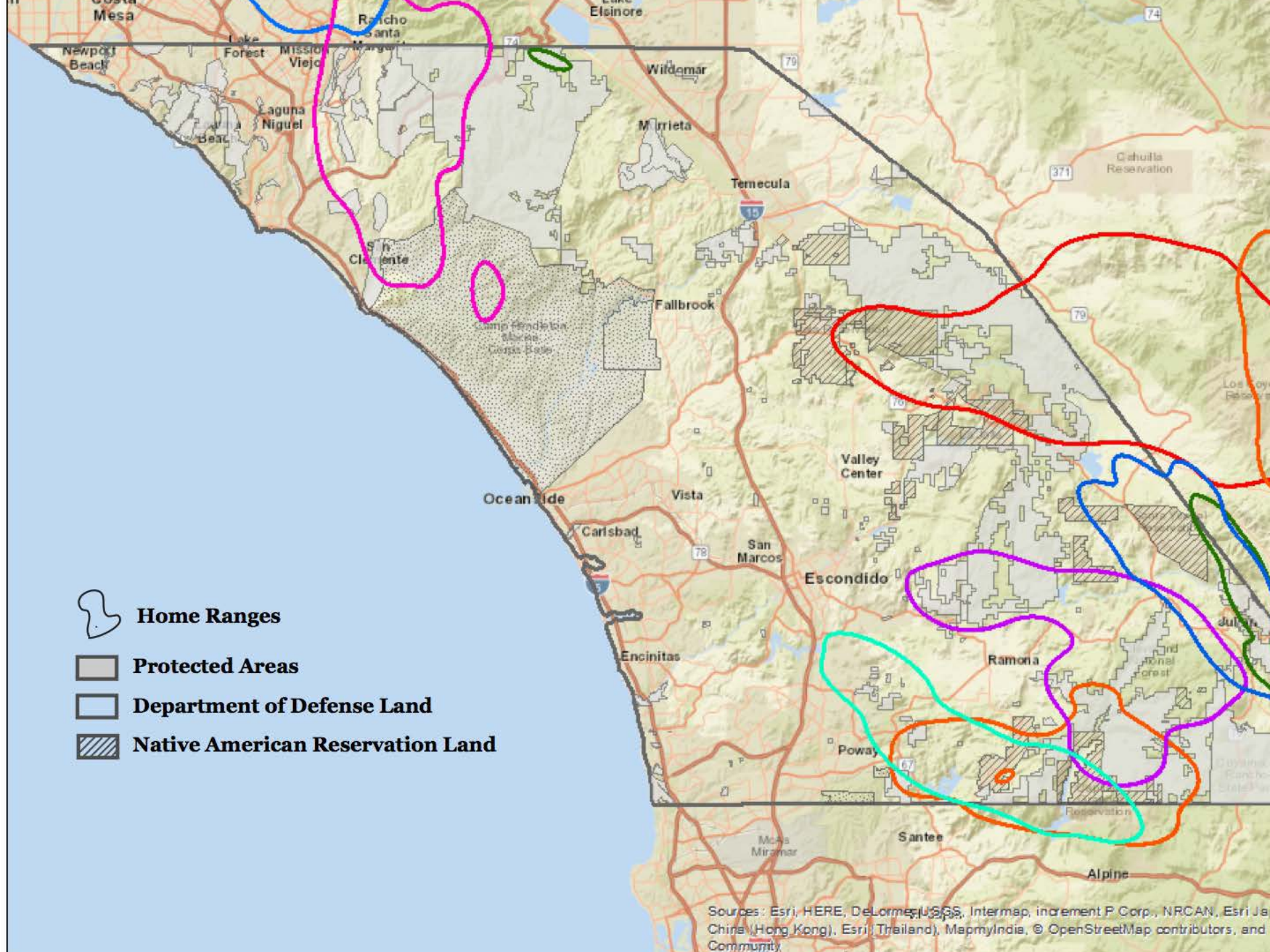
Project study area with 5 mile buffers around the highways that are focus of the study.

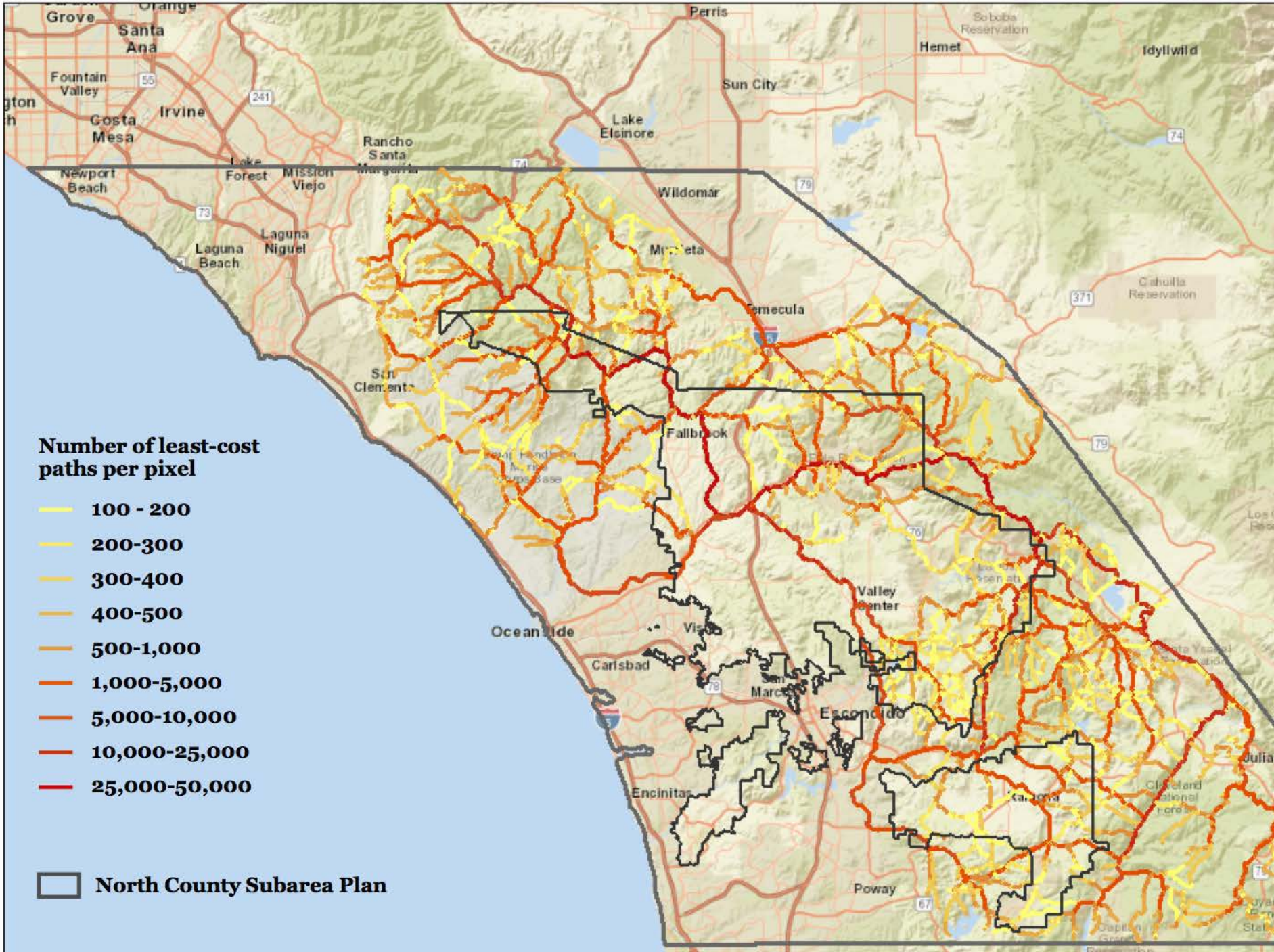


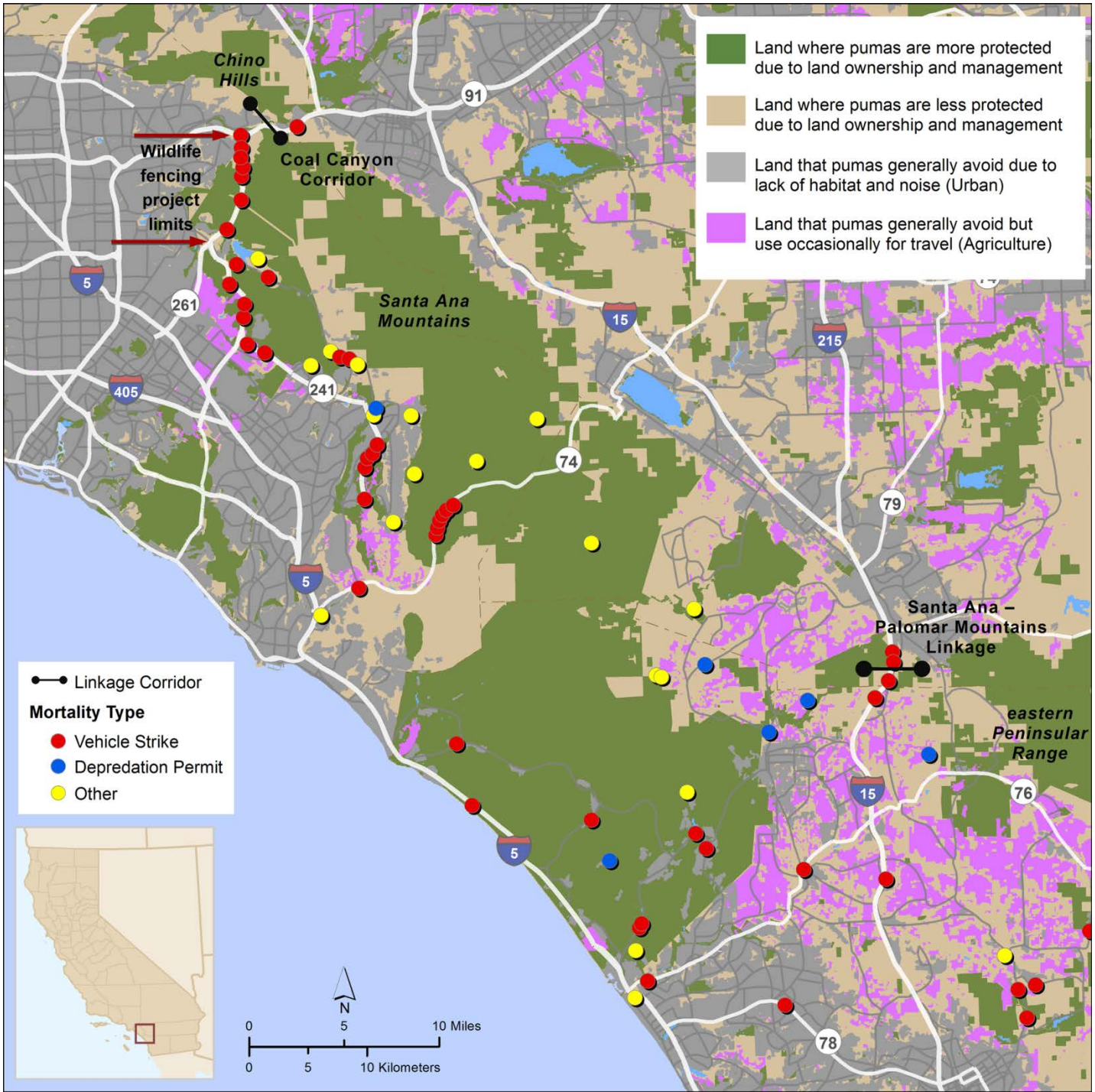

Greater Northern San Diego County Study Area
Over 350,000 GPS datapoints
North County Subarea Plan
Southern California Mountain Lion Project GPS telemetry Points
Banning
Corona
Anaheim
Long Beach
Santa Ana
Huntington Beach
Perris
Hemet
Cathedral City
Palm Desert
Indio
Mission Viejo
Lake Forest
Murrieta
Oceanside
Santee
El Cajon
San Diego
Chula Vista
Tecate
Tijuana
N
0 15 30 Kilometers
Sources: Esri, HERE, DeLorme, USGS, Intermap, increment P Corp., NRCAN, Esri Japan, METI, Esri China (Hong Kong), Esri (Thailand), MapmyIndia, © OpenStreetMap contributors, and the GIS User

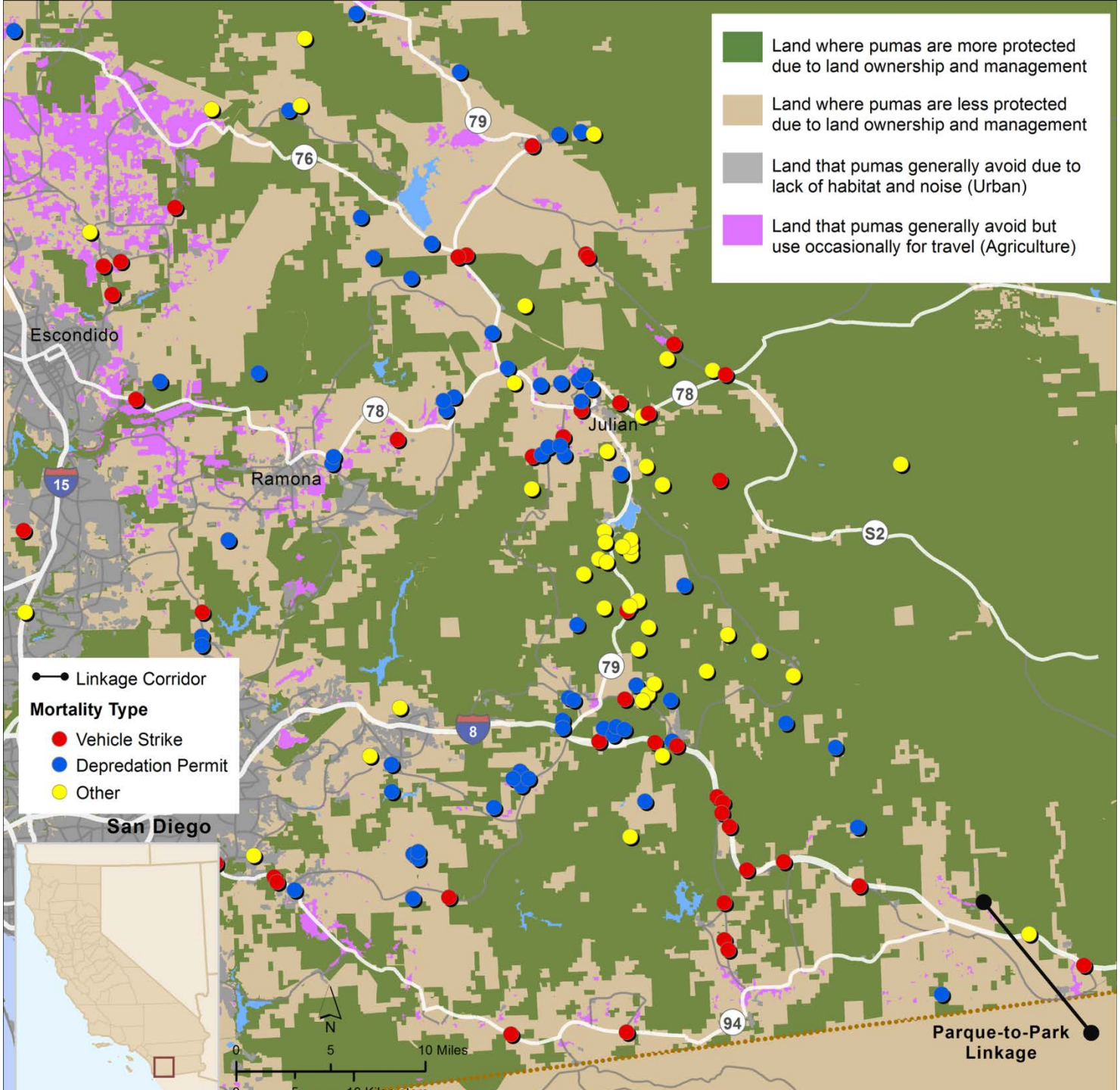

Over 130,000 points at 5 or 15 minute intervals
Mountain Lion GPS points for Movement Selection Function
North County Subarea Plan
N
0 15 30 Kilometers
Banning
Corona
Anaheim
Long Beach
Santa Ana
Huntington Beach
Perris
Hemet
Cathedral City
Palm Desert
Indio
Mission Viejo
Lake Forest
Murrieta
Oceanside
Escondido
Santee
El Cajon
San Diego
Chula Vista
Tijuana
Tecate
Cleveland National Forest
Anza-Borrego Desert State Park
Santa Rosa San Jacinto Mountains National Monument
Cahuilla Reservation
UNITED STATES
MEXICO
Sources: Esri, HERE, DeLorme, USGS, Intermap, increment P Corp., NRCAN, Esri Japan, METI, Esri China (Hong Kong), Esri (Thailand), MapmyIndia, © OpenStreetMap contributors, and the GIS User Community


In San Diego Co. 51 collared pumas
1,540 crossings of major highways
16% were struck (Vickers et al. 2015,201
Mountain Lion Location
"F105"
"F13"
"F18"
"F90"
"F95"
"M02"
"M107"
"M108"
"M109"
"M110"
"M118"
"M120"
"M122"
"M125"
"M17"
"M27"
"M32"
"M46"
"M53"
"M56"
"M64"
"M93"
Freeway
Highway
River
Body of Water
Conserved Land Ownership
Federal
Jointly Owned
Local Government
Native American
Non-Governmental Organization
Private
Regional Agency
State
Territorial
Unknown Landowner
N
SR-79
SR-76
SR-78
SR-67
SR-54
SR-94
SR-86


Home Ranges
Protected Areas
Department of Defense Land
Native American Reservation Land
Costa Mesa
Newport Beach
Lake Forest
Laguna Niguel
Wildomar
Murrieta
Temecula
Elsinore
Fallbrook
Camp Pendleton
Ocean Side
Vista
Carlsbad
San Marcos
Escondido
Valley Center
Encinitas
Ramona
Poway
Santee
Alpine
Cahuilla Reservation
Sources: Esri, HERE, DeLorme, USGS, Intermap, increment P Corp., NRCAN, Esri Ja
China (Hong Kong), Esri (Thailand), MapmyIndia, © OpenStreetMap contributors, and
Community


Number of least-cost paths per pixel
100 - 200
200-300
300-400
400-500
500-1,000
1,000-5,000
5,000-10,000
10,000-25,000
25,000-50,000
North County Subarea Plan
Perris
Hemet
Idyllwild
Sun City
Lake Elsinore
Wildomar
Temecula
Fallbrook
Valley Center
Oceanside
Carlsbad
Escondido
Encinitas
Poway
Rancho Santa Margarita
Lake Forest
Mission Viejo
Laguna Niguel
Laguna Beach
Newport Beach
Irvine
Costa Mesa
Fountain Valley
Santa Ana
Grove


Land where pumas are more protected due to land ownership and management
Land where pumas are less protected due to land ownership and management
Land that pumas generally avoid due to lack of habitat and noise (Urban)
Land that pumas generally avoid but use occasionally for travel (Agriculture)
Chino Hills
Coal Canyon Corridor
Wildlife fencing project limits
Santa Ana Mountains
Santa Ana – Palomar Mountains Linkage
eastern Peninsular Range
Linkage Corridor
Mortality Type
Vehicle Strike
Depredation Permit
Other
N
0 5 10 Miles
0 5 10 Kilometers
91
261
5
405
241
74
15
215
79
76
78


Land where pumas are more protected due to land ownership and management
Land where pumas are less protected due to land ownership and management
Land that pumas generally avoid due to lack of habitat and noise (Urban)
Land that pumas generally avoid but use occasionally for travel (Agriculture)
Escondido
Ramona
Julian
San Diego
79
76
78
15
8
S2
94
Linkage Corridor
Mortality Type
Vehicle Strike
Depredation Permit
Other
N
0
5
10 Miles
Parque-to-Park Linkage

Project Tasks as defined in the funding grants were:

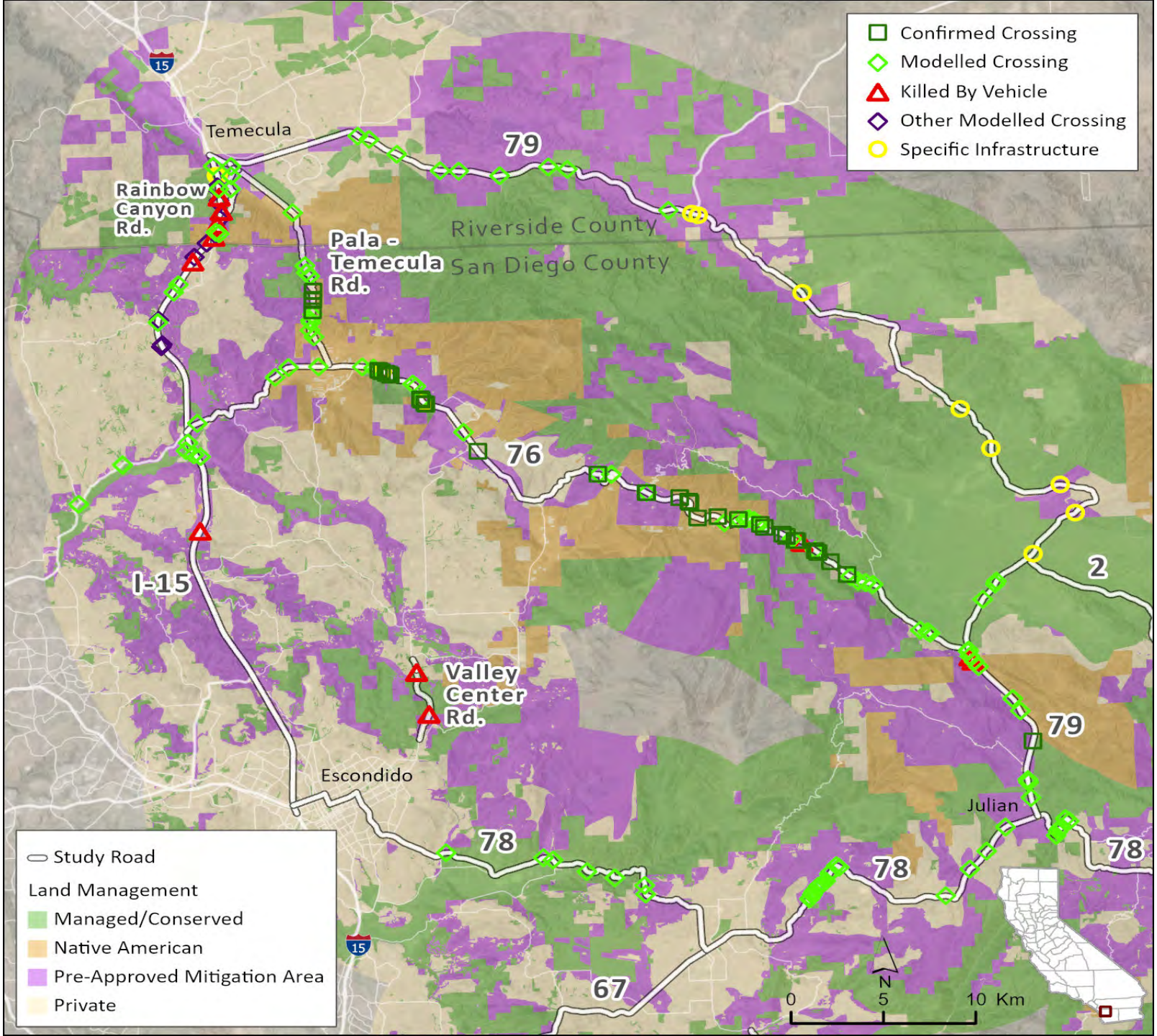
- Task 1 (NCCP-LAG): Conduct wildlife crossing infrastructure assessments for the approximately 7-mile portion of I-15 in the SA-ePR linkage region

- Task 1 (SANDAG):
- Conduct Highway Crossing Assessments and create Wildlife Crossing Improvement Plans for portions of I-15, SR's 76, 78, and 79, as well as other major highways

- Task 2 (NCCP- LAG): Collaborate with Cal Poly Pomona engineering faculty and students, and other highway engineers, to assess feasibility of infrastructure changes

- Task 3 (NCCP-LAG): Coordinate and consult with stakeholders on findings and create maps and other tools to illustrate findings.

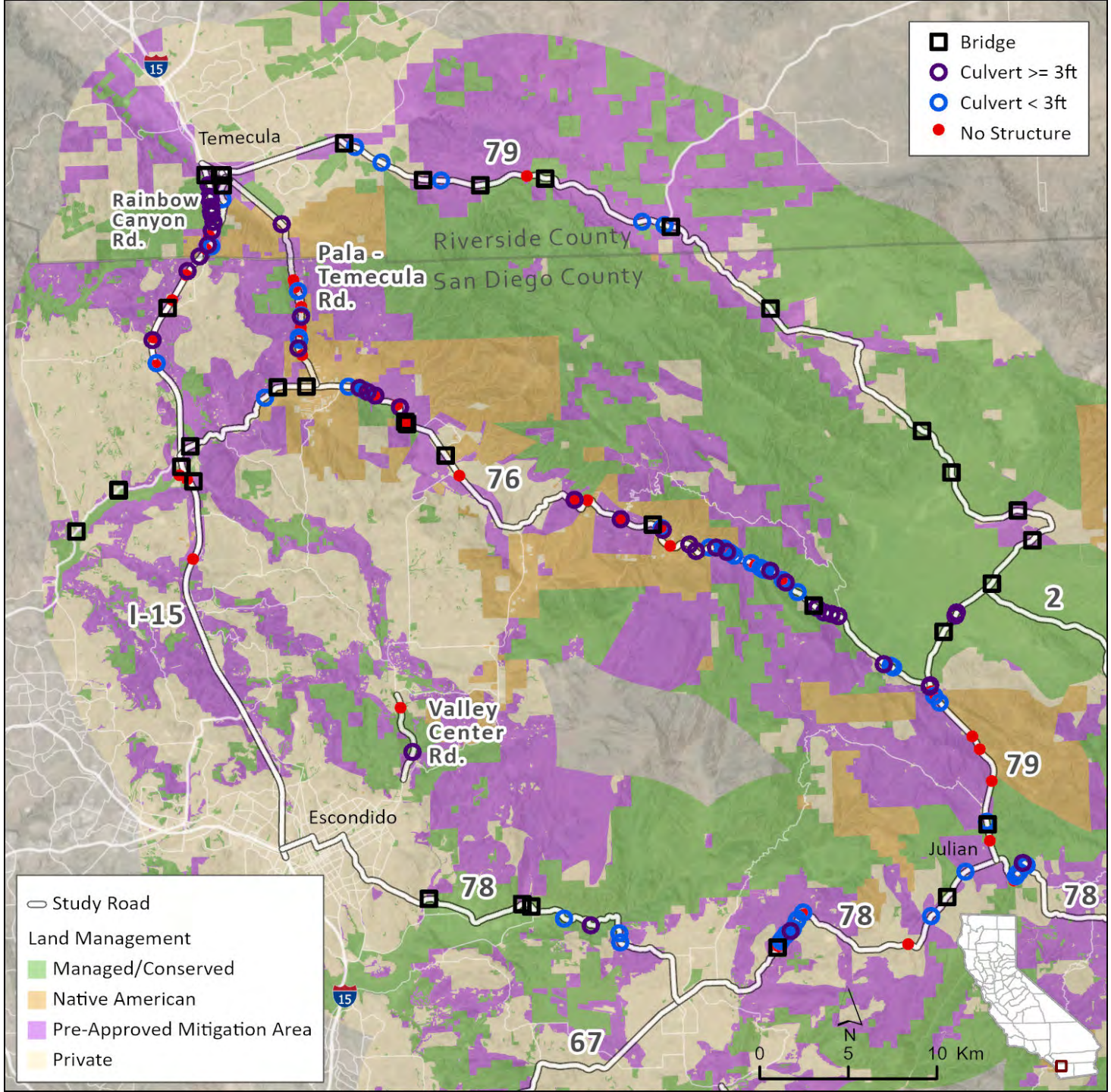
- **Potential crossing sites:**
- 190 sites examined – full data from 183 sites, 2 others with structure grades
- **Identified via:**
- Known successful crossings from cameras, or 5 to 15 minute frequency collar data (over 130,000 datapoints) – (n=53 – over half on SR76)
- Unsuccessful crossing attempts (Roadkill – n=11 [13 lions])
- Zeller least cost path modeling, previous modeling – (n=108)
- Sites named in Missing Linkages Report/expert opinion/other – (n=13)
- A few sites were too dangerous to access due to traffic and landscape factors


Confirmed Crossing
Modelled Crossing
Killed By Vehicle
Other Modelled Crossing
Specific Infrastructure
Temecula
Rainbow Canyon Rd.
Pala - Temecula Rd.
Riverside County
San Diego County
79
76
2
I-15
Valley Center Rd.
Escondido
Julian
78
67
Study Road
Land Management
Managed/Conserved
Native American
Pre-Approved Mitigation Area
Private
N
0
5
10 Km

- Grading of sites re infrastructure present

Structure Grade - 0= no structure, 1=culvert <3 ft, 2 = culvert 3 ft or more, 3 = bridge
Constraint/Plus Factor Score: 3 if can see through and trails, tracks, other evidence of use of structure by wildlife (ideal); 2 if can see through but no evidence of use, or if evidence of use but can't see through; 1 if can't see through and no evidence of use; 0 if full time water, accessibility compromised, or likely human presence at night.
Landscape score: 2 if suggests likely crossing point; 1 if minor contraints of landscape; 0 if significant landscape negatives
Confirmed crossing this location: 2 if yes; 0 if no

- Of the 185 sites examined and characterized:
- Culverts >3 ft dia: n=43 sites; 23%
- Bridges: n=36 sites; 19%
- Smaller culverts: n=49 sites; 26%
- No culvert or bridge: n=56 sites; 30%


Bridge
Culvert >= 3ft
Culvert < 3ft
No Structure
Temecula
Rainbow Canyon Rd.
Pala - Temecula Rd.
Riverside County
San Diego County
79
76
2
I-15
Valley Center Rd.
Escondido
Julian
78
67
Study Road
Land Management
Managed/Conserved
Native American
Pre-Approved Mitigation Area
Private
N
0
5
10 Km

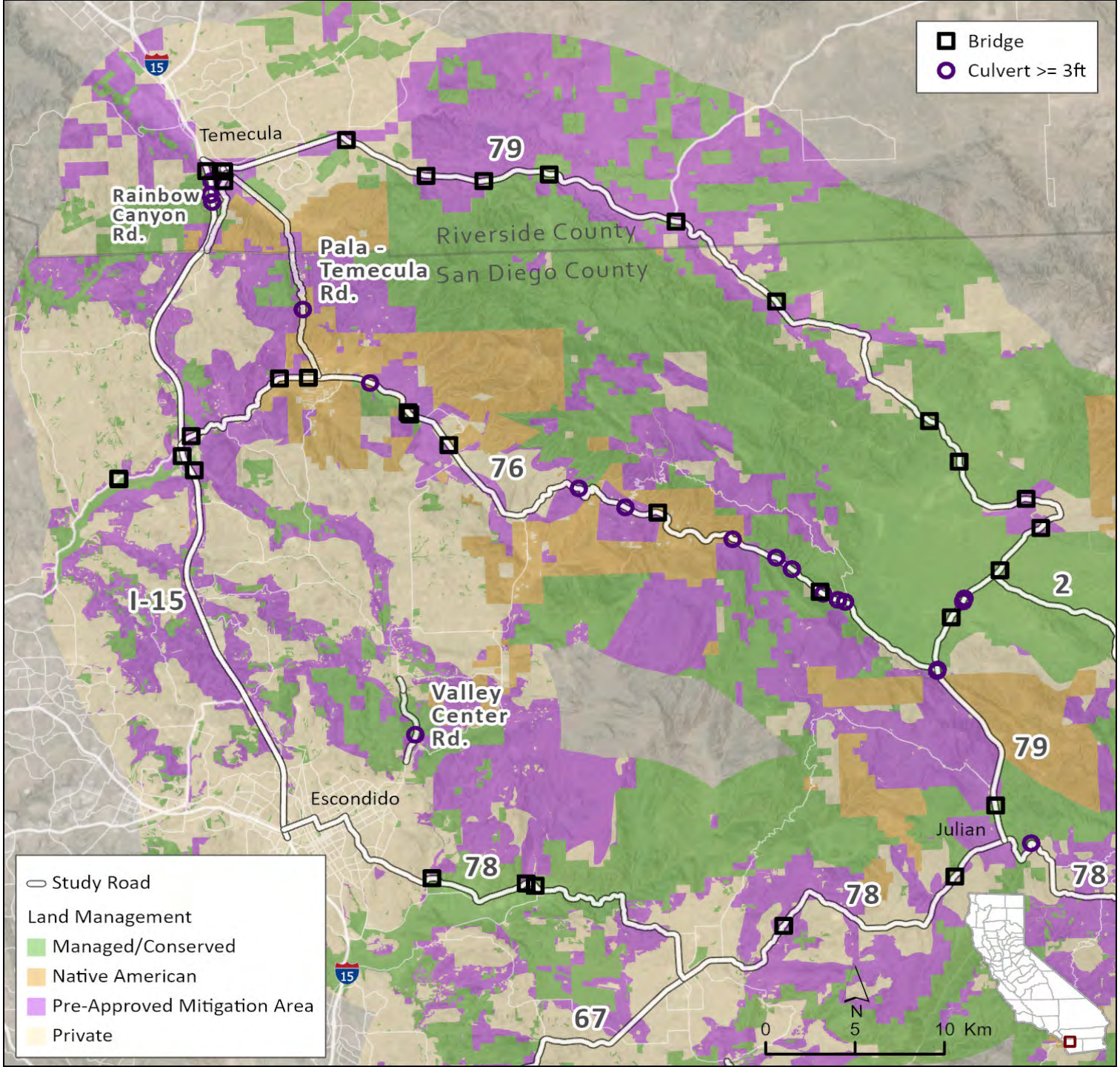

Bridge
Culvert >= 3ft
Temecula
Rainbow Canyon Rd.
Pala - Temecula Rd.
Riverside County
San Diego County
79
76
I-15
2
Valley Center Rd.
Escondido
Julian
78
67
Study Road
Land Management
Managed/Conserved
Native American
Pre-Approved Mitigation Area
Private
N
0
5
10 Km

Table 4. Number of sites examined on each highway, with structure types and number present. For bridges and larger culverts, the number of structures with no or only partial constraints is in parenthesis.

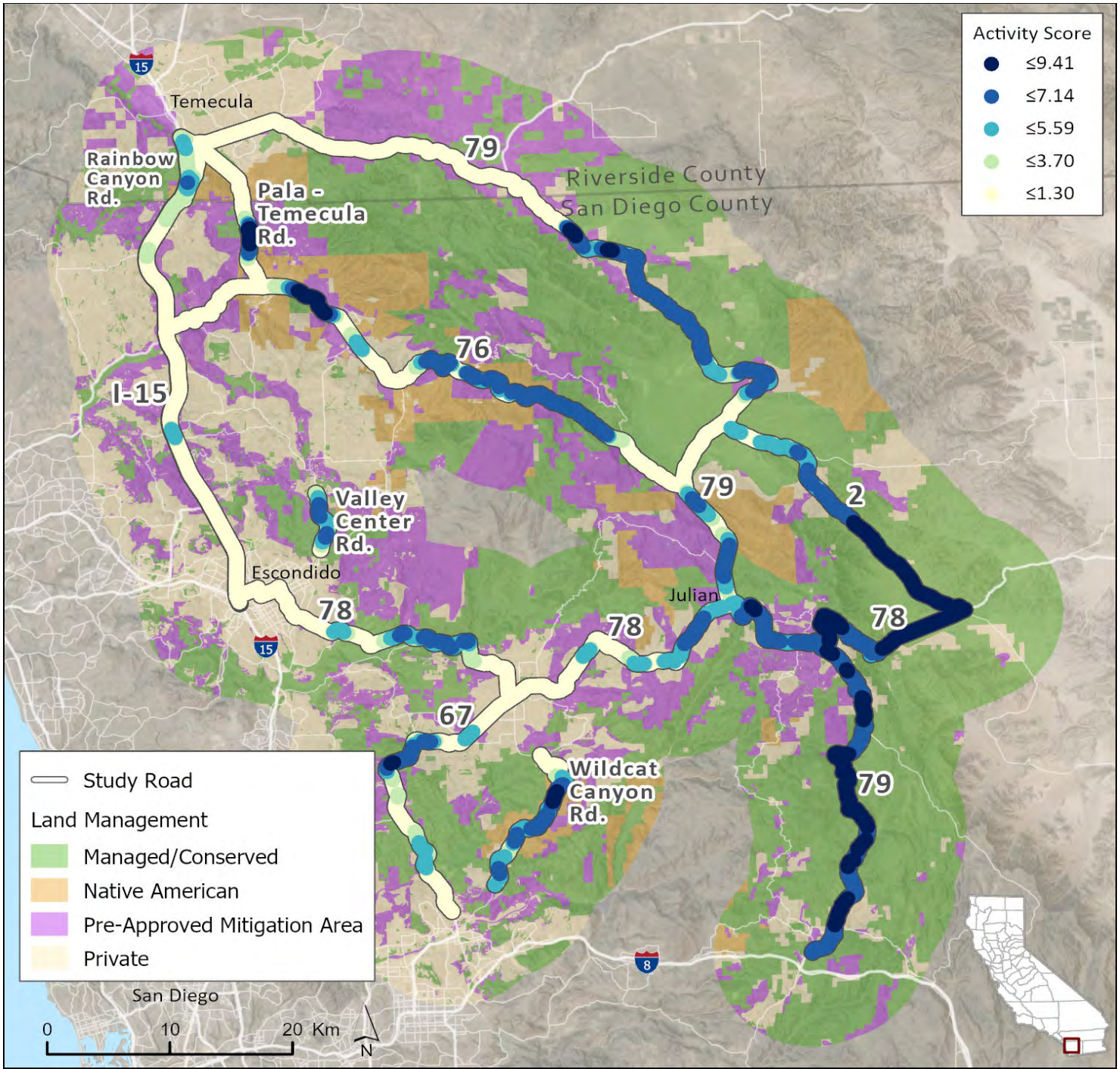
Highway name	Bridges	Culverts 3 ft or more	Culverts less than 3 ft	No Culvert or Bridge	Total sites examined
I-15	3 (2)	14 (5)	0	8	25 (7)
I-15/Old Hwy 395 jct	0	0	0	1	1 (0)
Rainbow Canyon Rd.	1 (1)	0	1	1	3 (1)
Old Hwy 395	2 (1)	0	2	1	5 (1)
Pechanga Parkway	1 (1)	1 (0)	0	0	2 (1)
Pala-Temecula Rd	0	2 (1)	4	8	14 (1)
SR-79	13 (13)	3 (3)	8	8	32 (16)
SR-76	11 (10)	19 (9)	16	23	69 (19)
SR-78	5 (5)	3 (1)	18	6	32 (6)
Valley Center Rd	0	1 (1)	0	1	2 (1)
Total Sites Examined	**36 (33)**	**43 (20)**	**49**	**57**	**185 (53)**

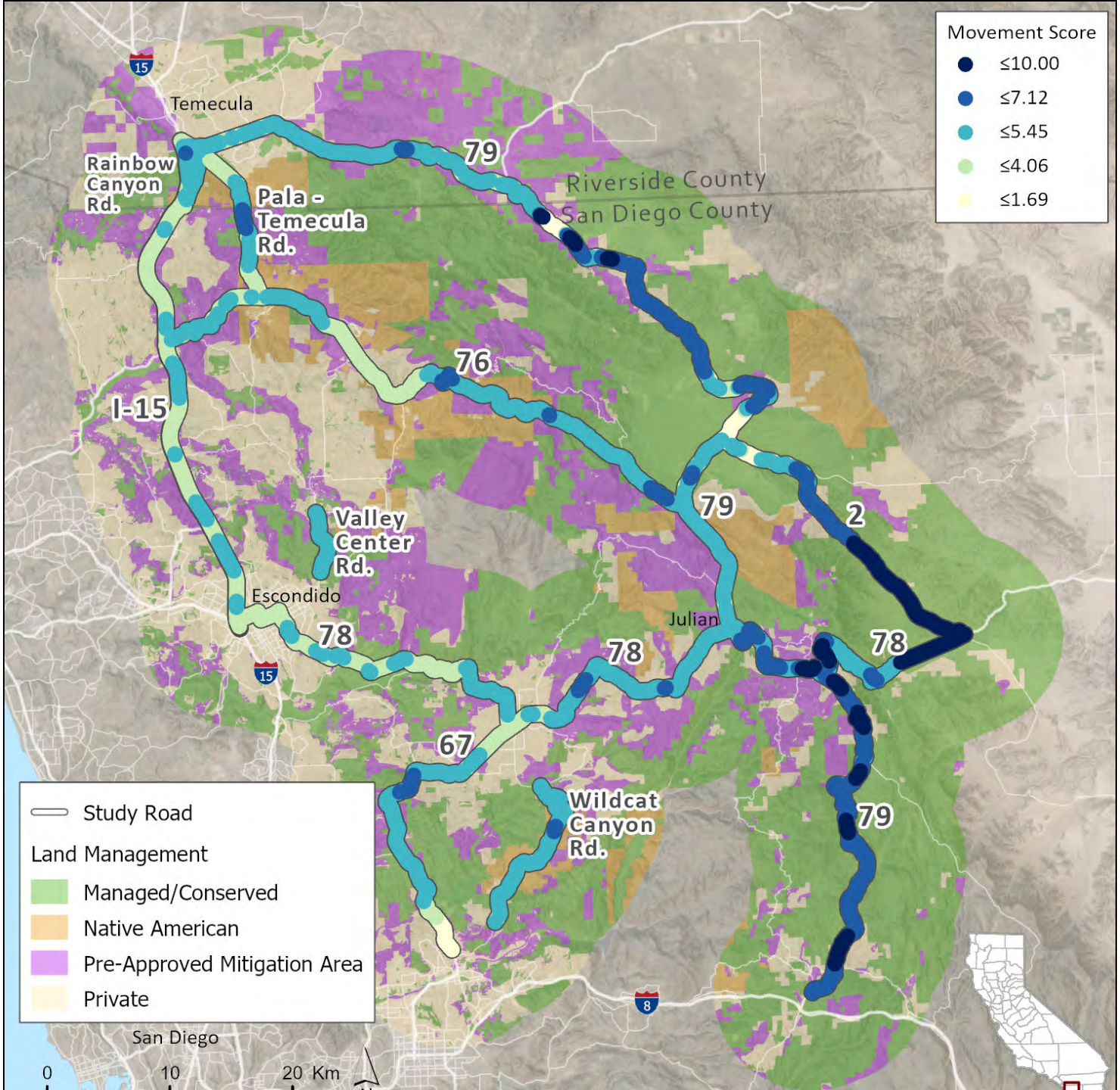
Information recorded at surveyed sites	
Survey ID	Structure type
Survey Date	Culvert distance below road
Highway name	Height
Highway number if not listed	Width
Location	Length
NEW Location?	Structure floor material
Drop Point (Lat/Long) (latitude)	Able to see through culvert
Drop Point (Lat/Long) (longitude)	Water?
Drop Point (Lat/Long) (speed)	Human presence likely at night?
Drop Point (Lat/Long) (direction)	Describe human presence potential
Drop Point (Lat/Long) (altitude)	Constraints
Drop Point (Lat/Long) (accuracy)	Describe constraint
Surveyor	Evidence of other animals?
Road type	Describe evidence of other animals present
Estimated width of road from one pavement edge to the other	Fencing present?
Landscape character suggestive of likely crossing point	Describe fencing type and height
Describe reason landscape character not conducive to crossing	Consider for camera?
Landscape and veg structure suggest corridor	Camera suggestions
Describe limitation of landscape and veg and which side of road	Comments
Other species observed	Management recommendations

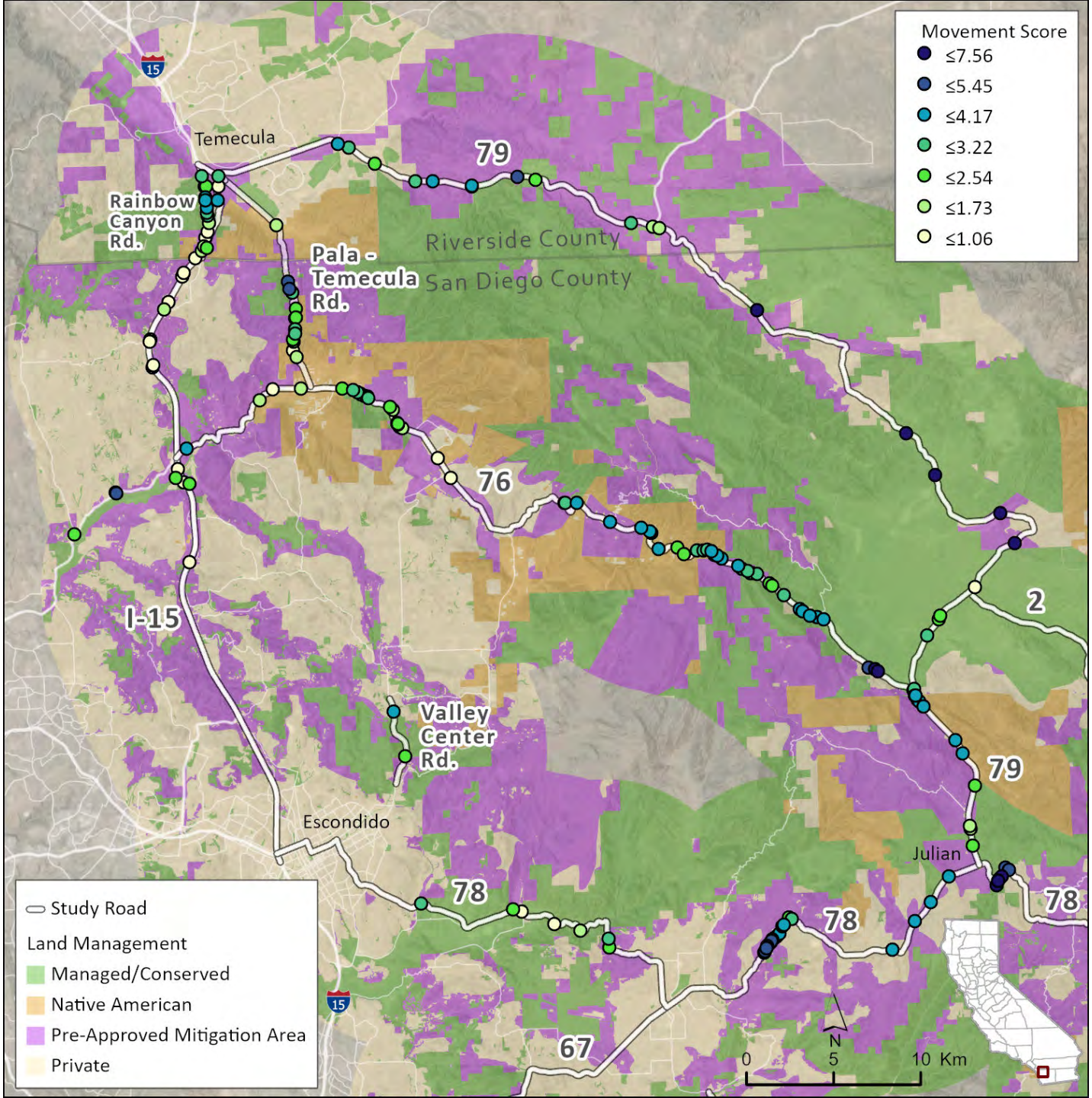
Software by Wildnote © - very useful

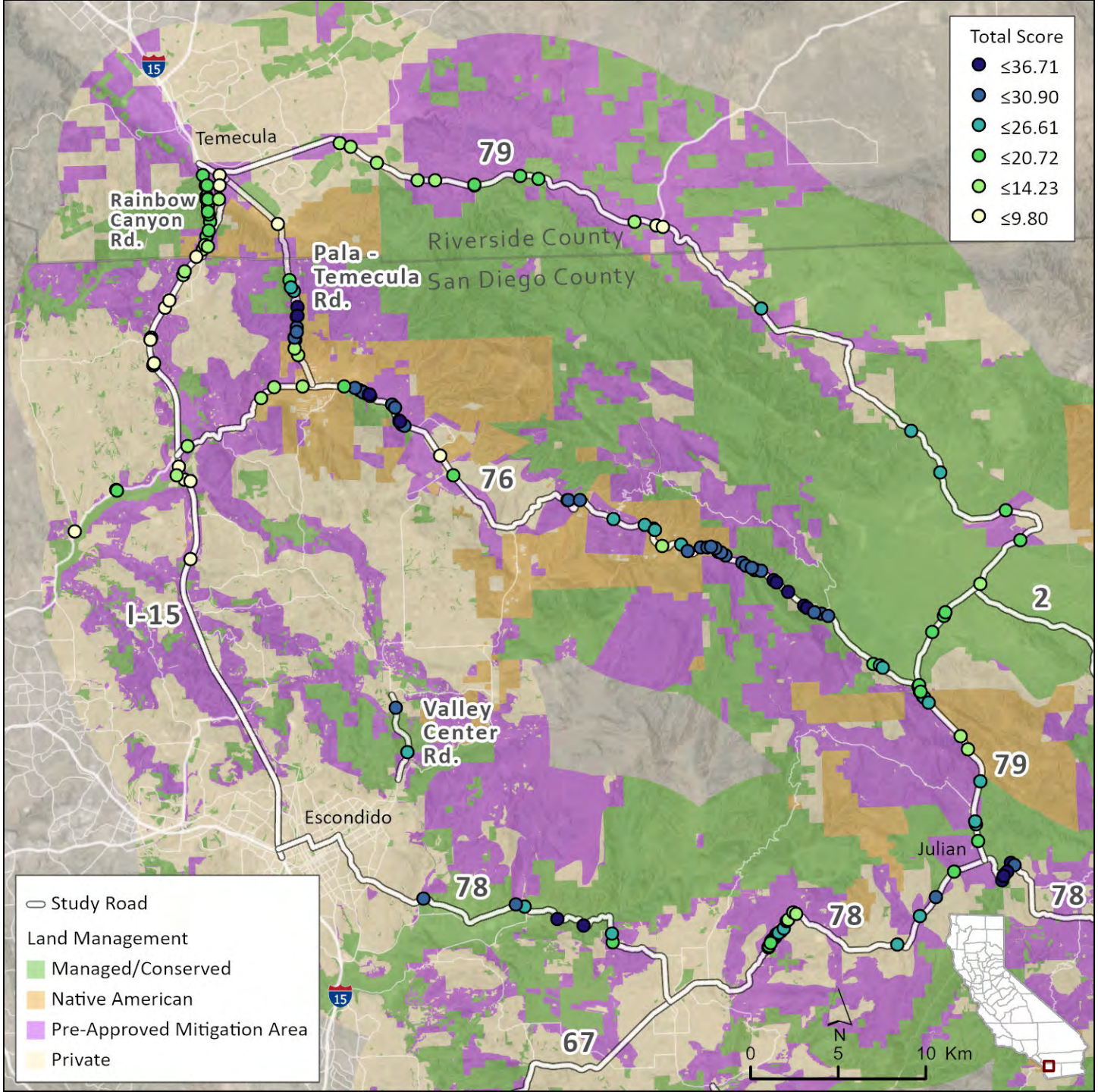
- **Brian Cohen scoring of the roadways:**
- Graded and scored points along the region highways at 100 meter intervals
- 4,378 points – 272 miles of roadway
- Scoring was scaled at 100, 500, and 1,500 meters

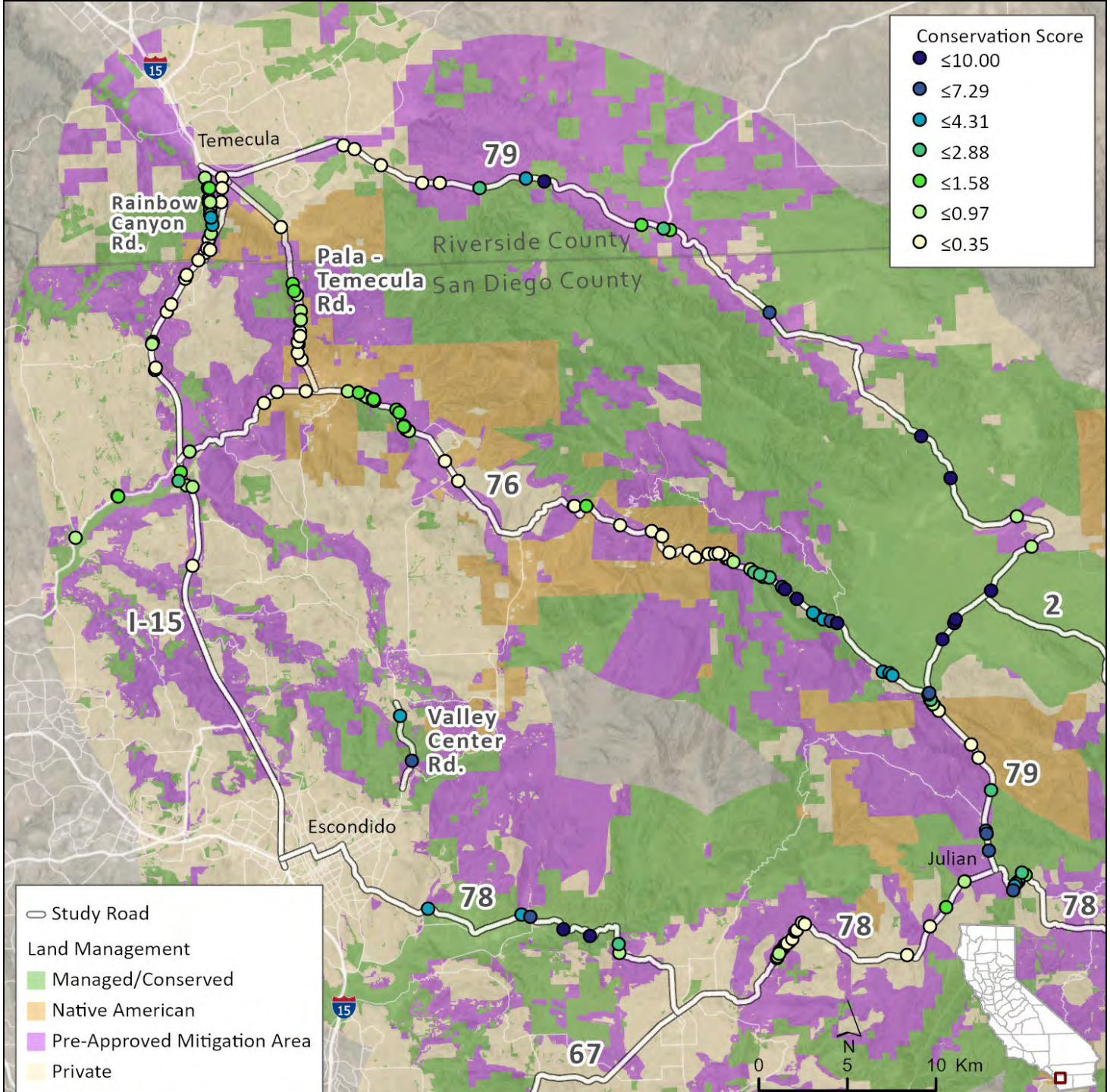
Title	Criteria	Scoring
Conservation score	Percentage of land within 100, 500, and 1,500 meters of a road point or examined site that is conserved	0 - 10
Habitat score	Quality of habitat for mountain lions within 100, 500 and 1,500 meters of a road point or examined site per K. Zeller habitat modeling	0 - 10
Resource score	Quality of resources for mountain lions within 100, 500 and 1,500 meters of a road point or examined site based on J. Dellinger resource modeling	0 - 10
Activity score	Numbers of mountain lion pathway 10 meter segments (based on GPS-Collar data) that lie within 100, 500, and 1,500 meters of a road point or examined site	0 - 10
Movement score	Likelihood of mountain lion movement within 100, 500, and 1,500 meters of a road point or examined site based on K. Zeller movement modeling	0 - 10
Observational score	Total of scores for crossing structure type (0-3); Lack of constraints on structures (0-3); Landscape structure / wildlife evidence (0-2), and confirmed crossing this location (0-2) based on on-the-ground road crossing site surveys	0 - 10
	Summary value for all scores	0 - 60


Activity Score
≤9.41
≤7.14
≤5.59
≤3.70
≤1.30
Temecula
Rainbow Canyon Rd.
Pala - Temecula Rd.
79
Riverside County
San Diego County
76
I-15
79
2
Valley Center Rd.
Escondido
Julian
78
78
78
67
Wildcat Canyon Rd.
79
Study Road
Land Management
Managed/Conserved
Native American
Pre-Approved Mitigation Area
Private
San Diego
0
10
20 Km
N


Movement Score
≤10.00
≤7.12
≤5.45
≤4.06
≤1.69
Temecula
Rainbow Canyon Rd.
Pala - Temecula Rd.
79
Riverside County
San Diego County
76
I-15
79
2
Valley Center Rd.
Escondido
Julian
78
78
78
67
Wildcat Canyon Rd.
79
Study Road
Land Management
Managed/Conserved
Native American
Pre-Approved Mitigation Area
Private
San Diego
0
10
20 Km

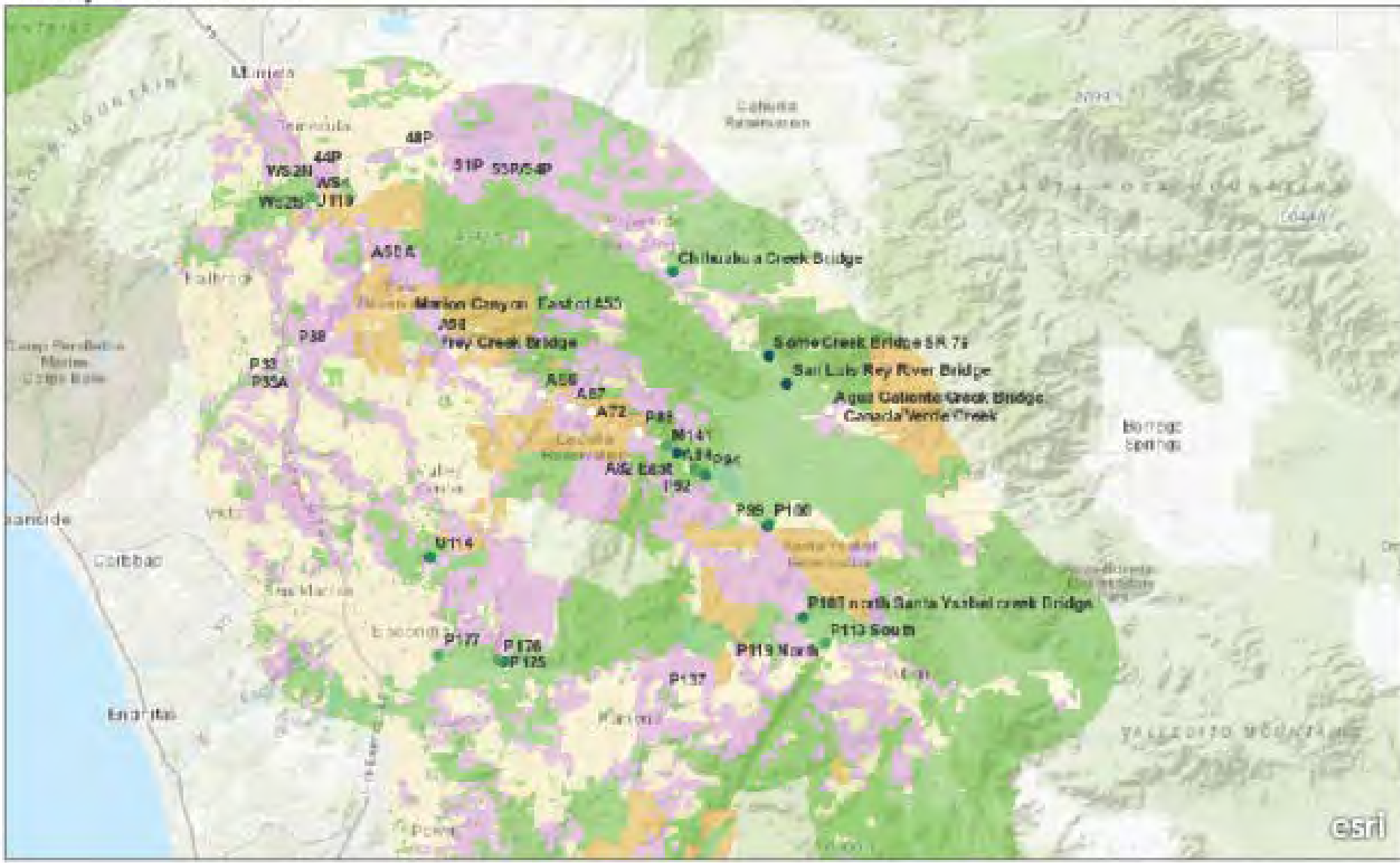

Movement Score
≤7.56
≤5.45
≤4.17
≤3.22
≤2.54
≤1.73
≤1.06
Temecula
Rainbow Canyon Rd.
Pala - Temecula Rd.
Riverside County
San Diego County
79
76
2
I-15
Valley Center Rd.
Escondido
Julian
78
67
Study Road
Land Management
Managed/Conserved
Native American
Pre-Approved Mitigation Area
Private
N
0
5
10 Km


Total Score
≤36.71
≤30.90
≤26.61
≤20.72
≤14.23
≤9.80
Temecula
Rainbow Canyon Rd.
Pala - Temecula Rd.
Riverside County
San Diego County
79
76
2
I-15
Valley Center Rd.
Escondido
Julian
78
67
Study Road
Land Management
Managed/Conserved
Native American
Pre-Approved Mitigation Area
Private
N
0
5
10 Km


Conservation Score
≤10.00
≤7.29
≤4.31
≤2.88
≤1.58
≤0.97
≤0.35
Temecula
Rainbow Canyon Rd.
Pala - Temecula Rd.
Riverside County
San Diego County
79
76
I-15
2
Valley Center Rd.
Escondido
Julian
78
67
Study Road
Land Management
Managed/Conserved
Native American
Pre-Approved Mitigation Area
Private
N
0
5
10 Km

- Based on infrastructure present, known crossings, and higher than average Activity and Movement scores only 39 of the 185 sites have both adequate infrastructure to support long term connectivity and a high potential for mountain lion use of the sites as those areas now exist
- Based on conservation scores only 8 of the top 39 sites have over 50% of the land conserved within a 500 meter radius

Survey Locations 2020

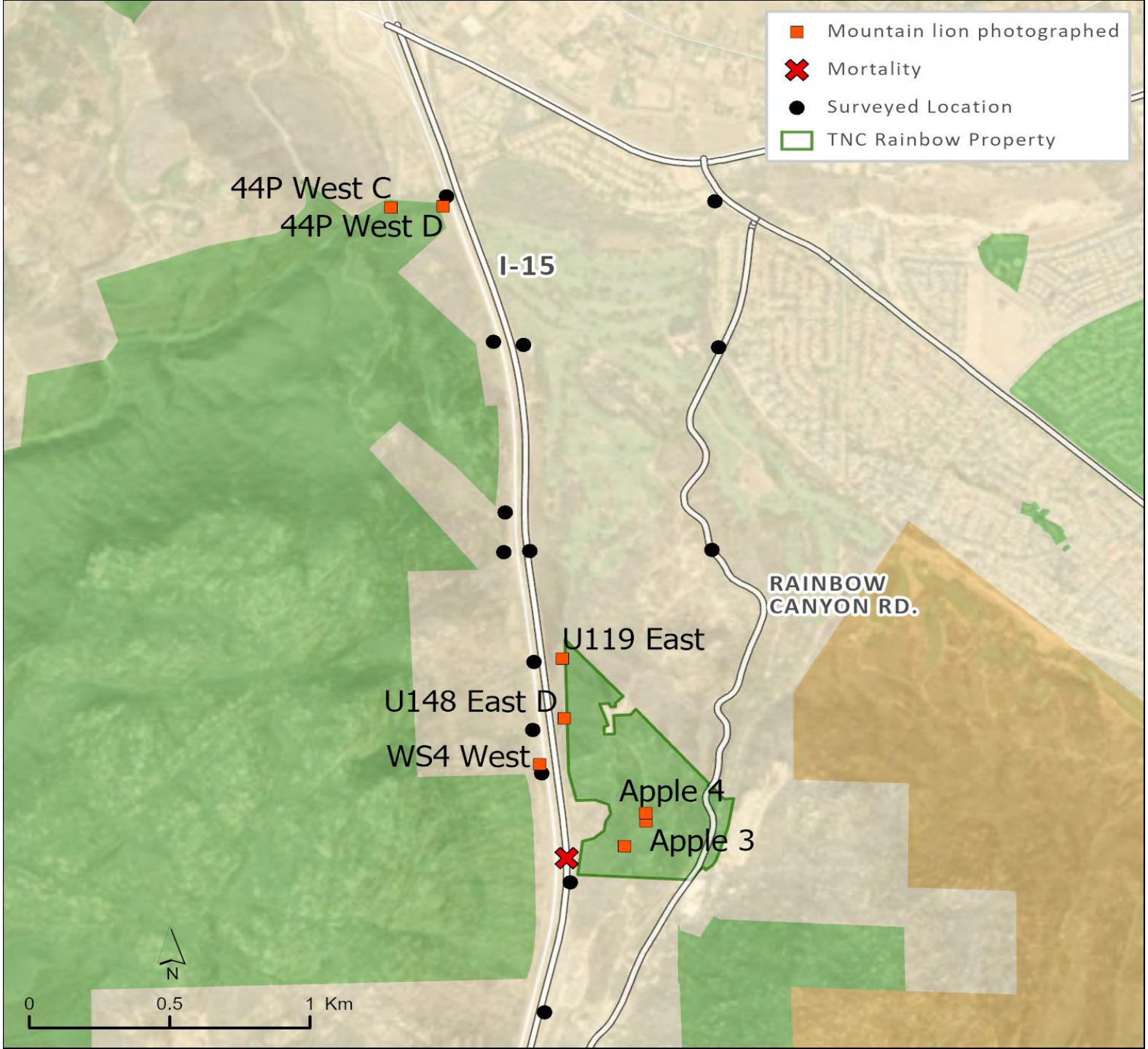


Esri, HERE, Garmin, USGS, NGA, EPA, USDA, NPS

Camera study at I-15 sites evaluated. All sites in the study had cameras present, as well as some sites on the TNC Rainbow Property adjacent to the freeway in area of proposed new crossing structure.

11 photos of lions since late 2018 and one mortality.

Site Name	General area	Latitude	Longitude	Number of mountain lion events	East or West Side of Highway
44P West C	SMER Gate	33.47428	-117.14068	1	West
44P West D	South trail closest to bridge	33.47427	-117.13932	1	West
WS4 West	I-15 West culvert	33.45466	-117.13611	1	West
U148 East D	Creek bed	33.45624	-117.13495	1	East
U119 East	East Creek bed/Culvert	33.45833	-117.135	1	East
Apple 3	TNC Rainbow Property along road	33.45256	-117.13515	4	East
Apple 4	TNC Rainbow Property along road	33.45284	-117.13204	1	East
M233 mortality site Dec 2018	I-15 near WS4	33.45141	-117.13520	1	
Apple 5	TNC Rainbow Property in Ravine	33.45172	-117.13281	1	East


Mountain lion photographed
Mortality
Surveyed Location
TNC Rainbow Property
44P West C
44P West D
I-15
RAINBOW CANYON RD.
U119 East
U148 East D
WS4 West
Apple 4
Apple 3
N
0
0.5
1 Km

Cal Poly Civil Engineering Assessment

Most feasible overcrossing site

Undercrossing site just to the north at head of draw on east side







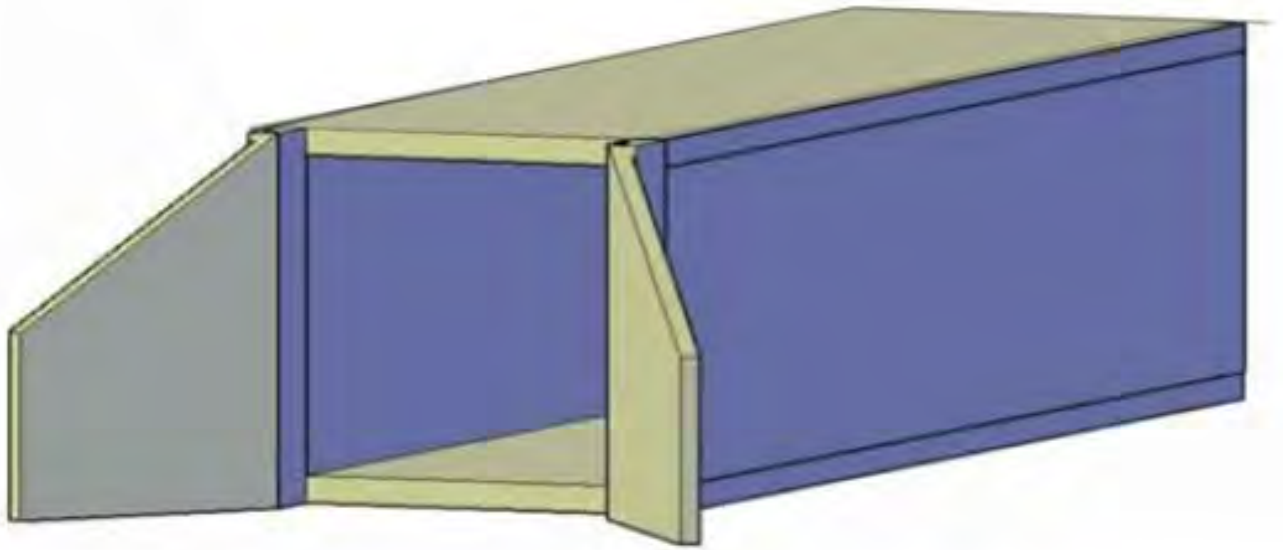
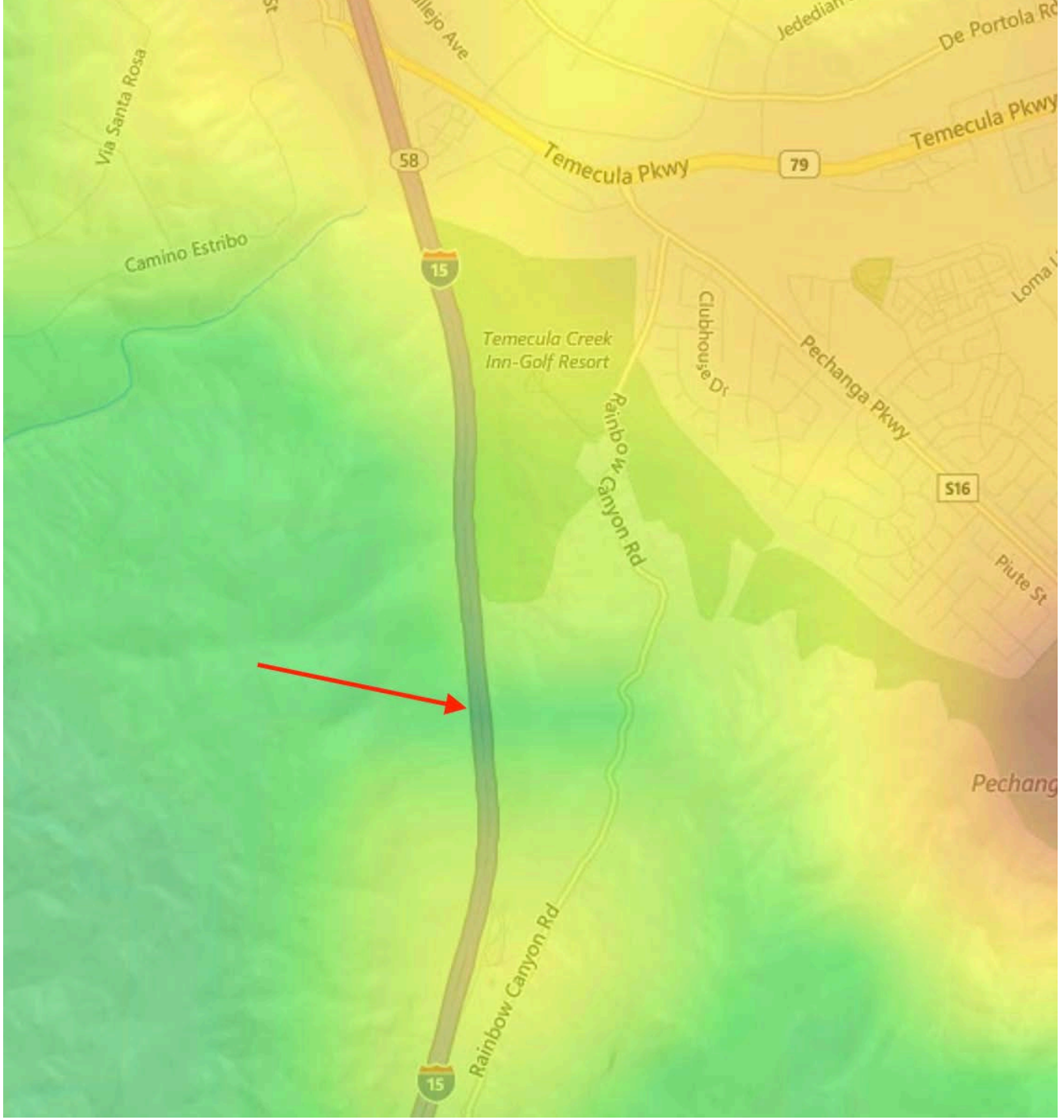


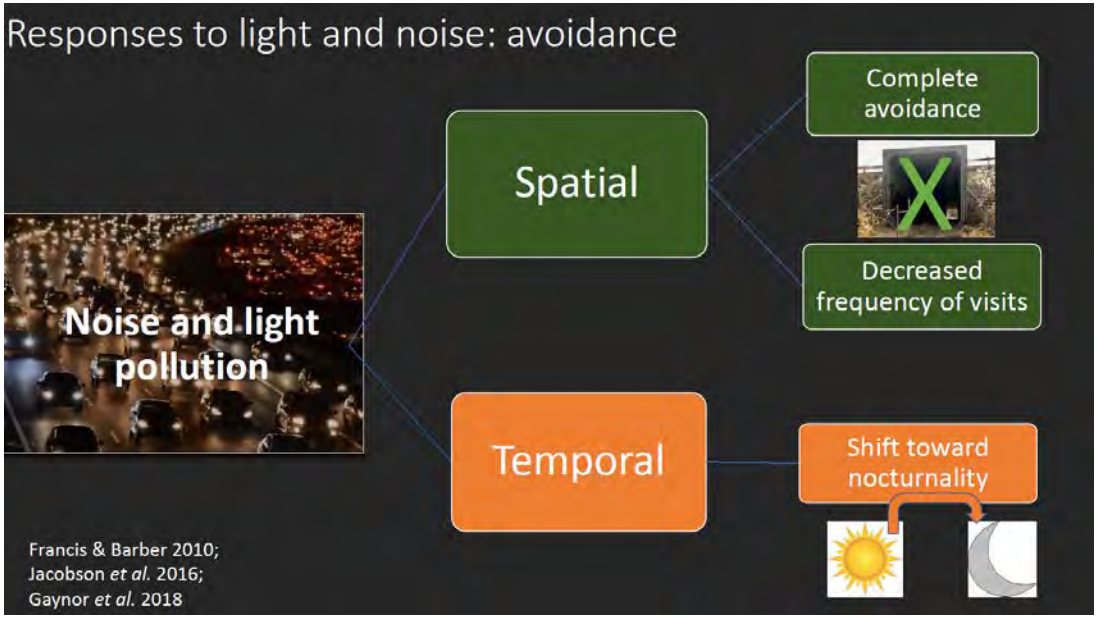
Figure 6.2. *Concrete Box Culvert Design.*

Light measurements from space. Darker areas on image are darkest on the surface. Darkest area is in the general location being considered for a new crossing.

Currently measuring light at ground level and on slopes leading down to a potential crossing site.



- Amy Collins sound measurements and paper pending
- Sound levels under the Temecula Creek Bridge were the same as levels right beside the freeway on the shoulder, suggesting sound dampening measures as suggested by CPP study are indicated



- Bottom line:
- Still adequate potential for safe crossing of regional highways – I-15 needs modifications at Bridge
- New structure north of Border check station would be HIGHLY likely to be successful
- New structure is feasible from an engineering perspective
- Light and sound studies support both Bridge mods and overcrossing so far

- Adequate infrastructure exists across the region's highways for mountain lion safe crossings

- However, of the 39 sites with adequate infrastructure and known crossings or high use levels by mountain lions, only 8 had over 50% or more conserved land in the vicinity

- Many of the adequate sites are in vicinity of less suitable sites and funneling fencing could make crossings safer for lions and people

On line resources and recent outreach:

CPP Student team presentation for the engineering students and faculty (their project won a top award) https://streaming.cpp.edu/media/0_nxln5xps, and a website detailing the findings of their portion of the overall project https://i15wildlifecrossing.wixsite.com/calpolypomona.

Additionally a webpage and podcast was developed by TNC highlighting the connectivity issues https://www.nature.org/en-us/what-we-do/our-priorities/protect-water-and-land/land-and-water-stories/a-path-for-mountain-lions/?src=e.dfg.eg.x.pod.F

A 9-episode series of short documentaries was developed by the UCD team that has been viewed online over 50,000 times at www.camountainlions.com.

On Facebook our new one hour documentary blending portions of our 9 part series with new footage aired April 14 on P22's Facebook page, as well as a Q and A session after the showing is here https://www.facebook.com/p22mountainlionofhollywood/videos/

We will forward links to the ARC GIS tools and databases that our team developed once the report is accepted as final by the agencies and the tools are streamlined a bit for easier use.

PLOS ONE

RESEARCH ARTICLE

Residential development alters behavior, movement, and energetics in an apex predator, the puma

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Abstract

Human development strongly influences large carnivore survival and persistence globally. Behavior changes are often the first measureable responses to human disturbances, and can have ramifications on animal populations and ecological communities. We investigated how a large carnivore responds to anthropogenic disturbances by measuring activity, movement behavior, and energetics in pumas along a housing density gradient. We used log-linear analyses to examine how habitat, time of day, and proximity to housing influenced the activity patterns of both male and female pumas in the Santa Cruz Mountains. We used spatial GPS location data in combination with Overall Dynamic Body Acceleration measurements recorded by onboard accelerometers to quantify how development density affected the average distances traveled and energy expended by pumas. Pumas responded to development differently depending on the time of day; at night, they were generally more active and moved further when they were in developed areas, but these relationships were not consistent during the day. Higher nighttime activity in developed areas increased daily caloric expenditure by 10.1% for females and 11.6% for males, resulting in increases of 3.4 and 4.0 deer prey required annually by females and males respectively. Our results support that pumas have higher energetic costs and resource requirements in human-dominated habitats due to human-induced behavioral change. Increased energetic costs for pumas are likely to have ramifications on prey species and exacerbate human-wildlife conflict, especially as exurban growth continues. Future conservation work should consider the consequences of behavioral shifts on animal energetics, individual fitness, and population viability.

Introduction

Habitat conversion is a primary driver of species extinctions and increases exposure of wildlife to anthropogenic disturbances [1]. These disturbances influence many integral animal behaviors (e.g., foraging, mating, and movement) [2] and transform species interactions [3±4].

Christopher C Wilmers. 6. University of California, Santa Cruz, www.ucsc.edu, Dr. Yiwei Wang. 7. Midpeninsula Regional Open Space District, www.openspace.org, Dr. Christopher C Wilmers. No funders played a role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

Conversion to low-density development at the wildland-urban interface is the fastest growing type of land use change in the continental United States [5] and is expected to continue expanding in the coming decades [6]. Although many species, including mammalian apex predators, continue to live at the wildland-urban interface [7], these regions may prove to be population sinks due to the increased risk of human-caused mortality or from the costs of adopting behavioral adaptations in response to human disturbances [8].

Behavioral changes by animals often provide the first measurable indication that individuals are responding to anthropogenic disturbance [9±11]. These behavioral responses can alter energetic budgets with important effects on individual fitness that may lead to population and community level changes. Movement behavior in particular carries rich information about where, when, and how an animal interacts with its surroundings, providing insight into the relationship between internal state and environmental factors [12]. Technological advances with GPS and accelerometer tracking devices now allow scientists to link animal movement behavior to caloric expenditure, which greatly increases our understanding of how animal energetics are impacted by human development at the landscape level. With the integration of accelerometers and traditional biologgers, we can monitor how natural and anthropogenic landscape structures change behavioral patterns and energy allocation in wild animals [13], with far ranging conservation implications for species living at the wildland-urban interface.

Large carnivores are frequently the first species to be lost from ecosystems as humans transform and develop landscapes [14]. Despite this, comparatively little is known about the behavioral and energetic responses of predators to development that could eventually lead to their local extirpation [15]. Large carnivores often respond to human disturbance and persecution through behavioral modifications much like prey species respond to predators [10]. Pumas (*Puma concolor*) have demonstrated behavioral responses to human developments by avoiding roads, moving quickly through developed areas, and changing temporal feeding patterns [8,16]. As human development continues to fragment previously intact landscapes, it becomes increasingly vital to understand how large carnivores adjust their behavior and energetic responses to anthropogenic perturbations. Only by better understanding these relationships can we implement protective policies that reduce human-wildlife conflict and promote their continued co-existence with humans [17].

Here we examined how human development alters daily behavior and energetics of pumas in the Santa Cruz Mountains of central California. We investigated the extent to which proximity to houses affected puma movements and daily activity budgets. These behavioral differences translate into differential energetic costs that progressively accumulate over time, which may have lasting repercussions on individual fitness[18]. We also investigated whether habitat type and time of day influenced how pumas responded to human development. In order to link behavior change to energetic impacts, we evaluated how human development affected the daily movement patterns and caloric expenditures of pumas using GPS tracks, which we calibrated using accelerometer data from a much finer temporal scale. Lastly, we explored the extent to which puma prey demands are altered in human-modified habitats and discuss potential consequences for recruitment of future generations.

Methods

Study species and area

Pumas are territorial, apex predators which live throughout diverse habitats in the Americas [19]. Individuals are primarily nocturnal and solitary, although females will typically raise and accompany cubs for up to 15±21 months after birth. In our study area in the Santa Cruz Mountains of California, pumas predominantly feed on black-tailed deer (*Odocoileus*

hemionus columbianus, 90% by biomass), but occasionally on other species, including wild boars (*Sus scrofa*), raccoons (*Procyon lotor*) and house cats (*Felis catus*) [20].

Our 1,700 km^2 study area encompasses a diverse landscape ranging from dense, urban development to large tracts of intact and relatively undisturbed native vegetation. Puma home ranges contain both protected and developed lands, with an average home range housing density of 21.7 ± 3.0 SE houses/km^2 (range 4.6±51.5) [8]. Even pumas that regularly move through or near residential areas also use nearby protected areas, allowing for comparison of movement behavior across a disturbance gradient within individual pumas. The vegetation is primarily forested (e.g., woodlands, hardwood and conifer forests) and shrubland (e.g., scrub and chaparral) habitats. It is bisected by a large freeway and further crisscrossed by numerous other smaller roads providing access to rural houses and developments. The climate is Mediterranean, with precipitation concentrated between November and April, and elevation ranges from sea level to 1155m.

Data collection

We captured 22 wild pumas (11 males, 11 females) from June 2010ÐMarch 2013 using trailing hounds, cage traps, or leg hold snares. Each animal was tranquilized using Telazol at a concentration of 100mg/mL (3.3±6.0 mg/kg estimated body weight) and outfitted with a GPS/VHF collar (3.7 kg; Model GPS Plus 1D, Vectronics Aerospace, Berlin, Germany). Six of the 22 animals were also equipped with a custom-built archival 3-axis accelerometer sampling continuously at 64Hz when activated [21]. The tri-axial accelerometer was mounted such that the x-axis was parallel to the anterior-posterior plane of the animal, the y-axis to the transverse plane, and the z-axis to the dorsal-ventral plane.

Accelerometers on pumas were programmed to record at a duty-cycle of 2 days on and five days off to maximize battery life. The GPS was programmed to acquire locations every 15 minutes during a 24-hour intense sampling period starting from noon one day each week. The Animal Care and Use Committee at UC Santa Cruz approved all animal-handling procedures (Protocols Wilmc0709 and Wilmc1101).

Data processing

During each 15-minute GPS sampling interval, we assigned one behavioral state (active or inactive) to each collared individual and considered these states to be mutually exclusive. We considered any distance greater than 70m between successive 15 minute GPS fixes to be an active period, and a distance smaller than 70m to be an inactive period. We used accelerometer measurements to determine the distance cutoff between activity states as follows. We used a random forest algorithm described in Wang et al. [22] to categorize 2-second increments of accelerometer measurements into mobile or non-mobile behaviors. These were then aggregated into 15-minute observation periods to match the GPS sampling periods. After inspecting the data visually, we identified 10% activity (i.e., 10% of accelerometer measurements categorized as mobile out of 15 minutes) as the cutoff between active and inactive periods. Because of the strong linear relationship ($r = 0.89$) between accelerometer defined activity and the distance traveled between GPS fixes, 10% activity recorded by accelerometers corresponded to 70 meters between GPS fixes.

Environmental and anthropogenic measurements

Our study animals inhabit a landscape primarily comprised of forested or shrubland habitats interspersed with developed areas. To examine how human development and habitat type affected puma behavior, we collected spatial information on buildings and habitat types

surrounding each puma GPS location. Using the Geographic Information Systems program ArcGIS (v.10, ESRI, 2010), we digitized house and building locations manually from high-resolution ESRI World Imagery basemaps for rural areas and with a street address layer provided by the local counties for urban areas. For each puma GPS position recorded, we calculated the distance in meters to the nearest house. We placed circular buffers with 150m radii around each GPS location and used the California GAP analysis data [23] to categorize the local habitat as either predominantly forested or shrubland. We chose a buffer size of 150m based on a previous analysis of puma movement responses to development [24].We also classified the time each GPS location was recorded as diurnal or nocturnal based on sunset and sunrise times.

Markov chains

We modeled puma behavior sequences as discrete-time Markov chains, which are used to describe activity states that depend on previous ones [25]. Here, we used first-order Markov chains to model a dependent relationship between the succeeding behavior and the preceding behavior. First-order Markov chains have been successfully used to describe animal behavioral states in a variety of systems, including sex differences in beaver behavior [26], behavioral responses to predators by dugongs [27], and impacts of tourism on cetacean behavior [28±29]. Because we were modeling behavior transitions with respect to spatial characteristics, we recorded the states of the puma (active or inactive) in the 15 minutes prior to and succeeding each GPS acquisition. We populated a transition matrix using these preceding and succeeding behaviors and examined whether proximity to houses influenced the transition frequencies between preceding and succeeding behavior states. Transition matrices are the probabilities that pumas remain in a behavioral state (active or inactive) or transition from one behavior state to another.

We built multi-way contingency tables to evaluate how sex (*S*), time of day (*T*), proximity to house (*H*), and habitat type (*L*) affected the transition frequency between preceding (*B*) and succeeding behaviors (*A*). Because high-dimensional contingency tables become increasingly difficult to interpret, we first used log linear analyses to evaluate whether sex and habitat type influenced puma behavior patterns using two three-way contingency tables (Before × After × Sex, abbreviated as BAS). Log linear analyses specifically test how the response variable is influenced by independent variables (e.g., sex and habitat) by using Likelihood Ratio Tests to compare hierarchical models with and without the independent variable [25]. We found that there were strong sex differences in activity patterns because adding *S* to the model greatly increased the goodness-of-fit (G^2) compared to the null model ($\Delta G^2 = 159.8$, d.f. = 1, $P<0.0001$), which assumed that succeeding behaviors only depend on preceding ones. Therefore, we evaluated data from male pumas separately from those of female pumas.

We then used another three-way contingency table for each sex to evaluate whether behavior patterns differed between habitats (*L*). We found that including habitat type significantly improved model fit for male ($\Delta G^2 = 7.9$, df = 1, $P<0.005$) but not female pumas ($\Delta G^2 = 3.18$, df = 1, $P = 0.0744$). Thus we evaluated three sets of data: all females, males in forests, and males in shrublands. For each dataset, we created four-way contingency tables (Before × After × House × Time) to evaluate how development and time of day affected behavioral transitions using the likelihood ratio methods described above.

Our null model (*BA*, *BHT*) is built such that succeeding behaviors (*A*) are only affected by behaviors in the previous time steps (*B*) and independent of proximity to houses and time of day. We tested whether including additional factors (proximity to house and time of day) improved model fit by comparing the null model with hierarchically more complex models. For example, the effects of proximity to housing on succeeding behaviors are evaluated by

comparing the goodness-of-fit (G^2) values for the null model and the model containing an interaction between succeeding behaviors and houses (*BAH*, *BHL*). We also tested the interaction between proximity to houses and time of day by comparing the saturated model (*BAHT*), which fits the data fully, to a less complex model without the interaction term (*BAH*, *BAT*, *BHT)*. Finally, we selected the best fitting model by minimizing the Akaike Information Crtierion (AIC) estimate.

Behavioral budgets

We tested whether transition matrices differed when pumas were close to houses or roads using the Z test for proportions [30]. We also estimated the amount of time pumas spent in each behavioral state by conducting an eigenanalysis on the transition matrix. Because Markov chains are ergodic matrices, we used the left eigenvector of the transition matrix to estimate the proportion of time pumas spent in each state [25]. We compared these values using a Z test of proportions and calculated 95% confidence intervals using the Wilson's score test [31].

Puma travel and energetic costs

For each puma, we identified all 24-hour intensive sampling periods during which GPS points were recorded every 15 minutes. At a fix rate of 4 times an hour, up to 96 GPS points are recorded throughout the day, equating to a total of 95 travel segments (straight lines between consecutive points). We removed any days from analyses that were missing more than 10% (i.e., 9 points) of potential GPS fixes. We determined the linear length of all travel segments and calculated the total daily distance (*D*) in km traveled by pumas by summing all travel segments and correcting for any missing GPS fixes using the formula:

$$D_{total} = D_{summed} \times 95/n \tag{1}$$

in which n represents number of actual recorded segments. Next, we calculated the minimum cost of transport (*COT*, W/kg) expended daily for each puma by adapting the equation developed by Taylor et al. [32]:

$$\mathrm{COT} = \sum_{\mathrm{i}}^{\mathrm{n}} 10.7(\mathrm{wt})^{-0.316} \times \mathrm{v_i} + 6.03(\mathrm{wt})^{-0.303} \tag{2}$$

in which *wt* is the weight (kg) of the animal when captured and v_i is the velocity of travel (m/s) between consecutive GPS points. *COT* has the units Watts/kg, which we converted to kcal/kg by applying the conversion factor 4.1868 Watt = 1 cal/s.

Lastly, we estimated the minimum number of black-tailed deer, the primary prey of pumas in our area, needed to sustain each puma given their daily minimum *COT*. We calculated the daily deer biomass (*DB*) needed to fulfill each puma's prey requirements using Eq 3 [33]:

$$DB\left(\frac{kg}{day}\right) = \frac{COT\ (kcal)}{1890\left(\frac{kcal}{kg}\right) \times 0.86 \times 0.88} \tag{3}$$

in which 1890 kcal represents the caloric content in each kg of wet deer tissue [34], and this value is then modified by multiplying it by the conversion efficiency (0.86) and the proportion of deer in a puma's dietÐhere estimated as 88% [20]. Finally, we used Eq 4 to convert the daily deer biomass into an estimate of the yearly deer requirements [33]:

$$\frac{Deer}{year} = \frac{DB\left(\frac{kg}{day}\right) \times 365\ days}{36.5\ kg \times 0.79} \tag{4}$$

in which 36.5 kg is the average weight of a black-tailed deer doe [35] and 0.79 is the edible proportion of the deer [34].

It is broadly understood that the energetic estimates generated using the equation developed by Taylor et al. [32] are the minimum estimates for *COT*. Even at 15-minute GPS sampling intervals, animals can deviate greatly from straight-line travel paths, thus expending many more kcals than estimated. In contrast, Overall Dynamic Body Acceleration (ODBA) measurements recorded by accelerometer collars, which sums the dynamic acceleration of the subject across three dimensions, provide a more precise measurement of energetic expenditure because it takes measurements at a rate of 64Hz [36]. Not all pumas were outfitted with accelerometer collars and we were unable to use ODBA alone to estimate energetic budgets. Instead we recorded ODBA values from two wild pumas whose accelerometers were active concurrent to the GPS intensive sampling periods. Using those values, we calculated the correlation between COT estimates from ODBA measurements and those estimated using velocities generated from intensive GPS sampling by Eq 2. This resulted in a correction factor that we applied to the energetic estimates of each puma in the study.

Development influences on puma movement

To quantify puma exposure to human development, we used ArcGIS (v. 10.1, ESRI, 2012) to create buffers of 150m around all GPS points within each 24-hour intensive GPS sampling period. We then calculated the number of houses encompassed within each buffer polygon and also recorded the time of day. For each day, we recorded the average housing density individual pumas were exposed to and the average distance pumas traveled between successive GPS locations during both nocturnal and diel periods. We hypothesized that pumas would use more calories by moving faster and further through areas with more houses in order to minimize their exposure to development [24,37]. However we also predicted that this relationship might be affected by time of day because pumas may prefer to stay hidden if they are in more developed areas during the day.

We used linear mixed effects models using restricted maximum likelihood estimation with the average diurnal and nocturnal calories burned between successive GPS points as the dependent variable. To select the best model, we used a top-down model selection approach to compare models with no random terms, with random intercepts, and with both random intercepts and slopes [38]. We started by fitting a linear model that included the full complement of fixed effects terms: sex of the puma (male coded as 1 and female as 0), time of day (day coded as 1 and night as 0), the average number of houses (log-transformed to account for all distributions being bound at zero), the interactions between sex and time of day, and the interaction between time of day and housing. In a second model, puma identity was included as a factor in the model to allow for random intercepts. For the third model, we also tested whether individual pumas responded to time of day, the log average number of houses, and their interaction differently by including random slopes for those terms. We used AIC to compare the three models to determine the optimal model structure. We examined the residuals for our final model visually to identify any obvious deviations from normality.

To quantify the difference in puma energetic expenditure between areas with low and high housing density, we calculated the average caloric expenditure by individual pumas in the top and bottom housing density quartiles of their home range for both days and nights. To maximize statistical power, only pumas with a minimum of 20 day and 20 night measurements were included in this analysis. We added day and night averages to get total daily difference in caloric expenditure. We calculated the percentage increase in calories used as the total daily difference between caloric expenditure for high and low housing density divided by the

average daily caloric expenditure for the individual puma. In order to conceptualize variation of human disturbances for individual pumas, we classified average housing density in the top and bottom quartiles into the following categories described by Theobald [5]: rural (greater than 0.0 and up to 0.062 houses per hectare), exurban (greater than 0.062 and up to1.236 houses per hectare), suburban (greater than 1.236 and up to 9.884 houses/hectare), or no housing. We used the package *nlme* [39] in R (v. 3.0.2, R Core Team, 2013) for all analyses.

Results

Log linear analyses

We recorded 78,242 GPS locations for 22 pumas, comprised of 6,967 behavioral transitions (e.g. active to inactive) for males in shrubland habitats, 11,379 transitions for males in forested habitats, and 21,977 transitions for females in all habitats. Log linear analyses revealed that both proximity to houses and time of day influenced puma activity levels, but this effect differed by sex, and by habitat type for males. Proximity to houses and time of day had a significant positive effect on the number of behavior transitions of male pumas in forests (Table 1). However, for males in forests, support for the interaction term (proximity to houses × time of day) was ambiguous because the two models had a ΔAIC of less than 0.2, indicating that they were statistically indistinguishable [40]. AIC comparison revealed that the best models for all female pumas and males in shrublands included the proximity to houses, time of day, and an interaction between the two (Table 1). This indicates that the time of day determined how pumas altered their movement patterns near development, which we discuss next.

Table 1. Results of log-linear analysis for all puma behavioral transition models.

Study Group	Model[ab]	ΔAIC[c]	Components added[a]	ΔG^2, *df*, *P*-value
Males, Forests	Null (BA, BHT)	72.0		84, 6, Ð
	Previous Location × House (BAH, BHT)	63.8	BAH	71.8, 4, 0.002
	Previous location × Time (BAT, BHT)	2.2	BAT	10.2, 4, <0.001
	Previous location × Time + Previous location × House (BAT, BAH, BHT)	0.01	BAT	4.01, 2, 0.001
			BAH	4.01, 2, 0.045
	Time × House (BAHT)	0.00	TH	0, 0, 0.135
Males, Shrubland	Null (BA, BHT)	53.4		65.4, 6, Ð
	Previous Location × House (BAH, BHT)	54.0	BAH	62, 4, 0.002
	Previous location × Time (BAT, BHT)	8.4	BAT	16.4, 4, <0.001
	Previous location × Time + Previous location × House (BAT, BAH, BHT)	11.5	BAT	15.5, 2, <0.001
			BAH	15.5, 2, 0.64
	Time × House (BAHT)	0.00	TH	0, 0, < 0.001
Females, All habitat	Null (BA, BHT)	90.8		102.8, 6, Ð
	Previous Location × House (BAH, BHT)	66.6	BAH	76.4, 4, <0.001
	Previous Location × Time (BAT, BHT)	41.3	BAT	49.3, 4, <0.001
	Previous Location × Time + Previous location × House (BAT, BAH, BHT)	24.5	BAT	28.5, 2, <0.001
			BAH	28.5, 2, <0.001
	Time × House (BAHT)	0.00	TH	0, 0, < 0.001

[a] A: Succeeding behavior; B: Previous behavior; T: Time; and H: Number of Houses.

[b] In null models, effects of time and number of houses were assumed to be independent of behavioral transitions. Succeeding behaviors (A) are only dependent upon preceding behaviors (B), and not on time of day (T) or proximity to housing (H). Subsequent models which incorporate the housing and time covariates and their interactions are listed below the null.

[c] ΔAIC values are in comparison to the top model for each study group.

https://doi.org/10.1371/journal.pone.0184687.t001

Behavioral budgets

All puma behavioral transitions showed contrasting responses to housing depending on the time of day (Fig 1). At night, all pumas regardless of sex or habitat were less likely to remain inactive, more likely to remain active, and more likely to transition between behavioral states near houses. In contrast, male and female pumas were more likely to stay inactive near houses during the daytime. However, male pumas in forests were also less likely to remain active near houses in the forest during the day whereas male pumas in shrublands were unaffected.

Both male and female pumas were generally more active at night than during the day. Male pumas near houses at night were active 26.9% and 21.1% of the time in forested and shrubland habitats, respectively, compared with 17.2% and 13.2% when they weren't close to human structures (Fig 2). Females were active 13.3% of the time when near houses at night, compared with only 7.5% when further away (Fig 2). In the daytime, puma activity was generally low, with females and males in forests exhibiting no difference in activity level in relation to proximity to houses (Fig 2). However, males in shrubland habitats were less likely to be active near houses (2.8%) than when far from houses (8%) during the day.

Energetic costs

Our COT estimates based on ODBA measurements from accelerometers for pumas 16M and 28F showed that our energetic expenditure estimates from GPS movement data greatly underestimated caloric intake. Applying the COT formula from Taylor et al. [32] to the intensive GPS sampling period, we estimated that 16M expended 2,492 and 2,296 kcals over two days and that 28F expended 1,793 kcals. In contrast, our COT estimates from ODBA for the same three days were about 2±2.5 times higher at 6,079 and 5,492 kcals, and 3,608 kcal, respectively. We used the results from a linear regression between the COT values calculated using 15 min GPS and ODBA measurements (intercept = 8.21, slope = 1.88; $r = 0.75$) to apply corrections factor to all puma energetic calculations.

We used 19 pumas (10 males and 9 females) to evaluate movement activities and energetics over 369 24-hour intense sampling periods (216 for females and 153 for males) (Table 2). Male pumas, averaging 53.3 kg ± 7.82kg (SD), traveled a mean of 7.43 km ± 2.2 km daily and expended 5,145 kcal ± 542 kcal (after factoring the correction factor). Females, averaging 39.8 kg ± 2.73 kg, were more sedentary and traveled a mean of 4.12 km ± 0.5 km daily and expended 4,760 kcal ± 555 kcal. If a puma only subsisted on a diet of black-tailed deer, we calculated that a male puma would need to kill a minimum average of 45.5 doe equivalents/year and that a female puma would need to kill 42 doe equivalents/year.

Development influences on puma energetics

We found that the model structure that included random intercepts and slopes for Puma ID minimized AIC values and fit the data better compared to a fixed-effects model (ΔAIC = 632) and the model with random intercepts only (ΔAIC = 23.4). The final model included all original fixed effects terms for sex, time, the log-transformed number of houses, the interaction between sex and time, and the interaction between time and number of houses (Table 3). As expected, males burned more calories than females during both nocturnal and diurnal hours (Fig 3). However, the influence of increased housing density on puma energetic expenditures differed depending on time of day, with pumas burning more calories between GPS points in more developed areas during nocturnal hours but not during diurnal hours.

Average daily caloric expenditure for individual pumas was consistently higher on days when pumas were in high housing density areas than in low housing density areas, constituting a 434.3 ± 130.3 SE kcal increase for females and a 513.3 ± 83.1 SE kcal increase for males

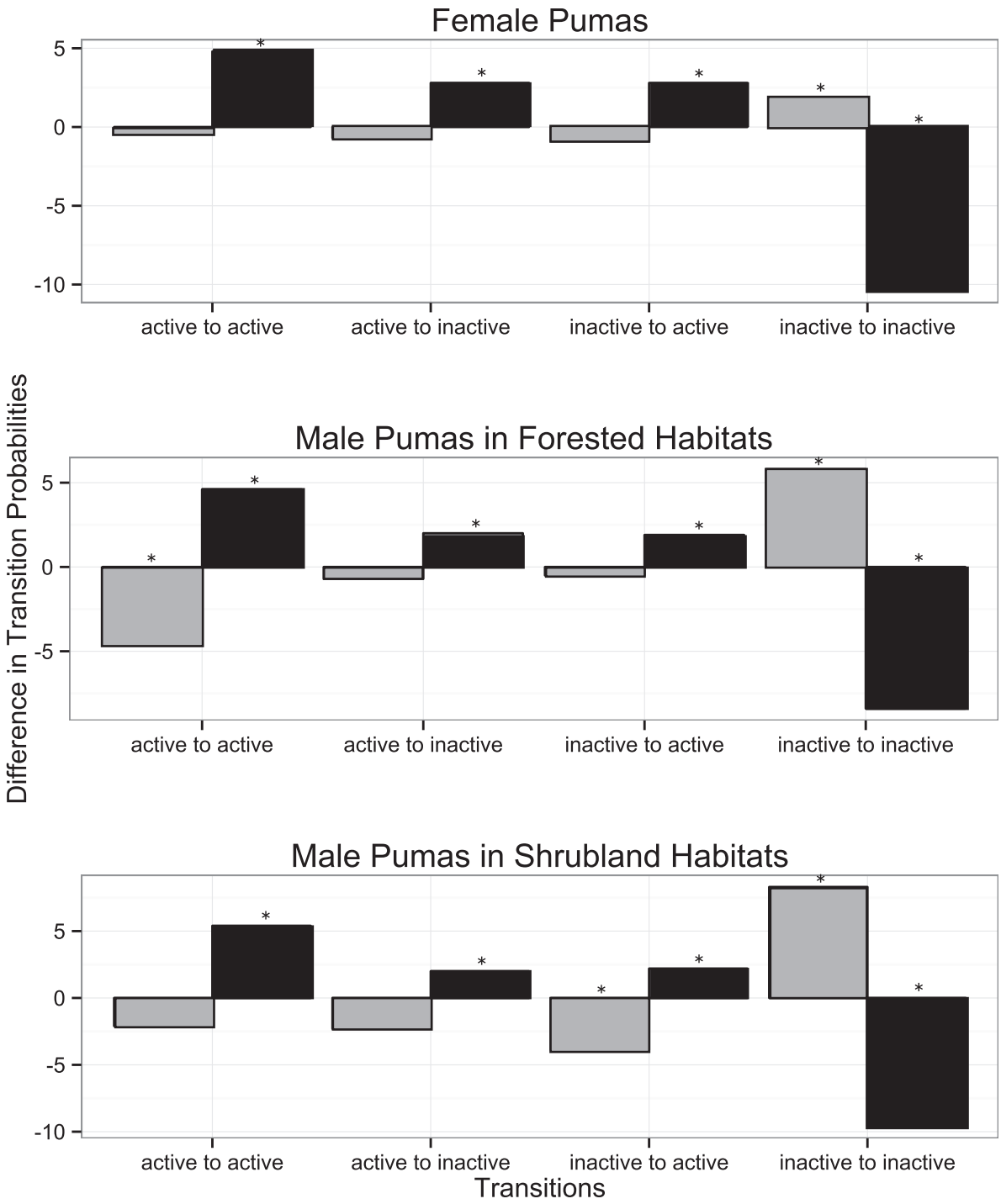

Fig 1. The effect of proximity to houses on the daytime (gray) and nighttime (black) transition probabilities between activity states for female pumas, male pumas in forested areas, and male pumas in shrubland habitats. Difference in transition probabilities is calculated as probability of transitioning between states when pumas are ≤150m from buildings subtracted by the probabillity of transitioning between states when pumas are >150m from buildings. A positive value means pumas are more likely to engage in those transitions when close to buildings than when further away. Asterisks above columns represent significant differences between transition probabilities close and far from houses ($P < 0.05$).

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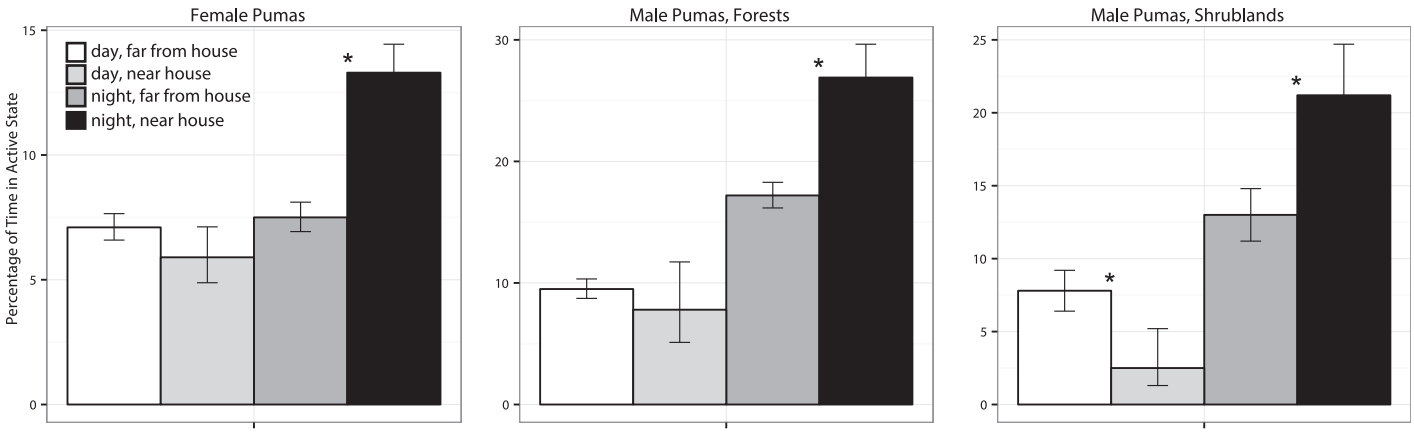

Fig 2. Proportion of time spent active for female pumas,male pumas in forests, and male pumas in shrublands ≤150m from buildings during the day (light gray) or night (black bars) and >150m from buildings during the day (white) or night (dark grey bars). Asterisks between paired columns represent significant differences between activity levels near houses and far from houses ($P < 0.05$). Error bars represent 95% confidence intervals.

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(Table 4). These differences in average daily caloric expenditure were equivalent to a mean total percentage increase of 10.1 ± 3.1 SE% of daily kcals used by individual females and 11.6 ± 1.8 SE% of daily kcals used by males. When the increase in daily calories is converted to the extra number of deer required annually by each puma, females would need to kill an additional 3.4 deer annually to meet higher energetic requirements, and males would need to kill 4.0 more deer.

Table 2. Mean (± standard error) of daily distanced traveled, daily caloric expenditure, and projected annual deer requirements of 9 female (F) and 10 male (M) pumas.

Puma ID	Days monitored	Daily distance (m)	Daily kcal/kg	Deer/year
7F	42	3236 ± 378	97.8 ± 0.6	36.3 ± 0.2
11F	22	3935 ± 489	104.5 ± 0.8	35.2 ± 0.3
18F	8	4001 ± 939	119.3 ± 1.7	40.0 ± 0.6
19F	35	3927 ± 495	107.9 ± 0.8	39.9 ± 0.3
23F	38	4389 ± 373	133.3 ± 0.8	48.0 ± 0.3
24F	15	3966 ± 462	145.0 ± 1.0	47.7 ± 0.3
25F	14	4493 ± 941	138.2 ± 2.0	48.1 ± 0.7
28F	24	4111 ± 606	129.9 ± 1.2	41.6 ± 0.4
29F	18	5060 ± 511	124.8 ± 1.0	42.2 ± 0.3
Female total	216	4132 ± 176	118.9 ± 1.1	41.6 ± 0.3
16M	12	10760 ± 1140	96.2 ± 1.5	50.4 ± 0.8
17M	8	4297 ± 706	95.0 ± 1.0	40.2 ± 0.4
22M	29	9830 ± 1091	91.2 ± 1.4	52.0 ± 0.8
26M	28	6743 ± 810	103.0 ±1.2	39.6 ± 0.5
27M	22	6853 ± 1000	99.5 ± 1.4	43.4 ± 0.6
31M	10	7047 ± 1298	94.8 ±1.8	46.1 ± 0.9
34M	17	6504 ± 727	90.1 ± 1.0	47.1 ±0.5
35M	19	4215 ± 484	97.3 ±0.7	38.8 ±0.3
36M	6	9192 ± 1874	96.4 ± 2.6	49.4 ± 1.3
37M	2	8877 ± 3	98.23 ± 0.1	48.4 ± 0.0
Male total	153	7334 ± 373	96.3 ± 0.6	45.0 ± 0.5

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Table 3. Results of final mixed effects model to predict puma activity.

Model Parameter	β	SE	t	*P*
Sex	5.50	2.84	1.94	0.069
Time	- 0.66	0.78	-0.85	0.395
Number of Houses (log-transformed)	1.21	0.28	4.26	< 0.001
Sex X Time	-3.10	0.97	-3.21	0.001
Time X Number of Houses	- 1.45	0.49	-2.95	0.003

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Discussion

This study explores how housing development influences puma behavior and energetics in a fragmented landscape. Our results suggest a clear relationship between proximity to houses and puma movement activity. This effect was modulated by the time of day, whereby pumas were more likely to be active and remain active when within 150m of development at night. We also found that pumas were more likely to transition between behavioral states when close to houses. These activity shifts may reflect discomfort with being in close proximity to humans and domestic animals or reaction to other abiotic disturbances from these sources, such as light pollution or human-associated sounds [41].

As we predicted, there was a significant positive relationship between distance traveled and the number of houses surrounding each puma's travel path. This pattern resulted in greater metabolic demand associated with higher densities of residential development. Both male and female pumas moved further and expended more calories in developed areas at night but not during the day, providing evidence that puma response to development was strongly influenced by the time of day. Although pumas only increased their movement activity near houses at night, we found that this still resulted in increased net energetic expenditure. Increases in distance traveled are unlikely to be influenced by deer availability, as occupancy of deer is ubiquitous across our study site in both developed and protected areas [20].

The increases in caloric expenditure we observed could in part explain observed increases in puma kill rate in developed areas [8]. To compensate for the higher energetic costs of living in developed areas alone, we found that pumas would need to kill on average a minimum of 3.4 and 4.0 more deer annually for female and male pumas, respectively. This estimated increase is likely conservative, as we have previously found that pumas in the most developed parts of our study area kill over 20 more deer per year than pumas in less disturbed areas [8]. Higher kill requirements based on increased movement may exacerbate other behavioral influences on energetics, including changes in feeding rates and handling time of prey [8] and altered diet composition [20].

Although pumas in our study area are not legally harvested, human-caused mortality is the leading cause of death for collared pumas. Hence, even in the absence of puma hunting, which is illegal in California, high human-induced mortality rates due to depredations give pumas strong incentive to alter their behaviors to minimize contact with people. Pumas fear humans in this human-dominated ecosystem, demonstrated by immediate responses to human stimuli [41], altered feeding behavior [8,24,41], reduced occupancy of developed areas [7], and strong avoidance of development when engaged in reproductive behaviors [24]. As large tracts of land increasingly transition from undeveloped to exurban development, non-lethal human disturbances will likely continue to alter puma behavior. As demonstrated here, changes in puma movement behavior has energetic consequences. The cumulative energetic cost of all behavior change in human-dominated systems is likely to exceed even the substantial estimated energetic requirements reported here.

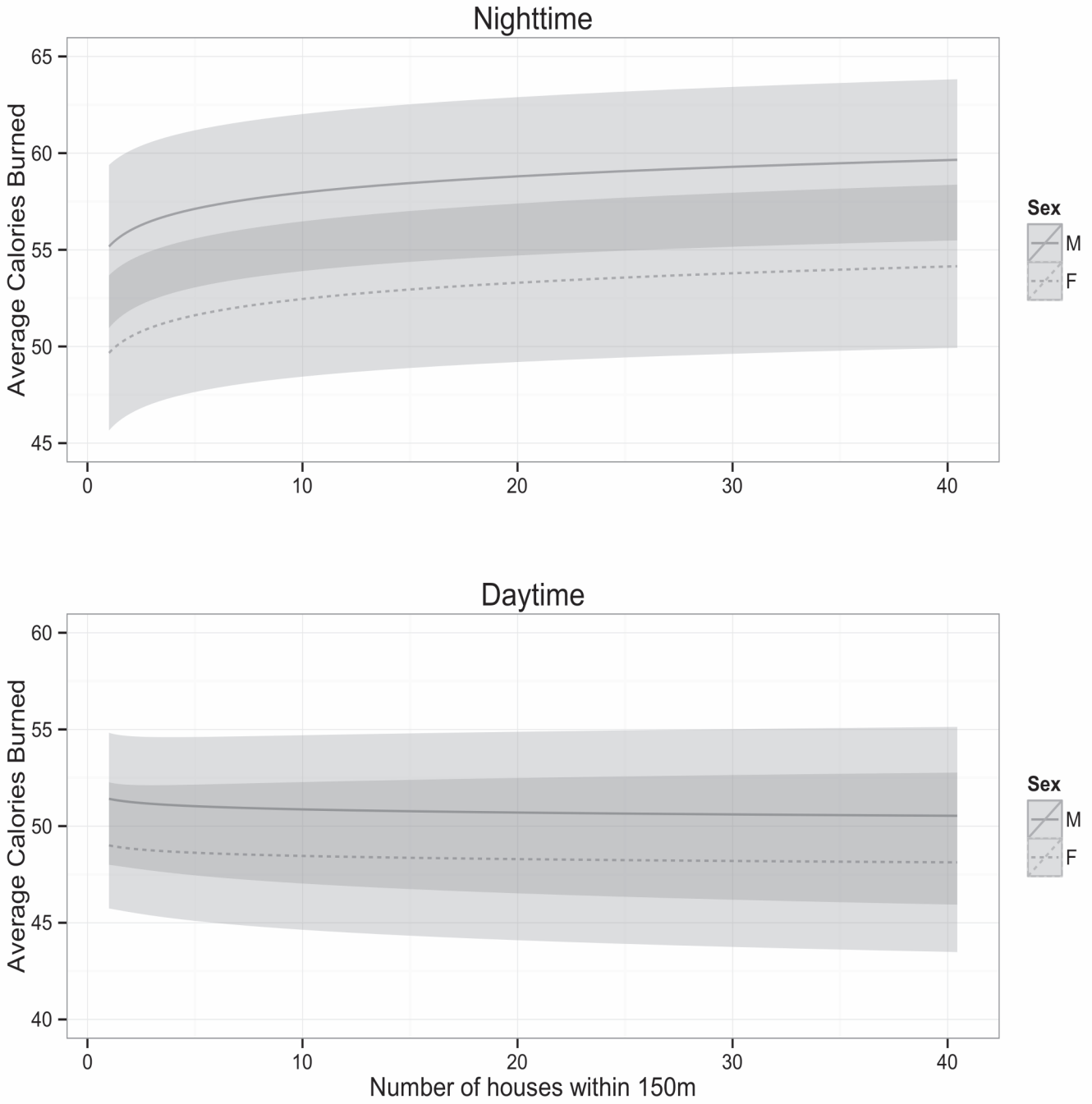

Fig 3. Predicted curves bounded by 95% confidence intervals relating the average calories expended between 15-minute GPS points and the average number of houses in a 150m radius around locations in nighttime and daytime. Predictions for males are indicated by the solid line and females are indicated by the dashed line.

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Increased energetic requirements are likely to disproportionalty impact females with kittens, given their higher energetic demands [34]. Kittens older than 6 months follow their mothers to kill sites to feed [42]; if these locations are close to development, their feeding times

Table 4. Caloric difference between time spent in high and low housing density areas relative to each puma.

Puma Sex	Puma ID	Difference in kcals (day)[a]	Difference in kcals (night)[a]	Total Difference (kcal)	Increase in Daily Calories (%)[b]	Change in annual deer consumption	Bottom 25% Housing Density[c]	Top 25% Housing Density[c]
Female	23F	-754.5	809.5	55.1	1.1	0.4	Rural	Suburban
	11F	94.1	19.8	113.9	2.9	0.9	No Housing	Exurban
	28F	128.7	128.3	256.9	5.7	2.0	No Housing	Exurban
	7F	124.9	206.3	331.2	8.3	2.6	No Housing	Exurban
	19F	509.1	10.5	519.6	12.3	4.0	No Housing	Rural
	25F	54.7	736.1	790.9	16.2	6.2	No Housing	Exurban
	29F	21.2	951.3	972.6	24.4	7.6	No Housing	Exurban
Male	26M	-23.5	328.6	305.1	7.2	2.4	No Housing	Exurban
	22M	114.9	288.1	403.0	7.5	3.1	No Housing	Rural
	17M	418.8	40.2	459.0	11.8	3.6	No Housing	Exurban
	27M	63.0	408.4	471.4	10.9	3.7	No Housing	Rural
	35M	2.8	543.6	546.3	12.9	4.3	No Housing	Exurban
	16M	343.1	551.9	895.0	19.3	7.0	Rural	Exurban

[a] Differences are calculated from average caloric expendature during days and nights spent in the top and bottom quartiles of housing density per puma.

[b] Increase in daily calories are measured as the total increase in caloric expendature divided by individual average daily caloric expendature.

[c] Housing density classifications are derived using categories described in Theobald (2005).

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may decline in response to disturbances [8]. Additionally, females may choose daytime resting locations further away from kill sites in developed areas, thus reducing the energetic gains kittens receive from carcasses. Although we could not track kitten survival during our study, most female pumas we tracked had kittens and lived in home ranges that encompassed developed areas. Future studies that measure kitten recruitment will shed light on the added energetic and survival costs of raising kittens in human-modified landscapes.

Our approach of using GPS and accelerometer data allowed us to obtain more accurate estamates of energetic use and requirements, which were likely underestimated in previous studies using GPS or telemetry data alone. The average activity levels of our study animals (20.8%) was relatively low compared to Beier et al.'s [37] estimates of 25% diel activity for pumas in southern California. This discrepancy may be due to methodological differences; Beier et al. [37] used the radio-telemetry to estimate the locations of animals, which is characterized by lower precision and sampling in comparison to GPS data. Pumas tracked in our study have some of the lowest travel distances (4±7 km/day) of any pumas studied, traveling less than half as far as those monitored by other studies [34,43]. However, despite their relatively short travel distances, our corrected estimates of puma energetic expenditures (average of 4,760 kcal for females and 5,145 kcal for males) was nearly twice as high as those of LaundrÊ [34] (average of 2,420 kcal for females and 3,144 kcal for males), which suggests that previous estimates of puma energetics from GPS or radio-tracked animals have considerably underestimated true field energetics. Metabolic costs derived soley from mimimum COT equations or telemetry-only tracking studies may woefully underestimate true large predator hunting costs due to their inability to account for additional energy demand associated with topographic complexity, substrate type, intermittent locomotion, maneuvering, feeding and weather [13,44,45].

Incorporating calibrated accelerometer datasets alongside GPS locations, as demonstrated here for pumas, allows for significantly finer-scale reconstruction of behavioral and energy budgets. Our accelerometer-corrected estimates for minimum annual deer consumption (42

deer/yr for females without kittens and 45.5 deer/yr for males) are likewise much higher than those predicted by LaundrÂ[34] (14.9 deer/yr for females and 19.4 deer/yr for males). Instead, our estimates are similar to the field-estimated kill rates of 25±84 deer/yr for pumas in our population [8].

Our study provides evidence that behavioral responses to human disturbance have energetic consequences to individuals. While previous research had focused primarily on how urbanization and development affect the persistence or declines in wildlife populations, more studies now examine the behavioral responses of these species as they adapt to increased human presence [8,46]. Understanding how animal motivations and behaviors are altered by human influences can shed light on why some species can continue to persist in human dominated landscapes while others become extirpated [47,48]. New technologies such as accelerometers can reveal much more than whether or not an animal is in an area, but elucidate how successfully the individual is able to move, feed, and reproduce [49]. Increasing awareness of the consequences of human-induced behavioral change in wildlife can contribute to more robust wildland-urban interface planning and reductions in human-wildlife conflict.

Currently, exurban or low density development is the fastest growing type of land-use change in the United States [50]. As low density development fragments previously intact landscapes, it could pose significant challenges to survival for wildlife due to cummulative effects of increased non-lethal human disturbance. By incorporating energetic measurements from accelerometers, we showed the substantial consequences of these changes in behavior on energetic costs and requirements. Changes in movement activity and behavior can provide the first indications of predator energetic responses to development. Large carnivores such as pumas occupy pivotal roles in ecosystems, and changes to their behaviors can lead to demographic effects that reverberate throughout the ecological community. In addition, as energetic needs increase with development, large carnivores may switch to domestic or synanthropic prey sources, exacerbating conflict with humans and threatening carnivore survival and population persistence. For all large carnivores, accounting for human-induced behavioral change should play a larger role in any conservation management strategy.

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A phantom road experiment reveals traffic noise is an invisible source of habitat degradation

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Decades of research demonstrate that roads impact wildlife and suggest traffic noise as a primary cause of population declines near roads. We created a "phantom road" using an array of speakers to apply traffic noise to a roadless landscape, directly testing the effect of noise alone on an entire songbird community during autumn migration. Thirty-one percent of the bird community avoided the phantom road. For individuals that stayed despite the noise, overall body condition decreased by a full SD and some species showed a change in ability to gain body condition when exposed to traffic noise during migratory stopover. We conducted complementary laboratory experiments that implicate foraging-vigilance behavior as one mechanism driving this pattern. Our results suggest that noise degrades habitat that is otherwise suitable, and that the presence of a species does not indicate the absence of an impact.

traffic noise pollution | songbird migration | habitat degradation | foraging-vigilance trade-off | perceived predation risk

Human infrastructure shapes animal behaviors, distributions, and communities (1, 2). A meta-analysis of 49 datasets from across the globe found that bird populations decline within 1km of human infrastructure, including roads (2). Observational studies of birds near roads implicate traffic noise as a primary driver of these declines (3). Road ecology research has also shown negative correlations between traffic noise levels and songbird reproduction (4, 5). Birds that produce low frequency songs, likely masked by traffic noise, show the strongest avoidance of roads (6).

There is now substantial evidence that anthropogenic noise has detrimental impacts on a variety of species (3, 7–10). For example, work in natural gas extraction fields has demonstrated that compressor station noise alters songbird breeding distribution and species richness (11–13). However, explicit experiments would help to further rule out other characteristics of infrastructure, such as visual disturbance, collisions, chemical pollution, and edge effects, which might be driving these patterns (3). In addition, although these studies implicate noise as a causal factor in population declines, many individuals remain despite noise exposure (3), but at what cost? Proposed causes of decreased fitness for birds in noise include song masking, interference with mate evaluation, nonrandom distribution of territorial individuals, disruption of parent-chick communication, reduced foraging opportunities, and/or alterations in the foraging/vigilance trade-off (3, 4).

Here we parse the independent role of traffic noise from other aspects of roads experimentally by playing traffic sounds in a roadless area, creating a 'phantom road'. We focus on birds during migratory stopover, because energy budgets are streamlined; foraging, vigilance, and rest dominate activity (14). To meet the amplified physiological needs of sustained nocturnal migratory flights, birds must increase foraging during periods of stopover while maintaining appropriate vigilance levels (14, 15). Any interference with foraging will decrease stopover efficiency and thus reduce migration speed, a likely surrogate for fitness (14), thereby increasing exposure to significant mortality risks during what can be the most perilous stage of a migratory bird's life cycle (16). Anthropogenic noise might disrupt the foraging-vigilance tradeoff by acting as a form of perceived predation risk (17, 18) or by reducing sensory awareness via distraction or acoustic masking (3, 19). Using the "phantom road" experimental approach, we previously conducted count surveys of bird distributions at this site, finding a decrease in overall bird numbers of more than 25% (20). We hypothesized that the subset of birds choosing to stay at the site would experience other negative effects of traffic noise, and we predicted that the birds that remained would exhibit lower body condition and reduced ability to increase body condition (i.e., reduced stopover efficiency) in noise.

To test these predictions we used an array of speakers to recreate the soundscape of a ~0.5 km section of highway along a ridge in southwest Idaho. This approach enabled us to turn the traffic noise *on* and *off* throughout fall migration at our phantom road site, and compare it with a nearby quiet control site, creating a modified before-after-control-impact design (Fig. 1). Alternating noise on/off every four days, we sampled a different set of migrants during each block as birds arrived and departed from the stopover site (*SI Text*). We measured sound levels (hourly level-equivalent, or LEQ) continuously during the season using acoustic recording units placed at mist net locations (Fig. 1*A*). We compared mist-net capture rate (birds/net/hr) across site (control vs. phantom road) and noise treatment (on vs. off) to investigate whether birds were leaving or staying when exposed to traffic noise (*SI Text*). Similar to our survey work (20), our best-fitting model indicated that capture rate decreased by 31% during phantom traffic noise playback, demonstrating that anthropogenic noise, independent of other road forces, fundamentally shapes bird distributions. However, 69% of birds remained despite the noise (Table S1, Dataset S1, and *SI Text*).

Significance

Using landscape-scale traffic noise playbacks to create a "phantom road," we find that noise, apart from other factors present near roads, degrades the value of habitat for migrating songbirds. We found that nearly one third of the bird community avoided the phantom road. For some bird species that remained despite noise exposure, body condition and stopover efficiency (ability to gain body condition over time) decreased compared with control conditions. These findings have broad implications for the conservation of migratory birds and perhaps for other wildlife, because factors driving foraging behavior are similar across animals. For wildlife that remains in loud areas, noise pollution represents an invisible source of habitat degradation.

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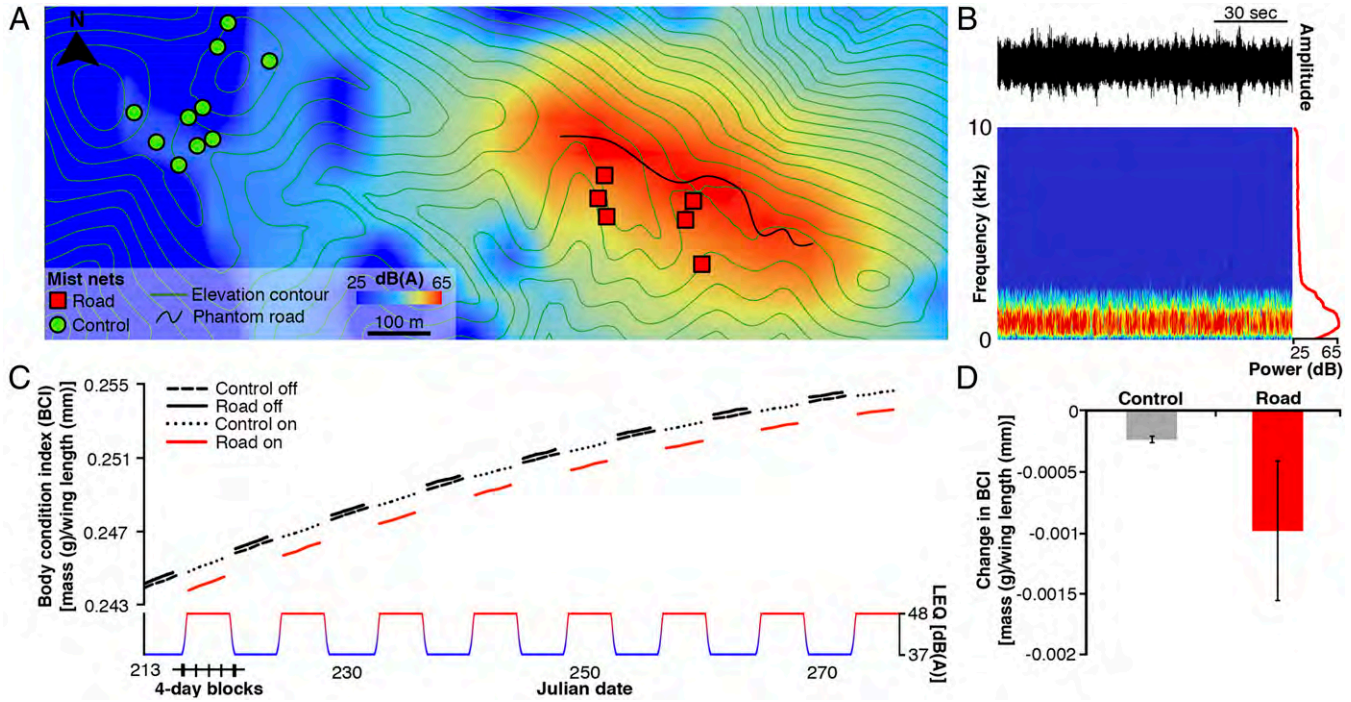

Fig. 1. Phantom road playback causes songbird body condition decline. (*A*) Estimated sound levels [dB(A) 1 h LEQ: The level of a constant sound over a specified time period that has the same energy as the actual (unsteady) sound over the same interval] during periods when speakers were on: from August through October 2012–2013 in the Boise Foothills, Idaho. Sound level was modeled using NMSim (Wyle Laboratories) (20). Circles (control) and squares (road) represent capture sites. With the noise on, mean sound levels at the phantom road capture sites increased by 11 dB(A) to 48 dB(A) (SE = 0.3), whereas the control site averaged 2 dB(A) louder with noise on (mean± SE; 41 dB(A) ± 0.2). With noise off, sound levels averaged 39 dB(A) (SE = 0.2) at the control capture sites and 37 dB(A) (SE = 0.3) at the phantom road. Elevation contours are 50 m. (*B*) A 2-min sample of the phantom road file displayed as an oscillogram, a spectrogram and a power spectrum. (*C*) Predicted values for body condition index (BCI) as birds add fuel throughout fall migration. Estimates are based on the AIC-best model for BCI for all captures combined, with species as a random intercept. A consistent full SD change in BCI is evident during each noise-on block (pattern of noise on blocks displayed along the *x* axis) throughout the migratory period. (*D*) Predicted mean change in BCI at the control and phantom road sites between noise off and noise on periods across the entire study. Error bars represent SE. These differences in BCI (and associated error) are derived from the average of the predictions presented in *C*.

Focusing on birds exposed to a gradient of sound levels, we examined differences in body condition index (BCI) of newly captured birds. BCI is a size-adjusted metric of body mass calculated as mass (g)/natural wing chord (mm). Small changes in BCI represent large differences in condition (21). During migration, high body condition signifies birds with the energy stores needed for long migratory flights (15). The best-fitting model showed that as noise exposure increased, overall BCI of the bird community remaining at the road site decreased (Fig. 1*C*, Table S1, Datasets S1 and S2, and *SI Text*). In fact, BCI in noise declined by a full SD compared with the community mean in control conditions. In the absence of noise, BCI of the songbird community at the phantom road site did not differ from the values at the control site, indicating both were suitable stopover locations (Fig. 1*C*). Models for individual species showed 5 of 21 species significantly decreased BCI in noise. Iterative exposure to noise during the multiple stopovers of saltatory migration may ultimately result in mortality (16) or, in a better case scenario, reduced fitness manifested from slower migration speed (14) which would likely impact fitness and survival in the subsequent life history stage (22).

Because we turned the phantom road off overnight to match typical diel traffic patterns, it is likely that nocturnal migrants (the majority of species in this study; see ref. 23) chose to land at our site when it was quiet, before the phantom road playbacks began in the morning. In effect, diurnally varying traffic noise might function as an ecological trap (24) for migrants. Although staying in traffic noise has a cost, the energetic outlay for individuals to leave a given site might be even greater. Birds with low body condition are less likely to embark on migratory journeys than those in good condition, and depending on the suitability of surrounding habitat, it may not be worth the risk to disperse once landed (25). We cannot differentiate whether the lower BCI we documented in traffic noise is the result of (*i*) higher body condition birds leaving the population or (*ii*) birds losing body condition over the duration of noise exposure. We saw both reduced mean body condition and reduced bird numbers, suggesting that at least some birds with the energetic stores to migrate chose to leave the site and escape the costs of remaining in noise (25).

To examine if the birds that remained in noise were suffering reduced ability to add migratory fuel (i.e., increase BCI), we regressed BCI of new captures against time of day to estimate stopover efficiency. Comparing stopover efficiency of individuals between sites provides an essential metric to compare the relative value of stopover habitat (*SI Text*). The best-fitting model for the entire songbird community included noise intensity level [dB(A)] although the confidence intervals overlapped zero (*SI Text*). For nine individual species, the best-fitting model included a noise variable, however the confidence intervals overlapped zero for all but 3 of these species (Table S1).

For MacGillivray's warblers, the best-fitting model showed that stopover efficiency substantially decreased with increasing decibel levels. MacGillivray's warblers did not show reduced capture rates in noise, and were the species that showed the strongest negative responses for both BCI and stopover efficiency, indicating that individuals stayed but did poorly in noise (Fig. 2*A* and Tables S1 and S2). In contrast, Cassin's finches had significantly increased stopover efficiency in noise and a decreased capture rate (Fig. 2*B* and

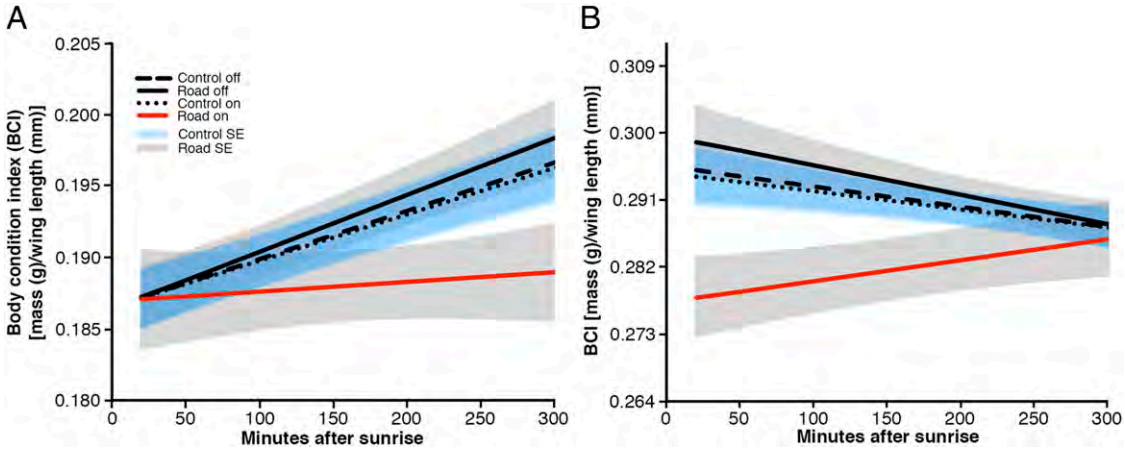

Fig. 2. Stopover efficiency is altered in noise. Predicted values for stopover efficiency for MacGillivray's warblers (*A*) and Cassin's finches (*B*). Estimates were made using average day of season using the AIC-best model for BCI for all captures combined. Values were predicted by inputting average dB(A) levels for each site. Values are shown for the control site noise off [avg. 42 dB(A)], control site noise on [43 dB(A)], phantom site noise off [40 dB(A)], and phantom site noise on [51 dB(A)]. Blue shading represents SE for the control site whereas gray shading represents SE for the phantom road.

Tables S1 and S2). This increase in stopover efficiency might reflect decreased competition for food resources in noise. Although stopover efficiency was increased in noise (Fig. 2*B*), Cassin's finches showed lower initial BCI in traffic noise (Fig. 2*B*), perhaps indicating individuals with higher BCI left the site during noise exposure. The best models for spotted towhees showed a reduced capture rate and also indicated different stopover efficiencies between on-off periods at the control and road sites with efficiency being negatively affected by noise along the phantom road (Fig. S1 and Tables S1 and S2).

It seems that for species impacted by noise, different strategies exist for managing the consequences, which might be based on differences in life history traits such as territoriality during stopover, migratory strategy, or flocking behavior. Our species-specific results show that birds may stay and incur a cost of remaining in noise (e.g., MacGillivray's warblers), or choose to leave (e.g., Cassin's finches). Leaving the noisy area may allow some species to avoid the costs of noise or a species may still experience the impacts of noise despite some individuals leaving (e.g., spotted towhees). Together, our observations of overall changes in the BCI of the entire bird community and of several individual species, as well as the changes in stopover efficiency of spotted towhee and MacGillivray's warbler, demonstrate that addition of traffic noise alone, without the other variables associated with actual roadways, can significantly decrease the value of a stopover site.

In support of our field results, we conducted a controlled laboratory study to test whether traffic noise alters the foraging-vigilance tradeoff in songbirds and could thus mechanistically underpin our field data (*SI Text*). We focused on the second most common species from our field study, white-crowned sparrow (*Zonotrichia leucophrys*), a species that also decreased BCI in noise, to investigate the reduction in foraging and increase in vigilance implied by our community-wide body condition analysis. We quantified head-down duration (i.e., foraging) and head-up rate (i.e., vigilance), because these are known measures of avian visual vigilance that change when auditory surveillance is limited and that correlate with food intake and ability to detect predator attacks (26). We also measured feeding duration (no. seconds per 8-min trial spent feeding) to quantify overall feeding bout duration. Using the same playback file as our field experiment, we played 61 dB(A) and 55 dB(A) traffic noise treatments, plus a silent control track [32 dB(A)] to foraging sparrows (n = 20). White-crowned sparrows decreased foraging by ~8%, increased vigilance levels by ~21%, and decreased feeding duration by ~30% when exposed

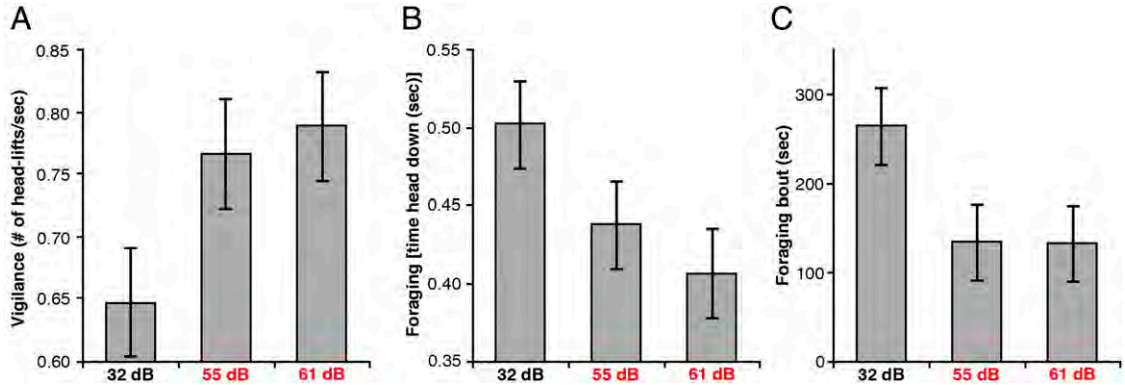

Fig. 3. The foraging/vigilance trade-off is altered in noise. White-crowned sparrows foraging in traffic noise at 61 and 55 dB(A) had reduced foraging rates (*A*), increased vigilance (*B*), and decreased foraging bout duration (*C*) compared with trials in ambient conditions [32 dB(A)]. Data are means ± SE. [Mean head up rate (head lifts/s) for 61 dB(A) = 0.79 ± 0.06, 55 dB(A) = 0.77 ± 0.05, 32 dB(A) = 0.65 ± 0.05. Mean head down duration (s): 61 dB(A) = 0.41 ± 0.03, 55 dB(A) = 0.44 ± 0.04, 32 dB(A) = 0.50 ± 0.04. Mean foraging bout duration (s): 61 dB(A) = 159.25 ± 28.0 55 dB(A) = 147 ± 32.5 32 dB(A) = 228 ± 33.7]. Birds showed more head lifts/s (β = 0.005 ± 0.002), decreased the amount of time spent with their heads down searching for seeds (β = −0.003 ± 0.001), and decreased total feeding duration (β = −4.589 ± 1.944; Movies S1 and S2) during noise playback compared with ambient conditions.

to traffic noise [61 dB(A); Fig. 3, Movies S1 and S2, and Dataset S3]. Vigilance behavior of individuals did not change based on the number of trials experienced, indicating birds did not habituate to the noise (*SI Text* and Table S2). During energetically demanding periods in a bird's life, increasing vigilance can reduce survival because of increased starvation risk (27). In contrast to song masking, which can be partially overcome by frequency shifting (28), release from masking is not possible for auditory cues necessary for aural vigilance (7). With limited auditory information, animals must resort to other methods such as visual scans to compensate for the increase in perceived predation risk, perhaps driven by masking of communication calls and predator-generated sounds (26, 29).

Our behavioral investigations in the laboratory offer compelling evidence that the body condition changes measured in the field were due at least in part to a change in foraging and vigilance behavior, but our field results could be due to a combination of factors that also deserve consideration. For example, noise might also increase physiological stress levels (ref. 30, but see ref. 31) that could cause additional declines in body condition. However, we view it as unlikely that noise can cause a stress response independent of a change in behavior. In addition, noise might indirectly change foraging rates through alterations in prey search time, sleep, or territoriality. For instance, our phantom road might have disrupted foraging behavior by reducing the acoustic detectability of insect prey (32) or reducing insect numbers. We did not test for changes in insect abundance or distribution, but because we found noise impacts on a mixed community of both frugivorous and insectivorous birds (Table S1 and Dataset S1), it seems unlikely that altered insect numbers explain a significant component of the observed patterns. Effects were consistent between the 4-d noise-on blocks throughout migration, despite documented seasonal variation in fruit and arthropod availability at the site (33), so it is more likely that changes in bird behavior drove these responses. Our experimental design was not able to determine whether noise disrupts territoriality or dominance hierarchies during stopover. However, both territorial and nonterritorial species showed negative effects of noise (23) (Table S1 and Datasets S1 and S4). We expect that a subset of these indirect effects plus the behavioral changes quantified in the laboratory contributed to the body condition declines seen in our field experiment. Because provisioning is a constant requirement for birds throughout the year, other effects of noise that occur outside of migration (e.g., refs. 4 and 5) would be in addition to, rather than instead of, the impacts we document here.

Previous work that failed to find a change in animal distributions near roads or other infrastructure has assumed a lack of negative impacts from loud human activities (2, 3). Our results demonstrate that individuals may remain in an area with high levels of noise yet suffer significant costs. We found that different species chose different strategies: to either leave noisy areas, or stay and perhaps incur the costs of noise (Fig. 1, Fig. S2, and Table S1). We exposed the bird community at our phantom road to sound levels similar to some suburban neighborhoods [~55 dB(A) hourly LEQ] (34). Many protected areas and high-value habitats are currently exposed to these levels, and would benefit from noise relief measures (35, 36). The impact of noise reaches far beyond the physical footprint of human infrastructure. Unlike other aspects of roads, noise impacts can be minimized without removing the road itself. Substrate alteration and speed limit reduction on existing roads can significantly lower decibel levels (34).

Our results reveal the need for attention to noise impacts beyond distributional shifts (3). For individuals that remain in areas disturbed by loud human activities, noise pollution represents an invisible source of habitat degradation that has been largely ignored: Traffic noise degrades habitat value but leaves no physical signs of change. Stopover habitat loss and degradation have been identified as major contributing factors to migratory songbird declines worldwide (37, 38). Migrants are exposed to an unknown risk landscape at stopover sites and must therefore rely heavily on increased vigilance to compensate (39–41). Unlike resident species, successful conservation of migratory species requires protection of habitats in breeding, wintering, and stopover locations (41). In addition, reduction in condition or delay in migration could have carry-over effects into the overwintering or breeding seasons (42). Further understanding of anthropogenic noise's impact on body condition is key, as it is an important predictor of fitness across taxa and life stage (22). When managing natural systems, we should ensure that the habitat we protect remains of high quality, including the quality of the acoustic environment.

All birds caught during this project were mist-netted and banded under the Intermountain Bird Observatory's federal permit (22929) and Idaho Department of Fish and Game permit (764–13-000039). All experiments were approved by Boise State University's Institutional Animal Care and Use Committee (006-AC12-007 and 006-AC13-002).

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Increasing impacts of climate change upon ecosystems with increasing global mean temperature rise

Rachel Warren · Jeff Price · Andreas Fischlin · Santiago de la Nava Santos · Guy Midgley

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Abstract In a meta-analysis we integrate peer-reviewed studies that provide quantified estimates of future projected ecosystem changes related to quantified projected local or global climate changes. In an advance on previous analyses, we reference all studies to a common pre-industrial base-line for temperature, employing up-scaling techniques where necessary, detailing how impacts have been projected on every continent, in the oceans, and for the globe, for a wide range of ecosystem types and taxa. Dramatic and substantive projected increases of climate change impacts upon ecosystems are revealed with increasing annual global mean temperature rise above the pre-industrial mean (ΔT_g). Substantial negative impacts are commonly projected as ΔT_g reaches and exceeds 2°C, especially in biodiversity hotspots. Compliance with the ultimate objective of the United Nations Framework Convention

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on Climate Change (Article 2) requires that greenhouse gas concentrations be stabilized within a time frame "sufficient to allow ecosystems to adapt naturally to climate change". Unless ΔT_g is constrained to below 2°C at most, results here imply that it will be difficult to achieve compliance. This underscores the need to limit greenhouse gas emissions by accelerating mitigation efforts and by protecting existing ecosystems from greenhouse-gas producing land use change processes such as deforestation.

1 Introduction

Effects of climate change are already being observed on a wide range of ecosystems and species in all regions of the world (Rosenzweig et al. 2007), in response to the 0.74°C rise (ΔT_g) in global mean temperature (GMT) that has been experienced since pre-industrial times (Solomon et al. 2007). Such responses include changes in phenology and shifts in species ranges (e.g. Walther et al. 2002; Root et al. 2003), whilst the first extinctions which are likely to be attributable to climate change—acting synergistically with disease—have already occurred in amphibians (Pounds et al. 2006; Bosch et al. 2006). Coral reef bleaching is expected to increase strongly with rising sea surface temperatures (Hughes et al. 2003). At the same time, the ocean has already acidified by 0.1 pH units since pre-industrial times (Solomon et al. 2007) due to the direct effects of increasing atmospheric concentrations of carbon dioxide from the pre-industrial level of 280 ppm to the 2005 level of 379 ppm CO_2 (Solomon et al. 2007).

The literature contains a growing number of studies that project for the future increasingly severe impacts that further anthropogenic climate change would have on ecosystems and species around the world (see the 71 studies referenced in Tables 2, 3, 4 and 5). Such studies typically identify the onset of some positive, but predominantly negative, impacts upon a species or ecosystem as the climate changes. However, these studies have largely been carried out independently from each other and have used a wide range of future climate scenarios. This makes it difficult to compare results and obtain a clear and aggregated picture of how impacts accrue with increasing global mean temperature rise. Such an aggregated picture is important for two reasons: firstly it addresses climate change at the appropriate scale, i.e. as a global phenomenon; and secondly it enables the evaluation of major policy recommendations, such as the much discussed 2°C limit suggested by the EU as both a "safe" and achievable level of global temperature increase. Existing reviews (Houghton et al. 2001; Thomas et al. 2004a; Hare 2006; Warren 2006) have not included the full range of recent literature and have not estimated uncertainties. Similarly to the summary given in Fischlin et al. (2007), this paper integrates the dispersed and fragmented literature on ecosystem impacts of projected climate change, often expressed at a regional level, into a set of tables of projected impacts for different levels of global mean temperature rise with respect to pre-industrial times, ΔT_g, providing an estimate of uncertainty in these levels. The tables report the main findings in terms of: range losses for species, habitats or entire ecosystems; extinction risks; and other biodiversity impacts caused by ecosystem degradations or declines in key populations due to anticipated climate changes.

2 Materials and methods

2.1 Literature search

A literature search was made to assess pertinent impacts of climate change on both terrestrial and marine ecosystems across the globe (Fischlin et al. 2007). Search engines were first used to identify references in the peer reviewed literature, and further references were then derived from information provided within these. Existing reviews (Gitay et al. 2001; Thomas et al. 2004a; Hare 2006; Warren 2006) were particularly useful in identifying additional references. All references were then reviewed for specific information about thresholds in local or global temperature change/sea level rise above which adverse consequences could be expected, and also for quantified projections of ecosystem or species changes associated with quantified local or global climate changes, taking note of the climate scenario and any general circulation model (GCM) used, and the treatment of dispersal and migration. Thus studies that contained insufficient detail about the climate scenario used, or that did not provide quantitative estimates of the resultant ecosystem or species changes, could not be included in the analysis. In particular, studies which reported only the general direction of trends in response to changing temperature or precipitation were deliberately excluded. In cases where more than one study addressed similar species or ecosystems, each study was included separately in the summary table, since it may be projecting different sensitivities due to the use of other climate change scenarios and/or assessing other kinds of impact responses.

2.2 Converting to a pre-industrial reference point for global mean temperature change

Information on the climate change scenario simulated by each original study was converted to a common pre-industrial reference point for temperature. Studies often refer to baselines of pre-industrial (<1850), 1960–1990 mean, 1990, or "present day" (e.g. 1980–1999). In this study the temperature rise between pre-industrial and the 1960–1990 mean is taken as 0.3°C and the temperature rise between pre-industrial and 1990 is taken as 0.6°C (Houghton et al. 2001); whilst that from the mid 1970s to 1990 is taken as 0.2°C (Houghton et al. 2001). Where studies report impacts as caused by a particular GCM simulation using the HadCM3 model, Table 7 of Arnell et al. (2004) was used to convert the temperatures to a common pre-industrial baseline.

While some of the literature relates impacts directly to global mean temperature increases, many studies refer only to local temperature rise, and hence upscaling from a local to a global scale is required. Upscaling was carried out as detailed below for the different classes of studies identified (Table 1) and also provided an opportunity to estimate the uncertainties arising from the use of different GCMs in climate projection. Whenever possible it was also considered whether the impact had been estimated based only on temperature change, or also on associated precipitation change.

When studies gave minimal detail about GCM scenarios, such as referring to them only as "CO_2 doubling scenarios", the original literature publishing that scenario was traced, and/or the model authors were contacted, in order to verify the global mean

Table 1 Detail of the upscaling methodology used to derive global mean temperature (GMT) change (ΔT_g) for the eight study classes a–h

Class	Description of study	Derivation of central estimate of GMT change ΔT_g	Derivation of range of GMT change
a	Relates global impacts directly to ΔT_g	ΔT_g by definition already provided: harmonised if necessary to pre-industrial	Not derived unless provided in original study
b	Relates local impact (e.g. x% species at risk of extinction) to regional temperature change without using GCM output	ΔT_g is the mean of values derived via upscaling procedure, using the cited regional temperature change	Range of values derived via upscaling procedure using the cited regional temperature change
c	Relates a local impact (e.g. y% species at risk of extinction) to regional temperature change while using the output of specific GCM(s)[2]	As not all studies provide the regional temperature change this may need to be derived by first downscaling for the appropriate timeslice (e.g. Gyalistras and Fischlin 1999). ΔT_g is then the mean of values derived via a subsequent upscaling of the downscaled regional temperature change	Range of values derived via upscaling procedure, using the downscaled regional temperature change
d	As b but regional precipitation change also used	As b	As b
e	As c but study uses also GCM simulated precipitation as well as temperature	Upscaling is not applicable, as procedure is based on temperature only. ΔT_g is derived from published values simulated by the used GCM(s)	Not derivable
f	Cases where upscaling is not possible because regional temperature changes are out of range of the GCM patterns available	Estimated from maps in Meehl et al. (2007) relating local and global temperature change	Not derivable
g	As c or e but GCM output comes from 3 or more different GCM models	Mean of values as simulated by the used GCM(s)	Range derived from published values simulated by the used GCM(s)
h	Cases where the key variable is sea surface temperature	Estimated from maps in Meehl et al. (2007) relating local surface air temperature over the sea to ΔT_g, since maps of SST were not readily available, and increases in surface air temperature over the ocean were assumed to approximate increases in SST	Not derivable

temperature increase corresponding to CO_2 doubling, taking into account the control CO_2 concentration as necessary.

2.3 Dynamics

Many reviewed studies do not consider a temporal dimension. There are two issues here (1) whether the climate scenario a study considers relates to transient or equilibrium climate change and (2) whether the projected ecological response is considered a steady state. Studies in class b project impacts without distinguishing between transient and equilibrium temperature change. However, most studies use models, which project the future long-term ecological response to a changed climate (i.e. a new steady state) while the climate scenario is a transient one: studies in classes c and e are typically based on transient climate change scenarios produced by GCMs, although there are a few which also include equilibrium temperature change scenarios. Hence, the ecological projections are *not* mere snapshots of a transient climate change and its concomitant response, rather do these studies artificially hold the transient climate constant and assume the ecosystem response to equilibrate, regardless of the time the system may need to actually reach such an equilibrium. Thus an important question is the time lag between the forcing temperature change, be it transient or equilibrium, and the ecosystem response (see Section 4). The upscaling procedure described below is based on transient GCM scenario outputs throughout.

2.4 Upscaling procedure

The upscaling procedure involved the use of $0.5 \times 0.5°$ resolution outputs produced from original $5 \times 5°$ resolution outputs of five GCM models HadCM3, ECHAM4, CSIRO2, PCM, and CGCM2, by using pattern scaling and downscaling methods (Christensen et al. 2007). These climate projections based on transient GCM outputs were available for the entire global land area at a resolution of $0.5 \times 0.5°$. They were produced from up to four IPCC SRES emission scenarios (Nakicenovic et al. 2000) providing 13 different GCM patterns on which to base the upscaling (available at http://ipcc-ddc.cru.uea.ac.uk). In each $0.5 \times 0.5°$ grid cell, 13 alternative twenty-first century time series of regional annual (or if required seasonal) temperature were thus available, each one expressed as the running 30-year mean temperature increase since 1961–1990 mean climate, to smooth inter-annual variability.

For each study in Table 1 of type b or c, the location was then related to a grid cell or to grid cells depending on how large an area the study covered. For each grid cell, all 13 upscaling calculations were carried out, to encompass the full range of inter-GCM and inter-scenario pattern variability as an uncertainty surrogate. The upscaling calculation was simply performed by examining any one of the 13 time series for a grid cell. A computer program calculated the date at which the regional temperature reached the temperature threshold which is referred to in the study of type b or c and therein associated with some particular impact on an ecological system. The program then used this derived date to identify the associated global temperature rise ΔT_g in the transient GCM runs, matching this same date, using if available the global temperature time series from the exact same GCM scenario as

Table 2 Projected impacts of climate change on various ecological systems and species as reported in the literature for different levels of global mean annual temperature rise ΔT_g, relative to pre-industrial climate (mean and range), showing also regional temperature change ΔT_{reg} relative to 1990 if provided by the literature: range losses for species, habitats or whole ecosystems

No.	ΔT_g above pre-ind °C	ΔT_g (range)	ΔT_{reg} above 1990 °C (range)	Impacts to unique or widespread ecosystems or population systems	Region	Taxa	Source
1	1.3	1.1–1.6	1	8% loss freshwater fish habitat, 15% loss in Rocky Mountains, 9% loss of salmon	N America	Fish	13
2	1.6			Bioclimatic envelopes eventually exceeded leading to 10% transformation of global ecosystems; loss of 47% wooded tundra, 23% cool conifer forest, 21% scrubland, 15% grassland/steppe, 14% savannah, 13% tundra and 12% temperate deciduous forest. Ecosystems variously lose 2–47% areal extent	Globe		6
3	1.6	1.1–2.1	1	Suitable climates for 25% of eucalypts exceeded	Australia	Plants	12
4	1.7	1.3–2.4	2	16% freshwater fish habitat loss, 28% loss in Rocky Mountains, 18% loss of salmon	N America	Fish	13
5	1.8			Mean latitude of range of *Aloe dichotoma* shifts S by 1.1° of latitude causing range loss	Namibia	Plants	68
6	<1.9	<1.6–2.4	<1	Range loss begins for Golden Bowerbird	Australia	Birds	4
7	1.9	1.6–2.4	1	Range loss of 40–60% for Golden Bowerbird	Australia	Birds	4
8	2.1			Without dispersal 17 common European deciduous trees variously lose 1–100% of their range (2 sp. lose 100%); whilst full dispersal could reduce this to 11 losing between 1–99% (2 sp. lose 99%) and 6 increasing their range by 42–303%	Europe	Plants	67
9	2.3	1.6–3.2	3	24% loss freshwater fish habitat, 40% loss in Rocky Mountains, 27% loss of salmon	N America	Fish	13
10	2.4			63 of 165 rivers studied lose >10% of their fish species	Globe	Fish	19
11	2.5	1.9–4.3		42% of UK land area with bioclimate unlike any currently found there; in Hampshire, declines in climate suitability space for curlew and hawfinch and gain for yellow-necked mouse; loss of montane habitat in Scotland; potential bracken invasion of Snowdonia montane areas	UK, Europe	Birds, mammals, plants	57
12	2.5			20–70% loss (mean 44%) of coastal bird habitat at 4 sites	USA	Birds	29

13	2.5	1.9–3.5		20% loss of coastal migratory bird habitat	Delaware, USA	Birds	36
14	2.7			32–70% of 111 European mammals studied lose >30% of current distribution whilst 24–35% undergo range expansions	Europe	Mammals	71
15	2.7			Bioclimatic envelopes exceeded leading to eventual transformation of 16% of global ecosystems: loss of 58% wooded tundra, 31% cool conifer forest, 25% scrubland, 20% grassland/steppe, 21% tundra, 21% temperate deciduous forest, 19% savanna. Ecosystems variously lose 5–66% of their areal extent	Globe		6
16	2.8	2.3–4.6	2.1–2.5	Cloud forest regions lose hundreds of metres of elevational extent, potential extinctions ΔT_{reg} 2.1°C for C America and ΔT_{reg} 2.5°C for Africa	C. America, Tropical Africa, Indonesia		17
17	2.8	2.1–3.1	3	Eventual loss of 9–62% of the mammal species from Great Basin montane areas	USA	Mammals	32
18	2.8			Most European bird distributions are reduced in area by 81% and displaced from 38–53% of their present location; 25% have ranges reduced by > = 90%. Avian species richness reduced by 9–60% depending on dispersal assumptions	Europe	Birds	65
19	2.8	1.9–3.8	3	38–54% loss of waterfowl habitat in prairie pothole region	USA	Birds	37, 38
20	2.9		3.2–6.6	50% loss existing tundra offset by only 5% eventual gain; millions of Arctic nesting shorebirds species variously lose up to 5–57% of breeding area; high Arctic species most at risk; geese species variously lose 5–56% of breeding area	Arctic	Birds	14
21	2.9			Lat. of N forest limits shifts N by 0.5° latitude in W Europe, 1.5° in Alaska, 2.5° in Chukotka and 4° in Greenland	Arctic	Plants	40
22	2.9			Substantial loss of boreal forest	China	Plants	15
23	3.0			66 of 165 rivers studied lose >10% of their fish species	Globe	Fish	19

Table 2 (continued)

No.	ΔT_g above pre-ind °C	ΔT_g (range)	ΔT_{reg} above 1990 °C (range)	Impacts to unique or widespread ecosystems or population systems	Region	Taxa	Source
24	2.4–4.0			431 bird species lose on average 76–89% of their present range, with new potential ranges overlapping original ones by 31–47% so that species richness declines locally by a mean of 9–56% depending on dispersal assumptions	Europe	Birds	73
25	3.3	2.3–3.9	2.6–2.9	Substantial loss of alpine zone, and its assoc. flora and fauna (e.g., alpine sky lily, and mountain pygmy possum)	Australia	Plants, marsupials	45
26	3.4			6–22% loss of coastal wetlands; large loss migratory bird habitat particularly in USA, Baltic and Mediterranean	Globe	Birds	35, 36
27	3.5	2.3–4.1	2.5–3.5	Loss of temperate forest wintering habitat of Monarch butterfly	Mexico	Insects	28
28	3.6	2.6–4.3	3	Bioclimatic limits of 50% of eucalypts exceeded	Australia	Plants	12
29	3.6	3.0–3.9		Parts of the USA lose 30–57% neotropical migratory bird species richness	USA	Birds	43
30	3.7			Bioclimatic envelopes exceeded leading to eventual transformation of 22% of global ecosystems; loss of 68% wooded tundra, 44% cool conifer forest, 34% scrubland, 28% grassland/steppe, 27% savannah, 38% tundra and 26% temperate deciduous forest. Ecosystems variously lose 7–74% areal extent	Globe		6
31	3.7	2.6–4.8	3	Up to 60% loss in upland stream macro-invertebrate abundance; local extinction of 4 taxa; 25% of mean species richness at risk of local extinction	UK	Invertebrates	62

32	4.0	3.3	47–78% of 111 European mammals studied lose >30% of current distribution whilst 13–33% undergo range expansions	Europe	Mammals	71
33	>>4.0	5	Bioclimatic limits of 73% of eucalypts exceeded	Australia	Plants	12
34	4.9		Without dispersal 17 common European deciduous tree species variously lose 15–100% of their range; full instantaneous dispersal could reduce this to 11 losing between 13% and 100% and 6 increasing their range by 3–320%	Europe	Plants	67
35	5.0		92–97% of 100 *Banksia* species studied experience range contraction, 9% expand	W Australia	Plants	74
36	5.2		62–100% loss of bird habitat at 4 major coastal sites	USA	Birds	29

A novel climate is a climate which is significantly different from the present climate whilst a disappearing climate is a climate that disappears from a given area, for example on a mountaintop or a coastline where geography prevents a species from tracking the changing climate. For further details see Williams et al. (2007)
Sources: 1—Thomas et al. (2004a), 2—Hoegh-Guldberg (1999), 4—Hilbert et al. (2004), 5—Rutherford et al. (2000), 6—Leemans and Eickhout (2004), 7—Williams et al. (2003), 8—Theurillat and Guisan (2001), 9—Sheppard (2003), 10—Eliot et al. (1999), 11—Symon et al. (2005), 12—Hughes et al. (1996), 13—Preston (2006), 14—Zöckler and Lysenko (2000), 15—Ni (2001), 16—Bakkenes et al. (2002), 17—Still et al. (1999), 18—Benning et al. (2002), 19—Xenopoulos et al. (2005), 20—European Climate Forum (2004), 21—Cox et al. (2004), 22—Thuiller et al. (2005), 23—Thuiller et al. (2006), 24—Midgley et al. (2002), 25—Hannah et al. (2002), 26—Peterson et al. (2002), 27—Erasmus et al. (2002), 28—Villers-Ruiz and Trejo-Vazquez (1998), 29—Galbraith et al. (2002), 30—Beaumont and Hughes (2002), 31—Kerr and Packer (1998), 32—McDonald and Brown (1992), 33—Halloy and Mark (2003), 34—Moriondo et al. (2006), 35—Nicholls et al. (1999), 36—Najjar (2000), 37—Sorenson et al. (1998), 38—Johnson et al. (2005), 39—Broennimann et al. (2006), 40—Kaplan et al. (2003), 41—Theurillat et al. (1998), 42—Forcada et al. (2006), 43—Price and Root (2005), 44—Siqueira and Peterson (2003), 45—Pickering et al. (2004), 46—Scholze et al. (2006), 47—Raven et al. (2005), 48—Cox et al. (2000), 49—Orr et al. (2005), 50—Malcolm et al. (2006), 51—Peck et al. (2004), 52—Pounds et al. (2006), 53—Arzel et al. (2006), 54—Bosch et al. (2006), 57—Berry et al. (2005), 58—Lucht et al. (2006), 59—Schaphoff et al. (2006), 60—McClean et al. (2005), 61—Williams et al. (2007), 62—Durance and Ormerod (2007), 63—Hawkes et al. (2007), 64—van Vuuren et al. (2006), 65—Huntley et al. (2006), 66—Lensing and Wise (2007), 67—Ohlemüller et al. (2006), 68—Foden et al. (2007), 69—Cramer et al. (2001), 70—Sekercioglu et al. (2008), 71—Levinsky et al. (2007), 72—Memmott et al. (2007), 73—Huntley et al. (2008), 74—Fitzpatrick et al. (2008)

Table 3 Projected impacts of climate change on various ecological systems and species as reported in the literature for different levels of global mean annual temperature rise ΔT_g, relative to pre-industrial climate (mean and range), showing also regional temperature change ΔT_{reg} relative to 1990 if provided by the literature: extinction risks

No.	ΔT_g above pre-ind °C	ΔT_g above pre-ind °C (range)	ΔT_{reg} above 1990 °C (range)	Impacts to unique or widespread ecosystems or population systems	Region	Taxa	Source
37	0.6			Amphibian extinctions/extinction risks on mountains due to climate-change induced disease outbreaks	Costa Rica, Spain, Australia	Amphibians	52, 54
38	1.6	1.2–2.0	0.7–1.5	9–31% (mean 18%) of species committed to extinction	Globe (20% terrestrial surface)	Plants, vertebrates and insects	1
39[a]	1.6			23–25% of bird species at risk of extinction, and 1–2% projected extinct	Western Hemisphere	Birds	70
40	1.7	1.2–2.6		38–45% of the plants in the Cerrado committed to extinction	Brazil	Plants	1, 44
41	1.7	1.3–3		2–18% of the mammals, 2–8% of the birds and 1–11% of the butterflies committed to extinction	Mexico	Mammals, birds, insects	1, 26
42	1.75	1.5–2.0		2–4% loss of global vascular plant diversity	Globe	Plants	64
43	1.9	1.6–2.4	1	7–14% of reptiles, 8–18% of frogs, 7–10% of birds, and 10–15% of mammals committed to extinction as 47% of appropriate habitat in Queensland lost	Australia	Reptiles, amphibians, birds, mammals	1, 7
44	2.1			41–51% loss in plant endemic species richness	S Africa, Namibia	Plants	39
45	2.1		1.4–2.6	13–23% of butterflies committed to extinction	Australia	Insects	1, 30
46	2.1	1.4–2.6		Bioclimatic envelopes of 2–10% plants exceeded leading to endangerment or extinction; mean species turnover of 48% (spatial range 17–75%); mean species loss of 27% (spatial range 1–68%)	Europe	Plants	22

47	2.2			3–16% of plants committed to extinction	Europe	Plants	1
48	2.2	2.1–2.3	1.6–1.8	15–37% (mean 24%) of species committed to extinction	Globe (20% terrestrial surface)	Plants, vertebrates and insects	1
49	2.2	1.7–3.2		8–12% of 277 medium/large mammals in 141 national parks critically endangered or extinct; 22–25% endangered	Africa	Mammals	23
50	2.3	1.5–2.7	2°C SST	Loss of Antarctic bivalves and limpets	Southern Ocean	Molluscs	51
51	2.3	1.5–2.7	2.5–3.0	Extinctions (100% potential range loss) of 10% endemics; 51–65% loss of Fynbos; including 21–40% of *Proteaceae* committed to extinction; Succulent Karoo area reduced by 80%, threatening 2800 plant species with extinction; 5 parks lose >40% of plant species	S Africa	Plants	1, 5, 24, 25
52	2.3	2.3–4.0	2.5–3.0	24–59% of mammals, 28–40% of birds, 13–70% of butterflies, 18–80% of other invertebrates, 21–45% of reptiles committed to extinction; 66% of animal species potentially lost from Kruger National Park	S Africa	Mammals, birds, reptiles, insects, other invertebrates	1, 27
53	2.3	2.2–4.0		2–20% of mammals, 3–8% of birds and 3–15% of butterflies committed to extinction	Mexico	Mammals, birds, insects	1, 26
54	2.3	1.6–3.2		48–57% of Cerrado plants committed to extinction	Brazil	Plants	1
55[a]	2.3			27–28% of bird species at risk of extinction, and 2–3% projected extinct	Western Hemisphere	Birds	70
56	2.3			Changes in ecosystem composition, 32% of plants move from 44% of area with potential extinction of endemics	Europe		16

Table 3 (continued)

No.	ΔT_g above pre-ind °C	ΔT_g above pre-ind °C (range)	ΔT_{reg} above 1990 °C (range)	Impacts to unique or widespread ecosystems or population systems	Region	Taxa	Source
57	2.4			Bioclimatic range of 25–57% (full dispersal) or 34–76% (no dispersal) of 5,197 plant species exceeded leading to extinction risks	Subsaharan Africa		60
58	2.5		2°C SST	Functional extinction of coral reef ecosystems (overgrown by algae)	Indian Ocean	Corals, fish	9
59	2.6			4–21% of plants committed to extinction	Europe	Plants	1
60	2.7			1–6 rodent species (1–5% of 111 mammals studied) committed to extinction	Europe	Mammals	71
61	2.8	2.5–3.0		Multimodel mean 62% (range 40–100%) loss Arctic summer ice extent, high risk of extinction of polar bears, walrus, seals; Arctic ecosystem stressed	Arctic	Mammals	11, 53
62	2.8			65 species at increased risk of extinction with high risk for endemic Scottish Crossbill, Imperial Eagle and Marmora's warbler	Europe	Birds	65
63	2.9		2.1–3.9	21–36% of butterflies committed to extinction; >50% range loss for 83% of 24 lat. restricted species	Australia	Insects	1, 30
64	2.9	2.6–3.3	2.1–2.8	21–52% (mean 35%) of species committed to extinction	Globe (20% terrestrial surface)	Plants, vertebrates and insects	1
65	3.1	2.3–3.7	2°C SST	Functional extinction of remaining coral reef ecosystems (overgrown by algae)	Globe	Corals, fish	2
66	3.1	2.5–4.0	2	High risk of extinction of Golden Bowerbird as habitat reduced by 90%	Australia	Birds	4

67	3.1	1.8–4.2	3–4	Risk of extinction of Alpine species	Europe	Plants	41
68	2.4–4.0			Of 40 endemic/near endemic species studied, 5–8 are threatened with extinction losing 90–100% of their original range	Europe	Birds	73
69	3.3	2.8–3.8	2	Risk of extinction of Hawaiian honeycreepers as suitable habitat reduced by 62–89%	Hawaii	Birds	18
70	3.3		3.7	4–38% of birds committed to extinction	Europe	Birds	1
71[a]	3.3			32–34% of bird species at risk of extinction, and 6–8% projected extinct	Western Hemisphere	Birds	70
72	3.5	2.0–5.5		Projected extinction of 15–40% endemic species in global biodiversity hotspots (narrow specificity)	Globe		50
73	3.6	2.6–3.7		30–40% of 277 mammals in 141 parks critically endangered/extinct; 15–20% endangered	Africa	Mammals	23
74	3.9			4–24% plants critically endangered/extinct; mean species turnover of 63% (spatial range 22–90%); mean species loss of 42% (spatial range 2.5–86%)	Europe	Plants	22
75	4.0	3.0–5.1	3	Likely extinctions of 200–300 species (32–63%) of alpine flora	New Zealand	Plants	33
76	4.0			1–10 species (1–9.% of 111 mammals studied) committed to extinction	Europe	Mammals	71
77	>4.0		3.5	38–67% of frogs, 48–80% of mammals, 43–64% of reptiles and 49–72% of birds committed to extinction in Queensland as 85–90% of suitable habitat lost	Australia	Reptiles, amphibians, birds, mammals	1, 7
78[a]	4.5			39–42% of bird species at risk of extinction, and 10–15% projected extinct	Western Hemisphere	Birds	70
79	>>4.0		5	57 endemic frogs/mammals eventually extinct, 8 endangered	Australia	Amphibians, mammals	7

Table 3 (continued)

No.	ΔT_g above pre-ind °C	ΔT_g above pre-ind °C (range)	ΔT_{reg} above 1990 °C (range)	Impacts to unique or widespread ecosystems or population systems	Region	Taxa	Source
80	>>4.0		7	Eventual total extinction of all endemic species of Queensland rainforest	Australia	Reptiles, amphibians, birds, mammals	7
81	5.0			22–24% of 100 *Banksia* species studied projected extinct	W. Australia	Plants	74
82[a]	6.9			50–57% of bird species at risk of extinction, and 19–30% projected extinct	Western Hemisphere	Birds	70

A novel climate is a climate which is significantly different from the present climate whilst a disappearing climate is a climate that disappears from a given area, for example on a mountaintop or a coastline where geography prevents a species from tracking the changing climate. For further details see Williams et al. (2007)
Sources: 1—Thomas et al. (2004a), 2—Hoegh-Guldberg (1999), 4—Hilbert et al. (2004), 5—Rutherford et al. (2000), 6—Leemans and Eickhout (2004), 7—Williams et al. (2003), 8—Theurillat and Guisan (2001), 9—Sheppard (2003), 10—Eliot et al. (1999), 11—Symon et al. (2005), 12—Hughes et al. (1996), 13—Preston (2006), 14—Zöckler and Lysenko (2000), 15—Ni (2001), 16—Bakkenes et al. (2002), 17—Still et al. (1999), 18—Benning et al. (2002), 19—Xenopoulos et al. (2005), 20—European Climate Forum (2004), 21—Cox et al. (2004), 22—Thuiller et al. (2005), 23—Thuiller et al. (2006), 24—Midgley et al. (2002), 25—Hannah et al. (2002), 26—Peterson et al. (2002), 27—Erasmus et al. (2002), 28—Villers-Ruiz and Trejo-Vazquez (1998), 29—Galbraith et al. (2002), 30—Beaumont and Hughes (2002), 31—Kerr and Packer (1998), 32—McDonald and Brown (1992), 33—Halloy and Mark (2003), 34—Moriondo et al. (2006), 35—Nicholls et al. (1999), 36—Najjar (2000), 37—Sorenson et al. (1998), 38—Johnson et al. (2005), 39—Broennimann et al. (2006), 40—Kaplan et al. (2003), 41—Theurillat et al. (1998), 42—Forcada et al. (2006), 43—Price and Root (2005), 44—Siqueira and Peterson (2003), 45—Pickering et al. (2004), 46—Scholze et al. (2006), 47—Raven et al. (2005), 48—Cox et al. (2000), 49—Orr et al. (2005), 50—Malcolm et al. (2006), 51—Peck et al. (2004), 52—Pounds et al. (2006), 53—Arzel et al. (2006), 54—Bosch et al. (2006), 57—Berry et al. (2005), 58—Lucht et al. (2006), 59—Schaphoff et al. (2006), 60—McClean et al. (2005), 61—Williams et al. (2007), 62—Durance and Ormerod (2007), 63—Hawkes et al. (2007), 64—van Vuuren et al. (2006), 65—Huntley et al. (2006), 66—Lensing and Wise (2007), 67—Ohlemüller et al. (2006), 68—Foden et al. (2007), 69—Cramer et al. (2001), 70—Sekercioglu et al. (2008), 71—Levinsky et al. (2007), 72—Memmott et al. (2007), 73—Huntley et al. (2008), 74—Fitzpatrick et al. (2008)
[a] Uniquely in this table, these five entries originate from a study which considers impacts by 2100 through a combination of climate change and land use change

Table 4 Projected impacts of climate change on various ecological systems and species as reported in the literature for different levels of global mean annual temperature rise ΔT_g, relative to pre-industrial climate (mean and range), showing also regional temperature change ΔT_{reg} relative to 1990 if provided by the literature: large-scale ecosystem collapse

No.	ΔT_g above pre-ind °C	ΔT_g above pre-ind °C (range)	ΔT_{reg} above 1990 °C (range)	Impacts to unique or widespread ecosystems or population systems	Region	Taxa	Source
83	2.5		2°C SST	Functional extinction of coral reef ecosystems (overgrown by algae)	Indian Ocean	Corals, fish	9
84	2.5	2.0–3.0		Major loss of Amazon rainforest with large losses of biodiversity	S America, Globe		21, 46
85	>2.5			Sink service of terrestrial biosphere saturates and begins turning into a net carbon source	Globe	Land ecosystems	58, 59
86	3.1	2.3–3.7	2°C SST	Functional extinction of remaining coral reef ecosystems (overgrown by algae)	Globe	Corals, fish	2
87	3.7			Few ecosystems can adapt	Globe		6
88	3.7			50% of nature reserves cannot fulfil conservation objectives	Globe		6

A novel climate is a climate which is significantly different from the present climate whilst a disappearing climate is a climate that disappears from a given area, for example on a mountaintop or a coastline where geography prevents a species from tracking the changing climate. For further details see Williams et al. (2007)
Sources: 1—Thomas et al. (2004a), 2—Hoegh-Guldberg (1999), 4—Hilbert et al. (2004), 5—Rutherford et al. (2000), 6—Leemans and Eickhout (2004), 7—Williams et al. (2003), 8—Theurillat and Guisan (2001), 9—Sheppard (2003), 10—Eliot et al. (1999), 11—Symon et al. (2005), 12—Hughes et al. (1996), 13—Preston (2006), 14—Zöckler and Lysenko (2000), 15—Ni (2001), 16—Bakkenes et al. (2002), 17—Still et al. (1999), 18—Benning et al. (2002), 19—Xenopoulos et al. (2005), 20—European Climate Forum (2004), 21—Cox et al. (2004), 22—Thuiller et al. (2005), 23—Thuiller et al. (2006), 24—Midgley et al. (2002), 25—Hannah et al. (2002), 26—Peterson et al. (2002), 27—Erasmus et al. (2002), 28—Villers-Ruiz and Trejo-Vazquez (1998), 29—Galbraith et al. (2002), 30—Beaumont and Hughes (2002), 31—Kerr and Packer (1998), 32—McDonald and Brown (1992), 33—Halloy and Mark (2003), 34—Moriondo et al. (2006), 35—Nicholls et al. (1999), 36—Najjar (2000), 37—Sorenson et al. (1998), 38—Johnson et al. (2005), 39—Broennimann et al. (2006), 40—Kaplan et al. (2003), 41—Theurillat et al. (1998), 42—Forcada et al. (2006), 43—Price and Root (2005), 44—Siqueira and Peterson (2003), 45—Pickering et al. (2004), 46—Scholze et al. (2006), 47—Raven et al. (2005), 48—Cox et al. (2000), 49—Orr et al. (2005), 50—Malcolm et al. (2006), 51—Peck et al. (2004), 52—Pounds et al. (2006), 53—Arzel et al. (2006), 54—Bosch et al. (2006), 57—Berry et al. (2005), 58—Lucht et al. (2006), 59—Schaphoff et al. (2006), 60—McClean et al. (2005), 61—Williams et al. (2007), 62—Durance and Ormerod (2007), 63—Hawkes et al. (2007), 64—van Vuuren et al. (2006), 65—Huntley et al. (2006), 66—Lensing and Wise (2007), 67—Ohlemüller et al. (2006), 68—Foden et al. (2007), 69—Cramer et al. (2001), 70—Sekercioglu et al. (2008), 71—Levinsky et al. (2007), 72—Memmott et al. (2007), 73—Huntley et al. (2008), 74—Fitzpatrick et al. (2008)

Table 5 Projected impacts of climate change on various ecological systems and species as reported in the literature for different levels of global mean annual temperature rise ΔT_g, relative to pre-industrial climate (mean and range), showing also regional temperature change ΔT_{reg} relative to 1990 if provided by the literature: miscellaneous impacts

No.	ΔT_g above pre-ind °C	ΔT_g above pre-ind °C (range)	ΔT_{reg} above 1990 °C (range)	Impacts to unique or widespread ecosystems or population systems	Region	Taxa	Source
89	0.6			Increased coral bleaching	Caribbean, Indian Ocean, Great Barrier Reef	Corals	2
90	<1			Marine ecosystems affected by continued reductions in krill possibly impacting Adelie and chinstrap penguin populations; Arctic ecosystems increasingly damaged	Antarctica, Arctic	Crustaceans	42, 11, 14
91	1.7	1–2.3	1°C SST	All coral reefs bleached	Great Barrier Reef, SE Asia, Caribbean	Corals	2
92	1.9	1.0–2.8		Most areas experience 8–20% increase in number ≥7 day periods with Forest Fire Weather Index > 45: increased fire frequency converts forest and Macquis to scrub, leads to more pest outbreaks	Mediterranean		34
93	2.0	1.3–2.3	1	21% decline in spring macro-invertebrate abundance in upland streams	UK	Invertebrates	62
94	2.1	1.0–3.2	1–2	Alpine systems in Alps can tolerate local temperature rise of 1–2°C, tolerance likely negated by land use change	Europe		8
95	2.2	–		Net primary production rises from 45–60 (pre-industrial) to 60–75 Pg C/year; net ecosystem production from zero (pre-industrial) to 2.5–7.5 Pg C/year	Globe		69
96	2.3	2.0–2.5		Fish populations decline, wetland ecosystems dry and disappear	Malawi (Africa), Great Lakes	Fish	20
97	2.4	2.0–3.5		4–20% of the earth's terrestrial surface experiences novel climate; 4–20% experiences disappearing climate	Globe		61
98	2.4	1.8–3.2	3	Extreme levels of mortality in loggerhead sea turtle	Southern US	Reptiles	63
99	2.6	1.6–3.5		Most areas experience 20–34% increase in number ≥7 day periods with Forest Fire Weather Index > 45: increased fire frequency converts forest and Macquis to scrub, causes more pest outbreaks	Mediterranean		34

100	2.8	1.2–4.5	1–3	Extensive loss/conversion of habitat in Kakadu wetland due to sea level rise and saltwater intrusion	Australia		10
101	2.8	2.5–3.0		Multimodel mean 62% (range 40–100%) loss Arctic summer ice extent, high risk of extinction of polar bears, walrus, seals; Arctic ecosystem stressed	Arctic	Mammals	11, 53
102	2.9	1.6–4.1		Threat of marine ecosystem disruption through loss of aragonitic pteropods	S Ocean	Crustaceans	49
103	2.9	1.6–4.1		70% reduction in deep-sea cold-water aragonitic corals	Ocean Basins	Corals	48
104	3.0			In a study of 1420 pollinator species feeding on 429 plant species, 17–50% experience disruption in food supply	Illinois, USA	Plants, insects	72
105	3.1	1.9–4.1	3–4	Alpine systems in Alps degraded	Europe		8
106	3.2	–		Net primary production rises from 45–60 (pre-industrial) to 72–93 Pg C/year; net ecosystem production from zero (pre-industrial) to 0–7 Pg C/year	Globe		69
107	3.3	2.0–4.5		Reduced growth in warm water aragonitic corals by 20–60%; 5% decrease in global phytoplankton productivity	Globe	Corals	2, 47, 48
108	4.0	2.5–4.5		12–39% earth's surface experiencing novel climate; 10–48% disappearing climate	Globe		61

A novel climate is a climate which is significantly different from the present climate whilst a disappearing climate is a climate that disappears from a given area, for example on a mountaintop or a coastline where geography prevents a species from tracking the changing climate. For further details see Williams et al. (2007)
Sources: 1—Thomas et al. (2004a), 2—Hoegh-Guldberg (1999), 4—Hilbert et al. (2004), 5—Rutherford et al. (2000), 6—Leemans and Eickhout (2004), 7—Williams et al. (2003), 8—Theurillat and Guisan (2001), 9—Sheppard (2003), 10—Eliot et al. (1999), 11—Symon et al. (2005), 12—Hughes et al. (1996), 13—Preston (2006), 14—Zöckler and Lysenko (2000), 15—Ni (2001), 16—Bakkenes et al. (2002), 17—Still et al. (1999), 18—Benning et al. (2002), 19—Xenopoulos et al. (2005), 20—European Climate Forum (2004), 21—Cox et al. (2004), 22—Thuiller et al. (2005), 23—Thuiller et al. (2006), 24—Midgley et al. (2002), 25—Hannah et al. (2002), 26—Peterson et al. (2002), 27—Erasmus et al. (2002), 28—Villers-Ruiz and Trejo-Vazquez (1998), 29—Galbraith et al. (2002), 30—Beaumont and Hughes (2002), 31—Kerr and Packer (1998), 32—McDonald and Brown (1992), 33—Halloy and Mark (2003), 34—Moriondo et al. (2006), 35—Nicholls et al. (1999), 36—Najjar (2000), 37—Sorenson et al. (1998), 38—Johnson et al. (2005), 39—Broennimann et al. (2006), 40—Kaplan et al. (2003), 41—Theurillat et al. (1998), 42—Forcada et al. (2006), 43—Price and Root (2005), 44—Siqueira and Peterson (2003), 45—Pickering et al. (2004), 46—Scholze et al. (2006), 47—Raven et al. (2005), 48—Cox et al. (2000), 49—Orr et al. (2005), 50—Malcolm et al. (2006), 51—Peck et al. (2004), 52—Pounds et al. (2006), 53—Arzel et al. (2006), 54—Bosch et al. (2006), 57—Berry et al. (2005), 58—Lucht et al. (2006), 59—Schaphoff et al. (2006), 60—McClean et al. (2005), 61—Williams et al. (2007), 62—Durance and Ormerod (2007), 63—Hawkes et al. (2007), 64—van Vuuren et al. (2006), 65—Huntley et al. (2006), 66—Lensing and Wise (2007), 67—Ohlemüller et al. (2006), 68—Foden et al. (2007), 69—Cramer et al. (2001), 70—Sekercioglu et al. (2008), 71—Levinsky et al. (2007), 72—Memmott et al. (2007), 73—Huntley et al. (2008), 74—Fitzpatrick et al. (2008)

used originally by the study to assess the impact. The process was repeated (1) for the other 12 GCM/emission scenarios and (2) for eight surrounding adjacent grid cells to test the sensitivity of the results in terms of spatial coherence when using a group of grid cells versus a single grid cell. For each GCM scenario, the average ΔT for the nine (central plus eight adjacent) grid cells was computed. The resultant collection of up to 13 global ΔT values gave the range of global annual mean temperature rise as listed in Tables 2, 3, 4 and 5. In cases where a study has referred to an area larger than a group of nine grid cells, either a cluster of disjunct groups or contiguous orographic features, such as a mountain range or a plain, were aggregated into several clusters of grid cell groups across the region. The entries in the tables reflect also the average and range of outputs over the appropriate clusters of groups of grid cells.

Large local temperature increases can lie outside the range of the outputs of the GCMs held in the database. If this was the case, the study was not included in the upscaling calculations. GCMs with temperature changes that were too low to reach the study value(s) were excluded. Table 6 in the Appendix details which GCMs were used in the upscaling. If more than two GCMs were thus out of range, we assumed case f (Table 1) to avoid underestimating ΔT_g. Note that the GCM time series for ΔT_g are provided with respect to an observed mean over the period 1961–1990, ensuring that correct temperature reference points were maintained in all upscaling.

3 Results

Tables 2, 3, 4 and 5 provide the resultant summary of key impacts on various ecological systems, ranging from the global level to that of individual, endemic species. The supplementary information in Table 6 in the Appendix provides for each entry from Table 2a–d information on the GCM runs used in upscaling, the climate variables considered by the impact study, and the category of the upscaling method we applied (a–h, see Table 1). 71 studies were found to provide sufficient quantitative climatic and ecological information for inclusion in Table 2a–d. Projected impacts were found for all major world regions, but only one study focused on Asia. Most studies were on terrestrial systems, whilst relatively few covered changes in the marine environment. Range losses and extinctions (Tables 2 and 3) were projected for many important taxa with vascular plants, birds, and mammals being particularly well represented. A significant number of studies also projected impacts on amphibians, reptiles, fish, butterflies, and freshwater or marine invertebrates. Table 2 also shows many projections for major losses of regional ecosystems as climate changes. Table 4 shows projections for large scale collapse in ecosystems, i.e. thresholds at which major components of the world's ecosystems become irreversibly damaged, positive feedbacks emerge, or their functioning, collapse. As global temperatures rise, many of these thresholds start to be crossed at around $\Delta T_g = 2.5°C$ above the pre-industrial level.

A key finding is that some significant negative impacts for range losses and extinctions (Tables 2 and 3), and also damages to marine ecosystems (Table 4), were projected to occur for values of ΔT_g below 2°C, especially in some biodiversity hotspots, and also globally for the diversity rich coral reef ecosystems ($\Delta T_g = 1.7°C$). However, it is also noticeable that, given the analyzed literature, projected impacts

increase in magnitude, numbers and geographic spread once a 2°C rise in global mean temperature is reached. Beyond this temperature rise the level of impacts and the transformation of the Earth's ecosystems become steadily more severe, with the potential collapse of some entire ecosystems, and extinction risks accelerating and becoming widespread. Additional positive feed-backs emerge causing land ecosystems to transition from their current status as a net carbon sink to a net carbon source.

4 Discussion

4.1 General

A large body of literature exists discussing the potential future impacts of climate change upon ecosystems, as reviewed in Fischlin et al. (2007). Much of this literature does contain only qualitative or no directly comparable quantitative projections of change or does not relate any quantitative estimates of change to quantitative changes in global climate. Previous integrating summaries of climate change impacts on wild species and ecosystems have suggested substantial ecosystem disruption with projected anthropogenic climate changes, and particularly the increased risk of species extinction (e.g. Thomas et al. 2004a, b). Such findings have been criticised partly because they did not reference the projected impacts to a consistent measure of climate change. In order to provide robust findings in a policy relevant manner, it is critical to reduce the uncertainty created by this lack of a common reference. Hence Warren (2006) and Hare (2006) both took steps to do so. The results reported here, through use of a common temperature reference point, confirm the likelihood of significant negative impacts of climate change first mooted in studies such as Thomas et al. (2004a, b), but provide a far clearer picture of the likely increase in scale of impacts with increasing levels of climate change, together with an indication of uncertainty associated with ΔT_g.

With our common referencing system, we can also address the question as to what extent the literature has sampled the range of climate change forcings of the next few centuries adequately for the observations made by this study to be valid. The likely range of temperature increase in 2100 is 1.1°C to 6.4°C above the 1980–1999 average (i.e. 1.6°C to 6.9°C above the pre-industrial level), showing that the literature currently does not sample the upper end of this range, with most studies considering only the range between 1.5°C and 4°C above pre-industrial). Within these limits however, a broad range of global annual mean temperature rises is sampled, owing to the many different scenarios and GCMs used. This is the case for those studies that are based on GCM scenario outputs as well as the many other regional scenarios based only upon potential local, non-GCM-scenario based climate changes. A small subset of the studies considers the effects of doubling CO_2 concentrations, whilst another subset is based on transient climate change simulations. Because different GCMs are used in these subsets, the resultant global mean temperature, and concomitantly precipitation, values vary considerably among climate models, in particular in cases where regional scenarios of climate change were derived. We believe the small subset of table entries referring only to CO_2 concentration doubling has not introduced a bias. Owing to a sampling of a relatively comprehensive temperature

range similar to that covered by many scenarios (0.3–6.4°C, IPCC 2007), the overall interpretation of the results is not biased by any artificial clustering of data around a particular global mean temperature rise.

The majority of the impacts found in the literature are negative, with the exception of those projecting increases in primary production. Whilst a higher productivity may indeed increase vegetation growth, this in itself can disrupt species assemblages and thereby degrade ecosystems. For example, in tropical forests increased concentrations of CO_2 are stimulating rapid growth by vines (Granados and Körner 2002), which can strangle large trees (Phillips et al. 2002); and increasing growth rate and turnover of trees could even result in lower carbon storage rates, thus reducing the forest's service as a carbon sink (Feeley et al. 2007). Hence, with the exception of enhanced growth at moderate climate change we have rarely identified definitively positive impacts of climate change upon ecosystems. Whilst some authors consider transitions from desert to grassland or grassland to forest as "positive" in terms of gains in net primary production, this often neglects the issue of transient dynamics between previous and new equilibrium, and threats to endemic and specialist organisms of the replaced environments. Some studies indicate transitionally an even lower productivity (e.g., Fischlin and Gyalistras 1997).

4.2 Uncertainties in the analysis

This study has considered the role of uncertainty only in a limited manner, as it is difficult to quantify. The uncertainty analysis carried out is limited by its dependency on downscaling and upscaling of pattern-scaled transient temperature outputs of GCMs, and thus is contingent on the assumptions of pattern regularity as assumed in most down-scaling procedures (e.g., Gyalistras et al. 1994), in particular that the patterns are constant over a particular temperature range. It is also assumed that the patterns are independent of the history of greenhouse gas forcing, whereas in actuality an equilibrium climate change pattern may differ from transient ones. Equilibrium patterns were not available for this analysis, but would be more suitable for use with studies of type b, or studies of type c or d which actually use outputs of equilibrium runs of GCMs. The uncertainty analysis also reflects only the different relationships between global and local temperature displayed by various GCMs, and not the relationship between global temperature and local precipitation changes. In some cases where impacts are strongly driven by precipitation and models differ widely for the location in question, for example entry 41, the loss of forest cover in the Amazon basin (Cox et al. 2004), this could be important.

Much of the literature reviewed here is based on a biogeographical or bioclimatic approach. Whilst this approach has been criticised for its shortcomings in largely ignoring some mechanisms such as physiological responses, the treatment of species–species interactions, the limited accounting for population processes or migration (Pearson and Dawson 2003; Pearson 2006), or the common assumption that current species distributions are in equilibrium with current climate, the approach has nevertheless proved capable of simulating known species range shifts in the distant and the recent past (Martinez-Meyer et al. 2004, Araujo et al. 2005), and furthermore, is generally corroborated by the observed responses of many species to recent climatic changes (e.g. Walther et al. 2002; Root et al. 2003; Rosenzweig et al. 2007) and climate-change induced changes in geographical species ranges, which are starting to

be reported (Thomas et al. 2006; Foden et al. 2007). However the approach remains nevertheless to be comprehensively and explicitly tested against the observational record (Midgley and Thuiller 2005), an opportunity that should be taken as soon as possible. Most of the studies reported in Tables 2 and 3 result from detailed analysis of well-studied species and ecosystems in a given locality. In the case of the global extinction rate estimates (Thomas et al. 2004a) there has been a debate as to the validity of the particular species–area relationship used to estimate extinction rates (Thuiller et al. 2004; Thomas et al. 2004b; Buckley and Roughgarden 2004; Harte et al. 2004; Lewis 2006). Whilst these estimates are based on extrapolation of studies of endemics, Thomas et al. (2004b) argue that this creates only a small bias because such a large percentage of global species are in fact endemics. The study of Malcolm et al. (2006) provides an overall estimate of extinctions of endemics in biodiversity hotspots that does not rely on bioclimatic modelling of individual species, and generally supports the findings of Thomas et al. (2004a), though the use of endemic–area relationships rather than simple species–area relationships indicates some reduced impacts.

Responses of species to changing climate will also be affected by biotic interactions, which affect the levels of space occupancy and dispersal; e.g. in alpine plant communities, mutualists are expected to be able to tolerate greater climate change than competitors at slow rates of climate change, whereas at faster rates they may be excluded by competitors if these can easily disperse into newly climatically suitable areas (Brooker et al. 2007).

4.3 Factors omitted or partly considered in this study and the underlying literature

4.3.1 Direct effects from raising atmospheric CO_2 concentrations

In Tables 2, 3, 4 and 5, the temperature column is essentially used as a proxy for the accompanying other changes, which will occur concurrently, such as precipitation change or elevated CO_2 concentrations. However, only a limited number of studies that project climate change impacts upon ecosystems consider concurrent changes such as the direct effects of elevated ambient CO_2 concentrations associated with local or global scenarios of temperature rise. This is particularly true of studies based on bioclimatic modeling, or niche-based modelling techniques that simulate species geographic range shifts. Despite increasing evidence that CO_2 fertilization effects on crop species have been somewhat overestimated in the past (Fischlin et al. 2007), those on wild plant species and particularly trees are corroborated by strong evidence (e.g., Ainsworth and Long 2005). This may remain a significant omission in the modeling of some ecosystem types. For example, CO_2 fertilization may differentially affect woody and herbaceous species, affecting the dynamics of forest–savanna–grassland conversions with major implications for biodiversity (Bond et al. 2003). Whilst a small number of entries in the tables derive from consideration of ocean acidification, the literature in this area is in its infancy. As oceans continue to acidify as atmospheric CO_2 concentrations rise concurrently with warming, there is significant potential for changes in marine food webs and hence the valuable ecosystem services that the oceans provide for humankind (Orr et al. 2005; Haugan et al. 2006).

4.3.2 Indirect effects of climate change

Tables 2, 3, 4 and 5, and the literature upon which they are based, largely document only the projected impacts on ecological systems resulting directly from climate changes such as changes in temperature and precipitation, the most commonly considered variables. However, there are a number of other impacts on ecosystems to be expected, that result from non climatic causes or indirectly via climatic changes. For example (1) wildfires and certain defoliating insects are projected to increase with warming (for example in boreal forests and the Mediterranean, e.g., Fischlin et al. 2007; Kurz et al. 2008), and decomposition rates will change by large percentages as rainfall changes (for example in deciduous forests in the USA, e.g. Lensing and Wise 2007) both of which is likely to have further impacts on forest and grassland ecosystems as well as causing substantive biotic feedbacks to the climate system; (2) secondary succession may last several centuries (Fischlin and Gyalistras 1997), thus delaying actual impacts and causing additional effects in other communities; (3) surprising ecological changes may also occur in marine and terrestrial communities with climate change if predators and prey become decoupled, or newly engage with each other, which could occur if they have differing phenological, geographical, and/or physiological responses to climate change (Price 2002; Burkett et al. 2005); (4) indirect impacts from sea ice melting, for example reductions in sea ice in the Antarctic are likely to have contributed to the dramatic 80% declines in krill observed since 1970 (Atkinson et al. 2004) with penguin populations already affected, and particularly if climate change shifts the Antarctic Circumpolar Current, krill could suffer further and the ecosystem could be severely impacted; (5) climate change is also projected to cause deglaciations, e.g. of the Himalayan region, which would adversely affect the hydrology of the downstream regions, e.g. of the Indian region including its ecosystems; (6) increases in the magnitude and/frequency of (intra-annual) extreme weather events are projected with climate change as climate variability increases (e.g. Schär et al. 2004; Meehl et al. 2007), all of which have a significant potential to affect ecosystems further (e.g. Fuhrer et al. 2006). Many impact models consider such effects only in a limited manner, e.g. because of a too coarse temporal resolution; (7) climate change may affect major modes of inter-annual cyclic variability such as El Nino, the North Atlantic Oscillation, or the Pacific Decadal Oscillation. GCMs do not capture such changes to a realistic extent and many impact models have only captured such climate variability effects to a limited extent if at all. Changes to these cycles are likely to affect ecosystems through for example, changed rainfall patterns and/or drought and fire incidence (e.g. Holmgren et al. 2001).

4.3.3 Land-use change

This meta-analysis focuses on the impacts of climate change and does not account for the effects of land-use change. More realistic impacts, notably those of species extinctions in 2100 and beyond, are likely to be greater than Tables 2, 3, 4 and 5 indicate, since land-use change is included in only one study (Sekercioglu et al. 2008), and is known to negatively impact biodiversity. These additional negative impacts from land-use change would only be avoided if effective stringent policies would soon be put into place that avoid further conversion of natural and semi-natural ecosystems to agriculture, landscape fragmentation, and/or other degradations within a

given type of land use as for instance also caused by intensification of agricultural practices. Owing to the development of human systems and their adaptation to climate change, including the potential use of biofuels as a mitigation measure, both of which may force new areas into cultivation, and the projected increases in global human populations, there are in fact rather to be expected increased pressures on extant land uses than the reverse. Some scenarios of future land uses have been developed for and reviewed in the Millennium Ecosystem Assessment (2005) and evince this overall trend.

Since land-use change is well known to be of critical relevance for biodiversity conservation, Lewis (2006) raised the concern that recent literature on potential extinctions due to climate change could distract conservationist's efforts in preventing land-use change in existing ecosystems, in particular with respect to avoiding deforestation. Jetz et al. (2008) projects losses of current ranges for 21–26% of the world's approximately 8,750 bird species by 2050, and for 29–35% by 2100, due to the combination of climate change scenarios from Solomon et al. (2007) and land-use change scenarios from the Millennium Ecosystem Assessment (MEA 2005). The need to provide for species to disperse successfully to reach areas that become newly climatically suitable increases the need for protecting existing ecosystems from land-use change. These findings suggest that avoided deforestation policies offer a crucial double benefit of reducing both climate change and land-use change impacts upon biodiversity. Thus, for these reasons we consider evidence that climate change can have severe impacts on biodiversity as presented in this analysis rather to provide an additional strong incentive for preserving existing ecosystems, including their protection from land-use changes, than an invitation to neglect conservation policies.

4.3.4 Dynamics

There are very few studies in the literature, which take into account the effect that the rate of climate change exerts upon ecosystems. This is also likely to be a key factor, since the slower the rate of change the greater is the potential for adaptation by dispersal or through natural selection for physical or behavioural characteristics better suited to a changed climate (for a recent review see Fischlin et al. 2007, notably Section 4.4.5). For very small amounts of warming there may be benefits in terms of increased productivity in ecosystems which are below their thermal optimum, for example in boreal forests. However, as temperature increases further the thermal optimum is passed, and the ecosystem begins to decline. It is the passing of such thresholds or "tipping points", the onset of negative impacts, which are the focus of the literature underlying this paper.

Some such "tipping points" are breached when a certain magnitude of climate change is reached. Regional features of the earth's climate system might also be disrupted, with concurrent un-quantified impacts upon ecosystems. For example, the Indian Monsoon might be disrupted (Zickfield et al. 2005). At the Earth system scale, as temperature continues to rise, additional positive feedback mechanisms may be activated. Examples are the saturation of the net carbon sink land ecosystems currently provide, the transition to a net source (Fischlin et al. 2007, Fig. 4.2), or the risk for the potential release of methane from tundra yedoma and permafrost (Fischlin et al. 2007) and perhaps beyond 2100 even clathrates from shallow seas. The weakening of the land sink, let alone the turning into a source, as well as a

release of substantive amounts of methane would cause a strong amplification of the greenhouse effect, greatly exacerbating the ongoing climate change.

Some such "tipping points" are breached when a certain rate of climate change surpasses the rate by which ecosystems can adapt naturally. During past phases of large climate changes, species have typically responded by shifting range rather than by evolving in situ (Davis and Shaw 2001). Ecosystems have been estimated to be able to withstand a temperature increase of only 0.05–0.1°C/decade (van Vliet and Leemans 2006), much slower than the current rate of 0.13°C/decade (Solomon et al. 2007) and hugely slower than the current rate near the poles of 0.46°C/decade, considered sufficient to cause serious ecosystem disruption. Foden et al. (2007) show how the currently observed migration rate of *Aloe dichotoma* (quiver tree), a Namib desert plant, in response to observed climate change, would be insufficient to keep pace with a moderate climate change scenario for 2050. Based on a comprehensive review of these issues Fischlin et al. (2007) concluded that "The resilience of many ecosystems is likely to be exceeded this century" for business-as-usual emissions scenarios (e.g. IS92a, A1FI, A2). Resilience is here understood as the capacity of ecosystems to adapt naturally and sufficiently fast to their changing environment without altering their mode of operation entirely.

This meta-analysis is based on impact studies that assume in many cases a new hypothetical equilibrium between the projected climate change and the impacted ecosystems. Typically the forcing climate change is then assumed to have remained constant indefinitely at the ΔT_g for which the impact was assessed and that the ecosystems are given sufficient time to adapt till the new estimated equilibrium has been reached. Most of the literature used in this analysis does not explicitly discuss the time dimension, but it can nevertheless be assumed in most cases that the ecosystem impacts in Table 5 might also occur if the temperature thresholds are breached transiently (i.e. local or regional temperature "overshoots") as simulated in various studies of the dynamics of climate change (O'Neill and Oppenheimer 2004).

Den Elzen and Meinshausen (2006) show that transient probabilities of exceeding various temperature thresholds might either be higher, or lower, than the equilibrium probabilities of exceedance of that threshold. Similarly Mastrandrea and Schneider (2006) show how probability of exceedance of temperature thresholds in stabilisation scenarios is a strong function of the pathway to stabilisation. Thus, one may argue that our assessment may indeed be questioned as the evolution of temperature and other concomitant climate change variables differ. However, the advantage of our approach is that the ranking of the impacts relative to the temperature increase as an indicator of climate change is unlikely to be affected even if the absolute values might have to be corrected as our understanding of these relationships progresses. In this respect our results can be viewed as being quite robust and conservative.

The question remains whether the impact models used have realistic sensitivities. Otherwise overestimations or underestimations of the impacts would have to be expected. The majority of the impact models we used here have considered changes in temperature as well as precipitation and many have also considered the beneficial effects from CO_2 fertilisation, in particular at the global level. This makes the models more likely to exhibit realistic responses to climate change than this was the case for many earlier studies, which followed less integrative approaches.

Nevertheless, the particular approach that many current state-of-the-art impact models follow may lead to biases. First in cases where the climate change was assumed to remain constant after having reached ΔT_g, the impact models that have

not yet reached the new equilibrium tend to underestimate the impacts. Secondly, if the magnitude of climate change exceeds rapidly certain tolerances, i.e. the fundamental niches, of impacted species, even long-lived species such as trees are likely to suffer mortalities before they are replaced by newly arriving, other species for which the new, climatic situations are more benevolent. Thus, in general the more rapid climate change, the more likely such transient ecosystem degradations become. Indeed, the modelling approaches generally followed do incompletely mimic such effects and for these reasons tend to rather underestimate than overestimate impacts. Finally, for other processes such as coral bleaching and local extinction of sensitive species, which can occur within a relatively short time span of a few years, transient temperature peaks might be very critical. If emissions are reduced in a manner such that there is transient overshooting of the final equilibrium temperature, impacts may then be considerably greater than indicated in Tables 2, 3, 4 and 5.

Therefore we consider the results from our meta-analysis to be in general rather conservative and it appears to be unlikely that they are biased towards overestimating the severity of the consequences of climate change for ecosystems. However, critical uncertainties remain, in particular because most impact models depend to a large extent on knowledge about the realized niches only. Should fundamental niches be significantly larger than the realized ones, overestimations of climate change impacts are bound to result. Indeed, the difficulties to assess the true fundamental niches of most species remain a relevant source of uncertainty (Kirschbaum and Fischlin 1996), a fact that still significantly constrains the ability of most currently used kinds of ecological models to assess climate change impacts.

5 Conclusions

A literature-based integrated assessment of the effects of climate change upon a wide range of ecological systems has shown that the negative impacts accrue as annual global mean temperature rise as little as 1.6°C (low end of the likely range of IPCC scenarios,[1] IPCC 2007) above the pre-industrial level, already with several examples of projected severe damages, range losses, and extinctions. As global temperatures reach and exceed 2°C above pre-industrial levels, negative impacts rapidly increase. This includes increases in range losses and extinctions and increasing damage to some critical ecosystem structure and functioning. As global temperatures increase further beyond 2°C above pre-industrial, the literature and models increasingly project impacts accruing to entire systems and becoming more widespread across a range of different species groups and regions. Several critical aspects of ecosystem functioning are projected to begin to collapse at a temperature of 2.5°C (Table 4). These represent either the potential collapse of entire ecosystems e.g. wide-spread impoverishment of coral reefs, or comprise impacts, which are in our judgement dangerous, because they likely imply irreversible damages, such as extinctions of key species, or the onset of positive feedbacks, such as CO_2 emissions, accelerating climate change. In our judgement, risking the widespread collapse of multiple global

[1]This value considers the multi-model projected lower end of the likely range of the IPCC SRES B1 scenario (IPCC 2007, Table SPM.3) of +1.1°C warming by 2100 relative to 1980–1999 and adding +0.5°C already realized global warming for period 1980–1999 relative to preindustrial climate.

ecosystems (Table 4) represents "dangerous anthropogenic interference" and would comprise a breach of compliance with Article 2 of the United Nations Framework Convention on Climate Change.

This meta-analysis confirms and expands upon the results of other assessments (Houghton et al. 2001; Hare 2006; Warren 2006; Fischlin et al. 2007), which have shown that climate change is a threat to ecosystems and species worldwide, with coral reef, Arctic, Mediterranean, and mountain ecosystems including many biodiversity hotspots being particularly at risk. Hare (2006) also identified substantial increases in risks to ecosystems and species beyond the EU 2°C target using "burning ember" diagrams. We consider that our study, with a more extensive literature review, using a tabular approach and including some uncertainty analysis, provides further strong justification for policies constraining annual global mean temperature change relative to preindustrial climate to no more than 2°C—at least from an ecosystem preservation point of view. This temperature would avoid the projected breaching of the aforementioned large-scale ecosystem collapses, as well as a large proportion of the onset of many of the projected negative impacts such as range losses, extinctions, ecosystem damages including disruptions of their structure and functioning. Since we identified some significant impacts in biodiversity hotspots such as amphibian extinctions in tropical forests and wide spread coral bleaching in reefs below a 2°C warming, protection of the majority of ecosystems would however require a more stringent target, as argued by Rosentrater (2005) for the Arctic.

Many of the impacts tabulated here appear to be clearly in conflict with Article 2 of the United Nations Framework Convention on Climate Change in not allowing ecosystems to adapt naturally. Minimising the rate of climate change is expected to also reduce the risks of climate change for ecosystems, although this aspect can not yet be well analysed with current techniques available to assess impacts. According to the precautionary principle it appears that a reduction in current and future land use change will give ecosystems and species the best chance to adapt to the climate changes that are projected to occur in the twenty-first century even under stringent mitigation policy. In particular, avoided deforestation is a policy which meets both these goals, although alone this policy is of course not sufficient to constrain climate change to 2°C above pre-industrial levels. Further analyses of many of the findings from this study made in an even broader context of climate change impacts on ecosystems can be found in Fischlin et al. (2007).

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Appendix

The Table 6 below contains detailed information concerning the underlying studies used in each entry of Tables 2–5, where column 1 is identical to column 1 of Tables 2–5, and the following abbreviations are used: **E** indicates an empirical derivation, **M** indicates a modelling study, a **number** refers to how many GCMs were used in the original literature. Other codes indicate if model projections included precipitation (**P**), ocean acidification (**pH**), sea ice (**SI**), sea level rise (**SLR**), sea

surface temperature (**SST**) or anthropogenic water use (**W**); dispersal assumptions from the literature. **D**—estimate assumes dispersal; **ND**—estimate assumes no dispersal; **NR**—not relevant since species/ecosystem has nowhere to disperse to in order to escape warming (e.g. habitat is at top of isolated mountain or at southern extremity of austral landmass). **IMAGE**, **BIOME4**, **LPJ**, **MAPSS** refer to specific models as used in the study, to assess climate change impacts, e.g. LPJ denotes the Lund–Potsdam–Jena dynamic global vegetation model (Sitch et al. 2003). **DVGM** refers to dynamic global vegetation model. GCM abbreviations used here: **H2**—HadCM2, **H3**—HadCM3, **GF**—GFDL, **EC**—ECHAM4, **CS**—CSIRO, **CG**—CG, **PCM**—NCAR PCM. Lower case a–h refers to how the literature was addressed in terms of up/downscaling and these are defined in Table 1. The GCM outputs used in the upscaling calculations are those used in the IPCC Third Assessment Report (TAR IPCC 2001) and are at 5° resolution: HadCM3 A1FI, A2, B1, B2 where A2 is an ensemble of 3 runs and B2 is an ensemble of 2 runs; ECHAM4 A2 and B2 (not ensemble runs); CSIRO mark 2 A2, B1, B2; NCAR PCM A2 B2; CGCM2 A2 B2 (each an ensemble of 2 runs). Where GCM scenario names only were provided further details were taken from: HadCM2/3 (Mitchell et al. 1995; Hulme et al. 1999; Arnell et al. 2004), http://ipcc-ddc.cru.uea.ac.uk.

Table 6 Supplementary to Tables 2, 3, 4 and 5: the table below contains detailed information on models and how the upscaling and downscaling were performed for each entry in Tables 2, 3, 4 and 5 and uses the same numbering scheme

Table no.	Entry no.	Details on type of study, models, model results, and methods used to derive the sensitivities as tabulated in Tables 2–5 for each table entry
2	1, 4, 9	M, 5, ND, c; ref. quotes 13.8% loss in Rocky Mountains for each 1°C rise in JJA temperature, upscaled with CS, PCM, CG
2	2, 15	M, 5, IMAGE, a; authors confirmed temperature baseline is year 2000 which is 0.1°C warmer than 1990
2	3	M, D, b; no GCM used in ref.; upscaled with H3, EC, CS, PCM, CG
2	14, 32	M, P, GDD, D&ND, a; ref uses B1 and A2 of H3 with ΔT rise of 2.4°C and 3.7°C respectively compared to the 1961–1990 mean
2	6, 7	M, P, NR, e; upscaled at several sites using H3, EC, CS, PCM, CG
2	5	M, H3, E4, P, D&ND, a; GFDL based estimates omitted due to lack of access to global temperature time series
2	10	M, H3, W, a; ref. uses B2 of H3 in 2070 that has a ΔT rise of 2.1°C with respect to the 1961–1990 mean
2	11	M, P, D, d; UKCIP02 high emission scenario used as central value; upscaled for Hampshire from UKCIP02 (Hulme et al. 2002) regional maps using H3, EC, CS
2	12	M, SLR, a; analysis based on transient 50% probability of sea level rise using the US EPA scenarios for ΔT of 2°C above 1990 baseline

Table 6 (continued)

Table no.	Entry no.	Details on type of study, models, model results, and methods used to derive the sensitivities as tabulated in Tables 2–5 for each table entry
2	13	M, H3, SLR, a; IS92a median ΔT 2.0°C above 1990 (Kattenberg et al. 1996, Fig. 6.20) and range 1.4–3.0°C
2	16	M, GE, P, NR, d; GENESIS GCM with 2.5°C rise for CO_2 doubling from 345 to 690ppm, 345 ppm corresponds quite closely to the 1961–1990 mean; upscaling then gives the range; across locations variously used H3, EC, CS, CG
2	17	M, NR, b; upscaled with H3, EC, CS, and CG
2	18	M, P, D, HadCM3, ECHAM4, GFDL, a; Huntley et al. (2006) give 2.5°C relative to 1961–1990 mean
2	19	M, 2, P, d, g; range is due to importance of ΔP, GFDL CO_2 doubling is from 300 ppm which is close to 1900 climate sensitivity in ref of 3.7; UKMO in 2050 is 1.6°C above 1961–1990 mean, 1.9°C above preindustrial
2	20, 21	M, H2, BIOME4, P, NR, c; A1 scenario of H2GS has ΔT of 2.6°C relative to 1961–1990 mean
2	22	M, BIOME3, P, d, f; H2 2080s has global ΔT of 2.6°C above 1961–1990 mean
2	23	M, H3, W, a; ref. uses A2 of H3 in 2070 that has a ΔT of 2.7°C with respect to the 1961–1990 mean and hence 2.5°C with respect to 1990
2	24	M, H3, GF, EC, P, D&ND, a
2	25	M, CS, P, d; upscaled with H3, EC, CS, CG
2	26	M, H2, SLR, NR, a; H2 2080s without aerosols has global ΔT of 3.4°C above pre-industrial (Hulme et al. 1999)
2	27	M, 2, P, D, d; study used CO_2 doubling scenarios—CCC ΔT at doubling is 3.5°C relative to 1900 whilst GFDL R30 is 3.3°C relative to 1900; upscaling gives range H3, EC, CG
2	28	M, D, b; upscaled with H3, EC, CS
2	29	M, CCC, P, D, d; CO_2 equilibrium doubling scenario has ΔT of 3.5°C relative to 1900; downscaled with CGCM and upscaled with H3, EC, CS, CG
2	30	M, 5, IMAGE, P,a; authors confirmed temperature baseline is year 2000 which is 0.1°C warmer than 1990
2	31	M, P, D (based on empirical calibration), d; upscaled with H3, EC, CS, PCM, CG
2	33	M, D, f; Meehl et al. (2007), Fig. 10.3.5 shows this occurs for ΔT ≥3.5°C above 1990
2	12, 34	M, D&ND, P, HadCM3, a; Ohlemüller et al. (2006) use HadCM3 projections quoted as ‘2.0, 4.8°C above 1931–1960 mean for entries 12, 34 respectively, add 0.1°C to convert to pre-industrial

Table 6 (continued)

Table no.	Entry no.	Details on type of study, models, model results, and methods used to derive the sensitivities as tabulated in Tables 2–5 for each table entry
2	35	M, 3, P, a
2	36	M, SLR, a; US EPA scenario of 4.7°C above 1990.
3	37	E
3	38	M, D&ND, a; 18% matches minimum expected climate change scenarios which Table 3 of Thomas et al. (2004a) lists as ΔT of 0.9°–1.7°C (mean 1.3°C) above 1961–1990 mean; 8 of 9 sub-studies used H2
3	39, 55, 71, 78, 82	M, D, a;
3	40	M, H2, P, ND, d; table 3 of Thomas et al. (2004a) gives global ΔT of 1.35°C above 1961–1990; HHGSDX of H3; downscaled with H3 then upscaled with H3, EC, CS, PCM, CG
3	41	M, H2, P, D&ND, d; Beaumont and Hughes (2002) give global mean temperature rise of 1.8°C relative to the 1961–1990 mean
3	42	M, D, P, a
3	43	M, D, b; upscaled using H3, EC, CS, PCM, CG
3	44	M, H3, P, D, d; H3 2050 SRES mean
3	45	M, H2, P, D, d, g; table 3 of Thomas et al. (2004a) gives global ΔT of 1.35°C above 1961–1990; upscaled with H3, EC, CS, PCM, CG; uses a local ΔT range across Australia
3	46	M, H3, P, D&ND, d; ref. uses B1 of H3 in 2050 with a ΔT of 1.8°C above the 1961–1990 baseline; downscaled with H3 and then upscaled with H3, EC, CG
3	47	M, H2, P, D&ND, d; studies used global annual mean ΔT of 1.7–2.0°C above 1961–1990 mean
3	48	M, P, D&ND, a; table 3 of Thomas et al. (2004a) mid-range climate scenarios have a mean ΔT of 1.9°C above 1961–1990
3	49	M, H2, P, D&ND, d; ref. refers to A2 of H3 in 2050 that has a ΔT of gives as 1.9°C above 1961–1990 (Arnell et al. 2004); downscaled with H3 then upscaled with H3, EC, CS, PCM, CG
3	50	H; upscaled using maps from WGI, chapter 10
3	51	M, 2, P, NR, d; scenarios on CRU website used with ΔT of 2.0°C above 1961–1990, agrees with Table 3 of Thomas et al. (2004a) which gives ΔT of 2.0°C above 1961–1990 mean; downscaled with H3 then upscaled with H3, EC, CS, PCM, CG
3	52	M, H2, P, D, d; the 66% is from a suite of 179 representative species, table 3 of Thomas et al. (2004a) lists global ΔT of 2.0°C above 1961–1990 mean, upscaled with H3, EC, CS, CG
3	53	M, H2, P, D&ND, d; table 3 of Thomas et al. (2004a) which gives ΔT of 2.0°C above 1961–1990 mean using HHGGAX; downscaled with H3 then upscaled with H3, EC, CS, PCM, CG

Table 6 (continued)

Table no.	Entry no.	Details on type of study, models, model results, and methods used to derive the sensitivities as tabulated in Tables 2–5 for each table entry
3	54	M, H2, P, ND, d; table 3 of Thomas et al. (2004a) which gives ΔT of 2.0°C above 1961–1990 mean using HHGGAX; downscaled with H3 then upscaled with H3, EC, CS, PCM, CG
3	56	M, IMAGE, P, D&ND; Bakkenes et al. (2002) gives the global temperature change relative to 1990
3	57	M, P, D&ND; ref. uses B1 in H3 in 2080s from (Arnell et al. 2004)
3	58	M, SST, h
3	59	M, H2, D&ND, d; ref. uses global ΔT of 2.3°C above 1961–1990 mean; downscaled with H3 and upscaled with H3, EC, CG
3	60, 76	M, P, D & ND, a
3	61	M, 15, SI, a; Arzel et al. (2006) uses 15 GCMs with A1B for 2080s, ΔT A1B 2080s multi-model from WGI, chapter 10, Fig. 10.3.2 is 2.5°C above 1990; ACIA uses 4 GCMs with B2, multi-model ΔT is 2.2°C over 1961–1990 or 2.0°C above 1990
3	62	M, P, D, HadCM3, ECHAM4, GFDL, a; Huntley et al. (2006) give 2.5°C relative to 1961–1990 mean
3	63	M, 10, P, D, d, g; Beaumont and Hughes (2002) give global mean temperature rise of 2.6°C relative to the 1961–1990 mean
3	64	M, P, D, ND, a; Table 3 of Thomas et al. (2004a) maximum climate scenarios have a mean ΔT of 2.6°C above 1961–1990 or 2.3°C above 1990
3	65	M, SST, h
3	66	M, P, NR, e; upscaled for several sites taken from maps in ref., using H3, EC, CS, CG
3	67	M, NR
3	68	M, 3, a, P, cloudiness, D & ND
3	69	M, NR, b; % derived from Table 1 in Benning et al. (2002) for all forest areas combined on the 3 islands studied; upscaling considers changes averaged over 3 islands and uses H3, EC, CS, CG
3	70	M, H3, P, D&ND, d, f; table 3 of Benning et al. (2002) lists global ΔT of 3°C above 1961–1990 mean
3	72	M, 7, BIOME3, MAPSS, P, D&ND, a; uses CO_2 doubling scenarios from Neilson and Drapek (1998) Table 2; control concentrations were obtained directly from modellers; thus deduced mean global mean ΔT for this study
3	73	M, H3, P, D&ND, d; ref. uses A2 in H3 in 2080 that has a ΔT of 3.3°C above 1961–1990 (Arnell et al. 2004)
3	74	M, H3, P, D, d, f; ref. lists ΔT of 3.6°C for A1 in H3 in 2080 relative to 1961–1990, downscaled with H3 and upscaled with H3, EC, CG

Table 6 (continued)

Table no.	Entry no.	Details on type of study, models, model results, and methods used to derive the sensitivities as tabulated in Tables 2–5 for each table entry
3	75	M, NR, b; upscaled with H3, EC, CG
3	77	M, NR, b, f; Meehl et al. (2007), Figs. 10.3.5 and 10.3.2 suggest global ΔT of 3.5°C relative to 1990
3	79	M, NR, b, f; Meehl et al. (2007), Fig. 10.3.5 shows this occurs for ΔT ≥3.5°C above 1990
3	80	M, NR, b, f
3	81	M, 3, P, a
4	83	M, SST, h
4	84	M, a
4	85	M, 2, P, LPJ; upscaled with H3, EC5
4	86	M, SST, h
4	87, 88	M, 5, IMAGE, a; authors confirmed temperature baseline is year 2000 which is 0.1°C warmer than 1990
5	89	M, 4, SST
5	90	E, SI
5	91	M, SST, h
5	92	M, P, NR, d; HadRM3PA2 in 2050, Fig. 13 in Moriondo et al. (2006) shows ΔT matching B2 of H3 of 1.6°C above 1961–1990 mean; downscaled with H3 and upscaled with H3, EC, CS, PCM, CG
5	93	M, P, D (based on empirical calibration), d, upscaled with H3, EC, CS, PCM, CG
5	94	E, P, D, b; upscaled using H3, EC, CS, PCM, CG
5	95	M, H2 with aerosols in 2050, a, 6 DVGMs, global temperature taken from Raper et al. (2001).
5	96	E, P, NR, a
5	97	M, a; Williams et al. (2007) use the B1 scenario from a mean of 9 GCM simulations used in IPCC (2007) which have a global temperature increase of 1–2.5°C averaging approximately 1.9°C above 1990 (hence 2.4 above pre-industrial)
5	98	M, d; upscaled using H3, EC, CS, PCM, CG
5	99	M, P, NR, d; HadRM3PA2 in 2050, taken from Fig. 13 of Moriondo et al. (2006)
5	100	M, CS, b; upscaled with H3, EC, CS, PCM, CG
5	101	M, 15, SI, a; Arzel et al. (2006) uses 15 GCMs with A1B for 2080s, ΔT A1B 2080s multi-model from WGI, chapter 10, Fig. 10.3.2 is 2.5°C above 1990; ACIA uses 4 GCMs with B2, multi-model ΔT is 2.2°C over 1961–1990 or 2.0°C above 1990
5	102, 103	pH, g; IS92a in 2100 has 788 ppm CO_2 and ΔT of 1.1–3.6°C above 1990
5	104	M, a;
5	105	E, P, D, e; upscaled with H3, EC, CS
5	106	M, H2 with aerosols in 2100, a, 6 DVGMs, global temperature taken from Raper et al. (2001)

Table 6 (continued)

Table no.	Entry no.	Details on type of study, models, model results, and methods used to derive the sensitivities as tabulated in Tables 2–5 for each table entry
5	107	pH, a; impact is at CO_2 doubling, T range given by IPCC (2007) for equilibrium climate sensitivity
5	108	M, a; Williams et al. (2007) use the A2 scenario from a mean of 9 GCM simulations used in IPCC (2007) which have a global temperature increase of 2–4°C averaging approximately 3.5°C above 1990 (hence 4°C above pre-industrial)

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RESEARCH ARTICLE

Climate-Related Local Extinctions Are Already Widespread among Plant and Animal Species

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Abstract

Current climate change may be a major threat to global biodiversity, but the extent of species loss will depend on the details of how species respond to changing climates. For example, if most species can undergo rapid change in their climatic niches, then extinctions may be limited. Numerous studies have now documented shifts in the geographic ranges of species that were inferred to be related to climate change, especially shifts towards higher mean elevations and latitudes. Many of these studies contain valuable data on extinctions of local populations that have not yet been thoroughly explored. Specifically, overall range shifts can include range contractions at the ªwarm edgesº of species' ranges (i.e., lower latitudes and elevations), contractions which occur through local extinctions. Here, data on climate-related range shifts were used to test the frequency of local extinctions related to recent climate change. The results show that climate-related local extinctions have already occurred in hundreds of species, including 47% of the 976 species surveyed. This frequency of local extinctions was broadly similar across climatic zones, clades, and habitats but was significantly higher in tropical species than in temperate species (55% versus 39%), in animals than in plants (50% versus 39%), and in freshwater habitats relative to terrestrial and marine habitats (74% versus 46% versus 51%). Overall, these results suggest that local extinctions related to climate change are already widespread, even though levels of climate change so far are modest relative to those predicted in the next 100 years. These extinctions will presumably become much more prevalent as global warming increases further by roughly 2-fold to 5-fold over the coming decades.

Author Summary

Climate change is an important threat to the world's plant and animal species, including species on which humans depend. However, predicting how species will respond to future climate change is very difficult. In this study, I analyze the extinctions caused by the climate change that has already occurred. Numerous studies find that species are shifting their geographic ranges in response to climate change, typically moving to higher elevations and latitudes. These studies also contain valuable data on local extinctions, as they document the loss of populations at the ªwarm edgeº of species' ranges (lower elevations

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and latitudes). Here, I use these data to show that recent local extinctions related to climate change have already occurred in hundreds of species around the world. Specifically, among 976 species surveyed, local extinctions occurred in 47%. These extinctions are common across climatic zones, habitats, and groups of organisms but are especially common in tropical regions (which contain most of Earth's species), in animals (relative to plants), and in freshwater habitats. In summary, this study reveals local extinctions in hundreds of species related to the limited global warming that has already occurred. These extinctions will almost certainly increase as global climate continues to warm in the coming decades.

Introduction

Anthropogenic climate change may be a major driver of biodiversity loss in the next 100 years, but the possible impacts of climate change on species survival remain highly uncertain [1±3]. Global mean annual temperatures increased by ~0.85ÊCbetween 1880 and 2012 and are likely to rise by an additional 1ÊCto 4ÊCby 2100 [4]. Modeling studies have predicted that various levels of species loss will result from this future climate change, ranging from 0% to >50% of all species currently known [3]. This uncertainty has many sources (e.g., different climate models and different hypotheses about species dispersal). One of the most important sources of uncertainty hinges on the details of how species respond to climate change. For example, if species can evolve rapidly enough in response to changing climate, then species extinctions due to climate change might actually be limited [5,6].

Species can potentially respond to climate change in several ways. The most important case to consider may be that when the species' present-day (realized) climatic niche no longer occurs within the species' current geographic range (because of the potential for global extinction of the species under these conditions). In this case, the possible responses of the species include the following: (i) undergoing niche shifts, such that the species' realized niche changes to incorporate these new climatic conditions (e.g., through plastic changes and/or by evolutionary adaptation to the modified abiotic and/or biotic conditions), (ii) dispersing to track the original climatic conditions over space (e.g., moving to higher latitudes or elevations), and (iii) going extinct [5±8]. While each of these responses has been shown in some cases (at least in local populations), the relative frequency of each is still unclear [7,8]. However, changes in species' geographic ranges have been especially well documented [9±11].

These data on geographic range shifts contain important but underutilized information on how species respond to climate change. Range shifts observed under climate change typically involve an overall shift towards higher latitudes and higher elevations [9±11]. These shifts can be composed of one (or both) of two types of changes (Fig 1): (i) range expansions at the cool edge of the species range (higher latitudes and elevations) and (ii) range contractions at the warm edge (lower latitudes and elevations). The presence of warm-edge contractions is critically important. A warm-edge contraction occurs when populations from one or more localities at the lowest latitudes or elevations of a species' regional distribution disappear (i.e., are inferred to no longer occur at those localities), leading to an overall shift in the species range towards higher latitudes or elevations. These contractions indicate that species are failing to shift their niches sufficiently to tolerate these new conditions and that these populations are instead going extinct (referred to as ªlocal extinctionº hereafter). This must be true regardless of the specific mechanism of local extinction (e.g., elevated death rates, increased emigration, or declining recruitment). The many papers that have assessed range shifts and that have included surveys of warm-edge populations can therefore provide a wealth of data about

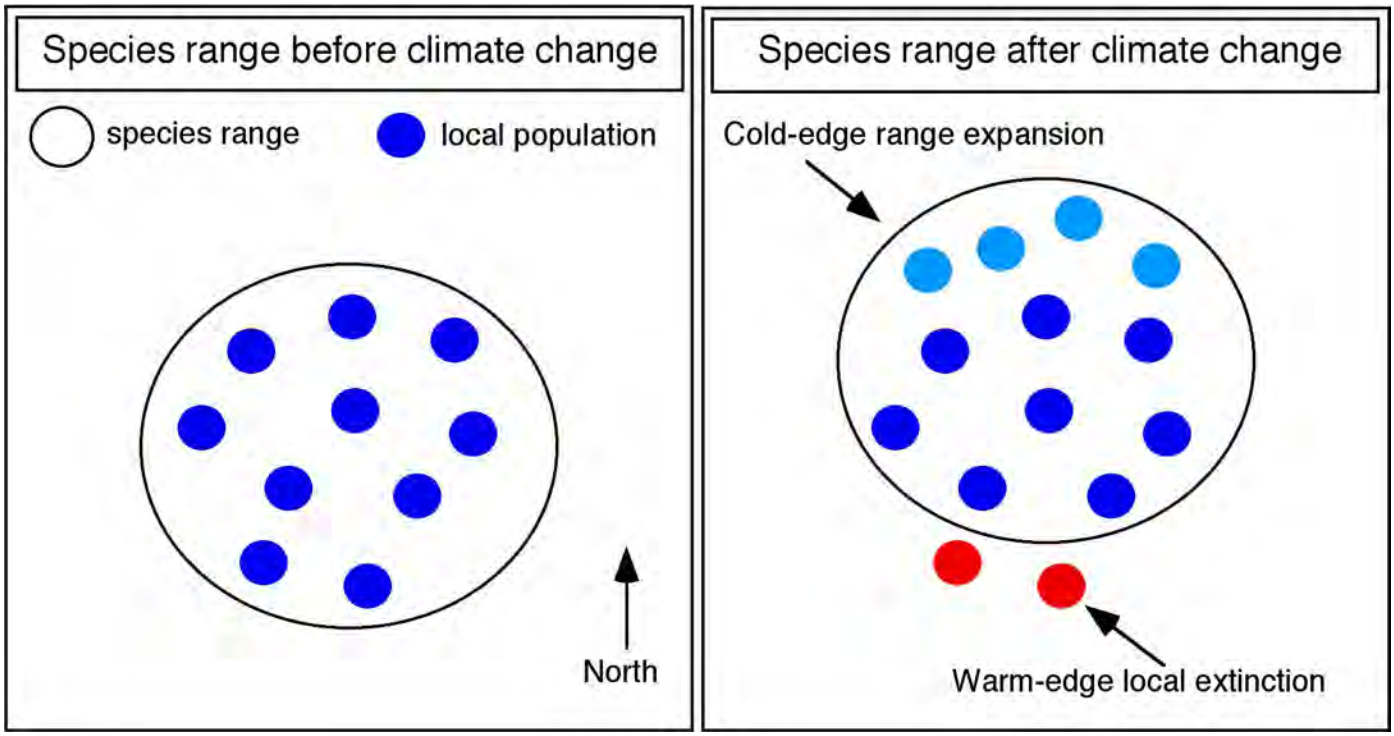

Fig 1. Hypothetical example illustrating the two components of a geographic range shift associated with climate change. The large open circle indicates the species' overall geographic range. Small dark blue circles indicate populations before climate change. After climate change, the overall geographic range is shifted northward (large open circle), both through the range expansion (new populations; small light blue circles) added at the northern, ªcoldº edge of the species range and range contraction (local extinction of original populations; small red circles) at the southern, ªwarmº edge of the species range. Similar patterns occur for range shifts along an elevational gradient. Modified from Cahill et al. [12].

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which species have (and have not) undergone local extinctions potentially related to climate change. These data are particularly useful because published papers on range shifts need not be strongly biased towards documenting warm-edge contractions, given that many studies that included data on warm edges also surveyed the cool edge. Thus, even though studies that failed to find any range shifts might go unpublished (a potential source of bias), studies that documented an overall range shift need not show a warm-edge contraction.

Here, I analyze the extensive data on range shifts to examine the prevalence of local extinctions related to modern climate change. I also provide a synthesis of inferred local extinction across habitats, climatic zones, and taxonomic groups. I systematically searched the literature for studies that examined shifts in species' ranges at their warm edges, shifts that were considered (in the original studies) to be related to current climate change. Hundreds of examples of local extinctions were found across diverse climatic zones, habitats, and taxonomic groups. Not all species exhibiting range shifts showed warm-edge contractions, but ~50% of the species surveyed had local extinctions inferred to be related to climate change. These results suggest that even the relatively small changes in climate that have already occurred are sufficient to cause widespread local extinctions and that many species may be unable respond to climate change fast enough to avoid extinction as global climate warms even further.

Results

The Web of Science was searched repeatedly between December 2014 and March 2016 using keywords related to climate change, range shifts, and local extinctions (see Materials and

Methods). All studies that monitored the warm edge of at least one species' range and that tied their results to climate change with explicit statistical analyses were included. Importantly, studies can document overall range shifts but need not find that the warm-edge populations that they examined had local extinctions.

A total of 27 studies (Table 1; [13±39]) met all the necessary criteria to address potential climate-associated warm-edge range shifts (see Materials and Methods). The sampled species were broadly distributed across clades (e.g., animals = 716; plants = 260) and regions (e.g., Asia = 332; Europe = 268; Madagascar = 30; Oceania = 58; North America = 233; South America = 55). Among the 976 unique species surveyed, 460 species had warm-edge contractions, and 516 did not (S1 Appendix). Therefore, local extinctions related to climate change are already very common (47.1% of species examined), even given the relatively modest rise in global temperatures that has occurred so far (less than 1ÊCincrease in global mean annual temperature; [4]).

These 976 species spanned many clades, habitats, and regions (Table 1; S1 Appendix). Comparison between those species that showed warm-edge contractions and those that did not provides potential insights into which species may be most sensitive to climate change, in terms of the climatic zones and habitats that they occur in and the clades that they belong to. Furthermore, there is no evidence that there were more species with local extinctions in studies that ended more recently, were of longer duration, or began earlier (based on midpoints for ranges of values; Table 1). Specifically, regression analyses of the proportion of species with local extinctions against (i) the study end date, (ii) the duration of the study, and (iii) the study start date all yielded nonsignificant results (end date: $r^2 = 0.001$, $p = 0.8910$; duration: $r^2 = 0.045$, $p = 0.2896$; start date $r^2 = 0.047$, $p = 0.2788$; after removing nine studies with four or fewer species: end date: $r^2 = 0.146$, $p = 0.1181$; duration: $r^2 = 0.132$, $p = 0.1376$, but unexpectedly trending towards fewer extinctions in studies with longer durations; start date $r^2 = 0.177$, $p = 0.0821$, with more extinctions in studies beginning more recently, not earlier). Therefore, the frequency of local extinctions was initially compared across species in different studies, regardless of differences in the duration, beginning, or end date of the study in which they were surveyed.

Overall, the frequency of local extinctions was similar (close to 50%) across most climatic zones, habitats, gradients, and clades. Nevertheless, there were some significant differences. First, local extinctions were significantly more common in species from tropical and subtropical regions (combined and referred to as tropical hereafter for brevity) than in those from temperate regions ($p < 0.0001$; Chi-squared test, testing the assumption of equal frequencies of local extinction among species between regions; subsequent p-values are also from Chi-squared tests). Specifically, 54.6% of the 504 included tropical species had local extinctions, whereas only 39.2% of the 472 temperate species did (Fig 2A). The pattern was even stronger when only considering terrestrial species on elevational gradients (54.6% of 504 tropical species versus 28.2% of 301 temperate species), which applied to all plants and most animals. In part, this pattern of more frequent tropical extinction arose from a much lower frequency of extinctions for temperate plants (59.4% of 155 tropical species versus 8.6% of 105 temperate species; $p < 0.0001$). The very low frequency of temperate extinctions in plants was based on a single study from very high latitudes [19]. Nevertheless, there were also significantly more local extinctions in tropical animals (52.4% of 349 tropical species versus 38.8% of 196 temperate species; $p = 0.0022$), if one compares terrestrial species on elevational gradients. This restriction also made them more comparable to the sampled plants (all from terrestrial, elevational gradients) and still encompassed most sampled animal species (76.1%; 545 of 716 species). Across all animals, the difference was not significant ($p = 0.2309$), possibly because of the influence of temperate marine and freshwater species (see below). Among the most well-

Table 1. Summary information on the 27 range-shift studies used to document local extinctions related to climate change. Studies are listed alphabetically by first author. The major taxonomic group surveyed is given (Taxon, all groups are animals except for ªPlantº), along with the total number of species surveyed (Total Species), the percentage of those species with one or more local extinctions (% Local Extinction), the general habitat type (Habitat; including terrestrial, freshwater, and marine), the climatic region (tropical-subtropical versus temperate), the geographic region where the study was conducted (note that North America here extends to Central America), the type of range shift (latitudinal, elevational), the dates of the initial survey and the resurvey, and the duration in between (for surveys and/or resurveys spanning multiple years, the midpoint of each was used to calculate the duration).

Reference	Taxon	Total Species	% Local Extinction	Habitat	Climatic Region	Geographic Region	Range Shift	Initial Survey	Resurvey Date	Duration
Angelo and Daehler [13]	Plant	4	50	Terrestrial	Tropical	Oceania (Hawaii)	Elevational	1966± 1967	2008	41.5
Beever et al. [14]	Mammal	1	100	Terrestrial	Temperate	North America	Elevational	1898± 1956	2003±2006	77.5
Brusca et al. [15]	Plant	27	56	Terrestrial	Tropical	North America	Elevational	1963	2011	48
Chen et al. [16]	Insect	208	56	Terrestrial	Tropical	Asia	Elevational	1965	2007	42
Comte and Grenouillet [17]	Fish	31	74	Fresh.	Temperate	Europe	Elevational	1980± 1992	2003±2009	20
Dieker et al. [18]	Insect	2	50	Terrestrial	Temperate	Europe	Elevational	1958± 1986	2008±2009	36.5
Felde et al. [19]	Plant	105	9	Terrestrial	Temperate	Europe	Elevational	1900	2008	108
Forero-Medina et al. [20]	Bird	55	29	Terrestrial	Tropical	South America	Elevational	1969	2010	41
Franco et al. [21]	Insect	3	100	Terrestrial	Temperate	Europe	Latitudinal	1970± 1999	2004±2005	20
Freeman and Freeman [22]	Bird	54	74	Terrestrial	Tropical	Oceania (New Guinea)	Elevational	1965	2012	47
Hiddick et al. [23]	Marine invertebrates	65	55	Marine	Temperate	Europe	Latitudinal	1986	2000	14
Hitch and Leberg [24]	Bird	1	100	Terrestrial	Temperate	North America	Latitudinal	1967± 1971	1998±2002	31
Menendez et al. [25]	Insect	39	54	Terrestrial	Temperate	Europe	Elevational	1981± 1993	2006±2007	24
Moritz et al. [26]	Mammal	27	41	Terrestrial	Temperate	North America	Elevational	1914± 1920	2003±2006	87.5
Myers et al. [27]	Mammal	8	12	Terrestrial	Temperate	North America	Latitudinal	1883± 1980	1981±2006	62
Nye et al. [28]	Fish	28	50	Marine	Temperate	North America	Latitudinal	1968	2008	40
Perry et al. [29]	Fish	10	40	Marine	Temperate	North America	Latitudinal	1997	2001	24
Ploquin et al. [30]	Insect	16	69	Terrestrial	Temperate	Europe	Elevational	1988± 1989	2007±2009	19.5
Pomara et al. [31]	Squamate	1	100	Terrestrial	Temperate	North America	Elevational	1965	2008	43
Raxworthy et al. [32]	Amphibian-Squamate	30	37	Terrestrial	Tropical	Madagascar	Elevational	1993	2003	10
Rowe et al. [33]	Mammal	4	25	Terrestrial	Temperate	North America	Elevational	1927± 1929	2006±2008	79
Rubal et al. [34]	Mollusca	7	29	Marine	Temperate	Europe	Latitudinal	1917, 1940	2011	94
Sheldon [35]	Insect	1	0	Terrestrial	Temperate	North America	Elevational	1977± 1978	2006	28.5
Telwala et al. [36]	Plant	124	60	Terrestrial	Tropical	Asia	Elevational	1849± 1850	2007±2010	159
Tingley et al. [37]	Bird	92	25	Terrestrial	Temperate	North America	Elevational	1900± 1930	1980±2006	78
Warren and Chick [38]	Insect	2	0	Terrestrial	Tropical	North America	Elevational	1973± 1974	2012	38.5

(*Continued*)

Table 1. (*Continued*)

Reference	Taxon	Total Species	% Local Extinction	Habitat	Climatic Region	Geographic Region	Range Shift	Initial Survey	Resurvey Date	Duration
Zuckerberg et al. [39]	Bird	31	71	Terrestrial	Temperate	North America	Both	1980± 1985	2000±2005	20

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sampled groups of animals, tropical extinction was significantly more common in birds (51.4% of 109 tropical species versus 37.1% of 124 temperate species; $p = 0.0284$), but not in insects (local extinctions in 55.2% of 210 tropical species versus 59.0% of 61 temperate species; $p = 0.6007$). For other animal groups, the species sampled here were either predominantly temperate (mammals, fish, and marine invertebrates) or tropical (squamate reptiles and amphibians), and so did not allow for similar within-clade comparisons.

Overall, the frequency of climate-related local extinctions (Fig 2B) was similar in terrestrial (45.6% of 835 species) and marine environments (50.9% of 110; $p = 0.2964$). In contrast, the frequency in freshwater species was substantially higher (74.2% of 31; $p = 0.0053$ across all three habitats). However, the estimate for freshwater species was based on a single study of European fishes [17]. Comparing fish only (all temperate) also supported a significantly higher frequency of extinction in freshwater environments relative to marine environments ($p = 0.0240$; local extinctions in 47.4% of 38 marine species versus 74.2% of 31 freshwater species). All marine species included here were temperate animals, but there was no significant difference in extinction frequencies between marine and terrestrial environments when only temperate animals were compared ($p = 0.1676$; marine: 50.9% of 110 species, terrestrial: 42.9% of 226 species). Terrestrial and freshwater species remained significantly different in this more restricted comparison ($p = 0.0011$).

The frequency of local extinctions (Fig 2C) was somewhat lower for species surveyed along elevational gradients relative to those on latitudinal gradients (elevational: 45.8% of 836 species; latitudinal: 55.0% of 140 species; $p = 0.0439$). Most (78.6%) species measured along latitudinal gradients were marine (and all marine studies focused on latitudinal gradients), and all were temperate. Again, most species included here were based on studies of elevational gradients in terrestrial environments.

Local extinctions were also broadly similar in frequency across taxonomic groups (Fig 3). Nevertheless, local extinctions were significantly more common ($p = 0.0018$) in animals (50.1% of 716) than plants (38.8% of 260). This difference was reduced when comparing only animals and plants on terrestrial, elevational gradients (47.3% of 556 animal species versus 38.8% of 260 plant species; $p = 0.0236$). Among these latter species, the plant±animal difference was nonsignificant for tropical species (and was actually reversed: local extinctions in 52.4% of 349 tropical animal species versus 59.4% of 155 tropical plants; $p = 0.1500$) but was strong for temperate species (38.6% of 207 temperate animal species versus 8.6% of 105 temperate plants; $p < 0.0001$).

The frequencies of local extinctions across different animal groups (Fig 3) were broadly similar to the overall value for animals (50.1%), but with higher values in insects (56.1% of 271 species; based on six studies; Table 1) and fish (59.4% of 69 species; three studies) relative to mammals (35.0% of 40 species; four studies), birds (43.8% of 233 species; five studies), amphibians (36.8% of 19 species; one study), and squamate reptiles (lizards and snakes; 41.7% of 12 species; two studies). Local extinctions were also broadly similar in frequency in various groups of marine invertebrates, including crustaceans (46.7% of 15; one study), annelids (64.5% of 31; one study), and molluscs (45.4% of 22; two studies). The frequency in echinoderms was lower (25.0%; one study) but was based on a very small sample size (4 species).

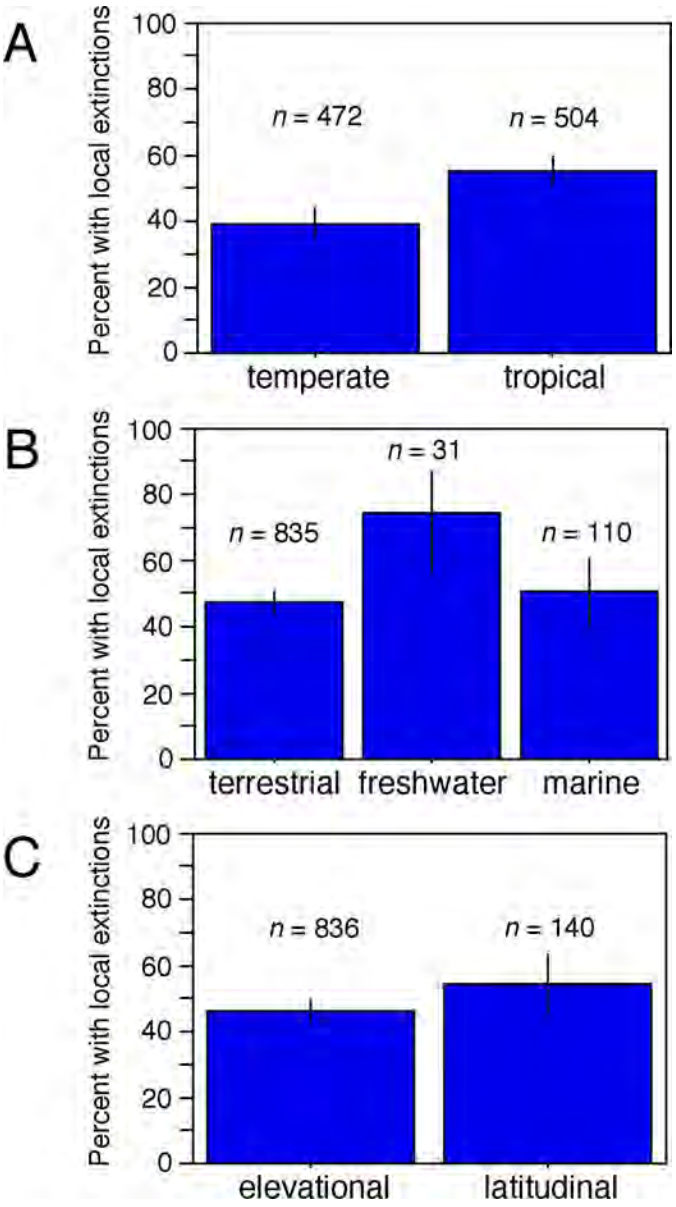

Fig 2. The frequency of local extinctions related to climate change across different climatic regions, habitats, and gradients. (A) Species are categorized as temperate or tropical (based on the location of the study), and the percentage of species with one or more local extinctions is shown, along with the sample sizes of species in each region. (B) Species are categorized as terrestrial, freshwater, or marine, and the frequency of species with local extinctions is shown (along with total species per habitat). (C) Species are categorized based on whether they were surveyed along elevational or latitudinal transects. Vertical lines indicate 95% confidence intervals on the estimated frequency of species with local extinctions.

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Results were generally similar using both general linear models (GLMs; see below) and general linear mixed models (GLMMs; see next paragraph). GLM results are given in full in S2 Appendix and are summarized here. Simultaneously including all 976 species and most variables (habitat [terrestrial versus freshwater versus marine], climatic regions [tropical versus temperate], taxonomic group [plants versus animals], survey type [latitudinal versus elevational], and study dates [start date, end date, and duration in between]) showed that most

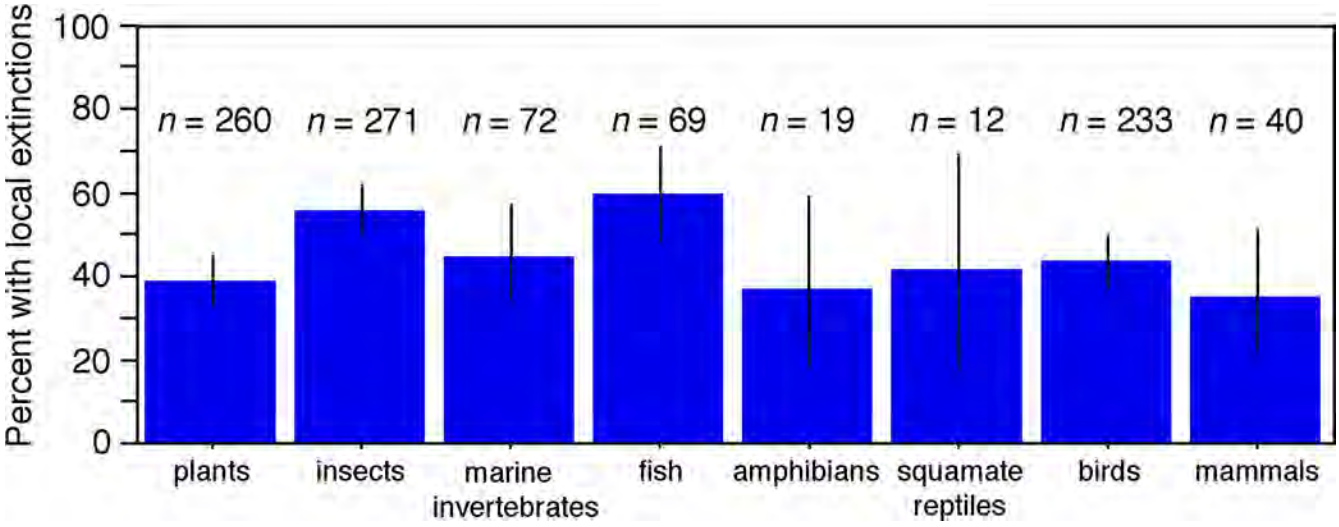

Fig 3. The frequency of local extinctions related to climate change across different taxonomic groups. The percentage of species with one or more local extinctions in each taxonomic group is shown, along with the total sample size of species surveyed in that group. For ease of presentation, four different groups of marine invertebrates (annelids, crustaceans, molluscs, and echinoderms) are shown together. Frequencies for these four groups were averaged to obtain a single value, and sample sizes of species across groups were summed. Squamate reptiles include lizards and snakes. Vertical lines indicate 95% confidence intervals on the estimated frequency of species with local extinctions.

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variables had significant effects on the frequency of extinction, except for the study dates. There were strong effects of habitat and climate ($p < 0.00001$) but weaker effects of taxonomic group ($p = 0.0246$). Results were similar when excluding study dates and taxonomic group. Including geographic regions showed that most regions had no significant effect (except for Madagascar and South America). Given that Madagascar and South America were represented by one study each, these region effects were not considered further. Furthermore, the effects of climatic region, habitat, taxonomic group, and survey type remained significant when geographic regions were included. Comparing species only on terrestrial elevational gradients (805 species in total) further confirmed the significant effects of climate and taxonomic group. Similarly, considering plants only (260 species) also confirmed the significant effects of climatic region. Considering only terrestrial animals on elevational gradients (545 species) showed a significant effect of climate ($p = 0.0023$) after removing study dates, which had no significant effect. Considering birds alone (233 species) and including climatic region, survey type, and study dates showed that climatic region, survey type, start date, and end date had significant effects. For insects (271 species), when including climatic region, study dates, and survey type, no variables were significant. For fish (69 species), a model including habitat (freshwater versus marine), study dates, and survey type showed that no variables were significant. However, habitat was significant if other variables were removed. Similarly, for temperate animals (367 species), a model including habitat, survey type, and study dates showed that only habitat and survey type were significant. Comparison of plants and animals on terrestrial elevational gradients (including study dates) showed that extinction is significantly different between temperate plants and animals (more common in animals), but not between tropical ones. Across animals, the effects of taxonomic group were limited and depended on the other variables included. If only taxonomic groups and study dates were included, then annelids, fish, and insects showed significantly more extinction ($p = 0.03 \pm 0.05$). Including habitat and survey type (and removing study dates) showed stronger effects in fish and annelids (as well as in crustaceans and molluscs), but not in insects.

Results were also broadly similar using GLMMs, with study identity included as a random effect. Results are summarized below and given in full in S3 Appendix. The impacts of study dates were somewhat counterintuitive (and rarely significant), and analyses including them sometimes failed. When most variables were included (habitat, climatic region, taxonomic group [plant versus animal], survey type, and study dates), all variables were significant except for study dates and taxonomic group, with strong effects of habitat, climatic region, and survey type. When study dates were removed, only habitat and survey type were significant. When geographic regions were included (and study dates excluded), only South America had a significant effect, and habitat, taxonomic group, and climatic region were significant or marginally significant. Comparing tropical and temperate species on terrestrial, elevational gradients showed significant effects of climatic region ($p = 0.0017$) and taxonomic group ($p = 0.0119$), but not of study dates. When study dates were removed, no variables were significant. Plants alone showed a significant effect of climatic region ($p < 0.0001$), but analyses failed if study dates were included. Animals on terrestrial, elevational gradients showed no significant effect of climatic region (again, study dates had to be excluded). Considering birds alone showed no significant effect of climate but a significant effect of survey type (excluding study dates). Insects showed no significant effects of climate or survey type, regardless of whether study dates were included. Analyses of fish failed unless study dates and survey type were excluded, but habitat alone (marine versus freshwater) had a significant effect ($p = 0.0265$). Analyses of temperate animals (367 species) including habitat, survey type, and study dates showed only habitat type as significant ($p = 0.0307$), but excluding study dates showed significant effects of habitat and survey type. Comparing only temperate plants and animals showed a significant effect of taxonomic group, when study dates were included ($p = 0.0116$) or excluded ($p = 0.0005$; study dates had no significant effect). In contrast, there was no significant effect of taxonomic group when comparing tropical plants and animals (504 species total; excluding study dates). Analyses of animals alone showed no significant effect of taxonomic group.

In summary, several patterns emerged as significant across all (or most) analyses. First, there were significant effects of climatic region overall, with extinction more common in tropical regions. This was present in plants across all analyses and generally present in animals. Animals showed significantly more extinction than plants overall and when comparing temperate, but not tropical, species. There were significant effects of habitat on animals overall (higher extinction in freshwater), even when considering fish alone. Finally, GLM analyses showed some effects of taxonomic groups across animals (with higher extinction in fish and annelids) and possibly in insects, molluscs, and crustaceans. The GLMM analyses did not show these group effects, possibly because many animal groups are included based on a single study.

Discussion

The results of this study show that local extinctions (inferred to be related to climate change) are already widespread and have occurred in hundreds of species. Roughly half of the 976 species that were surveyed for range shifts showed evidence of local extinctions (47%). This proportion was surprisingly similar across diverse climatic regions, habitats, and taxonomic groups. The results here suggest that even the modest changes in climate that have occurred so far are enough to drive local populations in many species to extinction. The results here also suggest that local populations in many species cannot shift their climatic niches rapidly enough to prevent extinction. This pattern of widespread local extinction seems likely to become even more prevalent as the global climate warms further (by roughly 2 to 5-fold [4]) in the next several decades.

The results here showed generally similar patterns of local extinction across climatic zones, habitats, and clades. Nevertheless, most analyses showed that local extinctions were

significantly more common in tropical species (Fig 2A), in freshwater species (Fig 2B), and in animals. A greater impact of climate change on tropical species has been predicted by several authors (e.g., [40±42]). This prediction is related to the narrower climatic niche widths for temperature-related variables in tropical species that are associated with reduced temperature seasonality in the tropics (e.g., [43,44]) and lower rates of temperature-related climatic niche change in tropical species (e.g., [42]). The results here provide support for this prediction based on documented local extinctions that have already occurred: species in tropical regions had local extinctions more frequently than those in temperate regions (54.6% versus 39.2%), especially when species were compared on terrestrial, elevational gradients (54.6% versus 28.2%). This pattern was strongest in plants and when animals were compared on terrestrial elevational gradients. Overall, these results further support the idea that the negative impacts of climate change on biodiversity are more frequent (per species) in tropical regions [40±42], where biodiversity is highest.

Climate-related local extinctions were also similar in frequency in marine and terrestrial species (Fig 2B) but were more common in freshwater species (although freshwater habitats were represented by a single study). Freshwater species may be especially susceptible to changes in precipitation patterns (e.g., drought), which can substantially alter or eliminate their habitats (e.g., [45]), quickly resulting in local extinction. In contrast, marine species may experience less impact from changes in precipitation. Furthermore, they may be buffered from temperature changes because they can potentially adjust the temperatures that they experience by movement within the water column (more so than is possible for most freshwater species; [46,47]).

The frequency of local extinctions was also broadly similar across diverse taxonomic groups (~35%±60%; Fig 3), including plants, insects, fish, amphibians, squamate reptiles, endothermic vertebrates (birds and mammals), and many marine invertebrates (annelids, crustaceans, and molluscs). However, local extinctions were significantly more common in animals than plants (and animals are far more species-rich than plants). They were also relatively common in insects (the most species-rich group of animals) and fish (the most species-rich group of vertebrates). Local extinctions were not particularly common in amphibians (36.7%) or squamate reptiles (41.7%), although both groups were included here based primarily on one study [32]. Nevertheless, both groups appear to have been strongly impacted by climate change overall. For example, many amphibian species have undergone sharp declines and global extinctions, many of which are thought to be caused by an interaction between climate change and an infectious disease (chytrid fungus; [48]). However, these chytrid studies were not included here because they were not focused on surveying warm-edge populations over time. Similarly, local extinctions related to climate change have been documented in many lizard species [49]. Again, these were not included here because they were not based on a systematic survey of warm-edge populations. Nevertheless, if the species studied by Sinervo et al. [49] were included here, the frequency of local extinctions in squamates would go from 41.7% (of 12 species) to 77.4% (of 124 species), but with the caveat that their study focused on documenting local extinctions and so might overestimate this frequency. It should also be noted that the well-publicized declines in amphibian populations globally are not necessarily inconsistent with the frequency of local extinction observed here. For example, a global assessment of amphibian populations [50] noted declines in 43% of amphibian species (compare to the 47% of all species here with local extinctions and the 37% for amphibians), but these declines also included those unrelated to climate change (e.g., habitat destruction and overexploitation). Thus, the frequency of climate-related declines here is not necessarily an underestimation relative to the declines documented by the global amphibian assessment [50].

A major conclusion of this study is that populations of many species are already unable to undergo niche shifts that are fast enough to prevent local extinction from climate change. The

rate is emphasized here because even if the absolute amount of niche change needed to avoid extinction might be attainable, it might require more time to achieve than is allowed by the rapid pace of anthropogenic climate change. Given this result, and that climate is predicted to change even further in the near future, the persistence of many species might depend largely on their ability to successfully shift their geographic ranges to higher latitudes or elevations and remain within their original climatic niche. Indeed, the summary here shows numerous instances of cool-edge expansions (in 367 of 904 species, with cool edges that were stable in 371 others and contracted in 166 others).

Unfortunately, these movements may be impeded for many species by one or more factors. First, human impacts may prevent species from successfully dispersing (including agriculture, roads, and urbanization), or these human impacts may simply leave them no habitat to disperse to (e.g., [51,52]). Second, many species are already confined to islands, peninsulas, and mountaintops, where dispersal to higher latitudes or elevations may not be possible (e.g., [53]). Third, even if dispersal is unimpeded by human or natural barriers, it may simply occur too slowly to allow species to remain within their climatic niche (e.g., [54,55]).

The combination of these potential limits to dispersal and the widespread local extinctions documented here is troubling. However, the results here do not rule out the possibility that rapid niche shifts will occur in some populations of many species in the future, preventing global extinctions. Indeed, roughly half of the species surveyed showed no local extinctions, and most species had some populations that persisted locally (but again, this is under the limited climate change that has already occurred). The future persistence of species will depend on many factors [6,8], including rates and patterns of climate change at each location, dispersal, niche shifts, local climatic microrefugia [56], and the contribution of population-level niche width to species-level niche width (e.g., whether species are broadly tolerant or locally specialized to different climatic conditions across their ranges [44]). Most importantly, I suggest that the patterns of present-day local extinctions obtained from range-shift studies should be part of the evidence used to predict species persistence in the future.

There are several potential sources of bias that may have influenced some aspects of these results but should not overturn the major conclusions. First, "local extinction" means that individuals of a given species are entirely absent from a location that they previously occupied. However, it can be difficult to distinguish between extinction and a substantial decline in abundance that causes the species to go undetected at a given location (e.g., [57]), and studies did not necessarily provide statistical evidence for the absence of a species at a site. Here, the estimates of previous researchers were used, and it was assumed that they adequately documented local absences (otherwise, their estimates of range shifts would also be erroneous). Furthermore, strong declines that make a species undetectable at a given site might soon lead to local extinction. Second, there may be a bias in terms of unpublished results. Specifically, some researchers who monitored the warm edge of a population but failed to find any changes associated with climate change may not have published their negative results. Such a reporting bias would lead to overestimating the proportion of species experiencing local extinction in this study. Nevertheless, local extinctions were still documented in hundreds of species across regions and clades, even if there are hundreds of additional species in which these local extinctions did not occur. Additionally, numerous species (n = 171) showed evidence of a cool-edge expansion without a corresponding contraction in the warm edge. Thus, a species can undergo a range shift but without local extinction, which should limit this source of publication bias. Third, it was assumed that previous researchers correctly associated the patterns that they observed with climate change. In theory, other factors such as overharvesting or habitat destruction may have contributed to the observed local extinctions in some cases (e.g., [21]).

Again, the analyses here primarily assume that the main conclusions of these previous studies were not erroneous.

Finally, despite the widespread pattern of warm-edge contractions and local extinctions, 521 species showed no local extinctions at the warm edge, indicating that they have successfully persisted in the face of the climate change that has occurred so far. However, even these species might still go globally extinct when global climate changes further. Additionally, contrary to the overall trend, 54 species were documented here as having expansions at both their warm edge and their cool edge (6.0% of 904 species with data on both cool and warm edges). One scenario by which this may occur is if cool-edge limits are set by colder temperatures (allowing expansion as global climate warms) and warm-edge limits are set by low precipitation (allowing warm-edge expansion), given that precipitation may increase in some areas because of climate change [4]. Indeed, some studies have found evidence for warm-edge expansions through this mechanism [58]. It is also important to note that local extinctions related to climate change need not be confined to the warm edge of the species range and so might actually be underestimated here. For example, there could be climate-related local extinctions far from the warm edge that are associated with certain microclimates (e.g., equatorially facing slopes at the cool edge of a species range; [59]).

In summary, the results here show that widespread local extinctions (seemingly related to climate change) have already occurred in hundreds of species, with broadly similar patterns of extinction across diverse clades, habitats, and climatic regions. Importantly, levels of climate change so far are limited relative to those generally predicted for the next 100 years [4]. The results here suggest that many species are unable to shift their niches rapidly enough to prevent local extinction. This inference of climate change outpacing niche change supports predictions from other sources, including transplant experiments in plants [60], phylogenetic analyses of rates of niche change in plants and animals [42,61,62], and projections based on selection, heritability, and temperature tolerances in lizards [49]. Local extinctions from climate change might also impact species that many human populations depend on for food, such as grasses (e.g., wheat, rice, and corn [62]). More generally, this study demonstrates that analyses of range shifts can provide extensive data on local extinctions related to climate change that have already occurred. These local extinctions offer a potentially important but underutilized source of information for the challenging task of predicting patterns of species survival and extinction in the future.

Materials and Methods

Selection of Studies

Web of Science searches were initially conducted from December 2014 to April 2015 using the Boolean search terms Topic = (global warming OR climate change) AND Topic = (local extinction OR range contraction OR range shift). A second Web of Science search was conducted between April 2015 and May 2015 to identify additional studies potentially missed by the first set of keywords, using the search terms TS = (global warm* OR climate change) AND TS = (extinction* OR contraction* OR range shift*), excluding results from TS = (global warming OR climate change) AND TS = (local extinction OR range contraction OR range shift). Each set of Web of Science results was sorted by relevance and then binned into subsets of 50. Searching was ceased when less than 1 in 50 studies per subset was relevant (see below for criteria). Finally, a third Web of Science search was performed on 1 March 2016 to find more recently published studies. This third search used the keywords TS = (global warm* OR climate change) AND TS = (extinction* OR contraction* OR range shift*). A total of 1,530 results were found in this third search. Results were sorted by relevance, and the first 300 (~20%) were examined. The last 40 of these 300 included no relevant studies.

Some additional studies were also found that were listed as references in the papers identified by these initial Web of Science searches. The reference list was also checked against a recent review study [11], which also conducted thorough searches of the literature on climate-related range shifts. Three studies were added from that survey which were not initially included here. Finally, several relevant studies were also found in the survey of Gibson-Renemer et al. [63], which had similar rules for inclusion of studies. Although those authors did not conduct a systematic search of the literature (as done here), they nevertheless included five studies not found in the searches described above. These were also added here.

In theory, the fact that ªextinctionº and ªcontractionº were included as keywords might have biased the results to include more papers documenting local extinctions and range contractions than would be obtained from a search of range-shift studies that excluded these as keywords (possibly leading to overestimation of the frequency of local extinctions). However, this seems unlikely in practice. First, these were included as ªorº keywords, along with ªrange shifts.º Examining the keywords and titles of the 27 selected papers showed that most were focused on overall range shifts, with no mention of local extinction (extinction or extirpation are mentioned in the titles of only 4 of 27 studies and as keywords in only 4 of the 21 studies with keywords; ªcontractionº is mentioned in only 1). Furthermore, the fact that the survey results here were checked against another recent review on range shifts [11], and that three missing studies were added, also makes this potential bias seem unlikely. In other words, if many range-shift studies were missed because of this bias, they should have been added at that point.

Overall, these searches were extensive but may not be truly exhaustive. Regardless, many studies were found that documented local extinctions, and finding more studies that did so would not overturn this main conclusion.

Studies were included that monitored one or more populations at the warm edge of a species' range (the edge that is lower in elevation or closer to the equator) over a relatively long time span. Studies were only included that spanned an interval of at least 10 years. The mean study duration was ~50 years (range = 14 to 159; Table 1). Studies were included that related their findings on range shifts to climate change through an explicit statistical analysis (but noting that these inferences could still be incorrect, for example, if other factors instead of climate change caused local extinctions of a particular species). The included studies all documented populations along elevational or latitudinal transects at two or more discrete time points.

Some recent studies have inferred climate-related range shifts based on overall trends in latitudinal and elevational distributions across a large number of localities over time, rather than systematically resurveying specific localities at different time points (e.g., [64]). These studies are valuable for documenting range shifts in general but were excluded here, since they do not unambiguously represent local extinctions (because the overall patterns described might be driven solely by range expansions instead).

Categorizing Species

Studies that documented warm-edge range contractions (and that were linked to climate change by the authors of the original studies) were considered evidence of climate-associated local extinction, regardless of changes at the cool edge. Studies differed in whether they reported changes at the population level (e.g., [28,37]) or species level (e.g., [33]). The analysis here was conducted at the species level. Therefore, if populations of the same species differed in the pattern of their range shifts, the species was categorized as showing evidence of local extinction if at least one population did so.

Most species were included in only one study. However, the plant species *Anthoxanthum odoratum* was included by both Angelo and Daehler [13] (in Hawaii) and Felde et al. [19] (in

Europe). However, since this species is not native to Hawaii, it was excluded from the dataset of Angelo and Daehler [13], along with all other nonnative species in that study.

For each study, it was noted whether the range shifts were elevational or latitudinal, as well as the general habitat of the organisms (i.e., terrestrial, freshwater, or marine), the higher taxa to which they belonged, the specific geographic location of the study, and whether the species occurred in a tropical or subtropical region (arbitrarily defined as within 35Êof the equator) or in a temperate region (>35Ê).Species were assigned to these climatic regions based solely on the location where they were surveyed, rather than on their overall geographic range. Species were also assigned to taxonomic categories, including plants, insects, fish, amphibians, birds, mammals, and squamate reptiles (i.e., lizards and snakes), as well as marine annelids, crustaceans, echinoderms, and molluscs. The beginning and end dates of the study were also noted (e.g., the date of the initial survey and the subsequent resurvey) and were used to estimate the duration of the study. Some studies provided a range of dates for the start and/or end date. In these cases, the midpoint of each range of dates was used to estimate the start, end, and duration (Table 1). Data for all species are provided in S1 Appendix.

The studies included (Table 1) spanned many geographic regions (e.g., North America, South America, Europe, Asia, and Oceania). Many studies were conducted in North America (n = 13; here extending to Central America) and Europe (n = 8), but the actual number of species sampled was more broadly distributed among regions (e.g., Asia = 332; Europe = 268; Madagascar = 30; Oceania = 58; North America = 233; and South America = 55). Africa and Australia were not represented, although nearby Madagascar and New Guinea were. The numbers of temperate and tropical species included were nearly equal. Further, there was no clear hypothesis for why particular continents alone should be an important factor influencing the frequency of local extinctions (e.g., separate from temperate versus tropical effects).

Statistical Analyses

Chi-squared analyses were initially used to compare the proportion of climate-associated local extinctions across some categories (i.e., tropical versus temperate; freshwater versus marine versus terrestrial; and latitudinal versus elevational gradients), testing the null hypothesis that frequencies of local extinction were equal between these categories. A series of analyses were conducted to assess whether frequencies of local extinction were higher in tropical regions relative to temperate regions, after accounting for the potential influence of different habitats, gradients, and clades (see Results). Similar analyses were conducted to assess the impacts of different habitats and clades (i.e., plants versus animals). However, potential analyses were restricted by the available data. For example, it was not possible to compare the effect of tropical versus temperate climates on marine or freshwater organisms, since only temperate marine and freshwater species were included here. For this reason, different sets of analyses were conducted for each question.

These analyses were then repeated using GLMs and GLMMs, both in R. These analyses were implemented treating the presence of warm-edge local extinction in a species as the binomial, dependent variable. GLMM analyses were conducted using the R package *lme4* [65]. GLMM analyses treated the study (from which the species data were obtained) as the random variable and the other variables as the fixed variables. GLM and GLMM analyses initially included all species and all or most variables and were then restricted to smaller sets of species (and variables) to test additional hypotheses and reduce potentially confounding effects (as in the Chi-squared analyses).

Phylogenetic information was not incorporated here, since phylogenies and comparable branch lengths spanning all the included species were not available (especially species-level

phylogenies for fish, insects, plants, and marine invertebrates). Nevertheless, some analyses were conducted to assess patterns within and between clades (see Results).

Supporting Information

S1 Appendix. Data for the 976 species used in this study.
(XLSX)

S2 Appendix. Results of GLM analyses, showing variable coefficients.
(DOC)

S3 Appendix. Results of GLMM analyses, showing variable coefficients.
(DOC)

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Scale Dependent Behavioral Responses to Human Development by a Large Predator, the Puma

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Abstract

The spatial scale at which organisms respond to human activity can affect both ecological function and conservation planning. Yet little is known regarding the spatial scale at which distinct behaviors related to reproduction and survival are impacted by human interference. Here we provide a novel approach to estimating the spatial scale at which a top predator, the puma (*Puma concolor*), responds to human development when it is moving, feeding, communicating, and denning. We find that reproductive behaviors (communication and denning) require at least a 4× larger buffer from human development than non-reproductive behaviors (movement and feeding). In addition, pumas give a wider berth to types of human development that provide a more consistent source of human interference (neighborhoods) than they do to those in which human presence is more intermittent (arterial roads with speeds >35 mph). Neighborhoods were a deterrent to pumas regardless of behavior, while arterial roads only deterred pumas when they were communicating and denning. Female pumas were less deterred by human development than males, but they showed larger variation in their responses overall. Our behaviorally explicit approach to modeling animal response to human activity can be used as a novel tool to assess habitat quality, identify wildlife corridors, and mitigate human-wildlife conflict.

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Introduction

Understanding the spatial scale of organismal response to human development is critical to unifying basic and applied ecology. How animals respond to human activity can influence population and community dynamics [1,2], serve as the basis for designing wildlife reserves and corridors [3], and inform the mitigation of human-wildlife conflict [4,5]. This is particularly true for large carnivores because of their vast home range requirements, disproportionate impacts on community composition [6], and central role in reserve design efforts [3].

Among mammalian carnivores, declining habitat fragment size leads to a predictable loss order of species according to body size and other ecological characteristics [7]. Large predator avoidance of smaller habitat fragments leads to mesopredator release - an increase in smaller predators and a consequent decrease in small mammals and birds [2]. While the pattern of human development can be to parcelize habitat into distinct fragments of varying size, human development (particularly in early stages) often consists of lines and blocks of developed areas that do not completely circumscribe natural areas, but instead create a variegated mosaic of natural and developed land [8]. In such variegated landscapes, the scales at which important animal behaviors related to survival and reproduction become impacted by human development will likely influence patterns of ecological function and determine the efficacy of conservation planning.

Perceptions of risk often shape landscape use by animals [9]. Individuals must balance the potential rewards gained from attaining food with the potential cost of being killed or displaced by a predator. This holds true for large carnivores as well [10,11], who often avoid humans - a major source of mortality. The scale at which large carnivores avoid humans is likely to be influenced by the type of behavior under consideration. Evolutionary theory predicts that the strength of selection on a behavior will correlate with the fitness consequences of that behavior [12]. If a large carnivore is displaced from its kill near humans, it might lose a meal, but the same individual displaced from an established communication post or den site risks losing mating opportunities or offspring. As such, we predict that reproductive behaviors will have undergone stronger selection pressure than non-reproductive behaviors, thus requiring a larger buffer from human development than non-reproductive behaviors. Furthermore, we predict that types of human development that provide more varied sources of human interference will be given a wider berth (i.e. residences will be more strongly avoided than arterial roads). Around residences human activity can include car traffic, people walking and talking, dogs barking, nighttime lighting and many other

potential activities that might negatively impact pumas. In contrast, arterial roads in our area are largely limited to intermittent car traffic.

Here we provide a novel approach to determining the spatial scale at which a large carnivore, the puma (*Puma concolor*), responds to human development when it is moving, feeding, communicating, and denning. We test whether the scale of response is different for reproductive (communicating and denning) versus non-reproductive behaviors (moving and feeding) and discuss how such analyses might be used as the basis for evaluating habitat quality, identifying wildlife reserves and corridors, and mitigating human-wildlife conflict. While our focus is on the puma, our approach should generalize to many other carnivore species and possibly other taxa as well.

Methods

Ethics Statement

The puma capturing, handling and monitoring for this research were reviewed by the Animal Care and Use Committee at the University of California, Santa Cruz (protocol #Wilmc1101). Approval for capturing, handling and taking samples from pumas was granted by the California Department of Fish and Game.

Study Area

We conducted our study in the Santa Cruz Mountains of California (Fig. 1a). The mountain range is bounded by the city of San Francisco to the north, several urban municipalities to the east, mixed farmland and residential development to the south, and the Pacific Ocean to the west. Our 17,000 km^2 study area overlaps Santa Cruz, San Mateo, and Santa Clara counties with elevation ranging from sea level to 1155 m. Vegetation communities on the west side of the mountains are dominated by redwood (*Sequoia sempervirens*) and douglas fir (*Pseudotsuga menziesii*) at low elevations, with patches of grassland, live oak (*Quercus* spp.), and coastal scrub immediately adjacent to the ocean. At higher elevations, mixed oak, conifer, and madrone (*Arbutus menziesii*) forests predominate. The land on the east side of the mountains is hotter and drier, characterized by shrub communities on ridges and south facing slopes, and mixed oak and bay laurel (*Umbellularia californica*) on north facing slopes and valleys. The climate is Mediterranean with the majority of annual precipitation occurring between November and April. Average annual precipitation varies from 58 cm to 121 cm throughout the mountain range.

Land use within the study area is varied as well. Large state and county parks and privately-held properties create a mosaic of relatively vast and intact areas of native vegetation. These large properties are bisected by varying amounts of development, from urban to rural. A major freeway (Highway 17) divides the study area. Agricultural activity is limited, with small vineyards, vegetable farms, and ranching operations (varying from a few goats to a few hundred cattle) interspersed throughout the mountains and along the coast.

Puma Capture and Collaring

Pumas were captured from 2008–2011 using trailing hounds, cage traps, or leg-hold snares and anesthetized with Telazol (Fort Dodge Laboratories, Fort Dodge, IA, USA). Once anesthetized, pumas were sexed, weighed, measured, fit with an ear tag, and collared using a combined GPS/radio telemetry collar (Model GPS Plus 1D, Vectronics Aerospace, Berlin, Germany). Collars were programmed to take a GPS fix every 4 hours and had a mean ($\pm$ se) fix rate of 86% ($\pm$1%). Data were remotely downloaded from the collar every 4 weeks via UHF or, alternatively, transmitted via cell phone towers every 1–3 days depending on collar configuration. Predicted battery life varied from 1–2 years depending on battery size. We attempted to recapture all pumas whose batteries failed prematurely or were scheduled to run out and fit them with new collars and/or batteries.

Behavior Determination

Previous studies on pumas have explored behavior time budgets [13], minimum area requirements [14], dispersal of juveniles in fragmented habitat [15], and the relationship between urban development and puma presence [16,17]. We expand upon these studies by using GPS data combined with extensive field reconnaissance to determine the spatial location of pumas while exhibiting four behaviors chosen to reflect both reproductive and non-reproductive activities: feeding, moving, communicating, and denning, and how these are influenced by natural and anthropogenic factors.

Feeding. We defined feeding sites as locations where pumas were likely to have killed a large prey, typically blacktail deer (Odcoileus hemionus columbianus). North American pumas are a generalist predator but are heavily dependent on a diet of large ungulates to survive and reproduce. In the Santa Cruz Mountains, pumas kill deer roughly once a week. Previous work found that GPS data can be used to accurately predict the locations of large prey, defined as mammals >8 kg, but not of small prey [18]; thus we chose to restrict our definition of a feeding site to places where pumas killed large prey. To find these locations, we classified potential feeding sites by generating GPS position clusters using a custom program integrated in the Geographical Information Systems program ArcGIS (v.10; ESRI, 2010) using the programming languages R (v.2.1.3.1; R Development Core Team, 2010) and Python (v. 2.6; Python Software Foundation, 2010). We adapted the algorithm developed by Knopff et al. [18] and identified possible feeding sites when two points occurred within 100 meters and six days of one another. We then calculated the geometric center between those two points. We expanded the cluster and recalculated the center if an additional point was located within 100 meters from the center and temporally separated from one of the original points by no more than six days. We iterated this process until no more points fit that criteria and moved on to the next potential kill site. After a cluster was identified, the program determined several descriptive characteristics of the cluster including: the coordinates for the geometric center of all points, the total amount of time between the first and last point of the cluster, the total number of points in the cluster, the number of night points in the cluster, the ratio of night to total points, the ratio of points in the cluster to points not in the cluster during the same time frame, a binary variable identifying whether the cluster lasted for more than 24 hours (1) or not (0), the number of cluster points adjusted for the success rate of the location fixes, and the fidelity to the cluster (number of points in the cluster subtracted by points away from the cluster). For each cluster, we also calculated the minimum, maximum, and average distances of all points from the center.

We visited 224 potential feeding sites identified by the clustering algorithm. We investigated the sites in reverse chronological order from the date the data were downloaded. We attempted to visit clusters within two weeks of the puma leaving the site, but occasionally waited longer because of logistical constraints. We programmed the geometric centers of each cluster into handheld GPS devices we carried into the field. Before proceeding to the cluster, we examined the spatial configuration of the points to determine whether we noticed any clumping of cluster points. If there was additional grouping within a kill site, we visually

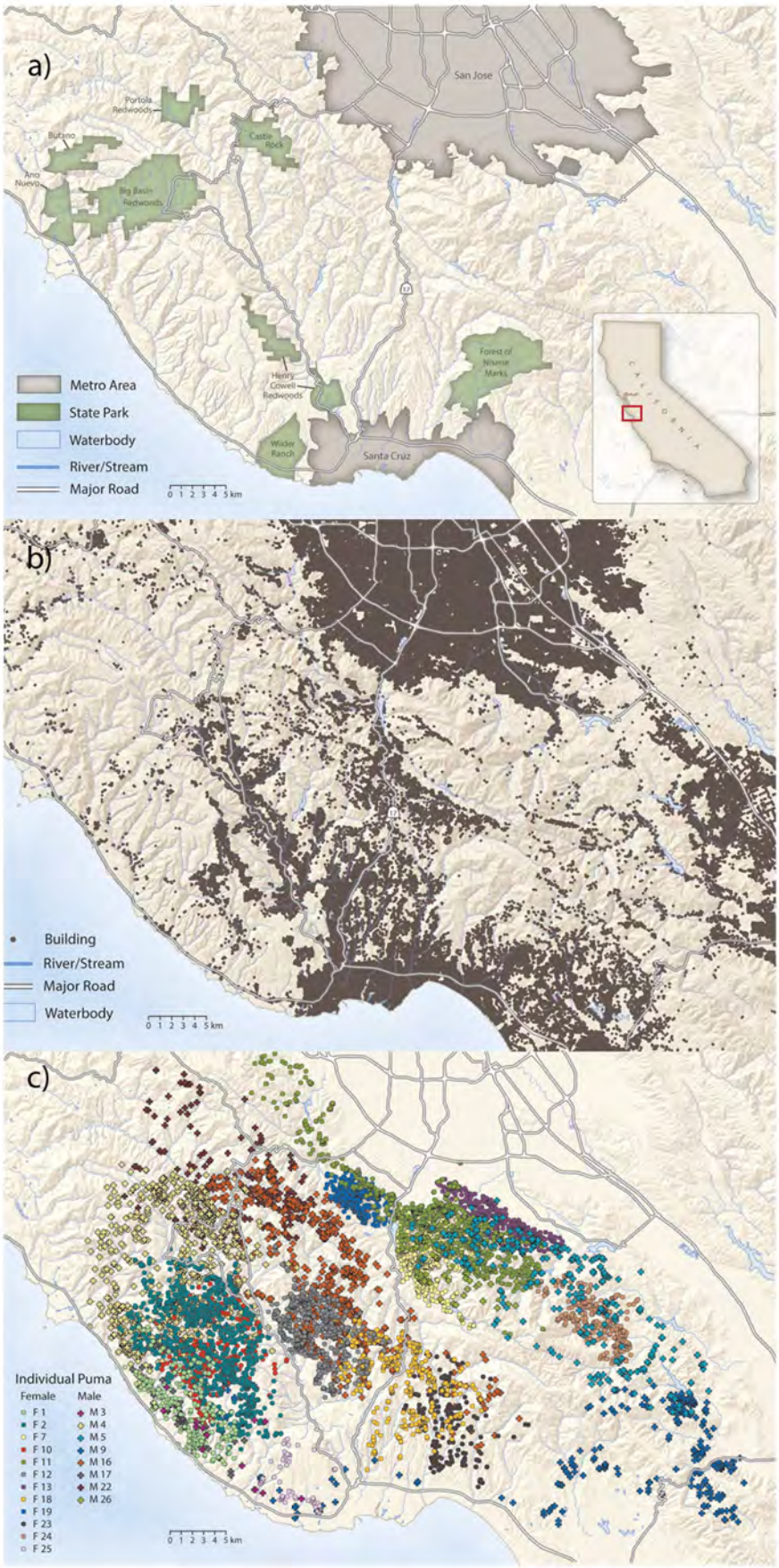
a)
San Jose
Portola Redwoods
Butano
Ano Nuevo
Castle Rock
Big Basin Redwoods
Forest of Nisene Marks
Henry Cowell Redwoods
Wilder Ranch
Santa Cruz
Metro Area
State Park
Waterbody
River/Stream
Major Road
0 1 2 3 4 5 km
b)
Building
River/Stream
Major Road
Waterbody
0 1 2 3 4 5 km
c)
Individual Puma
Female
Male
F 1
F 2
F 7
F 10
F 11
F 12
F 13
F 18
F 19
F 23
F 24
F 25
M 3
M 4
M 5
M 9
M 16
M 17
M 22
M 26
0 1 2 3 4 5 km

Figure 1. a) Map of the study area showing b) digitized housing locations and c) 4-hour movement locations of 20 pumas. Circles indicate females and pluses indicate males.
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estimated the centers and also programmed them into our GPS devices. We began our searches at the geometric centers of all clusters and spiraled outwards until we reached the maximum distance a point was recorded from the center. We searched each cluster for at least 30 minutes. If we located prey remains, we labeled it as a puma kill if the decomposition status matched the time-frame over which the cluster was generated. For each prey carcass we found, we determined the age class, gender and species.

Each cluster, y_i for $i = 1,\ldots, 224$, was coded as 1 if prey remains were found and 0 otherwise. We used a logistic regression model given by,

$$\begin{aligned} y_i &\sim Bin(1, p_i) \\ E(y_i) &= p_i \\ p_i &= \frac{e^{\beta_0+\beta_1 x_1+\ldots+\beta_n x_n}}{1+e^{\beta_0+\beta_1 x_1+\ldots+\beta_n x_n}} \end{aligned} \quad (1)$$

to estimate the probability, p_i, that a cluster was a kill using each of the cluster characteristics described above as predictor variables x with coefficients β. We selected the model with the lowest Akaike Information Criteria (AIC) [19] among all combinations of the predictor variables to estimate the probability that a cluster was a kill. We then used the intersection of specificity and sensitivity curves generated from the model as a break point in the probability [20]. Clusters with probability values above the break point were labeled as kills.

Movement. We defined movement locations as recorded GPS points not associated with a kill cluster or den site. Specifically, we removed all GPS points associated with a kill cluster (except for the first point to occur at the cluster) or den site from the GPS dataset. The remaining locations thus indicate periods when the pumas were likely moving or bedding.

Communication. Pumas communicate with each other through the use of scent markings called scrapes [21]. Scent marking is common among mammals and serves a dual purpose of advertising high competitive ability and attractiveness to the opposite sex [22]. Puma scrapes consist of a pile of leaves or duff that have been scraped together in a characteristic fashion on which they urinate [21]. The vast majority of scrapes are made by males, and are used to advertise their presence to conspecifics. Males will commonly scrape near trail junctions, ridges, kill sites, and on the sides of roads and trails. The same animals visit certain scrape locations that we call 'community scrapes' (defined as 3 or more scrapes within 9 meters squared of each other) repeatedly and mark adjacent to or on top of previous markings.

We located potential community scrapes using a modification of the custom program we developed for identifying kill sites, we located potential community scrape sites by finding clusters of male GPS locations where the male visited an area within 300 meters of a previous location two or more times, with visits separated by more than seven days. We then searched by foot all the trails, roads and ridge tops near the cluster. We recorded the actual GPS locations of each community scrape that we found with handheld GPS units. We also opportunistically recorded community scrapes in our extensive exploration of the study area while out investigating kill sites or trapping animals. Sites suggested by the GPS locations of returning males identified most of the community scrapes that we located. We maintained remote cameras at 44 (chosen so as to represent broad spatial coverage of the study area with different groups of pumas) of these sites for periods as long as 3 years, and in each case these were sites that were visited on a regular basis by territorial males. Females also visited community scrapes when looking for mates as evidenced by photographs of males and females together as well as GPS location data of males and females together.

Denning. Female pumas establish natal nurseries in thick vegetation or rock piles [21]. Females localize in these spots for a number of days after parturition and continue to return to the site for up to a few weeks until their offspring are mobile enough to change locations. We found dens by investigating female GPS data for clusters of points persisting for a week or more to which females made repeated return visits. In one case, the GPS unit on the puma's collar failed and so we located her den site by triangulating her location using VHF telemetry multiple times over several days. We then investigated these clusters between 4 to 6 weeks of the female first localizing there and recorded the location of where we found the kittens using a handheld GPS.

Statistical Analysis

We used resource selection functions (RSFs) under a use-availability design [23] to evaluate the relative puma preference for different habitat variables under each of the four different behavior types. The use-availability design generates relative probabilities of use by calculating the use of a habitat or environmental covariate relative to that covariate's availability to the animal. Preference, w, for environmental covariate, x, with coefficient, β, is often estimated using the exponential model,

$$w(x) = \exp(\beta_1 x_1 + \ldots + \beta_n x_n) \quad (2)$$

[24]. Different animals might respond differently to similar availabilities of environmental covariates, however. If this is the case, correct population-level inferences need to account for among individual differences [25]. This can be accomplished by adding a random effect which models variability among k pumas in their response to different covariates. The resulting mixed effects model thus allows for both conditional inferences about individual animals as well as marginal inferences about the population and correctly accounts for different sample sizes among individuals [26]. The model with interaction terms for the vector $\mathbf{x}$ of I covariates is given by,

$$w(x) = h^{-1}\left\{(\beta_0+\gamma_{0,k})\sum^{I}\left[(\beta_i+\gamma_{i,k})x_i\right] + x_i\sum^{I}\alpha_j x_j\right\} \quad (3)$$

for k pumas where the β's are fixed coefficients, γ's are normal random coefficients with mean 0 and covariance Ω, α's are fixed coefficients for interaction terms, and h is a log-linear link. We added an intercept term to the mixed effects model to allow for variation among pumas in sample size and selection probability [26]. We fit the model using the lmer package in R with a binomial link, which has been shown to provide accurate parameter estimates for log-linear models [27].

While variation in use patterns can be attributed to differences in behavior among individuals, they can also be caused by differences in the overall availability of habitat covariates among individuals [25,28]. As such, we tested for a functional response in

puma use of areas in relation to housing density by regressing the random coefficients from equation 3 corresponding to housing density against the mean level of housing density that each puma experienced.

We calculated 'use' locations (coded as a 1) as follows for each behavior: we coded movement 'use' as each GPS location not associated with a feeding cluster or den site, feeding 'use' as the center of each predicted kill cluster, communication 'use' as the location of each community scrape, and denning 'use' as the location of each den site.

We generated 'available' locations (coded as 0) by choosing random points from the movement paths of each puma. Specifically, we used a matched-case control design whereby for each movement 'use' location, we calculated 5 random 'available' locations by adding 5 random vectors to the previous 4-hour location. The angle of these vectors was chosen from a uniform $(0,2\pi)$ distribution, while the magnitude was sampled with replacement from a vector representing all the 4-hour movement distances, not associated with kill clusters, that the puma moved to during the period for which we collected data on it. In this way, we could then compare the actual location that a puma visited with 5 locations to which it could have visited. Data for which there was no GPS location 4 hours prior were discarded. Available locations for each behavior were then randomly sampled from this dataset such that a 5:1 ratio of 'available' to 'use' points was maintained for each behavior.

For the communication model, the sampling regime adopted to record 'use' locations resulted in some observations that were highly clustered in space and recorded in close proximity to one another. Data collected in this manner introduces spatial structure that can have detrimental effects on statistical inference and severely confound parameter estimates from regression models [29–31]. As such, to explicitly account for any latent spatial effects in the analysis, we adopted a spatial filtering framework based on spatial eigenvector mapping (SEVM) [32]. Also, because we could not definitively assign scrape locations to particular individuals, we conducted our RSF of communication at the population level only ($\gamma = 0$, eq. 3).

SEVM captures latent spatial structure in a dataset as a set of eigenvectors extracted from a connectivity matrix expressing spatial relationships among spatial units. Each eigenvector represents a synthetic covariate whose linear combination with other eigenvectors constitute a spatial filter, or a set of proxy variables that remove the inherent spatial structure from regression models by treating this spatial structure as a missing variable. In our implementation, we generated eigenvectors using Moran's Eigenvector Maps [33,34] based on a binary spatial weighting matrix with neighbor relationships constructed by connecting all points within a fixed distance threshold. To give more weight to short-distance effects, we defined the truncation distance using the intercept of spatial correlograms for residuals from spatially naive models. Eigenvectors were selected by adding each set to the model until the spatial autocorrelation of residuals, measured using a permutation based global Moran's I, were below a minimum desirable level ($p<0.05$). In this approach, we retained the eigenvector(s) best reducing spatial structure in our model and included them, along with other covariates, as predictors in the final specification. Calculations were performed using a modification of the spdep package in R [35].

Covariates. We included land cover, topographic, and fragmentation covariates as predictor variables in our models. All covariates were in a raster format at a nominal spatial resolution of 30 meters. We divided land cover into grassland, shrub, forest, and wetland cover types (US Geological Survey, Gap Analysis Program (GAP). May 2011. National Land Cover, Version 2). Pixels identified as agriculture were almost entirely rangeland. As such we collapsed these into our grassland cover type. For each pixel we also calculated its elevation, slope, aspect, and distance to the closest perennial water source.

Our human development covariates were derived from housing structures and roads. The location of each house or structure in the study area was digitized manually from high-resolution satellite imagery for rural areas, and calculated directly from a street address layer provided by the counties for urban areas (Fig. 1b). The reason for using two methods for digitizing house locations is that street address layers essentially provide the location of every mailbox, which for urban areas is typically quite close to the location of the house, while for rural areas might be up to a few kilometers away from the actual residence. The housing density of each 30 m×30 m pixel for our study area was then calculated from the housing points by applying a bivariate radially-symmetric Epanechnikov kernel with a scale parameter h to the location of each house and then summing the resulting densities at each 30 meter cell. The choice of h determines the width of the kernel and hence the relative strength of the housing impact as you move away from each house. At the landscape scale, large values of h result in housing density maps where the influence of human structures extends far into undeveloped land with a shallow slope. Small values of h, conversely, result in housing density maps where human influence falls off sharply when transitioning from human structures to undeveloped land. Consequently, different values of h will strongly influence the inference made about the impact of housing density on puma behavior. As such, we incorporated housing densities derived from multiple values of h varying from 10–2000 meters into our models and used model selection criteria to choose the best fitting h to the nearest 50 meters.

There are three broad categories of roads in our study area: arterial roads, which we define as roads with traffic speeds over 35 mph, neighborhood roads on which people live, and fire/logging roads which occur in undeveloped areas. Fire/logging roads are most likely an attractant to pumas because they facilitate travel, but we did not include these in our analysis because of the uneven accuracy of the data among properties. We also did not include neighborhood roads because these are highly correlated with housing locations such that our housing density layer captured the variance explained by neighborhood roads. For arterial roads, we included the distance to the nearest road of each location as a covariate.

For each behavior we fit models with multiple combinations of the predictor variables and chose the best models in each behavioral category as those that minimized the AIC. The scale of housing density which best fit data in each behavioral category was selected by finding the combination of covariates and housing density of scale h which minimized the AIC. We then evaluated our predictions by comparing housing density scales and slope coefficients (of the housing density and distance to arterial road variables) among behaviors. Due to the small sample size of den sites, we limited our analysis of this behavior to univariate fixed effect regressions of roads and housing density. Statistical models were fit using the lme4 package in R. All covariates were normalized $\left(\frac{x-\bar{x}}{std(x)}\right)$ to improve model convergence and to facilitate comparison of model coefficients among covariates. We also made sure that no candidate models had covariates exhibiting high levels of colinearity ($r>0.7$).

In order to illustrate possible extensions of our results, we used the resultant behavioral maps to predict corridors crossing Highway 17, – the major freeway and possible barrier to movement in our study area. We selected the largest patches

where communication and denning are unimpeded by housing density on either side of Highway 17. We then inverted and re-scaled relative use probabilities from our movement model to create a travel cost layer for pumas, which we used to calculate corridors of least-cost paths (using the Corridor function in ArcGIS 10.0) across Highway 17 between core areas.

Results

Here we report the results of data collected on 20 pumas (12 females, 8 males, see Fig. 1c for movement data). One of the males dispersed during the study period while the rest of the animals were residents. The mean (± se) number of days that we recorded location data from each puma was 203 (±28) days. We recorded 21,053 locations for a mean (± se) of 1052 (±166) locations per animal. We located 183 community scrape locations and 10 den sites from as many different females. Community scrape locations were distributed both near and far from male territorial boundaries.

We visited 224 GPS clusters and located prey remains at 115 of these. The model that best predicted ($\Delta AIC = 0$) whether a GPS cluster was a kill site included terms (coef, SE) for an intercept (−2.06, 0.42), binary variable identifying whether the cluster lasted for more than 24 hours (1.16, 0.41), fidelity to the cluster (0.05, 0.02), ratio of number of night points to total points (1.66, 0.56) and total number of night points (0.10, 0.07). The ability of the model to discriminate between kills and non-kills was 'excellent' as determined by an area of 0.80 under the receiver operator curve (ROC) [20]. Specificity (probability of correctly classifying a kill as a kill) and sensitivity (probability of correctly classifying a non-kill as a non-kill) curves intersected at a probability cut off of 0.485. This yielded a sensitivity of 70% and a specificity of 78%. At this cut off the algorithm predicted 105 kills. Applied to the entire GPS dataset, the algorithm predicted 667 kills.

The RSF analysis revealed that feeding, movement, communication, and denning were best fit by models with a housing density scale parameter, *h*, of 50 m, 150 m, 600 m and 600 m respectively (Table 1). These scales were not sensitive to which covariates were in the model (see supplemental information Table S1). At these scales, plots of the population level response of the relative probability of use in relation to housing density reveal an increasing negative slope as behavior changes from movement and feeding to communication and denning (Fig. 2). Housing density scale, *h*, influenced the magnitude of these coefficients, but comparison among behaviors at different scales still revealed strong differences (see supplemental information Table S1). The movement of pumas in response to housing density was variable, with males displaying a stronger aversion to houses than females (Fig. 3). Interaction terms also revealed that pumas were less deterred in their movement by housing when slopes were steep and more deterred by housing when near water. Arterial roads did not significantly influence puma movement, and were a small attractant to puma kill site selection ($\beta_{road} = -0.13$). Conversely, pumas selected against arterial roads when communicating ($\beta_{road} = 0.40$), especially in flat areas, and when denning ($\beta_{road} = 1.7$). The response of pumas to natural environmental covariates is detailed in table 1.

The final model for each behavioral category was used to generate spatial predictions of habitat use in relation to housing density for feeding (Fig. 4a), and communication (Fig. 4b). The mapped predictions reveal large-scale spatial differences between habitat appropriate for feeding and communication in relation to housing density. Maps of movement were similar to feeding, while maps of denning were similar to communication and are not displayed here. Corridor predictions based on the reproduction and movement maps correspond closely to where pumas have been documented to cross Highway 17 (Fig. 5).

Table 1. The best fit RSF model for each puma behavioral category (in italics).

	Fixed effects	**Coefficient**	**Std. error**
Feeding	gender	0.11	0.11
***h* = 50 m**	elevation	−0.60	0.11
	distance to road	−0.13	0.05
	grassland	−0.59	0.27
	housing density	−0.46	0.12
	gender x elevation	0.57	0.12
	Fixed effects	**Coefficient**	**Std. error**
Movement	gender	0.02	0.02
***h* = 150 m**	slope	−0.09	0.03
	elevation	−0.05	0.01
	distance to water	0.04	0.01
	grassland	−0.35	0.14
	forest	0.30	0.05
	shrub	0.30	0.05
	housing density	−0.51	0.09
	gender x housing density	0.32	0.11
	slope x housing density	0.15	0.03
	elevation x water	−0.05	0.01
	water x housing density	−0.09	0.03
	Random effects	**Variance**	**Correlation**
	housing density	0.03	
	slope	0.01	0.09
	Fixed effects	**Coefficient**	**Std. error**
Communication	housing density	−8.59	2.05
***h* = 600 m**	distance to road	0.40	0.15
	slope	−1.35	0.19
	road x slope	−0.85	0.19
	Fixed effects*	**Coefficient**	**Std. error**
Denning	housing density	−34.48	23.6
***h* = 600 m**	distance to road	1.70	0.52

*Coefficients estimated independently using univariate regressions due to low sample size.

Sample sizes for each analysis were as follows: Feeding –20 pumas, 667 kill sites; Movement –20 pumas, 21,053 movement locations; Communication –183 community scrapes; Denning –10 nurseries.

The scale, *h*, of housing density in the best-fit model is reported below each of the listed behaviors.

doi:10.1371/journal.pone.0060590.t001

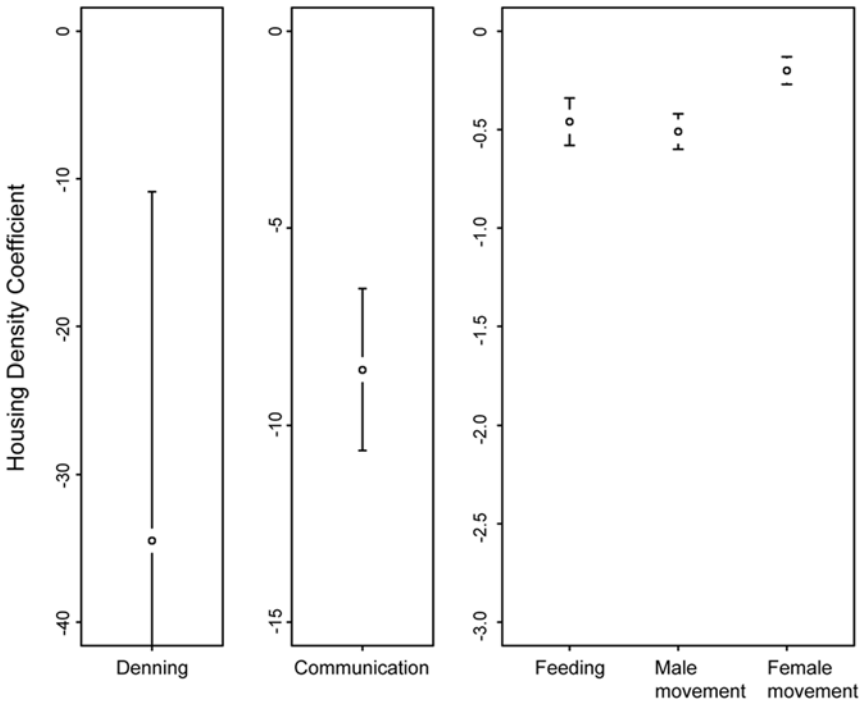

Figure 2. Relative sensitivities of each behavior to housing density as indicated by the fixed regression coefficient (± s.e.) of housing density in each behavioral model. These represent the relative log odds of pumas exhibiting each behavior for a unit change in normalized housing density holding other covariates constant. Note the difference in the y-axis scale among panels.
doi:10.1371/journal.pone.0060590.g002

Discussion

Our study examining the differential effects of human development on puma behavior revealed that pumas required a larger buffer from human development when exhibiting reproductive behaviors than non-reproductive behaviors. This is likely due to the fact that disrupting reproductive behaviors imparts a higher evolutionary cost than disputing feeding behaviors. As solitary animals with large home ranges, pumas use chemical and auditory cues to locate mates. These types of communication, however, are vulnerable to disruption by humans. Hikers, bikers and dogs can easily disturb chemical communication at scrape sites, which are often the first point of contact between males and females. Loud mating calls might also expose pumas to greater risk of disturbance or mortality from humans and/or dogs.

Previous work on puma movement has shown that pumas avoid residential development and 2-lane roads [16,17,36,37]. Furthermore, when they do move close to human dominated areas, their traveling speeds increase [37]. Interaction terms from our movement model indicated that pumas were more likely to use areas near houses when traveling on steep slopes and less likely to utilize areas near houses when close to water. These interactions likely reflect the pattern that human activity tends to increase near water sources and decrease on steep slopes. Pumas were also more deterred by houses than by arterial roads, indicating that they require a wider berth from more predictable sources of human interference. In fact, pumas only avoided arterial roads when they were engaged in reproductive activities and displayed no aversion when moving or feeding.

There was substantial individual variation in puma response to housing density. Females were less deterred by housing density than males and showed larger variation in their response overall. Similar to results by Kertson et al [16] and Burdett et al [17], neither sex displayed a functional response to housing density, indicating that tolerance of housing was not a function of its overall availability in their home range. Though we were not able to explain differences among males and females, we suspect that they are due to life history differences. Females caring for dependent young, especially large cubs with high energetic demands, are more likely to be food-limited than males, and might be attracted to neighborhoods where prey are more abundant. Males, conversely, are highly repetitive in their movements, moving between communication sites and seeking out females. Since communication sites are remote, this would lead to a lower variation in overall male landscape use in relation to human development. The one male that did show 'female-like' tolerance for human development was a dispersing animal, a life history stage during which pumas are known to exhibit tolerance for more developed areas as they seek out their own territories [15]. Thus it is likely that those animals most likely to take on the higher risk associated with developed areas are young pumas and females with large cubs. While individual pumas showed differential responses to housing density, they might also respond differently to the configuration of residential development. For instance development along a linear boundary might induce a different response than development that circumscribes habitat. Future work is thus needed to disentangle potential interactions between the density and configuration of residential development.

Pumas in our study responded to natural environmental covariates in a similar fashion as reported elsewhere [17]. They were generally attracted to shrub, forest and water, which provide good hunting and escape habitat, and were deterred by grassland [but see 38], which lacks effective stalking cover. We did not include a covariate for the spatial distribution of prey density because heavy forest cover, high housing densities, and rugged terrain precluded accurate estimation of this covariate. We note,

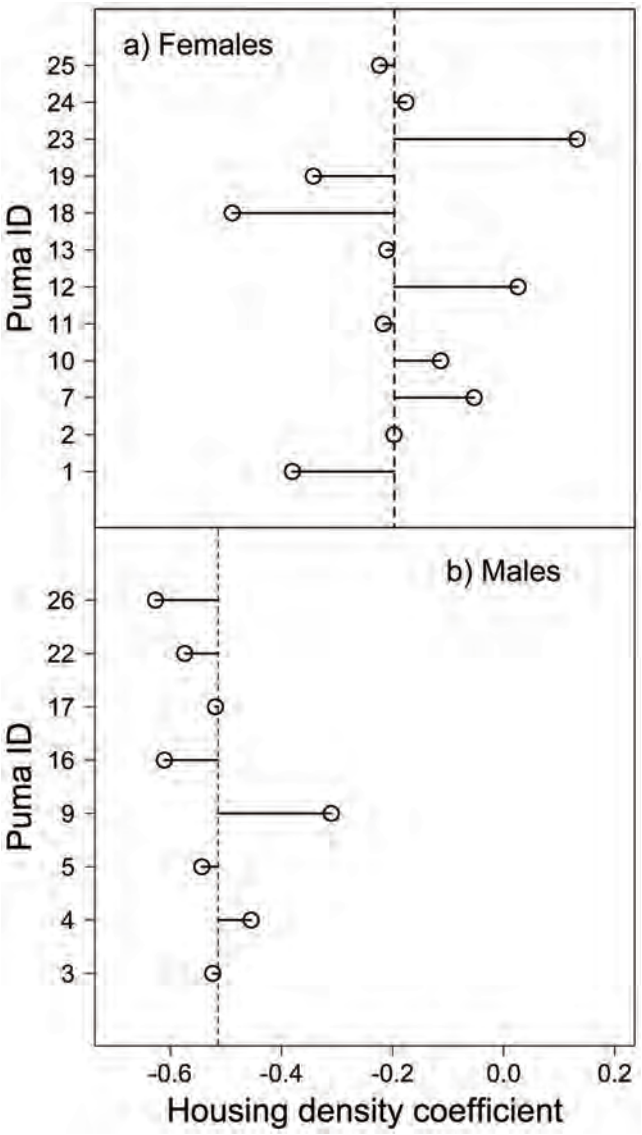

Figure 3. Estimates of the random effect coefficient of housing density for each puma are plotted in relation to the marginal prediction (dashed line) for a) females and b) males. Females were more tolerant of human development and displayed greater variation in their response than males, likely due to life history differences related to breeding and raising young. The sole dispersing male (M9) in our sample exhibited a tolerance of housing density more similar to that of females than other males.
doi:10.1371/journal.pone.0060590.g003

however, that deer, the primary prey of pumas in our study area, are known to be attracted to areas with higher housing density where they forage on high nutrient-irrigated gardens and landscaping [39]. As such, any bias induced in our model by not including prey density as a covariate would likely lead us to under predict the negative impact of human development on puma behavior.

Accurately measuring habitat quality is crucial to a variety of conservation and management issues. Recent work by Mosser et al. [40] using a 40-year spatially explicit dataset on African lion (*Panthera leo*) reproductive success and density revealed that areas of high reproductive activity were a better predictor of habitat quality than lion density, and that some areas of high lion density were actually population sinks. Common approaches to measuring habitat quality (such as RSF's of GPS location data), however, assume a direct positive relationship between population density and habitat quality. This can be problematic if some areas of high density are actually population sinks. Long-term datasets on reproductive success are exceedingly rare, however, while GPS data sets are increasingly common. Assuming that the spatial dependency of reproductive success correlates with reproductive behavior, the behaviorally explicit approach we have demonstrated here can be used to assess habitat quality by conducting an RSF on the spatial response of reproductive behaviors to human development and environmental covariates. While this assumption remains to be tested, it holds promise for improving rapid assessments of habitat quality using GPS location data combined with strategic field measurements.

An emerging goal among conservation practitioners is to identify movement corridors among patches of high quality habitat so as to ensure metapopulation persistence and allow for species range shifts under climate change [41]. Quantitative methods used to assess connectivity and define corridors such as least-cost modeling [42] and circuit theory [43] require the identification of both habitat patches and resistance landscapes. These are often determined using existing protected areas and expert opinion, respectively [44]. Our approach, conversely, explicitly defines these areas, whether they are currently preserved or not, using real data. Spatial predictions of reproductive behaviors can be used to identify core areas, while spatial distributions of relative movement probabilities can be inverted to define a resistance landscape. As illustrated in figure 5, the corridors we estimated using this approach accurately capture where pumas are crossing highway 17.

Areas of high human-wildlife conflict, where animals threaten livestock, crops or human safety, can be a significant source of animal mortality, and can help shape people's attitudes towards conservation [45]. This is evident from the mortality statistics for pumas in our study. Eight out of eleven adult puma mortalities to date were the result of depredations after pumas attacked domestic livestock. Similarly, Burdett et al [17] showed that pumas that selected for habitat nearer to humans had higher rates of mortality. Kertson et al [16] suggested that a threshold residential density exists at which puma-human interactions are likely to be maximized. Areas of intermediate feeding probability illustrated in Fig. 4a can serve as a predictive map of where such human puma conflict is most likely to occur. These are areas where pumas are moderately deterred by human development, but to which they will still make occasional foraging visits. It is during these visits that pumas are most likely to kill livestock (often pet goats in our area), and then be lethally removed by landowners for doing so. By identifying areas where conflict is most likely to occur, our model can help target education efforts designed to help landowners reduce losses of livestock to large carnivores, and consequently, reduce an important source of human-mediated large carnivore mortality.

The initial response by animals to anthropogenic changes in the environment is often behavioral [46]. By distinguishing the spatial response of distinct behaviors relevant to survival and reproduction in wild animals to human development, we are able to glean insights as to how animals are likely to respond to increased fragmentation in the environment and to identify strategic conservation regions. As new communities are planned, our analytical approach allows us to predict whether target species will cease communicating and denning, where human-wildlife conflicts are likely to take place, and how animals will use the landscape to move from one breeding area to the next. This approach can also

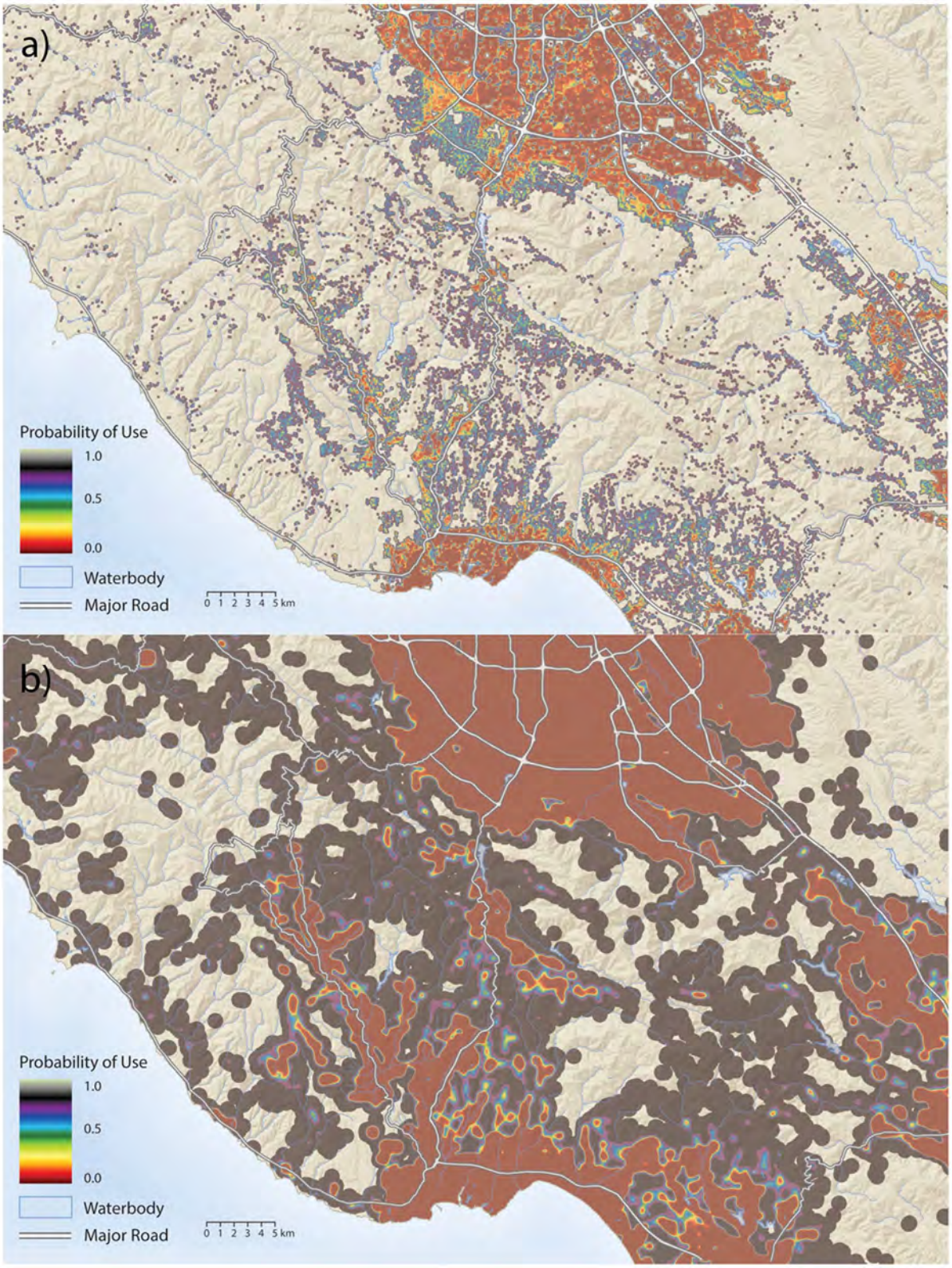

Figure 4. Maps of the study area displaying the relative probability of use by pumas in relation to housing density when they are either a) feeding, or b) communicating. Intermediate colors on the feeding map are areas that pumas are likely to avoid, but will still visit occasionally to hunt and feed. It is here that most puma mortality occurs over conflicts with livestock owners. The light colored areas on the communication map represent areas where pumas are not impacted by housing density when communicating (or denning). These areas would make good candidates for reserves.
doi:10.1371/journal.pone.0060590.g004

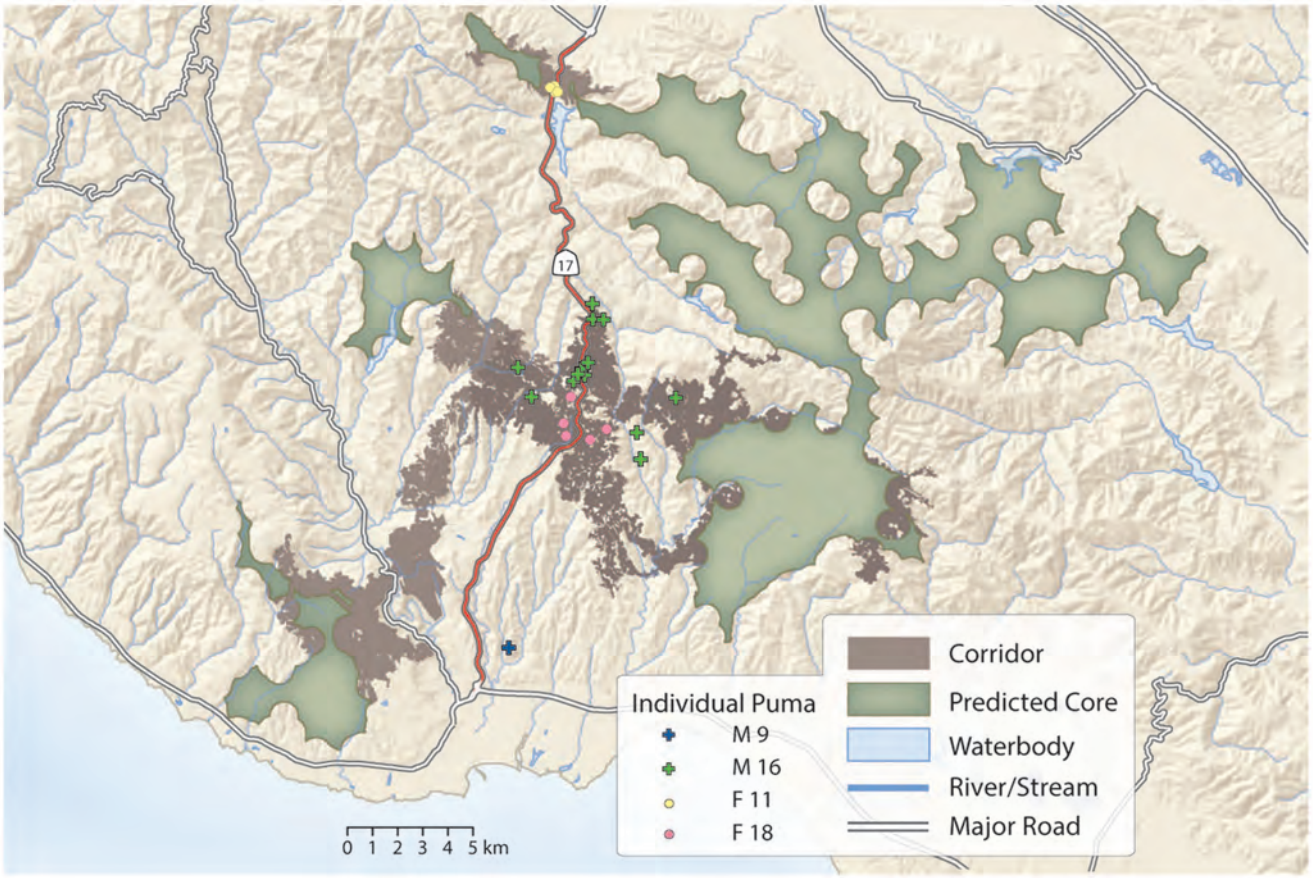

Figure 5. Map illustrating the top 0.5% least-cost corridors crossing Highway 17– the major freeway and barrier to movement in our study area. Predicted core areas on either side of the Highway 17 are those areas where reproductive behaviors are unimpeded by housing density. Corridors were generated using the puma movement model. For each consecutive pair of individual puma locations that bisect Highway 17 (representing crossing locations), we plot the location closest to the freeway.
doi:10.1371/journal.pone.0060590.g005

be used to mitigate the effects of increased human development by informing the location of wildlife reserves, corridors and education efforts.

Supporting Information

Table S1 Influence of covariate combinations on the optimal housing density scale, *h*, for each behavior.
(DOCX)

Table S2 The effect of different housing density scales, *h*, on the housing density coefficient for each behavior.
(DOCX)

Text S1 To ensure that our statistical procedure for choosing the behaviorally specific scales at which pumas are responding to housing density was not an artifact of different covariates in the best fit model for each behavior, we computed AIC scores across scales of housing density ranging from 50–1000 meters for each behavior, using the covariates from the best fit model of each behavior reported in Table 1.
(DOCX)

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Author Contributions

Conceived and designed the experiments: CCW. Performed the experiments: CCW YW PH YS MA JKW VY TW. Analyzed the data: CCW YW BN JKW. Wrote the paper: CCW YW BN PH MA VY TW.

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ORIGINAL PAPER

Using spatial characteristics of apex carnivore communication and reproductive behaviors to predict responses to future human development

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Abstract
A growing body of evidence has documented how wildlife alter their behavior in response to human encroachment. For carnivores, behaviors related to reproduction and communication are particularly sensitive to human disturbance and can provide an early warning indicator of development's negative impacts. Despite the important role carnivores play in an ecosystem, few tools have been developed to anticipate how future human development impacts these behaviors. We developed a set of models to understand spatial relationships between anthropogenic development and puma (*Puma concolor*) habitat selection for two critical reproductive behaviors: nursery habitat for raising young, and sites for communication with mates. Using geospatial location data from the Santa Cruz Mountains in California, USA, we found that female pumas use small nursery home ranges (9 km^{2} $\pm$ 1.72 SE) of predominantly natural habitat, potentially with low levels of human development ($<$ 1 housing unit per 40 acres), when supporting kittens $<$ 8 weeks old. Areas immediately surrounding ($\leq$ 600 m) puma communication sites were also almost entirely composed of undeveloped habitat or low-density development. When modeling projected human development compared to current land use, we found that increases in human development may eliminate 20% of current puma nursery habitat and nearly 50% of current communication site habitat. Future development will also increase the patchiness of suitable habitat, intensifying the difficulty of locating and accessing suitable areas for nurseries and communication. Focusing on the habitat needed to support reproductive and communication behaviors may be an effective way to prioritize conservation planning for pumas and other apex carnivores.

Keywords Anthropogenic development · Breeding habitat · Communication · Habitat loss · Habitat selection · *Puma concolor*

Communicated by Xiaoli Shen.

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Introduction

Early conservation efforts focused on setting aside large areas of land in order to preserve intact ecosystems, but conservation goals can no longer be accomplished by establishing protected areas alone (Wade and Theobald 2010; Wiersma and Sleep 2016; Kshettry et al. 2020). Increasing anthropogenic development necessitates creating viable conservation strategies that promote coexistence with wildlife across rapidly changing landscapes (Burdett et al. 2010; Visconti et al. 2016; Kshettry et al. 2020). Exurban development is the fastest growing land use type in the U.S, and currently occupies 25% of the lower 48 states (Theobald 2001; Theobald 2005). Within the next 25 years, exurban development is projected to increase by over 75%, with the highest rates of growth near coastal areas (Alig et al. 2004). Even modest growth in exurban areas may have large consequences for wildlife, making conservation planning for exurban areas critical (Burdett et al. 2010; Krausman et al. 2011; Wiersma and Sleep 2016). Our study seeks to evaluate how populations of a wide-ranging carnivore, *Puma concolor*, might respond to such exurban development. Specifically, we assess how two key behavioral characteristics, neonatal nursery sites and communication scrape sites, might be impacted by current and future development.

While some carnivore species may tolerate development (e.g. urban canids; Gehrt et al. 2010; Mueller et al. 2018), some species are displaced by areas with heavy human presence (Burdett et al. 2010; Wang et al. 2015; Vickers et al. 2015). Specifically focusing on pumas (*Puma concolor*), though they are not a wilderness-obligate species, there are no known urban puma populations (Gehrt et al. 2010). Further, suburban and even exurban development may present significant impediments to puma use (Burdett et al. 2010; Vickers et al. 2015; Benson et al. 2016). Pumas may live in open spaces adjacent to highly developed areas, however, they spend the majority of their time utilizing undeveloped parts of their home ranges. Previous research has shown that puma reproductive and communication behaviors are particularly sensitive to human activities (Beier et al. 1995; Burdett et al. 2010; Riley et al. 2014; Wilmers et al. 2013; Maletzke et al. 2017). Because nursery and communication site selection are essential for puma population persistence, their conservation is dependent on understanding how anthropogenic activity and development affects these behaviors.

When pumas are supporting neonate offspring, they transition from occupying large home ranges to localizing in a small area, adopting a central place foraging strategy as they make limited forays from their den or nursery site to secure food (Beier et al. 1995; Logan and Sweanor 2001). The areas surrounding nursery sites, or nursery home ranges, provide critical resources that directly affect survival of dependent young and population dynamics (Ross et al. 2010; Davies et al. 2016). Relative to other life stages, neonate mortality is often high, and neonates have high energetic demands. This makes selection of high-quality nursery habitat critical for reproduction and survival (Logan and Sweanor 2001; Laundré 2005). Understanding the specific habitat requirements during this restricted nursery home range period can help inform predictions of how development will impact future carnivore populations.

Communication sites are areas used for conspecific communication via scent marking and are important for selecting mates and defining territories (Allen et al. 2015). Males create communication sites, or scrapes, by using their hind feet to dig two shallow grooves with a mound of soil and duff at one end, and will sometimes urinate or defecate on the scraped mound of material (Allen et al. 2014). Male pumas communicate their presence to

competitors using scrapes (Allen et al. 2016), and advertise to females for breeding opportunities (Allen et al. 2015). Scrapes are often placed at prominent landscape locations, such as trail junctions, saddles, or under large trees. Communication sites are most frequently visited by males; however, these sites serve an important role to females as well (Allen et al. 2014, 2015). When a female is ready to breed, she will often linger at these locations and caterwaul to increase her chances of encountering a receptive mate (Logan and Sweanor 2001; Allen et al. 2015).

The Santa Cruz Mountains of California, USA, ranging from urban Silicon Valley to large areas of preserved open space, provided a backdrop for quantifying how varying levels of development affect puma behavior. Previous analyses conducted by Wilmers et al. (2013) suggested that anthropogenic development plays a key role in shaping habitat suitability for reproductive behaviors (i.e. communication and nursery sites), however that work did not assess the quality and characteristics of the habitat surrounding these sites. Here we extend that analysis by explicitly estimating habitat selection by females during their central place foraging phase (hereafter referred to as a nursery home range) and modeled current and future human development patterns. This allows us to more accurately model interactions between key puma behaviors and habitat availability in the context of human development. We hypothesized that pumas would avoid anthropogenic development, and anthropogenic development in our study would increase, thereby shrinking suitable habitat patches and increasing suboptimal matrix between patches.

Materials and methods

Study area

We conducted our study in the Santa Cruz Mountains of California, USA (Fig. 1). Our 1600 km^2 study area ranged from sea level to approximately 1155 m in elevation, with two distinct climactic zones: a cooler coastal climate on the west side, and warmer temperatures inland to the east. The climate was Mediterranean with hot, dry summers, and cool, wet winters; most of the annual precipitation occurs as rain between November and April. The study area encompassed a spectrum of human development and protected lands, creating a mosaic of land use where human density ranged from 0 to 40 housing units per acre (0 to 9884 housing units per km^2; see Table 1 for housing density categories and definitions). There were also large areas of preserved habitat managed by state, county, and city parks as well as private entities. In between were areas with human influence ranging from rural to urban development, as well as trails, fire roads, residential roads, and highways.

Field methods

We captured 45 free-ranging pumas from 2008 to 2014 with cage traps, leg hold snares, or trailing hounds as described in Wilmers et al. (2013). Puma capture, handling, and sampling protocols were approved by the Animal Care and Use Committee at the University of California, Santa Cruz (protocol #Wilmc1101), and the California Department of Fish and Wildlife. Individuals were tranquilized using Telezol (Fort Dodge Laboratories, Fort Dodge, IA, USA) and fitted with a GPS/VHF tracking collar (GPS PLUS, Vectronics

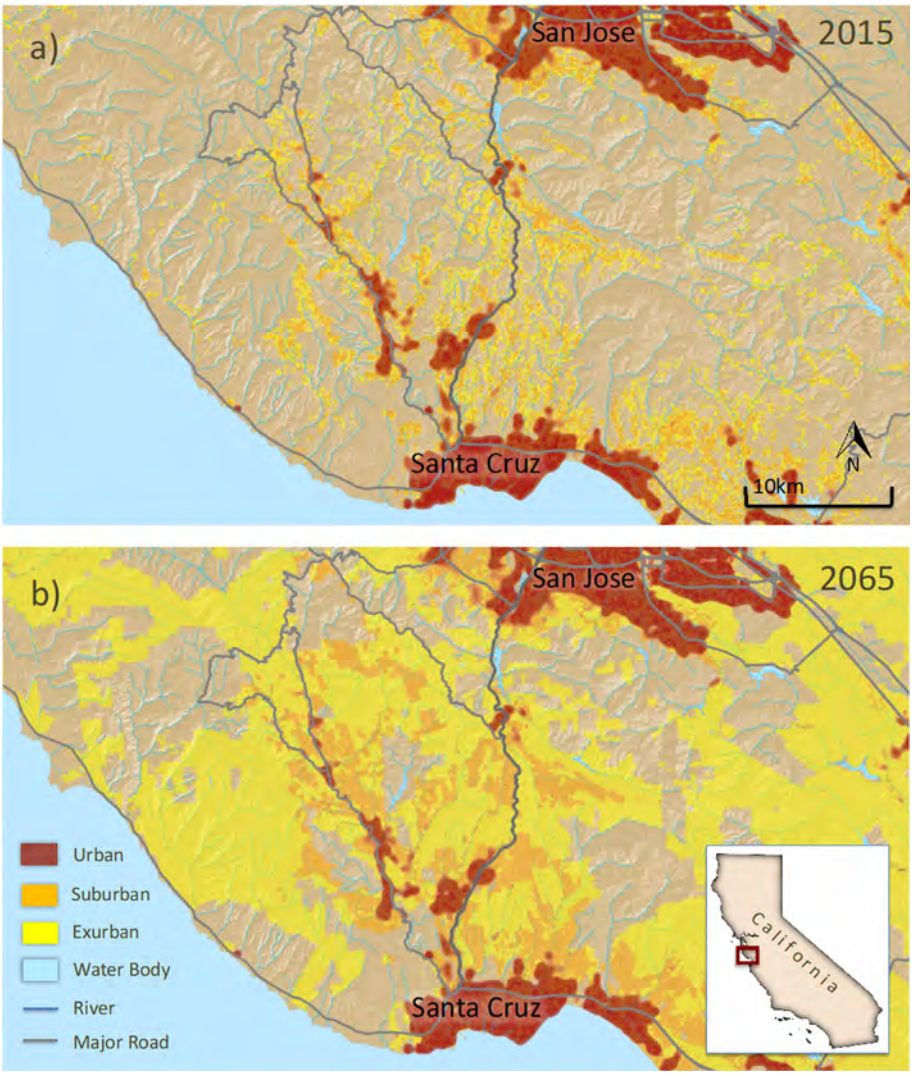

Fig. 1 Over the next 50 years, development is expected to greatly increase in the Santa Cruz Mountains, California, USA. The fastest growing projected land use change between 2015 (**a**) and 2065 (**b**) will be habitat shifting from lightly modified development to exurban development

Aerospace, Berlin, Germany). Collars were programmed to acquire a GPS location every 4 h, and the GPS data were remotely downloaded monthly via UHF, or transmitted via cellular phone towers every 1–3 days depending on collar program configuration and cell phone coverage.

We used female GPS collar data to locate potential nursery sites by searching for clusters of spatially aggregated GPS locations that persisted for > 1 week, and were characterized by repeated excursions by the female to and from the site. In one instance, the GPS collar failed and we used the collar's VHF signal to repeatedly triangulate the position of her nursery over the course of several days. We visited potential nursery GPS

Table 1 Recent (2015) and predicted (2065) land cover statistics of each development category, and the percent change from 2015 to 2065, for Santa Cruz, California, USA

Development category	Housing units per 100 km^2	Percent of study area		Percent change
		2015	2065	
Lightly modified (> 40 acres/house)	< 0.062	77.38	32.61	− 44.76
Exurban (2–40 acres/house)	0.062–1.236	6.43	49.23	+ 42.8
Suburban (0.25–1 acres/house)	1.236–9.884	11.07	12.63	+ 1.56
Urban (< 0.25 acres/house)	> 9.884	5.12	5.52	+ 0.4

clusters between 3 and 6 weeks of when the female first localized to confirm the site as a nursery by finding kittens or associated kitten sign. We then recorded the nursery coordinates using a handheld GPS unit, and subsequently monitored the female's movements in relation to the nursery as well as kitten fates.

We defined communication sites as frequently used scent marking areas containing ≥ 3 scrapes within 9 m^2 of one another (Allen et al. 2014). We located potential communication sites using an algorithm (described in full in Wilmers et al. 2013). The algorithm located sites within 300 m of previous locations in which males visited, with visits separated by > 7 days to eliminate feeding sites. Then we field-checked locations for scrapes and recorded site coordinates with handheld GPS units. We also located communication sites opportunistically during our extensive field activities, but sites identified by the algorithm comprised the vast majority of communication sites recorded.

Model variables

We used a digitized housing layer (described in Wilmers et al. 2013) to classify the current landscape into housing density categories as defined by Environmental Protection Agency Integrated Climate and Land-Use Scenarios (ICLUS) model (Bierwagen et al. 2009) (Table 1). We employed a spatially explicit regional growth model (SERGoM) developed by ICLUS (Bierwagen et al. 2009) to project future development in our study area (e.g. Burdett et al. 2010). SERGoM uses several categories of input to create projections, with special attention to exurban/low-density development (Bierwagen et al. 2009). For our analyses, we used the "base case" development projection as a conservative prediction of human development in Santa Cruz Mountains 50 years into the future (to the year 2065). This assumes a "business-as-usual" development pattern and the midline U.S. Census Bureau projection for population growth. For a detailed description of model assumptions, parameters, and alternative development patterns see Bierwagen et al. (2009). The SERGoM model produces a 100 m resolution raster of housing development categories.

We quantified habitat data by extracting landscape attributes for each point or area. Prior to conducting statistical analyses, we used a correlation matrix to identify independent variable collinearity ($|r| < 0.50$). All variables met this criterion and were retained in the model. As a continuous variable, slope (x) was normalized as follows (Zuur et al. 2007),

$$x_i^{\text{norm}} = (x_i - x^{\text{mean}})/std$$

When modeling future selection, we could not adequately predict distance to the nearest road with the SERGoM model because the model output does not explicitly map road locations. However, the distance to roads had a marginal influence on site suitability, and the SERGoM does implicitly incorporate road density into their model output. This allowed our model to account for the influence of roads by including their effects as a component of development.

Statistical methods

We processed all spatial data in Geographical Information Systems program ArcGIS (v.10.1; ESRI, 2012) and R (v.2.1.3.1; R Development Core Team, 2010), and used R for our statistical analyses. We used two packages in R: the lme4 package (Bates et al. 2015) with a binomial link for model fitting, and the adehabitatHS package (Calenge 2006) for the compositional analysis. We also used the LoCoH (Getz et al. 2007) and SERGoM (Bierwagen et al. 2009) tools in ArcGIS.

Home ranges

We used 95% adaptive local convex hulls (LoCoH; Getz et al. 2007) to estimate an annual home range for each puma. We restricted our analyses to mature resident pumas because subadult pumas are seldom involved in reproductive behaviors. We excluded data for pumas monitored fewer than 12 continuous months. To avoid overestimating home range size due to shifts in territories, we used the first year of GPS data for individuals with data spanning longer than 1 year (n = 24).

Modeling suitability: potential nursery home ranges in 2015

We assessed selection and avoidance in nursery home range areas in a use-availability framework (Manly et al. 2002). This analysis considered the relationship between habitat selection within animals' home ranges (3rd order selection, *sensu* Johnson 1980) and landscape features. We compared habitat characteristics in areas surrounding nursery sites to similar areas within individual home ranges using a compositional analysis (Aebischer et al. 1993). By defining used areas as "nursery home ranges," or areas females utilized as a central place forager while she was bound to the nursery with young, immobile kittens, this analysis allowed us to incorporate kitten-rearing behavior in nursery site selection. To determine the effect of surrounding habitat, we compared nursery home ranges to comparably sized random areas selected within female home ranges. We modeled this behavior by creating a nursery 95% LoCoH home range (Getz et al. 2007) for each nursery site by using the GPS points collected while the female had kittens < 8 weeks old. We created comparable "available" nursery areas by placing a buffer around each random point. The buffer size was determined by sampling with replacement from a vector representing the size of all used nursery home ranges. We then compared the percent composition of each type of anthropogenic development (Table 1) in used nursery home ranges compared to similarly-sized available areas, drawing 5:1 available:used areas at random from within each female's home range (Manly et al. 2002).

Next, we used the results from the nursery home range compositional analysis to model landscape-level habitat suitability. Selected nursery home range habitat provided a metric for suitable conditions, which we used in a moving window analysis to identify preferred

nursery area habitat within the study area. Specifically, we measured the percent composition of each development category (lightly modified, exurban, suburban, or urban) in nursery home ranges, and used the mean (± SE) amount of each type of development present to model suitable habitat across the study area. Positive t-values indicated a preference for the habitat type, and negative t-values indicated avoidance. For avoided development categories, we used the mean value, plus the standard error, as the maximum threshold for nursery home range suitability in our predictive model. For selected categories, we set the average value, minus the standard error, as the minimum threshold for modeling nursery home range selection. We used these mean values, plus or minus the standard error, to model habitat suitability across the study area, as well as project how suability will be influenced by development.

Modeling suitability: potential communication sites in 2015

Similar to the nursery analysis, we assessed selection and avoidance in communication sites in a use-availability framework (Manly et al. 2002). We performed two analyses that addressed selection at two different spatial scales—the first at the site, and the second at the area around each site. In each analysis, we defined "used" points or areas as locations in which we found communication sites, and drew "available" comparison locations at random from within each puma's home range (mapped using a 95% LoCoH) at a rate of 5:1 available:used (Manly et al. 2002).

For the first communication site selection analysis, we modeled site-level selection using a Resource Selection Function (RSF). The model variables were the four levels of development, as a categorical variable, and slope (the terrain steepness, calculated using a 3×3 cell moving window), as a continuous variable. These two habitat features were previously identified as the most important for predicting communication site selection (Wilmers et al. 2013).

For our second analysis, we compared development and slope in areas surrounding communication sites to equally-sized areas within individual home ranges. We quantified differences in used and available areas by placing a 600 m radius circle around each used and available communication site (Wilmers et al. 2013) and compared the slope and human development within used versus available areas using a compositional analysis (Aebischer et al. 1993). Originally modeled by Wilmers et al. (2013), the 600 m buffers represent the distance at which pumas are sensitive to human development when selecting communication sites.

Modeling future suitability: potential nursery and communication habitat in 2065

We mapped projected future housing density for the Santa Cruz Mountains for the year 2065 using the SERGoM GIS tool (Bierwagen et al. 2009). Using the tolerance/attraction thresholds generated from our compositional analysis (Table 2a), we created a moving window analysis to create binary (suitable/unsuitable) rasters for potential nursery home ranges and potential communication sites. In order to measure the distribution of suitable patches, we made a simulated puma home range grid with cell sizes the average size of a puma home range, and eliminated grid cells in urban areas, as these areas are unsuitable habitat for a puma.

Table 2 Human development in puma nursery and communication areas in the Santa Cruz Mountains, California, USA in 2015

Development category	Percent composition						
	a. Nursery areas	SE	Communication areas	SE	b. Female home ranges	SE	Study area
Lightly modified	94.0	4.0	97.6	0.4	85.5	1.4	75.9
Exurban	3.5	1.3	1.8	0.3	7.7	1.0	8.5
Suburban	2.5	1.9	0.6	0.2	5.5	0.87	12.3
Urban	0.1	0.0	0.1	0.01	1.3	0.02	3.3

Mean values for human development in nursery home ranges and within 600 m of communication sites (a), and mean values for female home ranges and the study area as a whole allow comparison between development levels in nursery areas (b)

Values are reported as percentages of each development category

We generated nursery LoCoHs, and used the mean size of successful nursery patches as a minimum area required to raise kittens to an age beyond the use of the first nursery site. In our analyses, we used binomial or quasibinomial regression to determine how projected development will affect the properties and distribution of suitable patches and sufficiently large patches and we incorporated slope into our modeled suitability using the estimated parameter coefficient. The ability of the model to discriminate between communication sites and non-communication sites was 'acceptable' as determined by an area of 0.79 under the receiver operator curve (Hosmer and Lemeshow 2004).

Results

We used GPS data from 15 female and 14 male pumas, which were monitored for a mean of 636 ± 102 SE and 428 ± 52 SE days respectively. We recorded 119,787 locations for a mean of 4130 ± 303 SE locations per animal. We documented 23 nursery home ranges for 12 female pumas (6 females had more than one nursery; Fig. 2). We also documented 299 communication sites from 13 males.

Nursery home range selection

The mean nursery home range area was 9 km^2 ± 1.72 SE (Fig. 2). Though some nursery home range areas contained low levels of exurban, suburban, or urban development, each of the documented nursery sites themselves (n = 23) was located in the lightly modified human development habitat category (Table 2). When selecting nursery home ranges, female pumas preferred predominantly lightly modified habitat over any other housing density category (compositional analysis: $mean_{nursery\ home\ range}$ = 94% ± 4 SE, $mean_{female\ home\ range}$ = 86% ± 1 SE, $p < 0.01$). Urban development made up a very small portion of the areas utilized while supporting young kittens (compositional analysis: $mean_{nursery\ home\ range}$= 0.0016% ± 0.0012 SE, $mean_{female\ home\ range}$ = 1.3% ± 0.02, $p < 0.01$, Table 2b).

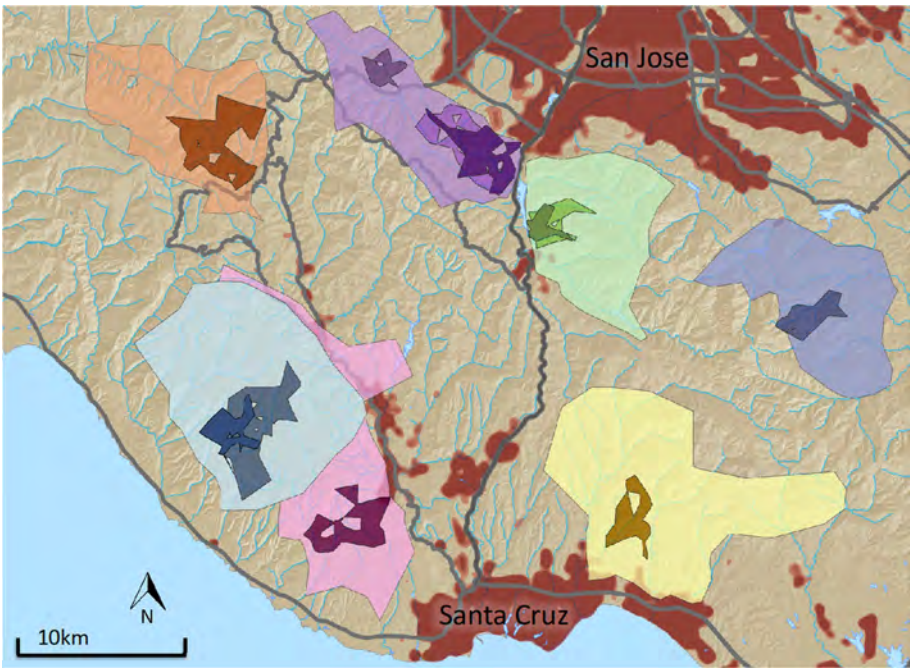

Fig. 2 Nursery home ranges in the Santa Cruz Mountains, California, USA between 2008 and 2014. An illustration of the difference between annual home ranges (translucent) and nursery home ranges (smaller opaque; area female utilized while maintaining a nursery), including urban and suburban areas in maroon. In cases where females had multiple nurseries, they are shown by different shades of the same color. For visual clarity, only a subset of the total 23 nurseries is shown

Communication site selection

Similar to nurseries, every communication site was located in lightly modified habitat (n = 299), and communication area composition was predominantly lightly modified habitat (Table 2). The RSF model suggested that male pumas significantly selected communication sites in undeveloped habitat ($\beta = 1.51 \pm 1.032$ SE) and relatively flat areas ($\beta = 0.03 \pm 0.124$SE), and they selected against urban habitat ($\beta = -10.06 \pm 309.12$ SE; Table 3a). Similar to site-level conditions, males selected undeveloped habitat within communication areas as well (compositional analysis: $\text{mean}_{\text{used}} = 98\% \pm 0.35$SE, $\text{mean}_{\text{random}} = 88\% \pm 1.00$ SE, $t_{299} = -8.07$, $p < 0.01$; Table 3b).

Future landscape for suitable nursery and communication sites

Over the next 50 years, models predict that high levels of lightly modified development will be converted to exurban development (Fig. 1). This shift would significantly reduce currently suitable habitat for communication sites and nursery home ranges (Fig. 3). In 2015, 75.9% of our study area was categorized as very lightly modified, the areas modeled as most suitable for nurseries and communicating, but by 2065 that number drops to 32.6% (Table 1). Every modeled female home range had sufficient nursery patches in 2015, or

Table 3 Models for puma communication site selection in 2015 in the Santa Cruz Mountains, California, USA

Habitat Variable	a	Communication RSF			b	Compositional analysis			
		Coefficient	SE	p		Mean percent		p	t
						Used	Available		
Slope		0.03	0.12	0.9					
Development category									
Lightly modified		1.51	1.03	< 0.01		97.59	88.35	< 0.01	− 8.07
Exurban		1.19	1.19	< 0.01		1.80	6.82	< 0.01	− 8.16
Suburban		0.98	1.02	< 0.01		0.62	4.64	< 0.01	− 6.28
Urban		− 10.06	309.12	0.7		0.01	0.15	0.5	− 1.77

(a) Resource selection function results comparing development at communication sites with available sites within male territories. (b) Compositional analysis results comparing the mean percent composition of each development category found within a 600 m radius of communication sites and areas of the same size randomly selected from male territories

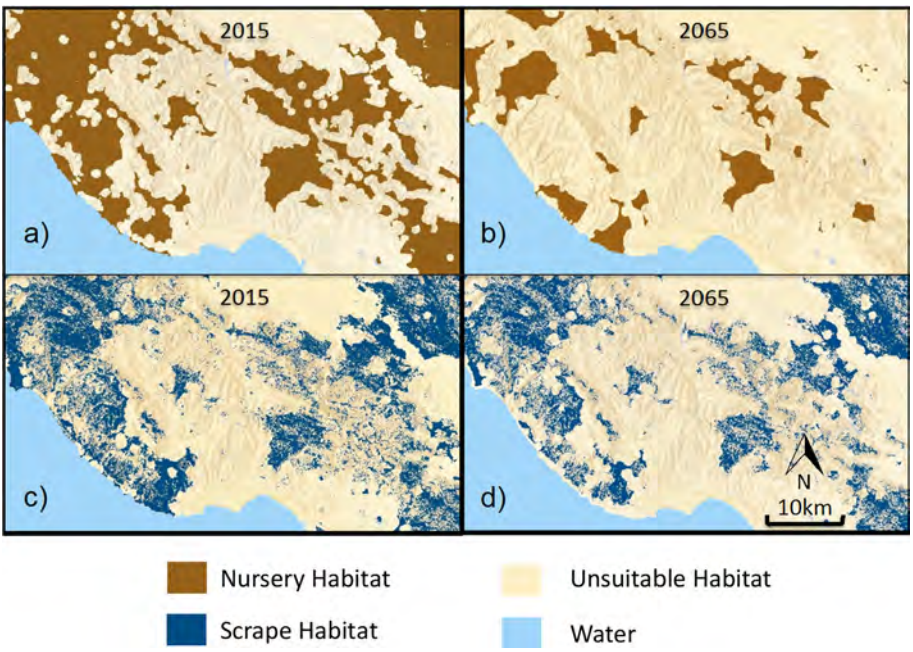

Fig. 3 Changes in puma nursery and communication habitat between 2015 and 2065 in the Santa Cruz Mountains, California, USA. The projected changes in spatial extent of suitable nursery habitat (in dark brown; panels **a** and **b**) and suitable communication habitat (in blue; panels **c** and **d**) habitat between 2015 and 2065. The matrix (tan) is a mix of habitat types, ranging from urban development to undeveloped natural habitats (namely mixed evergreen forest, redwood forest, oak savanna, chaparral, mixed oak forest, coastal prairie and coastal scrub, and sandhills). Future suitable habitat for each behavior is projected to shrink and become more fragmented

patches of continuous open habitat with low levels of urban, suburban, and exurban development, while only 77% had sufficient patches in 2065. Future suitable habitat patches are also projected to become farther apart (Fig. 3), with the average distance between sufficiently large nursery patches in 2065 projected to be three times the distance of 2015 (mean patch distance$_{2015}$: 787 m $\pm$ 117 SE, mean patch distance$_{2065}$: 2,749 m $\pm$ 260 SE; $p < 0.01$). A similar pattern was true for potential communication sites (Fig. 3). In 2015, 30% of the study area was considered suitable for communication sites, but our projections for 2065 reduced potential communication site area to 18%. Overall, remaining potential habitat is projected to shrink and became patchier, making suitable sites smaller and farther apart.

Discussion

We explored the relationship between anthropogenic development and puma nursery and communication habitat, and found habitat suitability for these behaviors were vulnerable to continued human development. Although suitable habitat may be utilized for only a short duration, pumas may breed at any time of year. Habitat suitable for breeding behaviors is likely to be disproportionately important for puma survival, making it important to consider these areas in conserve efforts (Boitani and Fuller 2000). Our future development projections suggest that nearly half of the lightly modified habitat that is key for these reproductive behaviors will be converted to exurban and suburban development by 2065. This would reduce available nursery habitat by 20% and potential communication habitat by nearly 50%, while making remaining habitat patchier and resulting in potential fitness costs for the population (Hinam and Clair 2008; Burdett et al. 2010; Gehrt et al. 2010). By explicitly modeling the spatial components of communication and nursery sites, we were able to predict how animals are likely to respond to increased development and fragmentation and help inform conservation efforts. Future studies on conservation planning may find it informative to explore spatial requirements for wildlife during sensitive periods (e.g., during the period of several weeks after giving birth when young are highly vulnerable). Focusing on the habitat requirements during infrequent, but highly important, activities may provide a critical tool for conservation planning efforts.

This study addresses female puma habitat use during the period in which they behave as central place foragers while raising immobile kittens, and highlights habitat with high conservation value with respect to puma reproduction. These areas require protective cover for kittens, as well as sufficient resources (prey, water, etc.) for the mother while supporting her growing young. When choosing nursery home ranges, female pumas avoided human development. Every documented nursery site was located in undeveloped habitat ($<$ 1 housing unit per 100 acres), and females tolerated only small amounts of low-level human development in areas surrounding the nurseries. This strong preference for undeveloped habitat likely has fitness implications, as habitat near humans has elevated populations of synanthropic carnivores (Wang et al. 2015) that could injure or kill vulnerable kittens. Humans themselves may pose real risks, but even the perception of risk could become taxing to a mother (Suraci et al. 2019). For example, when a female is disturbed, she will often abandon kills she needs to feed her young, elevating energetic costs during a period that is already energetically expensive, and move her kittens to a new nursery site (Logan and Sweanor 2001).

Similar to females, males also selected lightly modified habitat at the site- and area-level in relatively flat areas when creating communication sites. Pumas appear to select sites that maximize their opportunities for communication between conspecifics (*sensu* Allen et al. 2014), while minimizing interaction with human disturbance. The cues left at communication sites are both chemical and physical (Allen et al. 2014), and vulnerable to human disruption. Hikers, cyclists, domestic dogs, and other recreationalists may trample, mark over, or otherwise disturb communication sites, making communication sites better suited to areas with little human impact. In the Santa Cruz Mountains, an aversion to precipitous slopes greatly narrows the habitat available for scraping, and selecting against human development reduces it further. Inadequate access to scrape habitat could generate fitness costs from lack of communication with conspecific competitors and potential mates.

Future habitat development will likely alter the landscape for reproductive and communication behaviors. The habitat loss and increasing habitat patchiness projected in 2065 could confer large energetic penalties to female pumas and potentially reduce fecundity. Habitat patchiness may leave some females without any access to optimal nursery habitat, which could create an ecological trap in which females try to raise young in adverse conditions. Similar to other carnivore species, neonate kittens experience a higher mortality rate than any other age group (Logan and Sweanor 2001). Nursing females are also unable to traverse long distances in search of prey because they need to make kills to feed themselves, and then quickly return to their young. Attempting to raise offspring in heavily modified habitat would likely increase neonate mortality and shorten the inter-birth interval. Pregnancy, lactation, and rearing young are energetically expensive, and the more often these behaviors need to occur, the higher the cost (Oftedal and Girrleman 1989).

In addition to needing resources close to nursery sites, moving in more heavily fragmented habitat imposes other potential costs to females with young. Roads present a dangerous direct and indirect challenge to wildlife in general (Bennett 2017), and pumas specifically (Ernest et al. 2003; Riley et al. 2014; Vickers et al. 2015; Benson et al. 2016). Reduced patch suitability and increased distance between patches in the future will likely result in pumas crossing roads more frequently, and losing some patches from uncrossable roads. In addition, living in close proximity to people, as predicted in model projections of the future, exposes puma populations to increased human-derived mortality sources (e.g. conflict with livestock or companion animals (Orlando 2008), anticoagulant rodenticide exposure (Moriarty et al. 2012).

For males, limited access to suitable scrape sites could cause a breakdown of territorial boundaries and effective communication, increasing male–male conflict (Chanchani et al. 2018). Resident male pumas patrol their territories to refresh communication sites every 2 to 3 weeks (Allen et al. 2016). Males use scrapes to establish dominance as well as define boundaries (Allen et al. 2015), allowing competing males to avoid physically confronting one another (Logan and Sweanor 2001). Intraspecific strife can be an important population driver (Rankin 2007), especially as isolation from other puma populations increases (Riley et al. 2014). The impacts could range from low cost outcomes, such as inefficient use of time or energy, to fitness costs including bodily harm or death.

Communication sites also serve as a way for males to advertise themselves to potential mates (Allen et al. 2014) and provide a location for females to communicate their receptivity to breeding (Allen et al. 2015). Without these sites, males and females could have a more difficult time finding mates, resulting in decreased reproductive success across the population (e.g., Slabbekoorn and Ripmeester 2008). Breeding success is correlated with territory maintenance, as kittens are generally sired by a territory-holding male (Logan and Sweanor 2001; Allen et al. 2015). Thus, the ability to secure and hold a

territory can have significant implications for reproductive success of a particular male, with broader population-level implications as well (Logan and Sweanor 2001).

Historically, pumas were widely distributed, occupying nearly every habitat in the Americas from the desert to tropical rain forests (Logan and Sweanor 2001), suggesting a high degree of adaptability. Our analyses did not take into account behavioral plasticity to an increasingly human-dominated landscape, and with diminished access to ideal sites, pumas may compensate to some degree by substituting less preferred sites. Pumas have demonstrated the ability to adapt and persist in urban- or suburban-adjacent areas (Burdett et al. 2010; Riley et al. 2014). However, evidence suggests they are less adaptable to persisting within more developed environments than many other carnivore species, such as coyotes or foxes (Gehrt et al. 2010); puma populations studied in areas adjacent to human development have suffered from inbreeding depression and population declines (Burdett et al. 2010; Vickers et al. 2015; Benson et al. 2016; Gustafson et al. 2019). Our study area is situated in an area already highly impacted by people; local puma population genetics show a relatively high degree of inbreeding and isolation (Gustafson et al. 2019), which could indicate that they are already living on the lower end of their acceptable spectrum. If they are currently subsisting in suboptimal habitat, further flexibility may not be possible. In addition, increased development will likely have additional negative implications for dispersal permeability and gene flow (Riley et al. 2014; Vickers et al. 2015; Gustafson et al. 2019) and overall habitat loss (Burdett et al. 2010; Visconti et al. 2016).

Our study highlights the need for regional planning to pay special attention to development patterns. In the next 50 years, 96% of the land use change is predicted to transform currently suitable habitat to lower quality, non-preferred exurban development (Table 1; Fig. 1). Redirecting some of this development into higher density, more efficient development in suburban or urban areas would allow space for humans and wildlife populations to coexist. The pervasiveness of habitat loss and transformation make it all the more important to carefully develop around remaining habitat (Burdett et al. 2010; Wang et al. 2015; Visconti et al. 20165; Maletzke et al. 2017). We modeled the relationship between pumas and human development in the Santa Cruz Mountains, but these dynamics are likely playing out across puma's large distribution and our findings are likely transferrable to other carnivore species as well. In addition, gaining a better understanding of how habitat modification influences wildlife can also help garner public support for sound conservation practices, and guide future development plans to ensure that wild populations can thrive alongside human development.

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PLOS ONE

RESEARCH ARTICLE

Multi-level, multi-scale resource selection functions and resistance surfaces for conservation planning: Pumas as a case study

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Abstract

The importance of examining multiple hierarchical levels when modeling resource use for wildlife has been acknowledged for decades. Multi-level resource selection functions have recently been promoted as a method to synthesize resource use across nested organizational levels into a single predictive surface. Analyzing multiple scales of selection within each hierarchical level further strengthens multi-level resource selection functions. We extend this multi-level, multi-scale framework to modeling resistance for wildlife by combining multi-scale resistance surfaces from two data types, genetic and movement. Resistance estimation has typically been conducted with one of these data types, or compared between the two. However, we contend it is not an either/or issue and that resistance may be better-modeled using a combination of resistance surfaces that represent processes at different hierarchical levels. Resistance surfaces estimated from genetic data characterize temporally broad-scale dispersal and successful breeding over generations, whereas resistance surfaces estimated from movement data represent fine-scale travel and contextualized movement decisions. We used telemetry and genetic data from a long-term study on pumas (*Puma concolor*) in a highly developed landscape in southern California to develop a multi-level, multi-scale resource selection function and a multi-level, multi-scale resistance surface. We used these multi-level, multi-scale surfaces to identify resource use patches and resistant kernel corridors. Across levels, we found puma avoided urban, agricultural areas, and roads and preferred riparian areas and more rugged terrain. For other landscape features, selection differed among levels, as did the scales of selection for each feature. With these results, we developed a conservation plan for one of the most isolated puma populations in the U.S. Our approach captured a wide spectrum of ecological relationships for a population, resulted in effective conservation planning, and can be readily applied to other wildlife species.

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Introduction

Almost 40 years ago, Johnson [1] established a hierarchical framework for examining wildlife habitat use. He proposed ordering habitat selection from Level I (i.e. selection of the geographical range of a species) to Level IV (i.e. selection of feeding sites) and argued that, [a]This hierarchy of selection has a unifying nature. Habitat usage studies and investigations of feeding are no longer qualitatively distinct; they are simply of different orders[o]. Johnson's hierarchical framework set the stage for much of the recent research, thinking, and understanding of how wildlife use habitat [2].

Examining selection at these different hierarchical levels encourages wildlife habitat use to be understood as a cascading process conditional upon higher levels of selection. For example, avoidance of human development may be weak at one level of selection but strong at another [3±5]. Instead of using the outputs from each hierarchical level independently, DeCesare et al. [4] proposed integrating the predictive surfaces from resource selection functions (RSFs; [6]), across levels of selection. DeCesare et al. [4] referred to these integrated predictive surfaces as Scale Integrated RSFs. Following the nomenclature of McGarigal et al. [2] we will hereafter refer to these as Multi-level RSFs (ML-RSFs). These ML-RSFs provide the relative probability of habitat use at a lower level, for example Level III, conditional upon the relative probability of habitat use at a higher level, for example Level II.

In addition to being conceptually appealing, ML-RSFs offer a number of advantages. First, they may reveal differences in selection at different hierarchical levels, which is useful for conservation and management of wildlife. Second, they provide a single surface that synthesizes habitat use across different levels, making it easier for managers to digest and use [4]. Third, they are relatively simple to derive since the hierarchical conditional probabilities collapse into a simple equation that is the product of the two relative probability surfaces. Studies that are unable to use the same data for each hierarchical level, but produce RSFs for different levels of selection and obtain their product, are not truly conditionally nested, but are conceptually similar and approximate hierarchically nested levels (e.g. [5±7]).

We expand the concept of ML-RSFs to resistance surfaces. Resistance surfaces quantify how environmental parameters affect wildlife movement and are the basis for most connectivity and corridor models [8]. Resistance surfaces are conceptualized as the union of three processes, (1) the willingness of an organism to cross a particular landscape feature, (2) the physiological cost of moving across a landscape feature, and (3) the reduction in survival due to crossing a landscape feature [8, 9]. However, in practice, it is difficult to estimate resistance for these three processes simultaneously. Typically, one of two data types are promoted as the gold standards for estimating resistance for wildlife: movement data or genetic data [10±13]. Movement data have been promoted as an effective way to estimate resistance at fine scales, both temporally and spatially, through context-dependent analyses of animal pathways [10, 13, 14]. Resistance surfaces from movement data approximate the first resistance concept, the willingness of an individual to cross a feature. Genetic data, as used in landscape genetic analyses, estimate resistance by correlating environmental variables with estimates of gene flow. Through this process, variables that minimize fitness costs, increase survival, and result in successful dispersal and breeding are identified [12]. Thus, resistance surfaces derived from genetic data approximate the second two resistance processes, physiological and survival costs.

Previous studies have attempted to determine if movement data can be used to predict genetic connectivity, and vice versa [10, 15]. To date, the results have been equivocal. Cushman and Lewis [10] found many similarities between the resistance surfaces derived from these two data types for black bears in Idaho. Resistance surfaces between genetic data and an early season movement model had a correlation coefficient of ~0.4 and shared the same variables with the same relationship to movement. However, correlation between the genetic resistance

surface and the resistance surface derived from the late season movement model was much lower at ~0.1. In other analyses on roe deer in France, Coulon et al. [15, 16] found an avoidance of woodland with movement data and a preference for woodland with genetic data.

Instead of trying to compare resistance surfaces derived from these two data types, we argue their best use may be by combing them into a multi-level resistance surface (ML-RS), akin to the ML-RSFs described above. Genetic data reflect movement, dispersal and breeding over generations which is analogous to a higher organizational level that represents broader scales and longer temporal windows. Pathway data, on the other hand, represents movement over much shorter temporal periods and reflect real-time movement decisions by individuals, which is analogous to a lower organizational level. Just as it is difficult to discern Level III habitat selection by using a home range selection function, so too is it difficult to discern fine-scaled movement patterns with a landscape genetic analysis. Conversely, it is difficult to identify variables that result in successful dispersal and breeding using only movement data. By integrating these surfaces, all three resistance processes can be estimated.

Analyzing species habitat use and movement across hierarchical levels and integrating the results captures selection and behavioral processes at different extents and results in stronger inference and predictive abilities than using a single level alone [2, 4, 6, 17]. Multi-level selection and movement models can be improved upon conducting multi-scale analyses within each hierarchical level. Not only do individuals select for environmental variables at different scales within a hierarchical level [18±21], individuals may also select different scales for the same environmental variable among hierarchical levels [5, 7]. These scales of selection are most often represented by summarizing each variable of interest with ecological neighborhoods of varying sizes [22]. The scale that produces the highest model performance for each variable is often referred to as the `characteristic scale' of selection [23]. For example, in our previous work, we have shown that in Level III selection, pumas respond to human development variables at coarse scales and to natural features at finer scales [21]. Bauder et al. [5] found different scales of selection for multiple environmental variables for eastern indigo snakes across Levels II and III selection. Developing multi-level, multi-scale models captures a wide spectrum of ecological relationships for a population resulting in more meaningful conservation plans.

As a case study for developing a multi-level, multi-scale conservation plan, we use data from a long-term study on pumas (*Puma concolor*) in a highly developed region of southern California. Over 20 years ago, Beier [24, 25] concluded that the coastal Santa Ana Mountains puma population was becoming isolated due to increased urbanization and long-term population viability was dependent on maintaining permeability to the eastern Peninsular Ranges. More recent genetic analyses have shown that the Santa Ana Mountains population not only has the lowest genetic diversity of any population in California, but also shows signs of inbreeding [26], indicating a heightened need for connectivity. This is complicated by low adult survival rates in the Santa Ana Mountains population (55.8%), with humans (mostly via vehicle strikes) causing the majority of puma deaths [27]. A detailed puma conservation plan accounting for connectivity between the Santa Ana Mountains and the eastern Peninsular Ranges is needed and will directly inform conservation preserve design in northern San Diego County. We present a multi-level, multi-scale approach to conservation planning for pumas in northern San Diego and southern Riverside and Orange Counties.

Materials and methods

Study area and GPS collar data

The study area was located across much of the Peninsular Mountain Range in southern California spanning from southern Los Angeles and San Bernardino Counties in the north to the

U.S.±Mexico border in the south (Fig 1). Interstate 10 and the Salton Sea approximately defined the eastern boundary and the Pacific Ocean was the western boundary. The region is defined by a Mediterranean climate with hot dry summers and mild, wetter winters. Elevations range from sea level to 3200 m. Outside of urban areas vegetation is primarily composed of chaparral, coastal scrub, grasslands, and oak woodlands.

Between 2005±2015, pumas throughout the study area were captured and fit with GPS collars under California Fish and Wildlife Scientific Collecting Permit number 9875 and University of California Davis Institutional Care Use Committee authorization number 17233. Please see Vickers et al. [27] for capture details and protocols. Collar acquisition interval varied from five minutes to six hours. To avoid the use of data that may have large spatial errors, we removed two-dimensional fixes with a Position Dilution of Precision > 5 [28].

GIS data and predictor variables

We used predictor variables that have been shown to influence puma habitat use and movement. These included: elevation, percent slope, terrain ruggedness (calculated as total curvature in DEM Surface Tools; [29]), roads, urban areas, and land cover types aggregated for the study area [13, 30±32]. Variable details are provided in Table 1. All variables were represented with a 30 m spatial resolution.

Level II resource selection: Home range selection function

Because our study area is well within the geographic range of pumas [33], we assumed that probability of use was 100% for Level I selection. Therefore, we focused only on Levels II and III for our resource selection analyses.

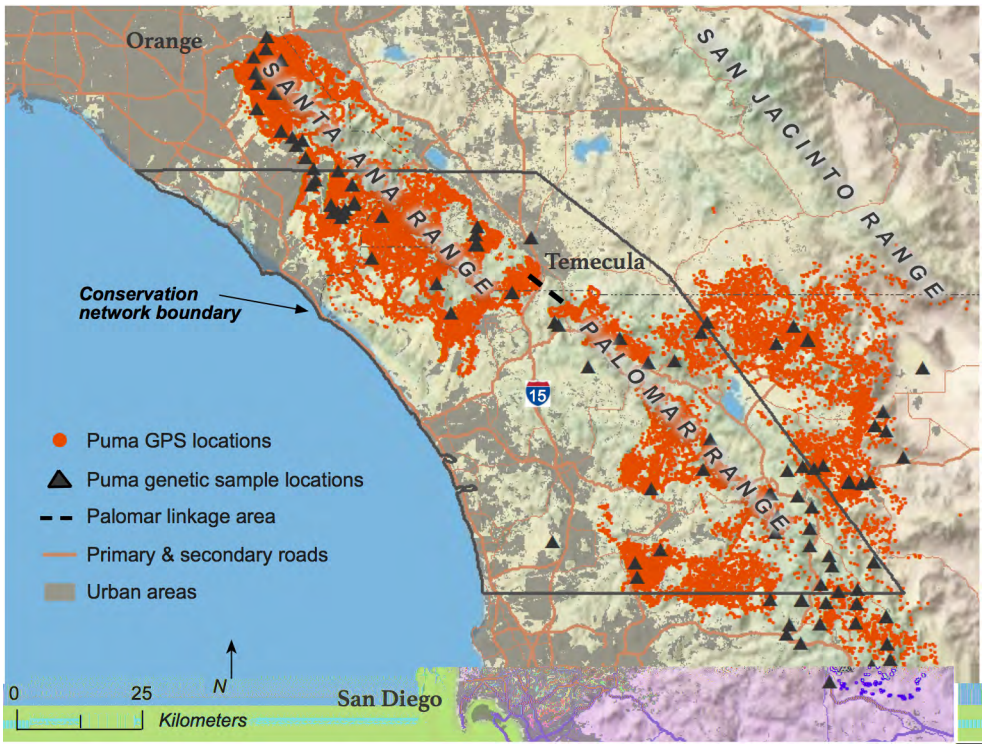

Fig 1. Southern California study area and conservation network sub-area with puma GPS telemetry and genetic sample locations used in the analysis.

https://doi.org/10.1371/journal.pone.0179570.g001

Table 1. Predictor variables used in the puma resource selection, movement selection, and landscape genetic analyses.

Variable	Source/Derivation	Year
Topographic features		
Elevation	USGS National Elevation Dataset	2009
Percent Slope	Derived from National Elevation Dataset	-
Terrain Ruggedness	Total curvature derived from National Elevation Dataset with DEM Surface Tools [29]	-
Land cover type		
Agriculture	Aggregated agricultural classes from CalVeg	2014
Chaparral	Aggregated chaparral classes from CalVeg	2014
Coastal Scrub	Aggregated scrub-type classes from CalVeg	2014
Coastal Oak Woodland	Aggregated woodland classes from CalVeg	2014
Grassland	Aggregated grassland classes from CalVeg	2014
Barren/Open Water	Aggregated barren and water classes from CalVeg	2014
Desert	Aggregated desert classes from CalVeg	2014
Riparian	Aggregated riparian classes from CalVeg	2014
Human development		
Urban	National Land Cover Data	2011
Roads; Classi®edas Primary, Secondary, and Tertiary	U.S. Census Bureau TIGER	2014
Roads; Classi®edas Primary, and Secondary	U.S. Census Bureau TIGER	2014
Roads; Classi®edas Primary	U.S. Census Bureau TIGER	2014

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All data analysis was conducted in the R software environment [34]. Home Range Selection Functions (HRSFs) were conducted in the same `used' and `available' framework typical of RSFs [35], where points distributed within empirical home ranges are the `used' data and points distributed within a buffer around the empirical home ranges are the `available' data. To estimate puma home ranges, we used pumas with at least five months of data. Based on prior analyses by Grigione et al. [36] and our observations of pumas in the study area, there is little variation in home range size among seasons, therefore we are confident five months is a sufficient amount of time to capture the full home range utilization of individuals. Data were visually examined to determine if individuals moved from their original home ranges to new home range areas during the study period. If home range shifts were identified, we excluded these individuals from the analysis. This resulted in a total of 31 pumas for the HRSFs (Males = 12, Females = 19) with collar duration ranging from five months to 32 months (mean = 10.87 months).

We followed the recommendations of Borger et al. [37], Bauder et al. [38], and Fieberg [39] to estimate puma home ranges and standardized our sampling regime among individuals by using only points from the longest collar fix interval (six hours) to reduce home range estimation bias. This subsetting resulted in a total of 24,911 locations with a per-individual mean of 811 points (range = 284±1535).

We used the *ks* package in R [40] to estimate kernel density home ranges using the reference bandwidth and an unconstrained bandwidth matrix. The unconstrained bandwidth matrix has been shown to produce a single volume contour, to encompass most of the input points, and to be less sensitive to fix rate and sampling duration than other home range estimators [38]. We identified our final home range boundaries as 90% of the entire utilization distribution for each individual.

For our used data, we randomly distributed points throughout the each puma home range. The number of points selected equaled the number of points used to estimate the home- range kernels. For our available data, we first calculated the maximum distance between points for each home range and identified the 95th quantile of this distribution. We then buffered all used home range points by this distance (43 km), which constituted our available area. Unique available points were randomly distributed throughout this available area in a 1:1 ratio with the used points.

We developed multi-scale HRSFs using a two-stage, pseudo-optimized approach [2]. We calculated our used and available data within 10 ecological neighborhoods of varying sizes (50 m, 100 m, 200 m, 500 m, 1000 m, 2000 m, 4000 m, 6000 m, 8000 m, 10000 m). These neighborhoods were weighted by a Gaussian kernel using the `kernel2dsmooth' function from the *smoothie* package in R [41]. In the first stage, we ran univariate logistic regression models to identify the characteristic scale of selection for each landscape variable as indicated by the lowest Akaike Information Criterion value corrected for small sample size (AICc; [42]). In the second stage, we combined the optimal scales for each landscape variable into a multiple logistic regression model (omitting the lesser performing variable of any pair that had a correlation greater than 0.6). Because we thought all the variables would have some influence on puma habitat use, we then used the `dredge' function in package *MuMIn* [43] to run all variable subsets and identify the best model.

Level III resource selection: Point selection function

We used the same individuals and GPS point locations in the Point Selection Function (PSF) as we used to estimate puma home ranges. We estimated the used data as the proportion (for categorical data) or mean (for continuous data) of each predictor variable within a 30 m uniform buffer around each GPS location. We estimated the available data within a larger ecological neighborhood around each used point weighted by a Pareto kernel. The Pareto kernel was derived from our empirical movement data (see Zeller et al. [21] for details). The used and available data were analyzed in a paired, or conditional, logistic regression framework [44]. Therefore, each used point was paired with a biologically relevant available area. This approach, also referred to as a context-dependent PSF, estimates habitat selection at each location across the study area based on its location and surrounding environment and allows us to model Level III habitat use [5, 21].

We examined multiple scales by varying the size of the Pareto kernel for estimating available. Nineteen different sizes of the Pareto kernel were determined by using the 5-min data to create empirical movement distributions. Specifically, we used the 5-min GPS data to calculate movement distances over a 5-min time period and fit a Pareto distribution to this empirical distribution using the *gPdtest* package [45]. We then subsetted the data at progressively longer time periods up to 6-hr and re-fit the Pareto to each of these empirical distributions of movement distances. This resulted in 19 Pareto kernels with the following distances representing 95% of the distribution: 241 m, 408 m, 681 m, 915 m, 1123 m, 1317 m, 1602 m, 1850 m, 2049 m, 2298 m, 2312 m, 2797 m, 3044 m, 3104 m, 3479 m, 3819 m, 3994 m, 4099 m, and 4461 m. The available data were calculated as the proportion (for categorical data) or mean (for continuous data) of each predictor variable around each used point weighted by each Pareto kernel. Movement time periods and estimated Pareto distribution parameters are provided in S1 Table.

We developed our multi-scale models using the same two-stage approach as described for the HRSFs. We ran the paired logistic regression models with the `coxph' function in the *Survival* package [46]. We had attempted to run these models in a mixed-effects framework to

account for individual variability, but had model convergence issues. To compensate for the lack of an individual level mixed-effect, we used robust standard errors, which are calculated by combining data into clusters such that the clusters are not autocorrelated [47±49]. Robust errors are often used to control for the individual level effects in paired regression models [47, 50]. We ranked the models using AICc and arrived at our final model by averaging any models that had a $\Delta AICc \leq 2$ from the best model. We used the robust standard errors when calculating confidence intervals for the model-averaged coefficients.

Estimating resistance from movement data

We performed Path Selection Functions (PathSFs) to estimate the relative probability of movement for pumas across the study area. Our previous work has shown that PathSFs are sensitive to fix interval and that, for pumas, biases are introduced with fix intervals of 1-hour and greater [13]. Therefore, for this analysis we used data from individuals with either a 5-min or 15-min fix interval for at least a 2-week duration. We created paths for each individual by connecting consecutive points for each 24-hour time period. This resulted in a total of 39 pumas (Males = 20, Females = 19) and 1,076 daily paths for the PathSF analysis (mean per individual = 30 days, median = 22 days, range = 14±106).

We used the same resource selection approach as for the PSFs above, but instead of points as our unit of inference, we used daily paths. The previously described scales and two-stage approach were used to develop multi-scale PathSFs.

Estimating resistance from genetic data

Between 2001±2016, blood or tissue samples were collected from 146 captured or deceased pumas across the greater study area. Nuclear DNA was extracted and characterized at 44 microsatellite loci, which met the assumptions of Hardy-Weinberg proportions and linkage equilibria as described in Gustafson et al. [51]. Of the 146 individuals, 139 were located in the study area and used for this analysis (Fig 1).

Landscape genetic approaches aim to correlate observed genetic distances among individuals or populations with geographic distances. These geographic distances are calculated as the least-cost distance or resistance distance among individuals across resistance surfaces defined *a priori*. We explored a number of different resistance hypotheses for each of our predictor variables. Specifically, we represented each variable with four ecological neighborhoods (100 m, 500 m, 2000 m, and 6000 m) weighted by a Gaussian kernel. Computational capacity limited us from testing a wider range of scales; therefore, we selected an array of scales we thought was biologically appropriate for this analysis. We then applied each of seven functions to transform the scaled variable into a resistance value of 1±100 (Fig 2). Positive or negative transformation functions were used to represent increasing or decreasing resistance with increasing values of that variable, respectively. We also used the inverse Ricker transformation to account for variables that might have a low resistance at moderate values. Therefore, for each variable we tested a suite of 28 *a priori* resistance surfaces.

With the *adegenet* package [52], we calculated pairwise genetic distances among all 139 individuals using Nei's genetic distance [53]. We calculated pairwise geographic distance by calculating the least cost path distance between all sample locations across each *a priori* resistance surface with the *gdistance* package [54]. We then compared all the *a priori* resistance surfaces for a variable by running univariate linear mixed effects models that accounted for the pairwise structure of the distance matrices following the maximum likelihood population-effects (MLPE) method [55, 56]. This method has recently been shown to outperform other

correlational methods in landscape genetics such as Mantel tests or multiple regression with distance matrices [57].

We used AICc to identify the most appropriate resistance surface for each variable. We assessed correlations among variables and removed variables from correlated pairs with higher AICc values. We then ran multiple regression models with all uncorrelated variables and fit all possible subsets of the variables. We ranked the multiple regression models using AICc and identified our top model.

Multi-level resource selection function and resistance surfaces

We predicted the relative probability of use across our study area from the HRSF by using the following formula $\hat{w}(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \ldots + \beta_p x_p)$ as recommended by Johnson et al. [35]. We predicted the relative probability of use from the PSFs and PathSFs in the paired framework described by Zeller et al. [13]. This approach requires `used' and `available' to be calculated for every pixel in the study area. We first calculated the proportion or mean of each variable within a 30 m fixed-width buffer at each pixel in our study area. We then calculated the proportion or mean of each variable at each pixel weighted by the Pareto kernel at the appropriate scale for that variable. This is akin to the `used' and `available' in the paired regression models and allows for a unique relative probability of movement to be identified for each pixel in the study area.

We converted the relative probabilities of the PathSF surface to resistance by subtracting the relative probabilities of movement from one and multiplying by 100. For the landscape genetics analysis, we derived our resistance surface by summing the resistance surfaces for the variables in the final model and rescaling from 1±100.

We multiplied the predictive surfaces from the Level II HRSF and the Level III PSF and rescaled the surface from 0±1 to obtain a single multi-scale ML-RSF. We quantile re-scaled the landscape genetics and PathSF resistance surfaces, multiplied them, and rescaled the surface from 1±100 to obtain a single multi-scale ML-RS.

Resource use patches and corridors

The greater Northern San Diego County area (including parts of southern Orange and Riverside Counties) was the focal landscape for our conservation plan. All further analyses were conducted on this subset of our original study area (Fig 1; Conservation Network Boundary).

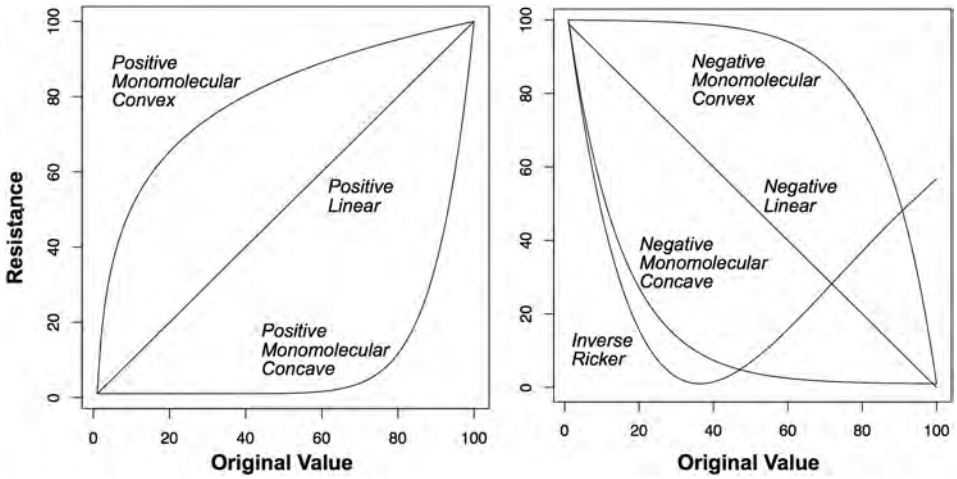

Fig 2. Functions used to transform the environmental variables to resistance, with a range of 1±100, for use in the landscape genetic analysis.

https://doi.org/10.1371/journal.pone.0179570.g002

To identify resource use patches, we first smoothed the ML-RSF surface using a Gaussian kernel with a bandwidth of 500 m. We then identified patches on this surface that had at least a 60% probability of resource use and were at least as large as the minimum observed female home range size.

To model corridors, we first probabilistically distributed 2000 source points on the ML-RSF surface within the resource-use patches. We then used UNICOR software [58] to identify resistant kernel corridors [9] across our ML-RS surface from the source points. Resistant kernels allow the identification of a maximum dispersal distance, which we set to 100 km for puma [27]. We identified landscape corridors by taking the top 75% of the resistant kernel surface.

We calculated the percent overlap between our conservation network (resource use patches and corridors) and the current and proposed protected area network to highlight gaps in protection for pumas and identify areas for future conservation attention. Current protected areas were identified from the California Protected Areas Database [59]. We considered Department of Defense, Native American Reservation, and large Water and Irrigation District lands as partially protected and included these as a separate category in our calculations. Proposed protected areas were lands designated as Pre-Approved Mitigation Areas by Orange, Riverside, and San Diego Counties.

Results

Level II resource selection: Home range selection function

Home range sizes varied from 41±497 km^2 (Mean = 231 km^2; Female mean = 188 km^2; Male mean = 316 km^2). Characteristic scales differed across predictor variables (Table 2), but pumas generally selected for coarser scales when establishing home ranges. Due to convergence errors, we were unable to fit the models for primary roads. We identified a single best model for puma home range selection (Table 3). This model indicates pumas select for home ranges with more rugged terrain, naturally barren areas, chaparral, coastal scrub, and grassland than the surrounding landscape and fewer areas of agriculture, desert, woodland, and urban.

Level III resource selection: Point selection function

Univariate model results indicate pumas had a mostly bi-modal response to landscape features at the third order of habitat selection (Table 2). Pumas responded to elevation, percent slope, chaparral, and coastal scrub at fine scales and responded to the other variables at coarse scales. Due to convergence errors, we were unable to fit the models for desert and primary roads.

After removing correlated variables, the global model was identified as the top model. Pumas preferred slightly more rugged terrain, riparian areas and woodland while avoiding high elevation, high slopes, agriculture, barren, chaparral, coastal scrub, grassland, urban, and primary, secondary, and tertiary roads (Table 4).

Estimating resistance from movement data

Pumas selected for more landscape variables at finer scales during movement than during resource selection (Table 2). After removing correlated variables, four top models were identified and beta coefficients were averaged. Pumas also showed more tolerance of landscape variables during movement than during resource-use events. Pumas avoided steep slopes, agricultural areas, urban areas, and roads during movement, but showed a preference for all other landscape variables in the final model, especially riparian and woodland areas (Table 5).

Table 2. Characteristic scales of selection for each predictor variable from the Level II and Level III selection functions, the Path selection functions, and landscape genetic analysis. Plus or minus indicates preference or avoidance of that variable for resource use or movement. The selected resistance transformation for the landscape genetic analysis are indicated by IR = inverse Ricker, NL = negative linear, NMCc = negative monomolecular concave, NMCv = negative monomolecular convex, PL = positive linear, PMCc = positive monomolecular concave, PMCv = positive monomolecular convex. Blank cells indicate model convergence failures.

Variable	Level II selection function		Level III selection function		Landscape genetics analysis		Path selection function	
	Scale (m)	*Sign*	*Scale (m)*	*Sign*	*Scale (m)*	*Trans-formation/ Sign*	*Scale (m)*	*Sign*
Topographic features								
Elevation	2000	+	241	-	6000	IR	241	+
Percent slope	8000	+	241	-	100	NMCc +	2797	-
Terrain ruggedness	10000	+	4461	+	500	IR	681	+
Land cover type								
Agriculture	6000	-	4461	-	6000	PL -	3819	-
Chaparral	4000	+	241	-	6000	NMCc +	3104	-
Coastal Scrub	500	+	681	-	500	NMCv +	241	-
Coastal oak woodland	10000	+	4461	+	2000	NMCv +	241	+
Grassland	10000	+	4461	-	500	PMCv -	2797	-
Barren/Open water	4000	+	3994	-	100	NL +	3104	-
Desert	8000	-			6000	PMCc -		
Riparian	10000	+	3497	+	500	NMCv +	1317	+
Human development								
Urban	2000	-	4461	-	500	PMCv -	241	-
Roads; Classi®edas Primary, Secondary, and Tertiary	10000	-	4461	-	500	PMCv -	3819	-
Roads; Classi®edas Primary, and Secondary	6000	-	4461	-	2000	PL -	4461	-
Roads; Primary only					500	PMCv -		

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Estimating resistance from genetic data

The linear mixed effect models resulted in identifying the characteristic scale and transformation for each variable in relation to the genetic distances among individuals (Table 2). Variables whose resistance increased with increasing values were agriculture, grassland, urban, and roads. Variables whose resistance decreased with increasing values were chaparral, percent slope, riparian, coastal scrub, and coastal oak woodland. Resistance for elevation and ruggedness were represented by an Inverse Ricker transformation, which decreases until middle values are reached, and then increases for the remaining values, indicating dispersal is facilitated at mid-elevation and mid-ruggedness values.

Table 3. Standardized beta estimates, robust standard errors, and 95% robust confidence intervals for the multivariate Level II Home Range Selection Function model variables.

Variable	Beta estimate	Standard Error	95% Con®dence Interval
Terrain ruggedness	0.95	0.01	0.94±0.96
Agriculture	-0.04	0.01	-0.05 ±-0.03
Barren	0.19	0.01	0.18±0.20
Chaparral	0.17	0.02	0.15±0.18
Coastal oak woodland	-0.05	0.01	-0.06 ±-0.05
Coastal scrub	0.15	0.02	0.14±0.16
Desert	-1.26	0.04	-1.28 ±-1.23
Grassland	0.11	0.02	0.1±0.12
Urban	-0.68	0.03	-0.70 ±-0.66

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Table 4. Standardized beta estimates, robust standard errors, and 95% robust confidence intervals for the multivariate Level III Point Selection Function model variables.

Variable	Beta estimate	Standard Error	95% Con®dence Interval
Elevation	-21.61	0.60	-21.99 ±-21.23
Percent Slope	-1.1	0.03	-1.12 ±-1.08
Terrain Ruggedness	0.09	0.01	0.08±0.09
Agriculture	-0.25	0.02	-0.23 ±-0.26
Barren	-0.06	0.02	-0.05 ±-0.07
Chaparral	-0.17	0.06	-0.21 ±-0.13
Coastal Scrub	-0.29	0.03	-0.03 ±-0.27
Grassland	-0.38	0.02	-0.40 ±-0.37
Riparian	0.38	0.04	0.35±0.40
Woodland	0.23	0.02	0.22±0.24
Urban	-2.18	0.16	-2.28 ±-2.08
Roads: Primary, Secondary, Tertiary	-0.06	0.02	-0.07 ±-0.05

https://doi.org/10.1371/journal.pone.0179570.t004

After accounting for correlations, the following variables were included in the multiple regression model: elevation, percent slope, agriculture, chaparral, coastal scrub, coastal oak woodland, grassland, riparian, urban, and primary roads. The global model was selected as the best performing model. To determine whether the variables explained the genetic distance among individuals more than Euclidean distance alone, we also ran a regression model with a simple Euclidean distance matrix among sample locations. This resulted in a ΔAICc of 278, which was much higher than any other model, indicating the environmental variables explained the genetic distance among individuals better than Euclidean distance alone. To determine whether long-term genetic processes were driven largely by fine scale movement data, we also calculated geographic distances among sample locations across our PathSF resistance surface and obtained low model support (ΔAICc = 247), indicating different drivers for long-term genetic connectivity.

Multi-level resource selection function and resistance surfaces, resource use patches, and corridors

Fig 3 presents the predicted relative probability of use surfaces for the HRSF, the PSF, and the combined ML-RSF. Home range centers tended to be located further from urban areas and in more mountainous terrain. The Level III selection surface also tended to select for non-urban

Table 5. Standardized beta estimates, robust standard errors, and 95% robust confidence intervals weights for the multivariate Path Selection Function model variables.

Variable	Beta estimate	Standard Error	95% Con®dence Interval
Elevation	9.22	1.00	8.51±9.94
Percent Slope	-1.35	0.21	-1.50 ±-1.20
Agriculture	-0.02	0.09	-0.08±0.05
Chaparral	1.44	0.30	1.37±1.51
Grassland	-0.02	0.28	-0.22±0.18
Barren/Open Water	-0.02	0.07	-0.07±0.04
Riparian	5.92	1.90	4.56±7.27
Woodland	2.87	0.36	2.61±3.13
Urban	-7.53	2.03	-8.98 ±-6.08
Roads: Primary, Secondary, Tertiary	-0.78	0.24	-0.95 ±-0.62

https://doi.org/10.1371/journal.pone.0179570.t005

areas, but this surface was more heterogeneous than the Level II surface, demonstrating finer-scale selection. The ML-RSF surface identified areas of Level III habitat selection conditional upon the higher Level II order of selection.

Fig 4 displays the resistance surfaces derived from the landscape genetics analysis, the PathSF, and the ML-RS. Similar to the probability of use surfaces at the higher order, the landscape genetic analysis resulted in developed areas having a high resistance for pumas and undeveloped, mountainous areas having a lower resistance. Though the coarse-scale patterns were similar for the resistance surface derived from the PathSF, this surface was more heterogeneous and reflected finer-scaled patterns of resistance to movement. The Spearman correlation coefficient between the landscape genetics and the PathSF resistance surfaces was 0.31. The ML-RS can be interpreted as resistance to movement at finer scales weighted by coarser-scale spatial and temporal processes.

Resource-use patches in the study area measured 2,577 km^2. Resistant kernel corridors connecting these resource-use patches measured 777 km^2 (Fig 5A). The current protected area network encompassed 35% of the puma resource-use patches in the study area and 47% of the landscape corridors outside of the resource use patches (Fig 5C). Adding the partially protected Department of Defense, Native American Reservation, and Water and Irrigation District lands increased current protection of resource-use patches to 61% and landscape corridors to 60% (Fig 5C). If 75% of the lands that are currently pre-approved for mitigation protection by Orange, Riverside, and San Diego Counties become protected (the 75% level is the target amount), then 88% of the puma resource-use patches will be fully or partially protected and 82% of the landscape corridors will be fully or partially protected (Fig 5D).

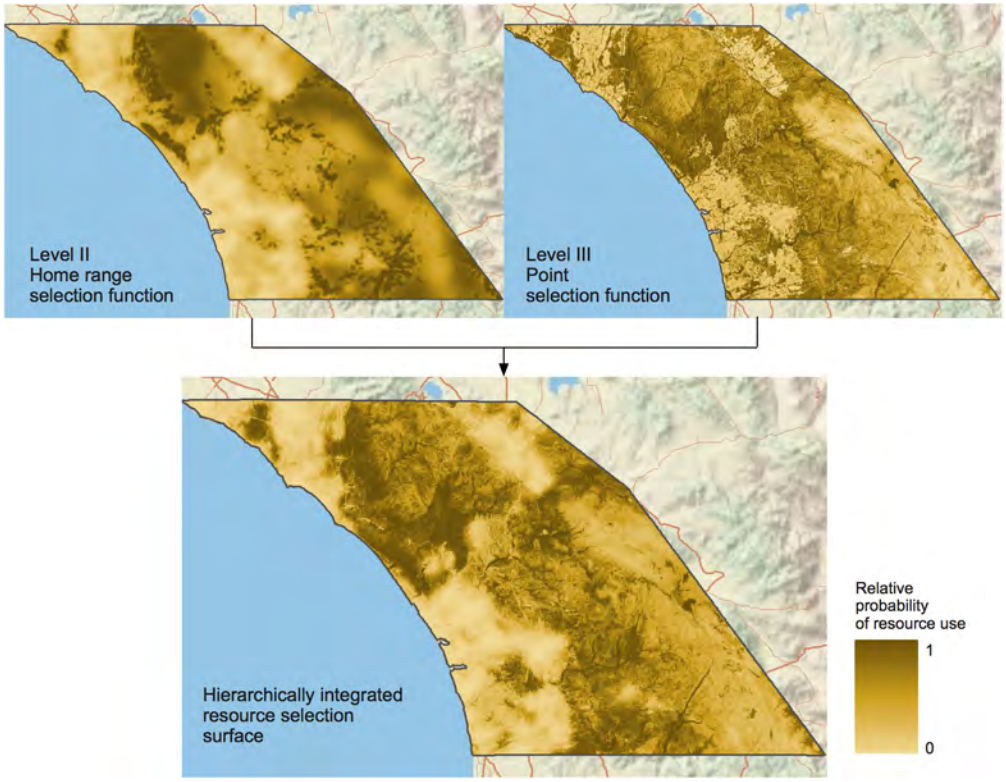

Fig 3. Predicted relative probability of use surfaces from the multi-scale Level II Home Range Selection Function, the multi-scale Level III Point Selection Function and the combined Multi-Level Resource Selection Function.

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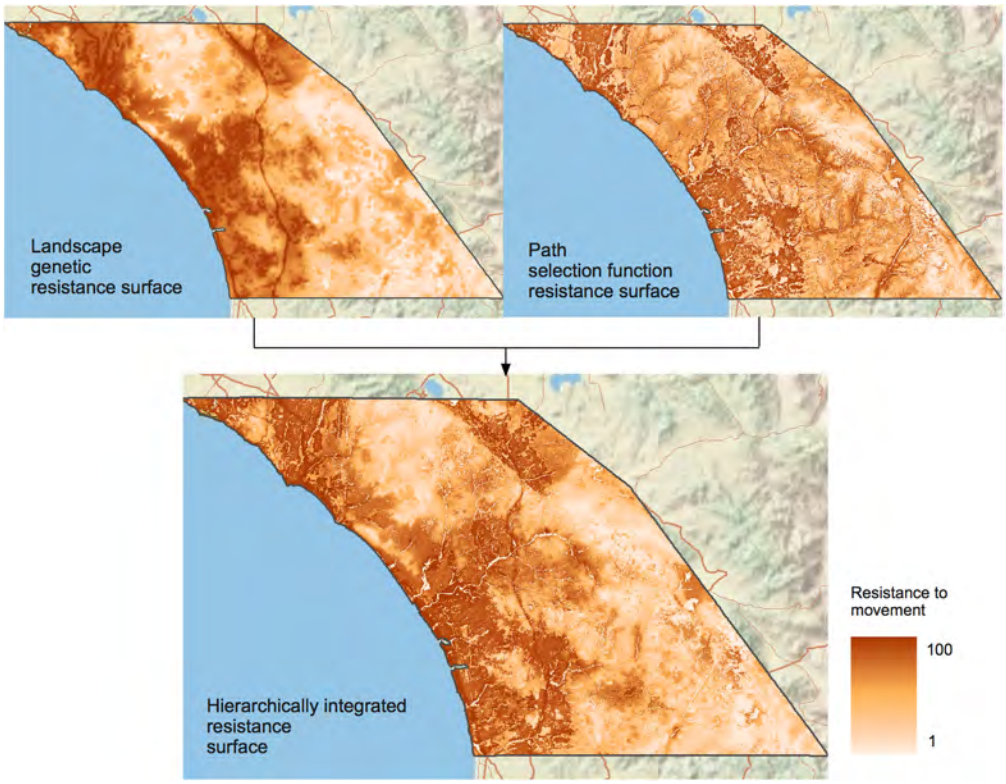

Fig 4. Resistance surfaces derived from the landscape genetics analysis, the PathSF, and the combined Multi-Level Resistance Surface.

https://doi.org/10.1371/journal.pone.0179570.g004

Discussion

Multi-level, multi-scale resource selection functions and resistance surfaces capture a wide spectrum of selection, movement and survival process. Multi-level, multi-scale resource selection models have been shown to outperform single-scale, single-level models, result in stronger inference and predictive capabilities [6, 7, 17, 21], and are the most appropriate for use in conservation planning [60]. However, to our knowledge, the multi-level, multi-scale framework had not been applied to resistance surfaces. Herein, we introduce a multi-level, multi-scale approach for developing resistance surfaces. Our ML-RS quantifies resistance in terms of all three previously sought-after processes: (1) willingness to cross, (2) physiological costs of crossing, and (3) direct survival impacts while crossing. When establishing landscape-level wildlife corridors, the ultimate objectives are to provide safe passage for migrants to access, establish residence, and successfully reproduce in new suitable habitats. Resistance surfaces that reflect real-time movement and decision-making of individuals, as well as the chances of surviving and reproducing, are conceptually more powerful than resistance surfaces that reflect only one of these three processes.

Our results showed similar coarse-scale patterns between the resistance surfaces derived from the genetic and movement data; however, details were present in the genetic surface that were not present in the movement surface, and vice versa. For pumas in our study, the resistance surface derived from the movement models consistently showed primary roads and urban areas as less-resistant features than the resistance surface derived from genetic data. These results reflect the ability and occasional willingness of pumas to travel through highly developed areas. Conversely, the movement data highlighted the importance of riparian areas

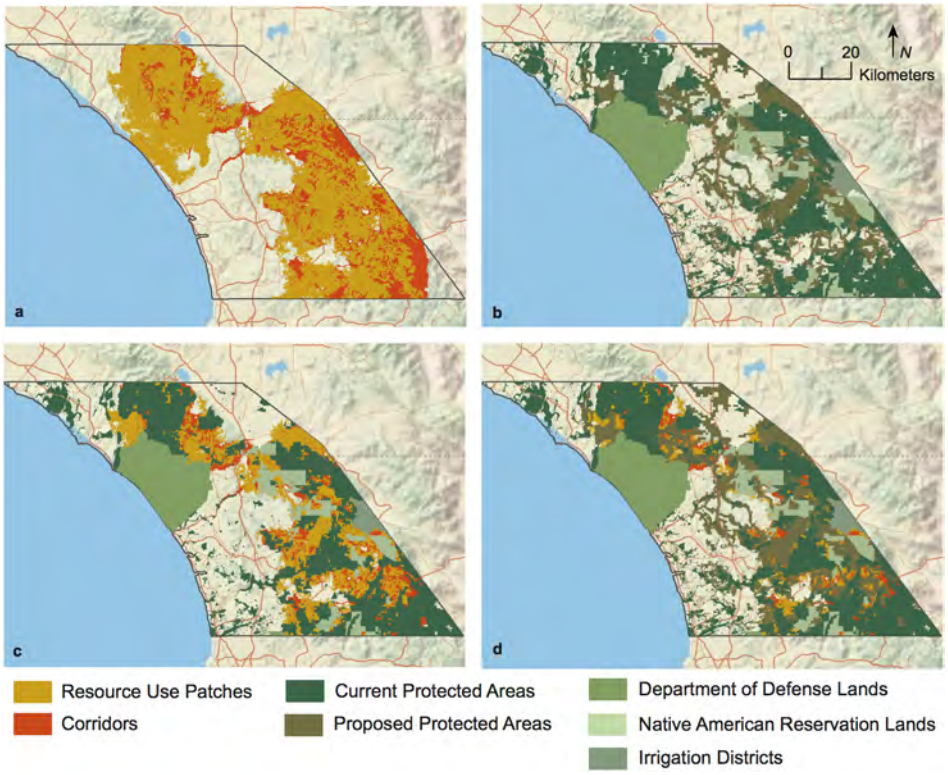

Fig 5. Puma resource use patches, landscape corridors, and the current and proposed protected area network.

https://doi.org/10.1371/journal.pone.0179570.g005

and canyons for puma movement, assigning consistently lower resistance values to these features than the resistance surface derived from genetic data. Combining these surfaces resulted in constraining fine-scaled movement (potential resistance) within areas more amenable to coarse-scale, generational success in dispersal and breeding (realized resistance).

We can further illustrate the advantages of a ML-RS through our collective knowledge of the Santa Ana Mountains puma population. This population inhabits what has been described as a large habitat fragment, isolated on all sides by roads, human development, and the Pacific Ocean [25]. The Palomar Linkage (Fig 1.; [61]) just south of the city of Temecula has been identified as the only potentially viable linkage between the Santa Ana Mountain puma population and those to the east. The Palomar Linkage connects natural areas on both sides of I-15, yet I-15 itself is a significant obstacle to puma movement. Genetic population assignment tests have shown that only seven males successfully crossed I-15 over the last 15 years; three immigrated into the Santa Ana Mountains from the Eastern Peninsular Range and four traveled from the Santa Ana Mountains to the Eastern Peninsular Range [51]. Of these seven, five are known to be deceased and the status of the remaining two is unknown. Offspring were only detected from one of the seven immigrants, M86, who migrated into the Santa Ana Mountains. M86 successfully bred and passed genetic material to 11 offspring before being hit by a car and killed. Of the 11 offspring, only two are confirmed to have survived to breeding age, yet the success of this one male was shown to significantly improve the genetic diversity of the Santa Ana Mountains population [51]. The seven males that crossed I-15 offer evidence of the occasional ability and willingness of pumas to travel through urbanized areas and across primary roads. The behavior of these individuals is therefore better represented with the movement resistance surface. In contrast, the physiological and survival costs of these movements,

exemplified by the low survival and breeding success of these seven pumas, are better reflected with the genetic resistance surface. The combination of these surfaces into a single ML-RS integrates all three of these processes and is a more appropriate representation of resistance for identifying landscape-level connectivity.

Consistent with other studies that conducted resource selection functions at multiple hierarchical levels, we found differences among levels in terms of variable importance and habitat preference for pumas [2, 4, 5, 7]. Of the variables present in both the Level II and Level III models, habitat use relationships differed for chaparral, coastal scrub, coastal oak woodland, and grassland. Chaparral, scrub, and grassland types were preferred for home range establishment, but were avoided while using resources within the home range. Our results for woodland were unexpected. Pumas are traditionally associated with woodland, but our Level II model showed an avoidance of woodland. We suspect this is the result of a relatively low occurrence of woodland in the Santa Ana and Palomar Mountain ranges compared with a higher amount of woodland in the greater extent used for the HRSF analysis. Therefore, this finding is likely an anomaly of study area extent and does not indicate a true avoidance [62]. As expected, woodland was preferred in our Level III model. Variables that were included in the final Level III model that were not present in the Level II model include primary, secondary, and tertiary roads, elevation, slope, and riparian areas. With the exception of woodland at the second order of selection, our results generally agree with other puma resource-use studies. We found topographic variables to be important at both hierarchical levels with a strong preference for rugged areas and an avoidance of areas with steep slopes [25, 30, 32]. We also found a strong avoidance of human development in the form of agricultural areas, urban areas, and roads [21, 30±32]. Home range sizes were also consistent with other studies of pumas in Mediterranean climates [63].

Similar to our findings across hierarchical levels of selection, we found some differences between the resistance models derived from the movement and genetic data. The genetic model included coastal scrub whereas the movement model did not and instead included the barren cover type. The genetic model only included primary roads whereas the movement model included the roads layer with all three road types: primary, secondary, and tertiary. For some variables, the models differed in their relationship with resistance. For example, the genetic model reflected decreasing resistance with increasing values of slope, and the movement model reflecting increasing resistance with increasing values of slope. For elevation, comparison is more difficult. The genetic resistance model selected the Inverse Ricker transformation, indicating lower resistance at moderate elevations and higher resistance for very low and high elevation areas. Given the paired nature of our PathSF model, we were unable to explore quadratic relationships and the resistance surface from the movement data reflected decreasing resistance with increasing elevation. Cushman and Lewis [10] compared black bear genetic models with early season movement models and found both to have the same variables with the same relationship to resistance, but observed different variables and different relationships when comparing genetic models with late season movement models. Coulon et al. [15,16] found roe deer exhibited different relationships to woodland areas with genetic and movement data. These differences are to be expected because, as argued above, resistance estimated from genetic data and resistance estimated from movement data represent different processes. This is further supported by our landscape genetic model performance results. We found the final resistance surface derived from the landscape genetic analysis to greatly outperform that derived from the PathSF analysis in predicting genetic distance, indicating potentially different drivers for long-term genetic connectivity.

Another possible advantage of combining the resistance surfaces from movement and genetic data lies in the difficulty of obtaining dispersal data. It is often argued that dispersal

data are more appropriate than data from within home-range movements for estimating resistance; however, dispersal data are much more difficult to obtain and often suffer from very small sample sizes. By using genetic data as a proxy for dispersal, and combining this resistance surface with one derived from within home-range movement, these surfaces may more closely approximate those obtained with empirical dispersal data, though more research is needed to support this hypothesis. We acknowledge the ML-RS may not be the most appropriate resistance surface to use for every application and recommend its use for landscape-level corridors only. For other applications, like pinpointing discrete road crossing locations or applications that reflect fine-scaled travel and real-time movement decisions, we argue that it is more appropriate to use a resistance surface estimated directly from movement data [11].

Our conservation network for pumas in the study area incorporated multiple scales of selection at two different hierarchical levels for both habitat use and resistance. In this heavily developed landscape, we found resource use and connectivity to be mostly confined to natural areas with only corridors extending into more developed areas. At present, only 35% of resource-use patches and 47% of corridors identified in this study are fully protected. Some additional lands offer partial protection, bringing the fully and partially protected lands to about 60% of the resource-use patches and corridors. Given the low adult survival rate (56%; [27]), low levels of heterozygosity and high incidence of inbreeding for pumas in this region [26], increasing protection of individuals and habitat is essential to their long-term survival [64]. The proposed protected areas identified by the three counties in the study area would greatly increase the amount of protection. However, many of these proposed protected areas are currently on private land and depend upon them being used as mitigation for development elsewhere. Road mitigation efforts are also needed given the low level of successful dispersal and breeding among pumas in the study area and the finding in Vickers et al. [27] that the most frequent cause of death for GPS-collared pumas was by vehicle collisions.

Our analysis was specific to pumas in southern California, yet the general approach may be applied to wildlife species worldwide. Many previous conservation networks have used a single organizational level, thereby omitting important behavioral and biological processes at other levels, and may result in incorrect inference and only partially effective conservation plans [2, 5, 7, 65]. By incorporating selection and movement at multiple hierarchical levels, correct inference may be made at each level. Furthermore, integrating results across levels will result in much stronger predictive surfaces for conservation. Modeling multi-scale relationships within each hierarchical level further strengthens these surfaces. Our thresholds for identifying the resource-use patches and landscape corridors were somewhat arbitrary, but are based on previously recommended thresholds [66] and provide a reasonable result for pumas in our study area. Echoing DeCesare et al. [4], additional research is needed to determine more biologically-based thresholds for creating binary conservation surfaces from continuously distributed ML-RSFs and connectivity surfaces derived from ML-RSs. Despite the strong conceptual and inferential advantages of multi-level, multi-scale approaches, a recent review of 173 multi-scale habitat selection studies found that only 8 (5%) used a combined multi-level, multi-scale approach, indicating this approach for research and conservation planning has been underutilized [2]. We offer the addition of multi-level, multi-scale resistance surfaces to this body of literature and recommend that multi-level, multi-scale approaches be used for identifying areas of resource use and landscape connectivity and for developing species conservation networks.

Supporting information

S1 Table. Time-intervals and associated radii of Pareto kernels used to define available habitat for point and path selection functions. We fit a Pareto distribution to the empirical

distribution of displacement distances at each time-period and defined the maximum radii of the Pareto distribution by either using the 95th quantile of the distribution, or the maximum observed displacement distance, whichever was smaller.
(DOCX)

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