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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

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.

<center>MATERIALS AND METHODS</center>

<center>*Study area*</center>

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 $\lambda_t$ (Lambda [population growth] at time t) as $N_t/N_{t-1}$, where $N_t$ is total population size at time $t$. We estimated $\lambda_s$ (stochastic lambda) across time periods of interest with the formula:

$$\frac{[\sum^{N_{years}} \ln(\lambda_t)]}{N_{years}}$$

We report median $\lambda_s$ from the distribution of values across all projections for simulations of interest. We estimated credible intervals for $\lambda_s$ 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 $\lambda_s$ 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 $\lambda_s$ in the absence of density-dependent limitations. We calculated sensitivity values ($S$) for each demographic parameter:

$$S = \frac{\text{Log}\lambda_s(\text{increased}) - \text{Log}\lambda_s(\text{original})}{\text{parameter(increased)} - \text{parameter(original)}}$$

and elasticity ($E$) for each demographic parameter following Morris and Doak (2002):

$$E = S \times \left(\frac{\text{parameter}_{original}}{\text{parameter}_{adjusted}}\right).$$

*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.

| Parameter | No immigration | | Observed immigration | | 1 immigrant/2 yr | | 1 immigrant/1 yr | |
|---|---|---|---|---|---|---|---|---|
| | Estimate | 95% HPD† | Estimate | 95% HPD† | Estimate | 95% HPD† | Estimate | 95% HPD† |
| Santa Anas | | | | | | | | |
| $\lambda_s$‡ | 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 | | | | | | | | |
| $\lambda_s$‡ | 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; $\lambda_s$, stochastic population growth.
† 95% highest posterior density credible intervals.
‡ Median value.
§ Effective population size (mean value).

rate was similar ($\lambda_s$ = 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 ($\lambda_s$ = 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 ($\lambda_s$ = 1.17 [1.11, 1.22]), whereas the predicted trend in the SAM did not differ from stable ($\lambda_s$ = 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 ($\lambda_s$ = 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
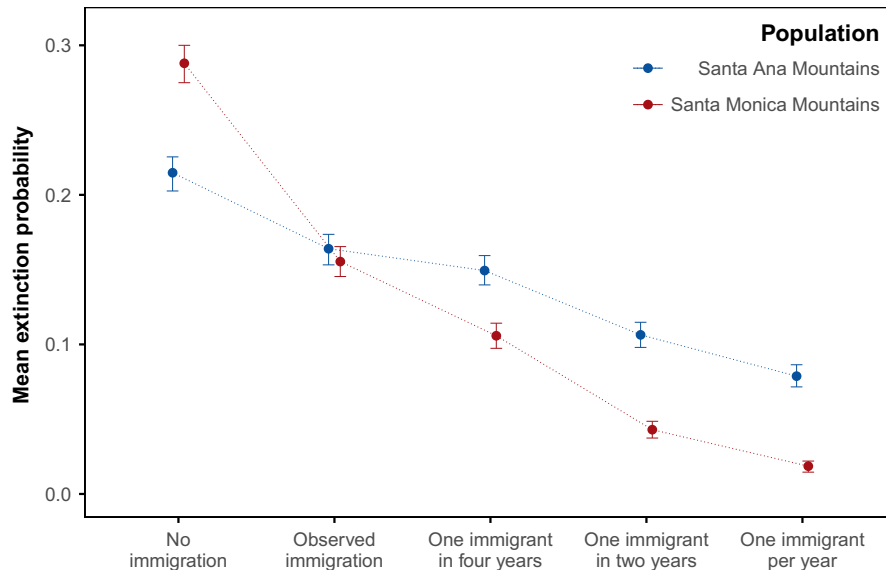
Fig. 2. Estimated extinction probability (without considering potential inbreeding effects) in 50 yr for mountain lion populations in the Santa Ana and Santa Monica Mountains from an individual-based population model based on 5,000 projections and varying levels of immigration.

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 $\lambda_s$ 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 $\lambda_s$ above 1, predicting a slightly increasing trend, whereas credible intervals overlapped 1 for all predictions of $\lambda_s$ 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
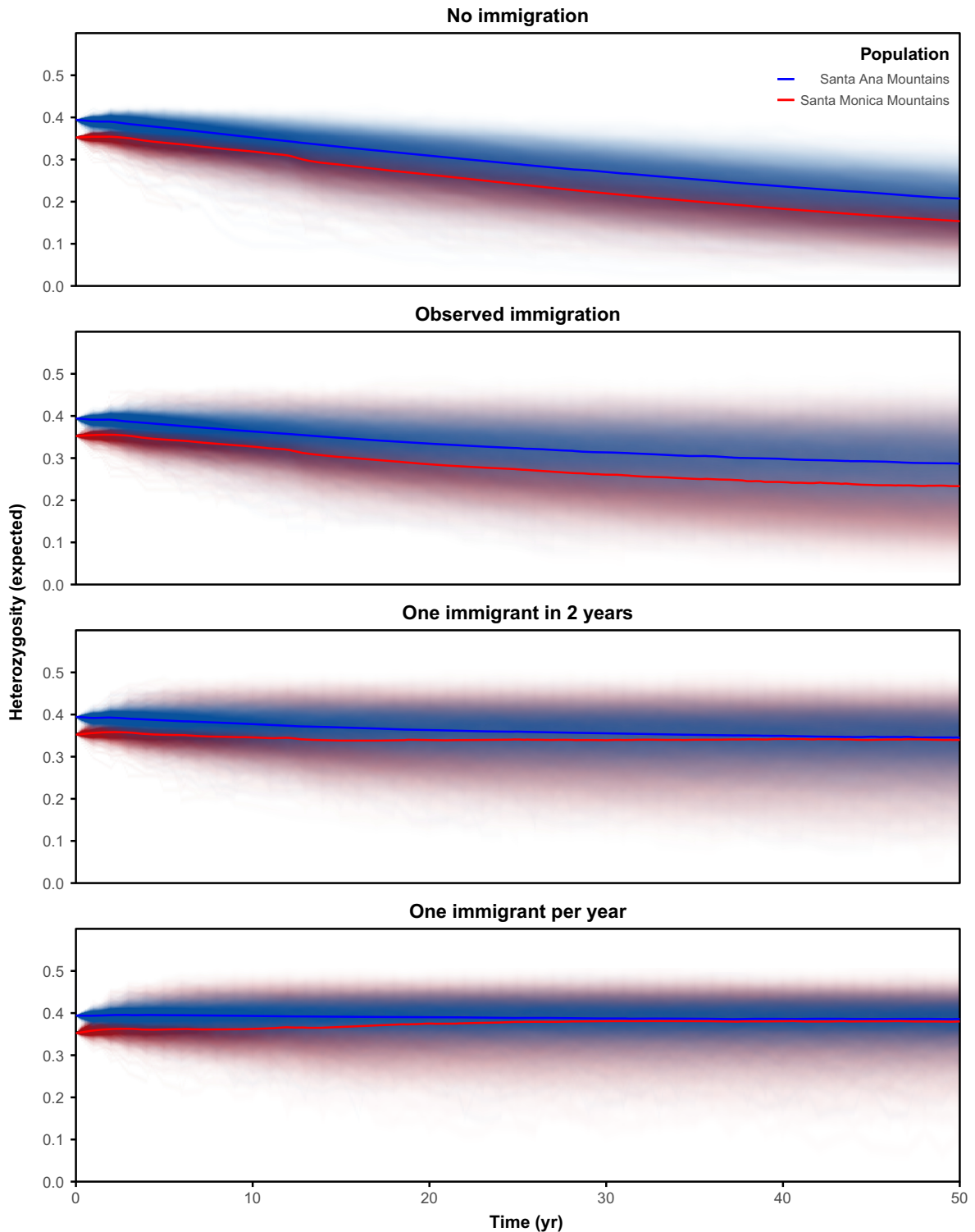
Fɪɢ. 3. Estimated expected heterozygosity over 50 yr for mountain lion populations in the Santa Ana and Santa Monica Mountains from and individual-based population model based on 5,000 projections and varying levels of immigration.

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 survival of breeding adults in a space-limited population provides few opportunities for mountain lions born in the SMM to breed.
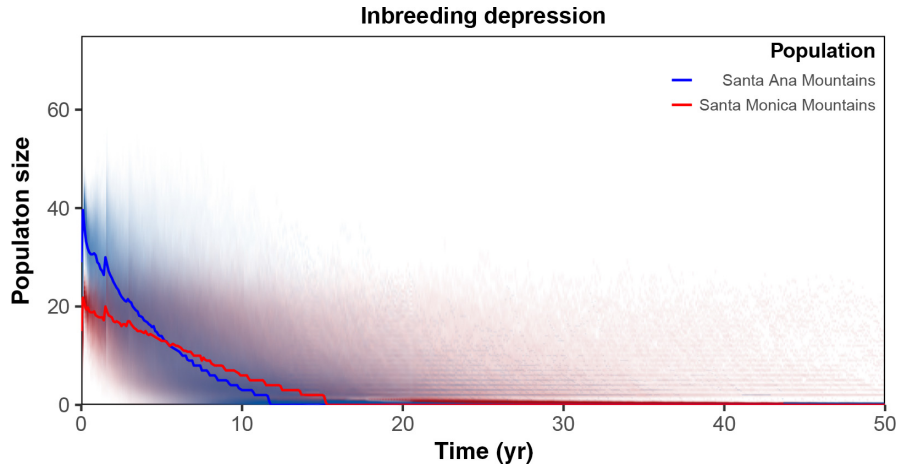
FIG. 4. Density-dependent demographic projections from individual-based population model showing predicted population sizes for mountain lions in the Santa Ana and Santa Monica Mountains over 50 yr based on 5,000 projections when we simulated inbreeding depression with the observed level of immigration.
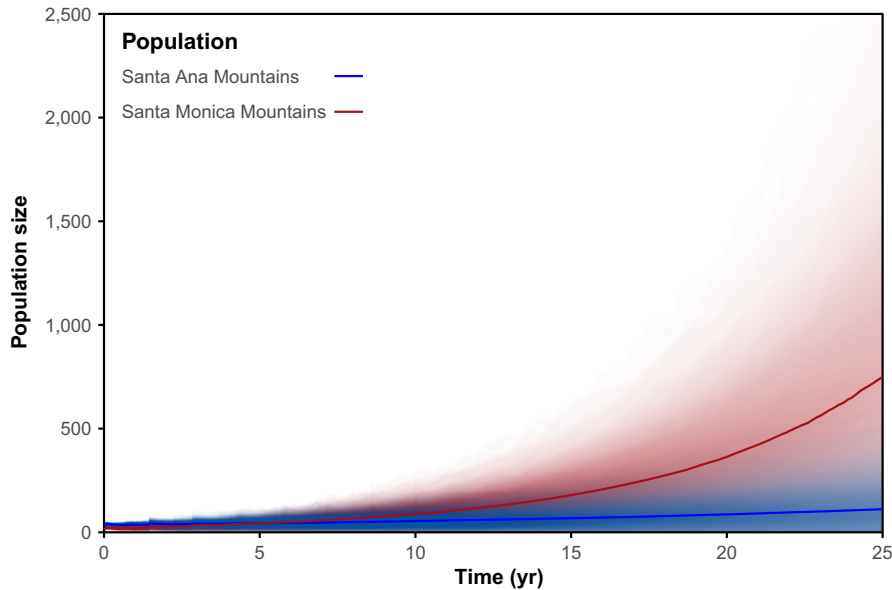


FIG. 5. Density-independent demographic projections from individual-based population model showing predicted mountain lion population size in the Santa Ana and Santa Monica Mountains over 25 yr based on 5,000 projections.

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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SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1868/full

DATA AVAILABILITY

Data are available on Zenodo: https://doi.org/10.5281/zenodo.2548917