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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 $[\hat{s}] = 0.68$, SE = 0.08) and adults ($\hat{s} = 0.81$, 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 (Andr n 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 Peninsular 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 km² 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-snare 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 Swenor, 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 non-parametric 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 \leq 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 ($\Delta AICc < 2$) 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

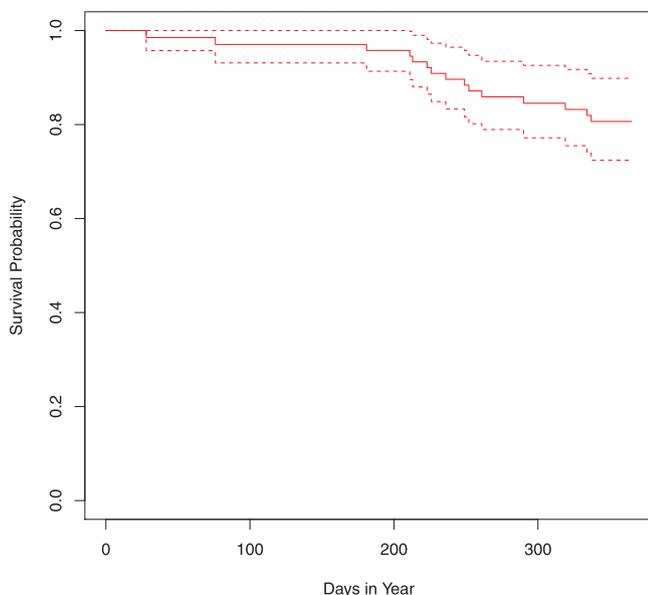


Fig. 2. Estimated annual survival probability and 95% confidence interval for adult mountain lions ($n = 29$) in greater Los Angeles.2002–2019.

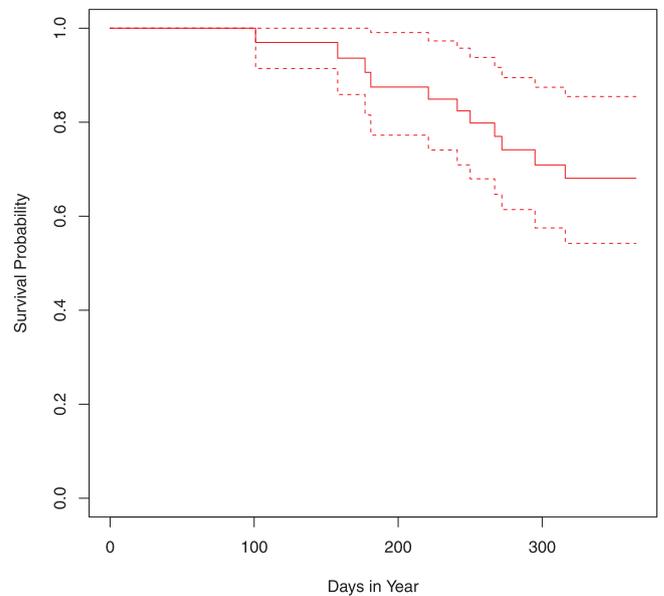


Fig. 3. Estimated annual survival probability and 95% confidence interval for subadult mountain lions ($n = 34$) in greater Los Angeles.2003–2019.

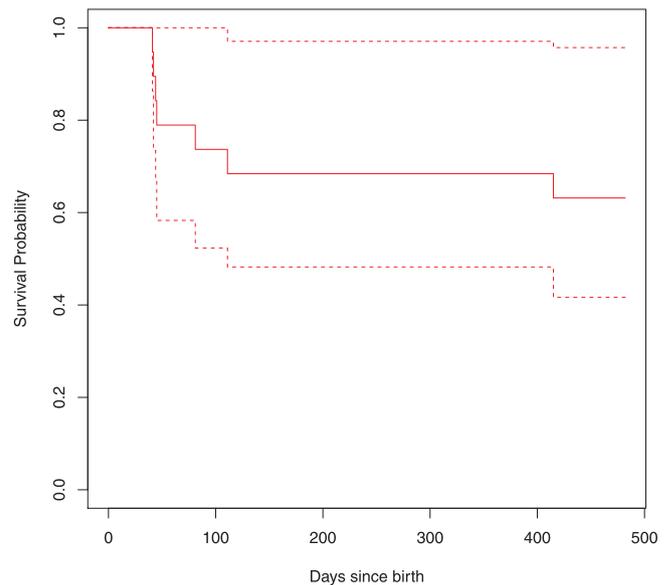


Fig. 4. Estimated survival probability to independence and 95% confidence interval for mountain lion kittens ($n = 22$ kittens from 10 litters) in greater Los Angeles.2004–2018.

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.

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 ($\Delta AICc = 0$). 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 ($\Delta AICc = 0.10$), further suggesting weak support for

a statistical difference between adults and subadults. Other models with $\Delta AICc < 2$ retained the dummy-coded variables of adults and males ($\Delta AICc = 1.26$) and the dummy-coded variable of males ($\Delta AICc = 1.10$), 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

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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References

- Andrén, H., Linnell, J.D., Liberg, O., Andersen, R., Danell, A., Karlsson, J., Odden, J., Moa, P.F., Ahlqvist, P., Kvam, T., Franzén, R., Segerstom, P., 2006. Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. *Biol. Conserv.* 131, 23–32.
- Beier, P., Riley, S.P.D., Sauvajot, R.M., 2010. Mountain lions (*Puma concolor*). In: Gehrt, S.D., Riley, S.P.D. (Eds.), *Urban Carnivores: Ecology, Conflict, and Conservation*, pp. 141–156 Baltimore.
- Benson, J.F., Hostetler, J.A., Onorato, D.P., Johnson, W.E., Roelke, M.E., O'Brien, S.J., et al., 2011. Intentional genetic introgression influences survival of adults and sub-adults in a small, inbred felid population. *J. Anim. Ecol.* 80, 958–967.
- Benson, J.F., Patterson, B.R., Mahoney, P.J., 2014. A protected area influences genotype-specific survival and the structure of a *Canis* hybrid zone. *Ecology* 95, 254–264.
- Benson, J.F., Mahoney, P.J., Sikich, J.A., Serieys, L.E., Pollinger, J.P., Ernest, H.B., Riley, S.P.D., 2016a. Interactions between demography, genetics, and landscape connectivity increase extinction probability for a small population of large carnivores in a major metropolitan area. *Proc. R. Soc. B: Biol. Sci.* 283, 20160957.
- Benson, J.F., Sikich, J.A., Riley, S.P.D., 2016b. Individual and population level resource selection patterns of mountain lions preying on mule deer along an urban-wildland gradient. *PLoS One* 11, e0158006.
- Benson, J.F., Mahoney, P.J., Vickers, T.W., Sikich, J.A., Beier, P., Riley, S.P., et al., 2019. Extinction vortex dynamics of top predators isolated by urbanization. *Ecol. Appl.* e01868.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*. Springer-Verlag, New York.
- Caughley, G., 1994. Directions in conservation biology. *J. Anim. Ecol.* 63, 215–244.
- Choate, D.M., Longshore, K.M., Thompson, D.B., 2018. Cougar dispersal and natal homing in a desert environment. *West. N. Am. Nat.* 78, 221–236.
- Clark, D.A., Johnson, B.K., Jackson, D.H., 2015. Monthly and annual survival rates of cougar kittens in Oregon. *Northwest Sci.* 89, 393–401.
- Elbroch, L.M., Marescot, L., Quigley, H., Craighead, D., Wittmer, H.U., 2018. Multiple anthropogenic interventions drive puma survival following wolf recovery in the Greater Yellowstone Ecosystem. *Ecol. Evol.* 8, 7236–7245.
- Ernest, H.B., Vickers, T.W., Morrison, S.A., Buchalski, M.R., Boyce, W.M., 2014. Fractured genetic connectivity threatens a southern California puma (*Puma concolor*) population. *PLoS One* 9, e107985.
- Fieberg, J., DelGiudice, G.D., 2009. What time is it? Choice of time origin and scale in extended proportional hazards models. *Ecology* 90, 1687–1697.
- Goodrich, J.M., Kerley, L.L., Smirnov, E.N., Miquelle, D.G., McDonald, L., Quigley, H.B., Hornocker, M.G., McDonald, T., 2008. Survival rates and causes of mortality of Amur tigers on and near the Sikhote-Alin Biosphere Zapovednik. *J. Zool.* 276, 323–329.
- Heisey, D.M., Patterson, B.R., 2006. A review of methods to estimate cause-specific mortality in presence of competing risks. *J. Wildl. Manage.* 70, 1544–1555.
- Hostetler, J.A., Onorato, D.P., Nichols, J.D., Johnson, W.E., Roelke, M.E., O'Brien, S.J., et al., 2010. Genetic introgression and the survival of Florida panther kittens. *Biol. Conserv.* 143, 2789–2796.
- Hostetler, J.A., Onorato, D.P., Jansen, D., Oli, M.K., 2013. A cat's tale: the impact of genetic restoration on Florida panther population dynamics and persistence. *J. Anim. Ecol.* 82, 608–620.
- Lambert, C.M., Wielgus, R.B., Robinson, H.S., Katnik, D.D., Cruickshank, H.S., Clarke, R., Almack, J., 2006. Cougar population dynamics and viability in the Pacific Northwest. *J. Wildl. Manage.* 70, 246–254.
- Logan, K.A., Swenaro, L.L., 2001. *Desert Puma: Evolutionary Ecology and Conservation of an Enduring Carnivore*. Island Press, Washington D.C.
- Lebreton, J.D., Burnham, K.P., Clobert, J., Anderson, D.R., 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* 62, 67–118.
- Lunn, M., McNeil, D., 1995. Applying Cox regression to competing risks. *Biometrics* 51, 524–532.
- Moss, W.E., Alldredge, M.W., Pauli, J.N., 2016. Quantifying risk and resource use for a large carnivore in an expanding urban-wildland interface. *J. Appl. Ecol.* 53, 371–378.
- Newby, J.R., Mills, L.S., Ruth, T.K., Pletscher, D.H., Mitchell, M.S., Quigley, H.B., et al., 2013. Human-caused mortality influences spatial population dynamics: pumas in landscapes with varying mortality risks. *Biol. Conserv.* 159, 230–239.
- Moriarty, J.G., Whited, L., Sikich, J.A., Riley, S.P.D., 2012. Use of intraperitoneal radiotransmitters to study mountain lion (*Puma concolor*) kittens. *Wildl. Soc. Bull.* 36, 161–166.
- Peduzzi, P., Concato, J., Kemper, E., Holford, T.R., Feinstein, A.R., 1996. A simulation study of the number of events per variable in logistic regression analysis. *J. Clin. Epidemiol.* 49, 1373–1379.
- Poessel, S.A., Breck, S.W., Fox, K.A., Gese, E.M., 2015. Anticoagulant rodenticide exposure and toxicosis in coyotes (*Canis latrans*) in the Denver Metropolitan Area. *J. Wildl. Dis.* 51 (1), 265–268.
- Pollock, K.H., Winterstein, S.R., Bunck, C.M., Curtis, P.D., 1989. Survival analysis in telemetry studies: the staggered entry design. *J. Wildl. Manage.* 53, 7–15.
- Riley, S.P.D., Bromley, C., Poppenga, R.H., Uzal, F.A., Whited, L., Sauvajot, R.M., 2007. Anticoagulant exposure and notoedric mange in bobcats and mountain lions in urban southern California. *J. Wildl. Manage.* 71, 1874–1884.
- Riley, S.P.D., Serieys, L.E., Pollinger, J.P., Sikich, J.A., Dalbeck, L., Wayne, R.K., Ernest, H.B., 2014. Individual behaviors dominate the dynamics of an urban mountain lion population isolated by roads. *Curr. Biol.* 24, 1989–1994.
- Robinson, H.S., Desimone, R., Hartway, C., Gude, J.A., Thompson, M.J., Mitchell, M.S., Hebblewhite, M., 2014. A test of the compensatory mortality hypothesis in mountain lions: a management experiment in West-Central Montana. *J. Wildl. Manage.* 78, 791–807.
- Ruth, T.K., Haroldson, M.A., Murphy, K.M., Buotte, P.C., Hornocker, M.G., Quigley, H.B., 2011. Cougar survival and source-sink structure on Greater Yellowstone's Northern Range. *J. Wildl. Manage.* 75, 1381–1398.
- Serieys, L.E., Lea, A.J., Epeldegui, M., Armenta, T.C., Moriarty, J., VandeWoude, S., Carver, S., Foley, J., Wayne, R.K., Riley, S.P.D., Uittenbogaart, C.H., 2018. Urbanization and anticoagulant poisons promote immune dysfunction in bobcats. *Proceedings of the Royal Society B: Biological Sciences* 285, 20172533.
- Therneau, T.M., Grambsch, P.M., 2000. *Modeling survival data: extending the Cox model*. Springer Science Business Media.
- Vickers, T.W., Sanchez, J.N., Johnson, C.K., Morrison, S.A., Botta, R., Smith, T., et al., 2015. Survival and mortality of pumas (*Puma concolor*) in a fragmented, urbanizing landscape. *PLoS One* 10, e0131490.