Received: 2 May 2022 | Revised: 8 January 2023 | Accepted: 11 January 2023

DOI: 10.1002/eap.2822

ARTICLE

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

Habitat fragmentation reduces survival and drives source–sink dynamics for a large carnivore

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Funding information
National Science Foundation, Grant/Award Numbers: 1255913, 0963022; Gordon and Betty Moore Foundation; Peninsula Open Space Trust

Handling Editor: Karen E. Hodges

Abstract

Rigorous understanding of how environmental conditions impact population dynamics is essential for species conservation, especially in mixed-use landscapes where source–sink dynamics may be at play. Conservation of large carnivore populations in fragmented, human-dominated landscapes is critical for their long-term persistence. However, living in human-dominated landscapes comes with myriad costs, including direct anthropogenic mortality and sublethal energetic costs. How these costs impact individual fitness and population dynamics are not fully understood, partly due to the difficulty in collecting long-term demographic data for these species. Here, we analyzed an 11-year dataset on puma (*Puma concolor*) space use, mortality, and reproduction in the Santa Cruz Mountains, California, USA, to quantify how living in a fragmented landscape impacts individual survival and population dynamics. Long-term exposure to housing density drove mortality risk for female pumas, resulting in an 18-percentage-point reduction in annual survival for females in exurban versus remote areas. While the overall population growth rate appeared stable, reduced female survival in more developed areas resulted in source–sink dynamics across the study area, with 42.1% of the Santa Cruz Mountains exhibiting estimated population growth rates <1. Since habitat selection is often used as a proxy for habitat quality, we also assessed whether puma habitat selection predicted source and sink areas. Patterns of daytime puma habitat selection predicted source areas, while time-of-day-independent habitat selection performed less well as a proxy. These results illuminate the individual- and population-level consequences of habitat fragmentation for large carnivores, illustrating that habitat fragmentation can produce source–sink dynamics that may not be apparent from other metrics of habitat quality. Locally, conserving high-quality source habitat within the Santa Cruz Mountains is necessary to support long-term puma population persistence. More broadly, source–sink dynamics may at play for other carnivore populations in similar fragmented systems, and linking landscape conditions

to population dynamics is essential for effective conservation. Caution should be used in inferring habitat quality from habitat selection alone, but these results shed light on metrics of selection that may be better or worse proxies to identify source areas for large carnivores.

KEYWORDS
carnivore conservation, habitat fragmentation, habitat selection, population dynamics, *Puma concolor*, source–sink dynamics, survival modeling

INTRODUCTION

Effective species conservation relies on an accurate understanding of habitat quality. Habitat quality is most rigorously quantified by linking habitat features to survival and reproduction to understand their influence on individual fitness and population dynamics (Mosser et al., 2009; Pulliam, 2000; Van Horne, 1983). Further, empirically linking habitat quality to fitness is essential for identifying important ecological dynamics, such as source–sink dynamics, which may not be evident in patterns of occupancy, distribution, or habitat selection (Pulliam & Danielson, 1991; Schlaepfer et al., 2002). However, quantifying the relationship between habitat features and fitness is notoriously difficult for wildlife species (Dias, 1996; Johnson, 2007), especially for species that are long-lived, exist at low densities on the landscape, or are cryptic or otherwise difficult to study—characteristics that typify many species of conservation concern (Cardillo et al., 2005). A rigorous understanding of habitat quality is particularly important in human-dominated landscapes, where species must coexist with humans and bear any associated costs of living alongside anthropogenic disturbance. However, few studies have explicitly modeled population growth relative to spatially-varying landscape conditions in human-dominated systems.

Large carnivore decline is widespread across the globe and conservation of large carnivore populations outside of protected areas and in human-dominated landscapes is essential for continued persistence of many of these species (Carter & Linnell, 2016; Ripple et al., 2014). However, living in human-dominated areas comes with a suite of direct and indirect costs. Direct anthropogenic mortality is often high for large carnivores, especially those living outside of protected areas (Darimont et al., 2015; Loveridge et al., 2017; Wolfe et al., 2015). In turn, large carnivores exhibit behavioral avoidance of humans, altering their movement (Suraci et al., 2019; Tucker et al., 2018), habitat selection (Abrahms et al., 2015; Nisi, Suraci, et al., 2022; Oriol-Cotterill et al., 2015; Wilmers et al., 2013), and feeding behavior (Smith et al., 2017) to avoid the risk of encountering people. These behavioral responses can carry substantial costs, including increased energetic expenditure during movement (Nickel et al., 2021) and reduced feeding times at kills (Smith et al., 2015). Thus, large carnivores in human-dominated areas experience elevated risk of anthropogenic mortality as well as sub-lethal costs associated with anti-predator behaviors that allow them to minimize the risk of such mortality (Frid & Dill, 2002). It is not known, however, whether or to what degree these indirect costs may scale up over time to impact individual survival.

Adult survival most strongly determines individual fitness and population growth for many large carnivore species, so reductions in survival often have consequences for population dynamics (Beckmann & Lackey, 2008; Benson et al., 2016; Heppell et al., 2000; Robinson et al., 2014). Understanding how habitat features are related to survival can facilitate rigorous evaluation of habitat quality for large carnivores in human-dominated environments and can reveal source–sink dynamics, which occur when certain areas support positive population growth while others cannot. Especially for territorial species such as pumas, source–sink dynamics may not be apparent from occupancy-based metrics, and long-term studies that relate population dynamics to habitat features are essential for elucidating these processes (Dias, 1996; O'Neil et al., 2020; Pulliam & Danielson, 1991; Van Horne, 1983). Identifying source–sink dynamics is of central conservation importance, as sources must be protected and conserved to maintain long-term population viability and understanding the mechanisms that produce sinks can enable conservation interventions (Dias, 1996).

Quantifying the relationship between habitat features and habitat quality for large carnivores in human-dominated environments can also shed light on when other, more easily obtainable metrics may be appropriate proxies for habitat quality (Stephens et al., 2015). Patterns of habitat selection are often used as a proxy for habitat quality under the assumption that animals select areas that confer higher fitness (Johnson, 2007). However, several ecological and behavioral processes may decouple habitat selection patterns from the true fitness value of an area or habitat type, including ecological traps and attractive sinks (Holt, 1997; Robertson & Hutto, 2006) as well as animal territoriality (Mosser et al., 2009;

O'Neil et al., 2020). Under these circumstances, habitat selection is expected to be an incomplete and potentially even misleading predictor of true habitat quality in terms of fitness. Additionally, habitat selection is often dynamic and scale-dependent. Habitat selection occurs at different scales, ranging from a species geographic range (first order) to subpopulation or home range selection (second order) to selection within home ranges (third order) to selection of specific resources within a used area (fourth order; Johnson, 1980). Habitat selection patterns also may change over the course of the day: for example, large carnivores often partition their daily activity to minimize overlap with human activity, generally exhibiting stronger avoidance of human development during the daytime (Kronfeld-Schor & Dayan, 2003; Nisi, Benson, & Wilmers, 2022; Oriol-Cotterill et al., 2015). It is thus likely that habitat selection patterns at certain scales or during certain times—for example, in the daytime when carnivores are most sensitive to human landscape features—will better predict population sources. Understanding to what degree habitat selection reflects population processes can shed light on when and how habitat selection can be used as an effective proxy, despite its limitations.

The puma (*Puma concolor*) population in the Santa Cruz Mountains, California, USA, presents an opportunity to quantify the impacts of exposure to human development on large carnivore survival and population dynamics. The Santa Cruz Mountains (SCM) consists of a mosaic of different levels of human use and residential development, including a considerable amount of exurban sprawl (Figure 1), which is the fastest growing land use type in the western U.S. (Theobald, 2005). While recreational hunting of pumas is illegal in California, pumas in this area still experience direct anthropogenic mortality, primarily due to retaliatory killings following livestock loss as well as vehicle strikes (Nisi, Benson, & Wilmers, 2022). Pumas also exhibit strong behavioral responses to humans in this system, including avoidance of human infrastructure, reduced activity in areas of high human presence, and reduced feeding time due to earlier carcass abandonment when near people, which have been shown to present substantial energetic costs (Nickel et al., 2021; Smith et al., 2015, 2017; Wilmers et al., 2013).

Here, we analyzed 11 years of movement, mortality, and reproductive data for 67 adult and subadult pumas to quantify the impacts of habitat fragmentation on puma survival, population dynamics, and source–sink dynamics, and to assess whether habitat selection reflects habitat quality with respect to population growth. Our overall hypothesis was that habitat fragmentation and conversion negatively influence survival and population growth of large carnivores. Specifically, we predicted that exposure to high housing density would be related to higher risk of mortality. We then parameterized a matrix population model to examine how population growth rates vary across the landscape, mediated by the relationship between adult survival and exposure to housing. Here we

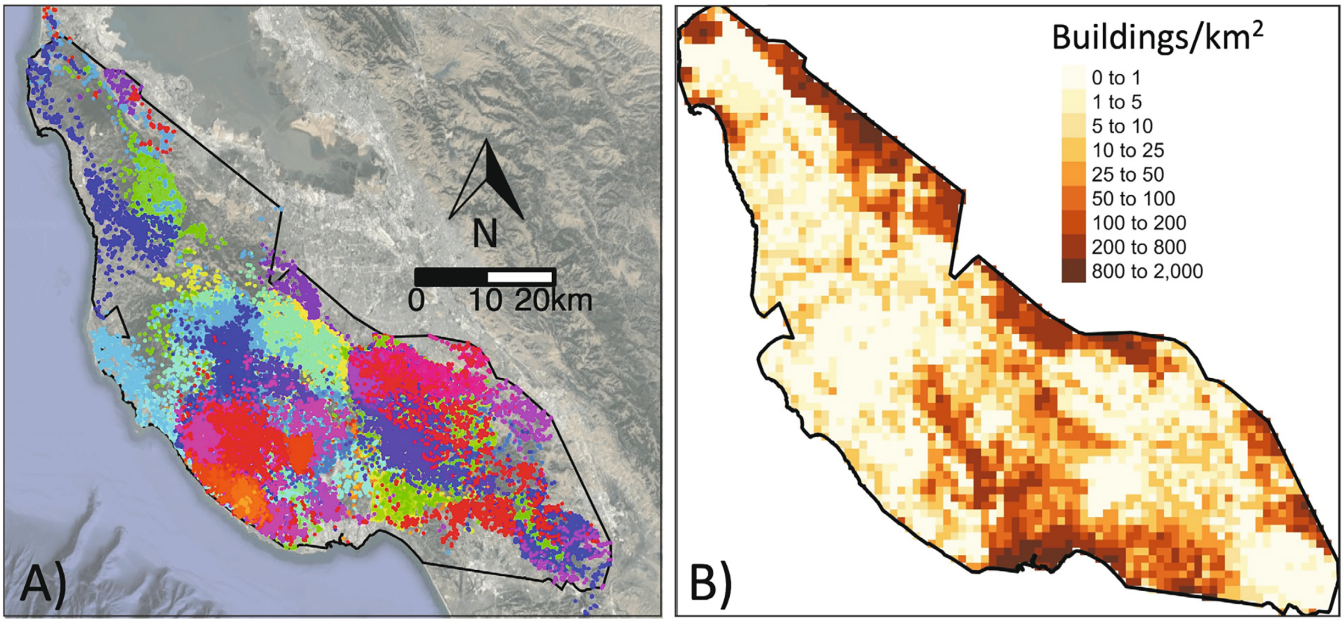

FIGURE 1 Maps of (A) puma GPS locations and (B) housing density at 1 km^2 resolution across our study area in the Santa Cruz Mountains, California, USA. In (A), colors correspond to unique individuals, though due to the high number of pumas monitored, some colors for different pumas appear similar.

predicted that source–sink dynamics will be evident, with areas of higher housing density being population sinks and more undisturbed areas serving as sources. Finally, we asked whether habitat selection metrics reflect predicted population growth, shedding light on proxies that can be used to estimate habitat quality when long-term population data is unavailable.

MATERIALS AND METHODS

Study system

The SCM is a 2800 km^2 area located in California's Central Coast (Figure 1). The SCM is bounded by Silicon Valley, San Francisco, and San Jose to the north, the Pacific Ocean to the west, the city of Santa Cruz and neighboring beach towns to the south, and mixed farmland, residential development, and a major interstate highway to the east. Within the SCM there is a mosaic of open space preserves, large state and county parks, privately held undeveloped properties which contain large swaths of relatively undisturbed native forests with various levels of exurban and rural residential development interspersed throughout. This creates a heterogeneous environment ranging from urban, suburban, and exurban areas to large tracts of intact, undeveloped habitat. At 1 km^2 resolution, 22.94% of the study area has no housing (0 houses/km^2), 38.86% is rural (0–6.18 houses/km^2), 27.76% is exurban (6.18–147.06 houses/km^2), 9.57% is suburban (147.06–1000 houses/km^2), and 0.86% is urban (>1000 houses/km^2, categories defined by Theobald, 2005).

Puma capture and monitoring

We captured adult and subadult pumas using trained hounds or box traps, and we anesthetized pumas with Telazol (Animal Use Protocol WilmC1402 issued by UC Santa Cruz to C. C. Wilmers). We fit pumas with GPS collars (Vectronics Aerospace GPS Plus, Berlin, Germany and Lotek, Seattle, WA, USA) that recorded locations once every 4 h. Due to GPS failure for two collars, we had VHF monitoring and mortality time information for two adult pumas but no or very limited GPS data. Those two animals were included for estimating overall survival rates for different age classes but were not included in spatial analyses.

We investigated mortality events of collared adult and subadult pumas following either (1) notification from California Department of Fish and Wildlife (CDFW) or California Highway Patrol about a retaliatory killing or vehicle strike, respectively; (2) mortality signal sent by collar over satellite network (which turns on following 12 h of a collar being stationary); or (3) UHF download of GPS data indicating that a collar had been in the exact same spot for multiple days. For cases 2 and 3, as soon as we received GPS data that suggested a mortality event had occurred, we investigated the location and attempted to determine cause of death from clues in the field. Specifically, we looked for indications of intraspecific mortality, including puncture wounds on the skull or crushed skull, or anthropogenic mortality, including gunshot wounds. When possible, we collected carcasses and sent them to CDFW Wildlife Investigations Laboratory for internal necropsies. If we were unable to determine cause of death, the cause was recorded as "unknown".

We also monitored puma reproduction. We identified natal denning events visually from puma GPS tracks by periods of time lasting longer than 3 weeks when female pumas localize to one cluster of points and make repeated excursions and returns to multiple (>2) different neighboring locations. We investigated a subset of these denning events, making field visits to count kittens at 2 weeks and to collar kittens at 4 weeks. Survival monitoring started upon collaring at 4 weeks, so we estimated litter size as the average number of kittens alive at the 4-week visit. We fit kittens with custom-made, expandable VHF collars (transmitters produced by Telonics Inc, Mesa, AZ), and monitored kittens weekly for mortality signals. When we heard mortality signals, we immediately investigated to determine whether the kitten had died or whether its collar had slipped.

Survival modeling

We used a Cox proportional hazards model (Cox, 1972) to relate mortality risk to spatial and demographic covariates for animals that were collared until their time of death. This approach models hazard, or instantaneous mortality risk, semi-parametrically, and allows for time-varying covariate effects and staggered entry and exit into the study (Fieberg & DelGuidice, 2009; Pollock et al., 1989). For this study, we used an annual recurrent design (Fieberg & DelGuidice, 2009), which allows the baseline hazard to vary over the course of the year (Appendix S1: Section S1). We used the *survival* package (Therneau, 2022) to conduct all survival analyses. First, to calculate overall age- and sex-specific survival rates, we fit a Cox proportional hazards model with an interaction between sex and age class (kittens [0–1 year], subadults [1–2 years], and adults [>2 years]) and calculated estimated survival rates using the *survfit* function.

Residential housing is the primary human use in the SCM, so we quantified exposure to anthropogenic impact

by calculating housing density (buildings/km^2) in puma home ranges. For these analyses, we only included only adult and subadult pumas, as kittens were not fit with GPS collars. To standardize home range calculation (Fieberg & Börger, 2012), we calculated housing density in home ranges fit over the 45 days prior to each event time. We chose 45 days as an interval as it was sufficient to encompass several home-range-crossing times for range-resident individuals (Appendix S1: Section S2; Calabrese et al., 2016; Fleming et al., 2014), and as such reflects long-term exposure to housing (Nickel et al., 2021). We used the adaptive local convex hull (aLoCoH) approach to fit home ranges over each 45-day period. Local convex hull approaches minimize Type 1 and Type 2 error, exhibit less bias compared to other estimator types, and were fit using the *tlocoh* package (Getz et al., 2007; Getz & Wilmers, 2004; Lyons et al., 2013). To shed light on whether habitat characteristics defined at the broad habitat scale or defined more tightly around areas most often used by an animal are more important in predicting mortality risk, we considered housing density calculated within 50% (core) and 95% (overall) home range extents.

We fit Cox proportional hazards models relating puma mortality risk to housing density exposure. We considered two models: a model with housing density and sex and a model with their interaction to investigate whether housing density influenced mortality risk differently between males and females. We considered a sex-specific relationship because previous studies have shown that survival rates and drivers of mortality risk differ between male and female pumas (Logan & Sweanor, 2001; Ruth et al., 2011). We fit these models with housing density calculated from the 50% and 95% home ranges. This modeling approach thus allowed us to evaluate (1) whether the relationship between housing density and mortality risk was mediated by sex and (2) whether characteristics of core or overall home ranges more strongly predicted mortality risk. We used Akaike's Information Criterion corrected for small sample size (AIC_c) to evaluate support for models (Burnham & Anderson, 2002). All models included a cluster term by individual to allow for robust standard error calculation and account for the lack of independence between multiple rows of data for the same individual (Therneau & Grambsch, 2000).

Matrix population modeling

We used the relationship between housing density and mortality risk to make inference on population growth rates across the study area via matrix modeling. We specified a single-sex (female-only), stage-specific matrix (Caswell, 2000) as follows: $\boldsymbol{n_{t+1}} = \boldsymbol{A}\boldsymbol{n_t}$, in which $\boldsymbol{n_t}$ is a vector of population sizes for each stage and $\boldsymbol{A}$ is a projection matrix:

$$\boldsymbol{A} = \begin{bmatrix} 0 & 0 & 0.5LbS_a \\ S_k & 0 & 0 \\ 0 & S_s & S_a \end{bmatrix},$$

where S_k, S_s, and S_a are stage-specific survival rates for kittens (0–1 year), subadults (1–2 years), and adults (>2 years), respectively, L is mean litter size, and b is mean birth rate (number of breeding events per year). Estimated population growth rate (λ) was calculated by the dominant eigenvalue of the matrix $\boldsymbol{A}$ (Caswell, 2000).

We estimated vital rates from puma monitoring data. Fecundity is a product of birth rate and litter size. The birth rate was calculated by dividing the number of denning events by the amount of time females were wearing collars recording 4-h GPS data. We conducted a Chi-square test and the kitten sex ratio was not statistically different from 0.5 (22 females, 34 males, $\chi^2 = 2.57$, $p = 0.11$), so we assumed a 0.5 sex ratio for the matrix population model.

We estimated S_k and S_s from our demographic-only survival model with an interaction between sex and age class (Table 1). For S_a, we used the best-fit housing density exposure model, which included an interaction between sex and housing density, to calculate estimated survival rates at different housing densities.

From the raster of housing density, we projected the best-supported model of adult female survival across the study area at 1 km^2 resolution. From this layer, we calculated estimated population growth rate (λ) across the study area. We also report estimated λ values from a

TABLE 1 Estimated annual survival rates for pumas in the Santa Cruz Mountains by sex and age class.

Sex	Age class	Survival rate	95% CI		Deaths
Female	Kitten	0.59	0.32	1.00	4
	Subadult	0.68	0.31	1.00	1
	Adult	0.83	0.74	0.92	13
Male	Kitten	0.29	0.13	0.64	10
	Subadult	0.43	0.19	0.98	4
	Adult	0.69	0.59	0.82	17

Note: Sample sizes include data from both VHF and GPS collared individuals. Due to GPS failures, for two adult pumas we had VHF monitoring and mortality time information but no or very limited GPS data. Those two animals are included to estimate these survival rates but were excluded from the spatial analyses.

matrix that includes the upper and lower 95% confidence intervals (CIs) for the estimated female survival rate, to illustrate the variability in λ associated with uncertainty in adult survival.

Comparing metrics of habitat quality

To test the degree to which habitat selection is a reliable indicator of habitat quality, we first fit population-level habitat selection models using resource selection functions (RSF, Manly et al., 2002). Next, we used logistic regression to quantify the relationship between whether a grid cell was a source ($\lambda \geq 1$) or sink ($\lambda < 1$) area and the predicted relative selection strength for that grid cell. Second-order selection (selection of a home range from the larger landscape) and third-order selection (selection of locations within home ranges) describe how animals select habitat in a hierarchical manner, are often linked to components of fitness for animals, and are commonly studied for large carnivores (e.g., Basille et al., 2013; Fattebert et al., 2015; McLoughlin et al., 2005; O'Neill et al., 2020; Wilmers et al., 2013). We fit models for second- and third-order selection to consider whether habitat selection at both scales reflected estimated population growth rate.

Resource selection functions quantify habitat selection by comparing used locations to available locations through the exponential function, $w(\boldsymbol{x}) = \exp(\boldsymbol{\beta x})$, with $\boldsymbol{x}$ a vector of spatial covariates and associated coefficients $\boldsymbol{\beta}$ (Manly et al., 2002). For both orders of selection, used locations were GPS locations recorded by collars at 4-h intervals. For second-order selection, available locations were drawn across the study area extent. For third-order selection, available locations for each individual were drawn from within that individual's 95% minimum convex polygon. For each order, we drew five available locations for each used location.

The same models were considered for both orders of selection. Predictor covariates included habitat features shown by prior analyses to be important determinants of puma habitat selection, including housing density and its quadratic term, slope, topographic position, distance to nearest perennial stream, percent vegetation cover, and an interaction between slope and topographic position (Nisi, Benson, & Wilmers, 2022, see Appendix S1: Section S3 for full covariate descriptions). Additionally, a previous analysis found that the relationship between relative selection strength and housing density for pumas in the SCM is conditional on time of day (day/night, defined by sunrise and sunset times for each day; Nisi, Benson, & Wilmers, 2022). It is possible that selection during one time of day may be a better proxy for identifying source areas. While it is inappropriate to include time-of-day specific behavior for a second-order habitat selection model as that selection process operates over longer periods of time, we were able to consider this for third-order models by fitting one model to all data (both daytime and nighttime points), one model to daytime locations, and one model to nighttime locations. We thus had four habitat selection models to consider: one second-order selection model (combined daytime and nighttime locations) and three third-order models (combined, daytime-only, and nighttime-only models). For full details on RSF fitting and specification, see Appendix S1: Section S3.

From these models, we calculated the relative selection strength (RSS), relative to mean habitat conditions, for each 1 km^2 grid cell across the study area for each model. This gave us four maps of relative selection strength. We next used logistic regression to relate whether or not a grid cell was expected to support population growth or decline (coded 1 = source grid cell with $\lambda \geq 1$ vs. 0 = sink grid cell with $\lambda < 1$) to relative selection strength from each our four models (second-order combined, third-order combined, third-order daytime, and third-order nighttime). We assessed goodness of fit for each model by calculating the area under the receiver operating characteristic curve (AUC). We conducted all analyses in R version 3.6.0.

RESULTS

We observed 33 mortality events from the 65 adult and subadult pumas monitored with GPS collars from 3/11/2009–10/19/2020. Of GPS-collared deaths of females ($N = 13$ deaths from 31 GPS-collared females), 5 were directly human-caused (2 retaliatory killings, 1 poaching event not related to livestock depredation, and 2 vehicle collisions) and 8 were from other causes (1 disease, 1 intraspecific mortality, and 6 unknown causes that were unlikely to be directly caused by humans). Of GPS-collared male deaths ($N = 20$ deaths from 34 GPS-collared males), 12 were directly human-caused (9 retaliatory killings and 3 vehicle collisions) and 8 were not directly caused by humans (3 intraspecific mortalities and 5 from unknown causes). We also observed 14 deaths of the 42 kittens collared and monitored between 6/6/2009 and 3/4/2020. Overall survival rates were higher for females than males, and higher for adults compared to kittens and subadults (Table 1). These estimates include data from 2 additional adults who did not have sufficient spatial data to be included in the spatial mortality risk analysis. We also observed 35 denning events over a cumulative female-monitoring-time of 61.8 years,

resulting in an observed birth rate of 0.565 litters/female/year. The mean observed litter size was 2.24 kittens, resulting in a mean kitten production rate per female of 1.27 kittens/year.

Sex mediated the relationship between housing density and mortality risk, and housing exposure in a puma's core home range was more informative than in their overall home range for predicting mortality risk (Table 2). Females living in more developed areas experienced heightened risk compared to females in more remote areas, but males experienced similar risk across the gradient of housing density (Figure 2). For females, the reduction in expected annual survival rates associated with housing exposure was substantial, with females in exurban areas (25 buildings/km^2) exhibiting a predicted 18.8-percentage-point reduction in annual survival relative to females in remote areas (0 buildings/km^2; Figure 2).

The reduction in female survival in more developed areas had population-level consequences. For example, parameterizing population matrix models with expected female survival rates at 3 levels of housing density shown in Figure 2, the expected population growth rate is 1.113 in remote areas (0 buildings/km^2; upper and lower estimates: 1.040, 1.181 calculated from upper and lower 95% CI on adult female survival), 1.037 (0.952, 1.135) in rural areas (5 buildings/km^2), and 0.945 (0.840, 1.071) in exurban areas (25 buildings/km^2). Furthermore, projecting expected puma population growth rate across the study area shows that source–sink dynamics are at play in the SCM, with 57.9% of the study area exhibiting $\lambda \geq 1$ and 42.1% exhibiting $\lambda < 1$ (Figure 3). The expected

TABLE 2 Model coefficients and ΔAIC_c results for Cox proportional hazards models relating puma mortality risk to housing density.

	Covariate				
Home range extent	**Housing**	**Sex**	**Housing*sex**	**AIC_c**	**ΔAIC_c**
Core	0.7 (0.283)*	0.902 (0.421)*	−0.727 (0.362)*	280.248	0.000
Overall	0.583 (0.256)*	0.926 (0.409)*	−0.723 (0.405)•	281.641	1.393
Core	0.315 (0.189)•	0.609 (0.389)		282.492	2.244
Overall	0.234 (0.194)	0.7 (0.381)•		284.820	4.572

Note: Housing density was measured in core (50% aLoCoH) and overall (95% aLoCoH) home ranges, and two models were considered: one with and one without an interaction between housing density and sex. Coefficient estimates are included with robust standard errors in parentheses with an * indicating $p < 0.05$ and a • indicating $p < 0.10$. ΔAIC_c values show comparisons between each model and the best model.

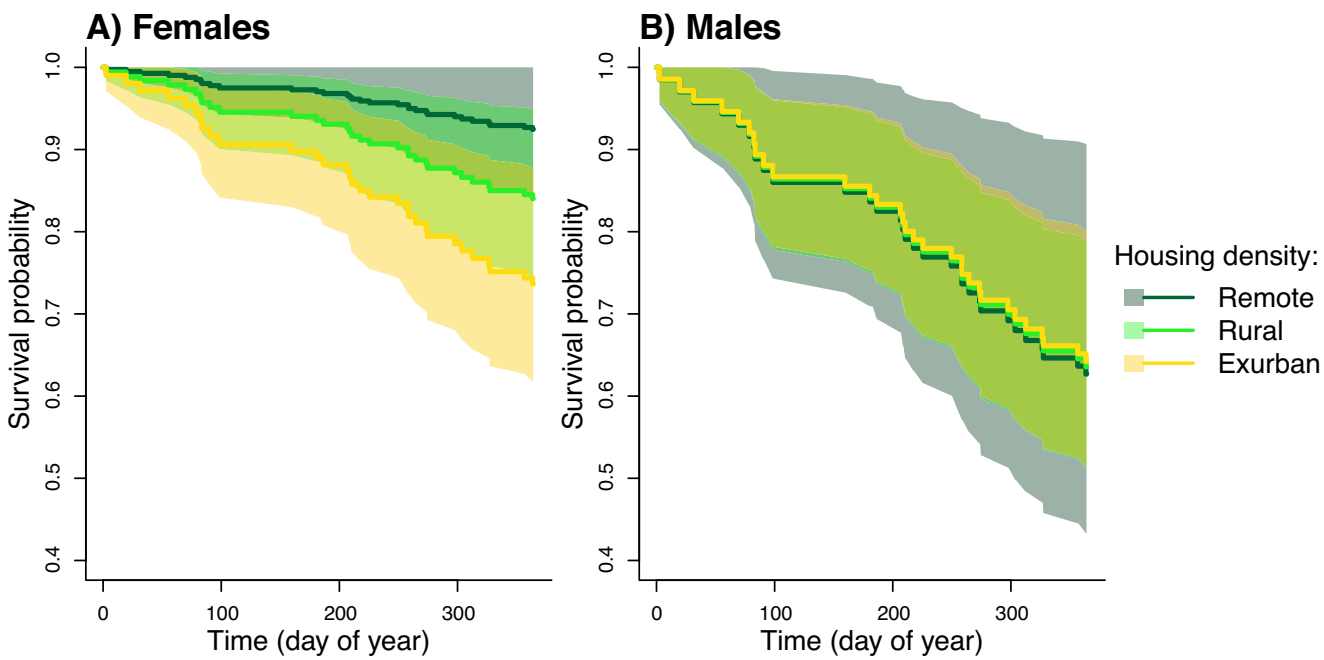

FIGURE 2 Predicted annual survival curves for (A) female pumas and (B) male pumas across three levels of housing density in the Santa Cruz Mountains. Remote, rural, and exurban housing densities refer to 0, 5, and 25 buildings/km^2, respectively, in an individual's 50% home range. Shaded areas are 95% CIs and day of year corresponds to the calendar year starting January 1.

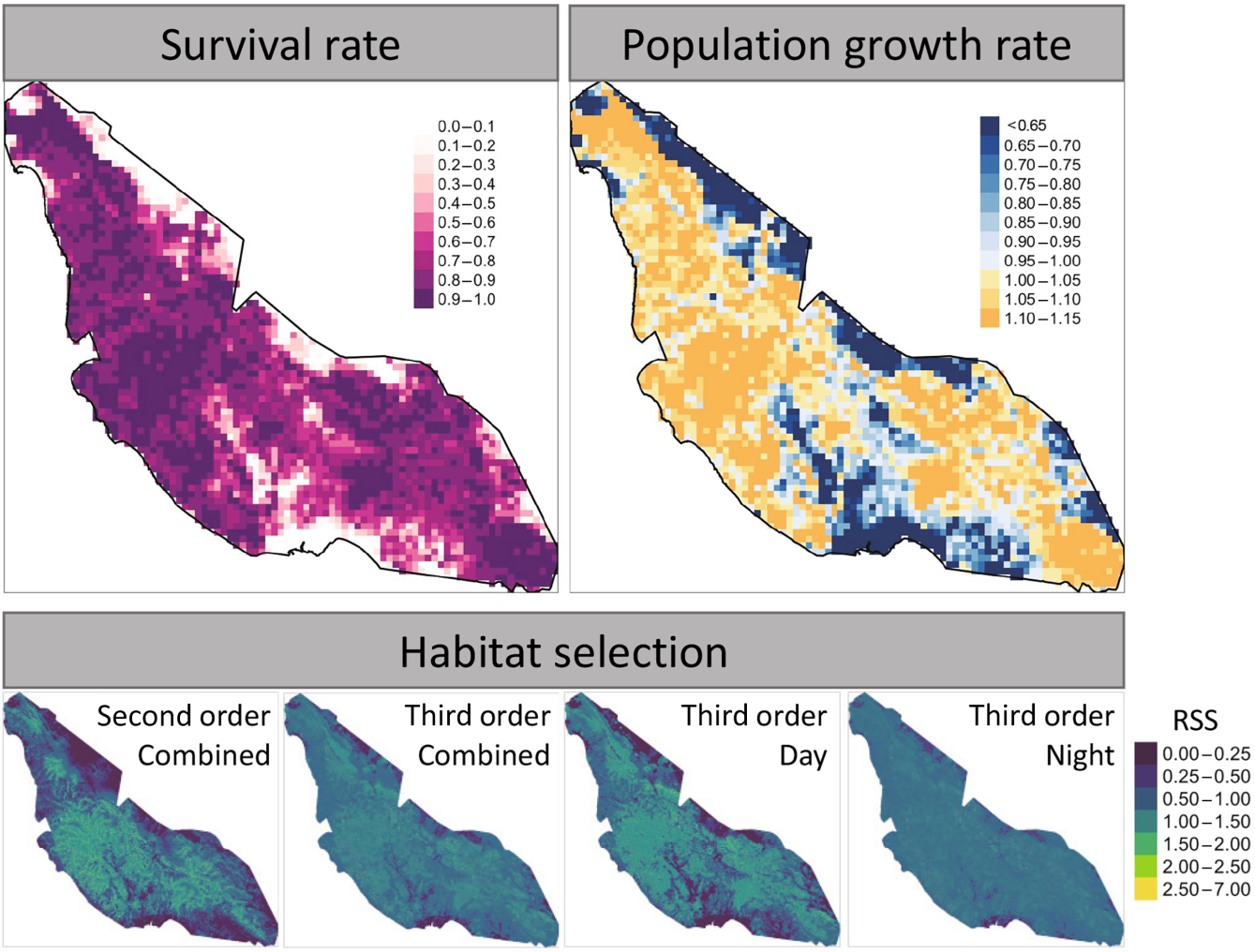

FIGURE 3 Puma population processes and habitat selection patterns in the Santa Cruz Mountains. The top left panel shows estimated adult female puma survival rates and the top right panel shows corresponding estimated puma population growth rates (λ) across the study area. The bottom row shows relative selection strength (RSS) across the study area, at the second and third orders of selection. Combined models were models that included both daytime and nighttime puma locations, while day and night models included only locations from that respective time of day. Third order daytime selection was most predictive of predicted population growth rate across the study area.

population growth rate when adult female puma survival is set at its mean for this population (0.826, 95% CI: 0.742, 0.921) was 1.025 (0.950, 1.110). Adult female survival was the most elastic vital rate with an elasticity of 0.581, and fecundity, kitten survival, and subadult survival all had elasticity values of 0.140.

Relative selection strength quantified by different habitat selection models all were positively related to whether a grid cell was predicted to be source habitat ($\lambda \geq 1$), though they varied in their predictive ability (Figure 3, Table 3, Appendix S1: Figure S1). Third-order daytime habitat selection was the best predictor of source areas and performed well as a proxy (AUC = 0.814; Table 3). Nighttime habitat selection (at the third order) performed the most poorly, with an AUC <0.70 (AUC = 0.658). Second-order selection was more strongly driven by vegetative cover than third-order models (Appendix S1: Table S1), and performed worse than daytime or combined third-order selection, but better than nighttime selection. Full habitat selection modeling output is presented in Appendix S1: Table S1.

DISCUSSION

Exposure to human development led to reduced female puma survival, which drove source–sink dynamics in this fragmented, human-dominated landscape. Female pumas living in more human-dominated areas experienced heightened mortality risk compared to females living in more remote areas. In turn, reduced survival rates in more developed areas suggested negative population

TABLE 3 Coefficient estimates and area under the receiver operating characteristic curve (AUC) values for logistic models predicting population status in a grid cell (1 = source area with $\lambda \geq 1$ or 0 = sink area with $\lambda < 1$) from puma habitat selection quantified as relative selection strength (RSS).

Order	Time	Coefficient estimate		AUC
		Intercept	RSS	
Second	Combined	−1.005 (0.002)*	1.747 (0.003)*	0.721
Third	Combined	−3.39 (0.005)*	4.259 (0.006)*	0.770
Third	Day	−2.511 (0.004)*	3.422 (0.004)*	0.814
Third	Night	−2.277 (0.006)*	2.904 (0.006)*	0.658

Note: Second- and third-order habitat selection were considered. For third-order selection, models were fit to all data (combined day and night points) as well as to daytime and nighttime locations respectively. Coefficient estimates are included with standard errors in parentheses and * indicating $p < 0.001$.

growth rates in these places—resulting in source–sink dynamics across the SCM with wide portions of habitat likely unable to support population growth.

Exposure to higher housing density drove mortality risk for female pumas, but not males, likely reflecting differences in causes of death as well as behavioral and energetic costs experienced by male and female pumas. Most deaths of female pumas were not directly caused by people, and previous research from this system has documented sex-specific indirect behavioral and energetic costs. While deer kill rates of male pumas are not affected by housing density, female pumas exhibit higher deer kill rates in areas of higher housing density (Smith et al., 2015), driven by earlier carcass abandonment and incomplete consumption (Smith et al., 2017). This presents significant energetic costs for females since hunting and killing deer requires substantial energetic expenditure (Williams et al., 2014). Taken together with these results, this suggests that indirect energetic costs experienced by female pumas in more developed areas may scale up over time to negatively impact survival. Additionally, relative to females, males experienced more mortality that was directly caused by people, primarily retaliatory killing following livestock loss. Previous work has shown that retaliatory killing risk peaks at intermediate housing densities rather than scaling directly with housing density, after controlling for puma time allocation (Nisi, Benson, & Wilmers, 2022). Together with this work, this suggests that heightened retaliatory killing risk at intermediate levels of housing may decouple overall mortality risk from housing density for males.

This reduction in female survival drove source–sink dynamics across our study area. Remote, wildland areas were associated with survival rates that result in positive population growth, while more developed exurban areas contain sufficient development to cause a reduction in survival likely below what supports a stable population over time. While the overall population growth rate was stable, these results indicate that further development of the SCM has the potential to expand sink habitat and threaten puma population viability. Source areas should be protected to support long-term puma persistence in this area, and further development in existing source areas is detrimental for puma population viability. We caution, however, that preventing further development of marginal-quality sink habitat, especially sinks that border source areas, is also essential for puma conservation. Such marginal-quality sink habitats contribute to supporting higher population size and improved viability (Howe et al., 1991) by serving as corridors buffering or connecting high-quality source habitat (Smith et al., 2019; Wilmers et al., 2013) as well as habitat for younger animals to bide their time until they can take over better quality territories for themselves. This sink habitat also allows for a larger population of pumas in the SCM than would exist if all sink habitat were eliminated—which is particularly important given their low genetic heterozygosity and effective population size (Gustafson et al., 2019). We acknowledge that population growth rate estimates projected from upper and lower 95% CIs for adult female survival in rural and exurban areas overlap 1, making it difficult to definitively separate these estimates from a stable trend, though wide CIs are likely driven by our relatively small sample sizes for this hard-to-study species. Low-density exurban development and rural sprawl are the leading cause of land-use change in the United States and often surround or are adjacent to protected areas (Theobald, 2001, 2005), so the dynamics that we describe for the SCM puma population could be at play for other populations of large carnivores living in similar environments.

It is important to understand where source areas are across a landscape, but often, long-term demographic data required to relate population dynamics to habitat features are not available for a given population or system. Habitat selection can be easier to quantify and is often treated as a proxy for habitat quality (Johnson, 2007; Stephens et al., 2015). Here, daytime patterns of

puma habitat selection strongly predicted whether a grid cell was expected to be a source area. Animals in human-dominated environments partition their activity to use higher-risk areas at night, when human activity is generally lower, and often become more nocturnal overall (Gaynor et al., 2018; Suraci et al., 2019). Our results suggest that the increased sensitivity and spatial partitioning that pumas exhibit during the daytime may more accurately reflect where source areas are across a landscape. This is a novel insight that would benefit from repetition in other species and systems—if this pattern is shown to be general, then daytime selection may be more useful in inferring where source areas are for species that exhibit temporal partitioning of space and activity related to risk from humans. However, we note that other important behavioral and population processes for pumas and other carnivores—such as foraging and dispersal—may be better revealed by patterns of nighttime habitat selection (Morrison et al., 2015; Smith et al., 2015). Habitat that enables dispersal and connectivity is essential for supporting long-term population persistence and genetic diversity and should be taken into account in conservation planning (Gustafson et al., 2019; Rio-Maior et al., 2019). When possible, it is ideal to relate habitat characteristics directly to fitness metrics rather than inferring habitat quality by proxy (Gaillard et al., 2010; Mosser et al., 2009).

Compared with other puma populations, survival rates in this system were higher than those seen in hunted populations (e.g., Robinson et al., 2014; Wolfe et al., 2015), but lower than those in remote areas free from hunting (e.g., Logan & Sweanor, 2001). Relative to other non-hunted, urban-adjacent puma populations in California, survival rates in the SCM are higher than what is seen in the Santa Ana and Eastern Peninsular Ranges (Vickers et al., 2015) but are slightly lower than survival rates in the Santa Monica Mountains (Benson et al., 2020). Together, this suggests that even when pumas are protected from hunting, living in fragmented landscapes presents survival consequences.

While we lack sufficient data to relate fecundity to housing density, we emphasize that reproductive success likely varies across the study area in a way that would exacerbate source–sink dynamics relative to what we present in this paper. Previous research suggests that puma reproduction decreases with increasing development, as pumas strongly avoid human development when selecting den site locations, indicating that these areas are poor quality for puma reproduction (Wilmers et al., 2013; Yovovich et al., 2020). As adult female survival was the most elastic vital rate in our analysis, consistent with other puma populations (Benson et al., 2016; Robinson et al., 2014), we expect that the impacts associated with human development on survival would be stronger than any reproduction-mediated impacts of development on puma population growth. However, we emphasize that additionally accounting for nuances in puma reproduction as they relate to housing density would almost surely reveal even stronger source–sink patterns than what we have presented here.

Overall, this work emphasizes the vulnerability of a population of large carnivores living in a human-dominated landscape: while currently stable, further development could threaten long-term viability for pumas in the SCM by expanding population sinks and reducing population sources. Exurban development is a common and growing component of land use change in the western United States (Theobald, 2005), and this study shows that even relatively low levels of rural and exurban development negatively impact habitat quality for large carnivores. Large carnivore persistence in human-dominated landscapes is essential for their conservation (Carter & Linnell, 2016), but for this to be possible, we must understand how anthropogenic features impact population vital rates as well as any thresholds in levels of human use or disturbance that reduce long-term viability. Here we emphasize that though pumas can coexist with humans within a matrix of low-density residential development, they experience costs in doing so that reduce their individual fitness, producing population-level consequences. In linking anthropogenic features to individual fitness to population dynamics, this study underscores the importance of relating habitat quality to population processes and sheds light on mechanisms by which other large carnivore populations in many systems may be impacted by human development.

AUTHOR CONTRIBUTIONS

Anna C. Nisi and Christopher C. Wilmers conceived the project idea and plan of analysis; Richard King, Anna C. Nisi, and Christopher C. Wilmers conducted fieldwork and collected data; Anna C. Nisi conducted analysis and led the writing of the manuscript with substantial input from Christopher C. Wilmers and John F. Benson. All authors gave meaningful contributions to this manuscript.

ACKNOWLEDGMENTS

Thank you to the California Department of Fish and Wildlife for permission to conduct research and to the landowners in the SCM who granted us land access. We thank Barry Nickel for computing and data support, and Troy Collinsworth, Chris Fust, Paul Houghtaling, Joe Kermish-Wells, Sean McCain, Blue Milsap, Yasaman Shakeri, Justine Smith, Dan Tichenor, Yiwei Wang, Cliff Wylie, and Veronica Yovovich for assistance in the field. This work was funded by National Science Foundation

grants 0963022 and 1255913 and by the support of the Gordon and Betty Moore Foundation and the Peninsula Open Space Trust.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Nisi, 2023) are available from Figshare at https://doi.org/10.6084/m9.figshare.19686345.v1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Nisi, Anna C., John F. Benson, Richard King, and Christopher C. Wilmers. 2023. "Habitat Fragmentation Reduces Survival and Drives Source–Sink Dynamics for a Large Carnivore." *Ecological Applications* e2822. https://doi.org/10.1002/eap.2822