Title

Cryptic Neighbors: Connecting Movement Ecology and Population Dynamics for a Large Carnivore in a Human-Dominated Landscape

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CRYPTIC NEIGHBORS: CONNECTING MOVEMENT ECOLOGY AND POPULATION DYNAMICS FOR A LARGE CARNIVORE IN A HUMAN-DOMINATED LANDSCAPE

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By

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TABLE OF CONTENTS

List of Tables iv

List of Figures v

Abstract vii

Dedication ix

Acknowledgments x

Introduction 1

Chapter 1 – Temporal scale of habitat selection for large carnivores: balancing energetics, risk and finding prey 5

Chapter 2 – Unreliable human cues create an ecological trap for a large carnivore in a human-dominated landscape 53

Chapter 3 – Habitat fragmentation reduces puma survival and drives source-sink dynamics 88

Chapter 4 – Wildfire vulnerability, carbon emissions, and wildlife habitat quality across the wildland-urban interface 119

Conclusion 145

References 147

LIST OF TABLES

Table 1.1. Coefficient estimates for lion iSSA 33

Table 1.1. Coefficient estimates for puma iSSA 34

Table 1.S1. Model selection for models with interactions with boma distance for lions 50

Table 1.S2. Model selection for models with interactions between movement and habitat covariates for lions 51

Table 1.S3. Model selection for models with interactions between movement and habitat covariates for pumas 52

Table 2.1. Model selection for retaliatory killing location RSF [$w_{rk}(\boldsymbol{x})$] and locations of mortality from other sources 78

Table 2.2. Model selection for population-level movement SSF [$w_{mvt}(\boldsymbol{x})$] 78

Table 2.S1. Coefficient estimates for the best-supported puma movement SSF 87

Table 3.1. Estimated annual survival rates for all sex and age classes 114

Table 3.2. Univariate models relating housing density to mortality risk at different spatial and temporal scales 114

Table 3.3. Model selection for logistic models relating population status (growth or decline) to habitat selection (RSS). 114

LIST OF FIGURES

Figure 1.1. Relative selection strength of slope and distance to boma by lions across temporal grains 30

Figure 1.2. Relative selection strength of slope and housing density by pumas across temporal grains 31

Figure 1.3. Effects of habitat covariates on lion and puma movement 32

Figure 1.S1. Distributions of covariates across temporal grains 40

Figure 1.S2. Variance in habitat covariates within and across matched-case strata for all temporal grains 41

Figure 1.S3. Spline correlograms of Moran's *I* across distance for residuals 42

Figure 1.S4. Sex-specific relative selection strength of slope and distance to boma for lions across temporal grains 43

Figure 1.S5. Sex-specific relative selection strength of slope by pumas across temporal grains 44

Figure 1.S6. Sex-specific relative selection strength of housing density by pumas across temporal grains 45

Figure 1.S7. Relative selection strength of slope and housing density for 17 pumas >2 years old across temporal grains 46

Figure 1.S8. Effects of habitat covariates on puma movement for 17 pumas >2 years old 47

Figure 1.S9. Sex-specific effects of habitat covariates on lion movement 48

Figure 1.S10. Sex-specific effects of habitat covariates on puma movement 49

Figure 2.1. Retaliatory killing risk peaked at intermediate housing densities, creating a mismatch between risk and puma behavior during high-risk times 79

Figure 2.2. Distribution of locations of retaliatory killings and other mortalities for collared pumas across the housing density gradient 81

Figure 2.3. Maps showing relative risk of retaliatory killing ($w_{rk}(\boldsymbol{x})$), relative probability of nighttime selection ($w_{mvt}(\boldsymbol{x})$), and ecological trap habitat across the SCM study area 82

Figure 2.4. Box plots showing the inter-kill intervals for all collared pumas 83

Figure 2.S1. Two time allocation controls for retaliatory killing risk 86

Figure 3.1. Predicted annual survival curves for females and males across 3 levels of housing density 115

Figure 3.2. Projected annual survival rates and estimated population growth rate across the study area 116

Figure 3.3. Relationship between predicted population status (growth [$\lambda > 1$] or decline [$\lambda < 1$]) and relative selection strength 117

Figure 4.1. Maps of land use category, household C footprint, and puma habitat quality metrics across the study area 136

Figure 4.2. Burn risk, household C emissions, and puma habitat quality across land use categories 138

Figure 4.3. Changes in burn risk, household C footprint, and habitat quality across the gradient of housing density 139

Figure 4.S1. Spatial layers for puma habitat quality and household C footprint 141

Figure 4.S2. Mean household C footprint (tCO_2e) across land use categories 142

Figure 4.S3. Sector contributions to household C footprints across land use categories 143

Figure 4.S4. Housing density classifications by land use category 144

ABSTRACT

CRYPTIC NEIGHBORS: CONNECTING MOVEMENT ECOLOGY AND POPULATION DYNAMICS FOR A LARGE CARNIVORE IN A HUMAN-DOMINATED LANDSCAPE

Anna C. Nisi

Understanding how habitat impacts population dynamics is essential for wildlife conservation, especially in heterogeneous, human-dominated landscapes. In these areas, animals may alter their movement behavior to manage the risks and costs of living in fragmented areas, which may help wildlife coexist alongside people. These interrelated concepts – how habitat quality and animal space use influence individual fitness and population dynamics, and whether animal behavior may mediate these relationships – are of particular conservation importance for large carnivores, as conservation in human-dominated landscapes is essential for the continued persistence of many carnivore species. In my dissertation, I quantify the links between movement ecology, behavior, and population dynamics for pumas *(Puma concolor*) in the fragmented Santa Cruz Mountains of California. I explore the behavioral strategies employed by large carnivores in response to humans (Chapter 1) and investigate whether these strategies help them avoid the risk of being killed by people (Chapter 2). I also quantify how living in more developed areas influences puma survival and how that scales up to impact population dynamics and viability (Chapter 3). Finally, taking a broader view, I investigate the intersections between several environmental impacts driven by low-density exurban development, including wildlife habitat quality, household carbon emissions, and wildfire risk and vulnerability (Chapter 4). This work illustrates that while carnivores exhibit complex behavioral strategies in human-dominated landscapes, their behavioral flexibility alone is insufficient for human-carnivore coexistence. Rather, land use strategies that minimize further development of wildland areas are necessary to support viable carnivore populations, and would confer multiple environmental benefits to people as well as wildlife.

DEDICATION

To my parents,

and to the pumas

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I would first like to acknowledge the indigenous peoples on whose land I have lived and conducted research for the last six years. The land acknowledgement used at UC Santa Cruz was developed in partnership with the Amah Mutsun Tribal Band Chairman and the Amah Mutsun Relearning Program at the UCSC Arboretum.

> *The land on which we gather is the unceded territory of the Awaswas-speaking Uypi Tribe. The Amah Mutsun Tribal Band, comprised of the descendants of indigenous people taken to missions Santa Cruz and San Juan Bautista during Spanish colonization of the Central Coast, is today working hard to restore traditional stewardship practices on these lands and heal from historical trauma.*

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INTRODUCTION

When we picture large carnivores, we tend to imagine them in remote areas, far away from much human influence. However, carnivores can and do live closely alongside us in more human-dominated landscapes, and indeed, their conservation in these areas is essential for the continued persistence of many carnivore populations and species (Chapron et al. 2014, Carter and Linnell 2016). Large carnivores require a lot of space and exist at low densities, which makes them particularly sensitive to habitat destruction and habitat fragmentation (Cardillo et al. 2004, Crooks et al. 2011, Ripple et al. 2014). However, these extensive spatial requirements also make essential their conservation in more human-dominated areas – while undeveloped land, including protected areas, is centrally important to carnivore conservation, the spatial extent of these areas is generally insufficient to support most large carnivore species (Di Minin et al. 2016). This means that from a purely practical standpoint, carnivores must be able to coexist with humans in shared landscapes.

Beyond being a practical necessity, carnivore presence in human-dominated landscapes can benefit both people and ecosystem health. Large carnivores are keystone predators in many ecosystems and can have cascading, ecosystem-wide effects through their regulation of prey and mesocarnivore species (Ripple et al. 2014). In addition to this regulatory role in their ecosystems, these effects may benefit humans as well. For example, carnivore suppression of deer, through both reduction of deer numbers alongside changes in deer behavior, is associated with reduced roadkill events, which are costly to and dangerous to humans as well as wildlife (Gilbert et al. 2017, Raynor et al. 2021). Additionally, large carnivore suppression of mesocarnivores may ripple through the rodent community and carry cascading benefits to zoonotic disease dynamics (Levi et al. 2012, Ripple et al. 2013). In sum, carnivore conservation in landscapes that they share with humans presents benefits to both.

However, living more closely alongside humans comes with direct and indirect costs, which are important to understand from a conservation perspective. Carnivores are killed by people at a rate higher than any non-human predator (Darimont et al. 2015), and direct anthropogenic mortality is a problem for many carnivore species outside of protected areas (e.g., Vickers et al. 2015). In turn, carnivores commonly exhibit fear responses to the perceived presence of humans (Smith et al. 2017, Suraci et al. 2019a), which can carry indirect behavioral and energetic costs (Smith et al. 2015, Wang et al. 2017, Nickel et al. 2021). In some cases, these behaviors may facilitate human-carnivore coexistence (Carter and Linnell 2016, Suraci et al. 2019b), though this depends on carnivore behaviors reflecting important sources of anthropogenic risk.

While research has described many costs that carnivores experience in human-dominated landscapes, less is understood about the impacts of these costs on carnivore population dynamics. This is due in large part to the difficulty of characterizing relationships between habitat characteristics and population processes for such cryptic and low-density species (Dias 1996, Johnson 2007). However, understanding relationships between habitat characteristics and population vital rates is essential for robustly characterizing habitat quality (Van Horne 1983, Pulliam 2000, Mosser et al. 2009) and understanding potential impacts of future land use change.

Broadly, my dissertation aims to understand how humans and carnivores can coexist in shared landscapes. I explore several key components of that puzzle: including characterizing carnivore behavioral responses to humans, assessing the impacts of living in these landscapes on individual fitness and population dynamics, and considering what humans can do to further carnivore conservation in these areas. I consider the puma (*Puma concolor*) population in the Santa Cruz Mountains of California as a model system. The Santa

Cruz Mountains is emblematic of a common, accelerating form of land use across the Western United States: low-level residential development in and alongside wildland areas.

First, I use high-resolution spatial data and integrated Step Selection Analyses to characterize how carnivores balance multiple goals, including avoiding risk from humans, managing energetic constraints, and finding prey, in human-dominated landscapes (Chapter 1). I look for commonalities across two species – pumas in the Santa Cruz Mountains and lions (*Panthera leo*) in the rangeland system of Laikipia County, Kenya – and describe how temporal scale is an important ecological and methodological consideration in habitat selection analyses. This analysis shows that carnivores exhibit complex, scale-dependent behavioral responses to human features, allowing them to avoid human cues in space and human activity in time, while managing energetic concerns.

Next, I investigated to what degree puma fear responses to humans allow them to avoid the risk of anthropogenic mortality (Chapter 2). I model puma habitat selection alongside the risk of the leading source of human-caused mortality: retaliatory killings following livestock depredation. Here, I ask whether cues that pumas respond to reflect how actual risk from humans is distributed, finding a mismatch between cues and risk that leads pumas to select the riskiest areas during the riskiest times, and results in an ecological trap.

I then consider how living in more fragmented areas impacts puma survival and population dynamics (Chapter 3). I used Cox proportional hazards models to relate puma survival to short- and long-term exposure to human development, finding that long-term exposure to human development reduced survival for female pumas. I then used matrix population modeling to calculate and map expected population growth rates across the study area and identify source-sink dynamics. Finally, I consider whether and how more easily accessible metrics – such as habitat selection – may be used as proxies for habitat quality as defined by population dynamics. This work contributes a rare analysis of the impact of habitat characteristics on carnivore demography, which addresses the unexplored question of how exurban development influences population viability.

Finally, I take a wider view encompassing other pressing environmental issues in California (Chapter 4). Alongside wildlife habitat, wildfire risk and per-capita carbon emissions are strongly driven by land use patterns. I quantify how each environmental impact varies across the spectrum of housing density, finding alignment between the three. This result suggests that urban infill, or further densification of urban areas, could be a win-win-win strategy in terms of having low wildfire vulnerability, per-household emissions, and impact on wildlife habitat quality.

CHAPTER 1

Temporal scale of habitat selection for large carnivores: balancing energetics, risk and finding prey

Abstract

1. When navigating heterogeneous landscapes, large carnivores must balance trade-offs between multiple goals, including minimizing energetic expenditure, maintaining access to hunting opportunities, and avoiding potential risk from humans. The relative importance of these goals in driving carnivore movement likely changes across temporal scales, but our understanding of these dynamics remains limited.
2. Here we quantified how drivers of movement and habitat selection changed with temporal grain for two large carnivore species living in human-dominated landscapes, providing insights into commonalities in carnivore movement strategies across regions.
3. We used high-resolution GPS collar data and integrated step selection analyses to model movement and habitat selection for African lions (*Panthera leo*) in Laikipia, Kenya and pumas (*Puma concolor*) in the Santa Cruz Mountains of California across eight temporal grains, ranging from 5 minutes to 12 hours. Analyses considered landscape covariates that are related to energetics, resource acquisition, and anthropogenic risk.
4. For both species, topographic slope, which strongly influences energetic expenditure, drove habitat selection and movement patterns over fine temporal

grains but was less important at longer temporal grains. In contrast, avoiding anthropogenic risk during the day, when risk was highest, was consistently important across grains, but the degree to which carnivores relaxed this avoidance at night was strongest for longer-term movements. Lions and pumas modified their movement behavior differently in response to anthropogenic features: lions sped up while near humans at fine temporal grains, while pumas slowed down in more developed areas at coarse temporal grains. Finally, pumas experienced a trade-off between energetically efficient movement and avoiding anthropogenic risk.

5. Temporal grain is an important methodological consideration in habitat selection analyses, as drivers of both movement and habitat selection changed across temporal grain. Additionally, grain-dependent patterns can reflect meaningful behavioral processes, including how fitness-relevant goals influence behavior over different periods of time. In applying multi-scale analysis to fine-resolution data, we showed that two large carnivore species in very different human-dominated landscapes balanced competing energetic and safety demands in largely similar ways. These commonalities suggest general strategies of landscape use across large carnivore species.

Introduction

Habitat selection, defined as disproportionate use of habitat features relative to their availability, provides a window into the drivers of animal decision-making by reflecting how animals balance fitness-related goals as they move around a landscape (Rosenzweig, 1981, McLoughlin et al. 2006). Habitat selection has long been recognized as a scale-dependent process, and often, drivers of habitat selection change depending on the scale of analysis (Johnson 1980, Boyce 2006, Mayor et al. 2009, McGarigal et al. 2016). Comparing habitat selection across spatiotemporal scales (i.e., longer-term over larger distances versus shorter-term over smaller distances) can reveal fitness-relevant trade-offs and hierarchical relationships between goals that would not be apparent if only a single scale were considered, which can have implications for conservation and management (Rettie and Messier 2000, Hebblewhite and Merrill 2009, Bastille-Rousseau et al. 2015).

The concept of scale encompasses both grain (the spatial or temporal resolution of data; e.g., pixel size for spatial covariates or how frequently animal locations are sampled) and extent (size of study area in space and/or duration of study in time; Wheatley and Johnson, 2009, McGarigal et al., 2016). Much scale-dependent habitat selection research has focused either on the spatial grain of habitat covariates or on comparing selection across broad spatiotemporal scales (McGarigal et al. 2016), which can elucidate drivers of behaviors that operate over longer periods of time (e.g., days to weeks to months) including migration, dispersal, and territoriality (Hebblewhite and Merrill 2009, DeCesare et al. 2012, Bastille-Rousseau et al. 2015, Zeller et al. 2017). The relative importance of landscape features also likely varies over finer temporal grains (i.e., within a day), and broader cross-scale comparisons may overlook important drivers and tradeoffs of short-term habitat selection. For example, short-term movement over the course of minutes may be driven by fine-grain topographic variation that determines how much energy an animal must expend during each movement event (Nickel et al. 2021), while tracking mobile prey or avoiding temporally variable predation risk (Kohl et al. 2018) may drive movement decisions over the course of hours to days (Suraci et al. 2019b). Examining how selection changes across finer temporal grains may elucidate relationships and potential trade-offs between drivers of fine-scale movement and selection.

If selection behavior changes across temporal grain, the resolutions at which researchers choose to sample animal movement (minutes to hours to days) may implicitly represent separate hypotheses about the scale at which habitat covariates are relevant to an animal and may obscure dynamics occurring at other grains (Wiens 1989, Wheatley and Johnson 2009). Historically, habitat selection studies have been conducted at the temporal resolution at which GPS data were collected (usually 1-12 hours between subsequent GPS locations; Bastille-Rousseau et al. 2018), often without explicit consideration of the implications of that choice. Advances in GPS collar technology now allow researchers to observe animal movement at a much higher resolution (Cagnacci et al. 2010), and thus to examine the drivers of animal movement and habitat selection at different temporal grains, ranging from short-term, fine-scale steps to movements over longer periods of time. If movement and/or habitat selection behaviors change with temporal grain, analyses conducted at a single temporal resolution may overlook grain-dependent patterns that can shed light on behavioral processes.

Large carnivore conservation in human-dominated environments is increasingly recognized as important to global conservation efforts (Carter and Linnell 2016), and understanding large carnivore spatial ecology in these systems can elucidate mechanisms that enable human-carnivore coexistence (Suraci et al. 2019b). Globally, large carnivores experience high rates of anthropogenic mortality (Ripple et al. 2014). As a result, large carnivores spatially avoid anthropogenic features (Wilmers et al. 2013, Abrahms et al. 2015) and exhibit temporal shifts in activity and habitat use to minimize the risk of encountering humans (Ordiz et al. 2011, Suraci et al. 2019b, Wilmers et al. 2021). In addition to avoiding anthropogenic risk, large carnivores must also balance the high energetic demands that come with carnivory, including substantial time spent in locomotion required to regularly hunt and kill large-bodied prey (Gorman et al. 1998). In some cases, avoiding anthropogenic risk and balancing high energetic demands may be in conflict with each other, for instance if areas of high resource quality (e.g., higher prey density) are also riskier. In such cases, animals are expected to exhibit temporal partitioning to avoid these areas during risky times (e.g., during the day, when humans are most active) but relax their avoidance during times of lower risk (Kronfeld-Schor and Dayan 2003). Carnivores may also face trade-offs between energetically efficient movement and risk avoidance if avoiding human features results in energetically sub-optimal movement strategies (e.g., moving through more rugged terrain; Nickel et al. 2021). Both energetic constraints and fear responses to humans are widespread across large carnivore species in different environments, but how they inform movement and habitat selection over shorter temporal grains remains unknown.

Here, we investigate scale-dependent drivers of short-term movement and habitat selection for populations of two large carnivore species, African lions (*Panthera leo*) and pumas (*Puma concolor*), living in two very different human-dominated environments: the livestock-wildlife rangelands of Laikipia County, Kenya, and the urban-adjacent Santa Cruz Mountains of California. Both species demonstrate strong behavioral responses to anthropogenic features. In the rangeland system of Laikipia, African lions alternatively exhibit spatial and temporal avoidance of livestock herding, the primary human use of the landscape, but may trade off safety with prey availability due to the overlap of high-quality herding areas and high-quality habitat for native large herbivores (Oriol-Cotterill et al. 2015a, 2015c, Suraci et al. 2019b). In the rugged Santa Cruz Mountains, low-level residential housing is the primary anthropogenic land use. Pumas exhibit strong fear responses to human presence and avoid housing (Wilmers et al. 2013, Smith et al. 2017).

We used integrated step selection analysis (iSSA; Avgar et al. 2016) to compare lion and puma habitat selection and movement across 8 temporal grains, ranging from 5 minutes to 12 hours. In modeling movement and habitat selection jointly, this approach allowed us to ask how habitat features related to energetic expenditure and anthropogenic risk impacted both the selection and movement processes for lions and pumas. We also asked whether and how the influence of covariates on movement and habitat selection changed with temporal grain, which could shed light on strategies that these species use to balance multiple goals in human-dominated landscapes. Applying this analysis to two species – lions and pumas – allowed us to explore and identify commonalities in how large carnivores manage trade-offs between energetics and risk via habitat selection across multiple scales.

Materials and Methods

Study systems and GPS collaring

Laikipia County is located in northern Kenya. Our 1040 km^2 study area was comprised of six commercial ranches consisting of semiarid *Acacia* savannah and open grasslands. These properties are managed for conservation as well as livestock production and support abundant native large herbivore populations, and use traditional livestock practices in which livestock are moved into bomas, or temporary livestock corrals, at night, and are let out to graze under the supervision of herders during the day (O'Brien et al. 2018). Bomas are the centers of human activity on the landscape, and humans present substantial risk to lions, with human-caused deaths accounting for 117 out of 133 mortalities for monitored lions between 1999-2016 (L. Frank, unpublished data). Bomas likely also represent areas of increased prey availability for African lions given that boma locations overlap with high-quality forage for native large herbivores. For further description of the study area, see Frank 2011 and Oriol-Cotterill et al. 2015a. The Laikipia study system has an elevational range from 1271-1931m and is largely flat with some escarpments. Slope ranges from 0-34° with a median slope of 1.16°.

The Santa Cruz Mountains are in the Central Coast region of California, and consist of a gradient of human residential development, including open space areas as well as exurban, suburban, and urban areas across the 2,800 km^2 study area. Habitat types include mixed redwood (*Sequoia sempervirens*) forests, mixed oak (*Quercus sp.*) forests, and chaparral. Pumas in the Santa Cruz Mountains experience high rates of anthropogenic mortality, accounting for 17 of 32 deaths of collared adults and subadults between 2008 and 2020 (A.C. Nisi, unpublished data). For further description see Wilmers et al. 2013. The Santa Cruz Mountains is more topographically rugged than Laikipia, with an elevational range from 0-1333m, slope ranging between 0-48° and a median slope of 4.38°.

Lions and pumas were captured and fitted with GPS collars set to record a GPS location every 5 minutes (Vectronics Aerospace GPS Plus or Vertex, Berlin, Germany; see Appendix 1.S1 for description of animal capture). Data were collected from 14 African lions (9 females, 5 males) and 20 pumas (10 females, 10 males) from 23 Sep 2014 to 14 Feb 2016 and 15 May 2015 to 9 Oct 2018, respectively. All African lions were adults, and 17 of 20 pumas were adults, with the remainder being subadults (ranging from 17-20 months).

Statistical analyses

We used integrated step selection analysis (iSSA) to quantify habitat selection. Step selection analyses (SSA) are a type of resource selection function (RSF; Johnson 1980) that define availability based on movement, with available points generated by simulating random steps from the movement path (Fortin et al. 2005, Thurfjell et al. 2014). Integrated step selection analysis is a further extension of SSA, and allows for the movement and habitat selection processes, and how they are influenced by habitat covariates, to be modeled jointly (Avgar et al. 2016). The movement-driven definition of availability makes temporal grain an important consideration for SSAs, since available points represent locations where an animal could have visited over a certain interval of time (Thurfjell et al. 2014). Applying iSSA to movement data at different temporal grains can thus allow us to compare drivers of movement and selection across temporal grains. We considered 8 distinct temporal grains for this analysis: 5, 15, and 30 minutes, and 1, 2, 4, 8, and 12 hours. Because step lengths (distance between subsequent GPS locations) increase with temporal grain, the temporal resolution of GPS data used in habitat selection analyses is inherently linked to the spatial extent of analysis (Fig. 1.S1 and 1.S2).

We subsampled 5-minute GPS tracks for lions and pumas to construct datasets at each temporal grain. For example, the 15-minute dataset was obtained by selecting every third 5-minute GPS location, and so on. Next, we excluded all non-movement points, which for both species we defined as used points that were < 20m from the previous point for each dataset (Dickie et al. 2020). The 20m cutoff corresponds to the average GPS error for pumas in the Santa Cruz Mountains and agrees with empirically determined step length cut-offs between stationary and moving behaviors for African lions in Laikipia (Suraci et al. 2019b).

For each dataset, we generated 20 available points for each used point by generating random step lengths and turning angles and projecting from the previous location. Step lengths were drawn from exponential (lions) and gamma (pumas) distributions fitted to the empirical data (Avgar et al. 2016). The choice of distribution was motivated by AIC and q-q plots. For both species, turning angles were drawn from Von Mises distributions fitted to the empirical data.

Habitat and movement covariates

For both African lions and pumas, models included anthropogenic features (distance to bomas for lions and housing density for pumas), topographic slope, and percent cover, all of which have been shown to be important for large carnivore movement (Suraci et al. 2019b, Nickel et al. 2021).

For African lions, boma locations were monitored for the duration of the study on the properties to which we had access. To account for the fact that African lions may have been responding to bomas on unmonitored neighboring properties, locations that were <1km from the study area boundary or >5km away from the nearest active boma were excluded (as in Suraci, Frank, et al., 2019). Distance to boma was log-transformed to account for the stronger response at short distances relative to longer distances (Suraci et al. 2019b).

For pumas, housing density was calculated by manually digitizing locations of houses from high-resolution satellite imagery, and fitting an Epanechnikov kernel with a radius of 150m around each housing point, which is the most informative spatial grain for puma movement (Wilmers et al. 2013). Housing density was cube-root-transformed to ameliorate its long right tail and make its coefficient more interpretable after covariate standardization.

Landscape topography is expected to strongly influence energetic expenditure during movement (Shepard et al. 2013); therefore, we included topographic slope for both species. We also included percent vegetative cover (Appendix 1.S2), which may provide hunting opportunities as well as offer more safety in areas close to people for both species. Topographic slope, percent cover, and housing density were rasterized at 30m resolution.

To allow the joint inference on habitat selection and movement, we included movement covariates in all models: step length for lions and the natural log of step length for pumas, as recommended for step lengths drawn from exponential and gamma distributions, respectively (Avgar et al. 2016). We also included directional persistence: $\cos(\theta_t - \theta_{t-1})$, where θ_t is the angle from the x-axis of the step ending at the used or available point and θ_{t-1} is the angle of the prior step. Values range from -1 to 1, with values closer to 1 representing straighter movements.

All covariates were standardized (centered by mean and scaled by standard deviation) within each dataset to facilitate coefficient interpretation (Schielzeth 2010).

We used Pearson’s correlation to test for collinearity between all pairs of covariates. No two pairs of covariates had an $|r|$ >0.17 for African lions or >0.36 for pumas.

Model fitting and interpretation

Coefficients were estimated via conditional logistic regression, fit with the *clogit* function from the *survival* package (Therneau 2015). We used generalized estimating equations (GEE) to account calculate robust standard errors to account for temporal autocorrelation (Appendix 1.S3; Prima et al. 2017).

Model specification reflected *a priori* hypotheses about how carnivores balance avoiding risk from humans with energetic constraints and differed slightly between species according to study area characteristics. Model selection was conducted in three stages for each species. We predicted that both species may avoid human features more strongly during the day than at night, so we first tested for diel changes in the response to anthropogenic covariate by evaluating the support (quasilikelihood information criterion; QIC) of models that included (or not) a time-of-day interaction with the anthropogenic covariate alongside topographic slope, cover, and movement covariates for each temporal grain. Models with ΔQIC <2 were considered to have support (Pan 2001). Next, we tested for interactions between habitat covariates by evaluating the respective support of candidate models differing in their covariate interaction structure. For both species, we predicted that proximity to human features may lead animals to relax their avoidance of slope in order to avoid risk from humans (Nickel et al. 2021), so we considered models that had an interaction between slope and bomas or housing density. We also hypothesized that lions may avoid bomas less strongly where there was higher vegetation cover that could allow them to move undetected (Suraci et al. 2019b); hence, we considered an interaction between boma and cover. Cover exhibited very low variation in the Santa Cruz Mountains (Fig. 1.S1) so we did not consider this interaction for pumas. For pumas, we also tested for a quadratic response to slope, hypothesizing that pumas may select for intermediate slopes that may allow them to reduce risk from people while avoiding high energetic costs of traversing very steep slopes. Because Laikipia is much flatter than the Santa Cruz Mountains, we did not include this interaction for lions. Finally, we considered whether habitat covariates mediated movement through models that included interactions between slope, cover, and anthropogenic covariate with step length and directional persistence, hypothesizing that movement strategies may vary across risky to safe and rugged to flat areas. For example, animals may either speed up or slow down when near human risk to minimize exposure or increase crypsis (Suraci et al. 2019a), and slower, more tortuous movement in rugged terrain likely would reflect how animals mediate movement behavior to manage energetic constraints (Nickel et al. 2021). We selected a single model structure for each species to interpret across grains. When best-supported model structure differed between grains, we chose the structure that received consistent support across grains (Appendix 1.S4, Tables 1.S1-1.S3). To interpret the effects of habitat covariates on selection across temporal grains, we calculated the relative selection strength (RSS) across the range of each focal habitat covariate relative to the same reference location across grains (Appendix 1.S5; Avgar et al. 2017). To assess whether there were differences in habitat selection between males and females, we re-fit the top model separately for individuals from each sex. While all African lions were adults, there were 3 pumas that were <2 years old (all between 17-20 months) and that thus could be pre-dispersal- and dispersal-age (Logan and Sweanor 2001a). To ensure that puma results were not biased by age class, we re-fit the top model to data excluding the 3 individuals <2 years old and compared results with the model fit to all pumas.

While grain-dependent responses may reflect meaningful behavioral processes (Wheatley and Johnson 2009), it is also possible that grain-dependent selection patterns could emerge purely as a function of changing availability domain (i.e., changes in the relative availability or distribution of different habitat types with changing temporal grain size) either through a functional response or patterns of spatial variation in covariates (Beyer et al. 2010). We compared covariate distributions (medians and upper and lower quartiles) at each temporal grain. If covariate availability was relatively constant across grains, a functional response was unlikely to have produced grain-dependent patterns. To assess how patterns of covariate variation changed with temporal grain, we calculated the within-strata variance (i.e., within groups of matched used and available locations), calculated as the mean variance of each matched-case stratum, and the overall (across-strata) variance at each temporal grain. Covariates that exhibited higher spatial autocorrelation would have particularly low within-strata variance at short grains relative to long grains, and may thus impact fine-grain selection less strongly than longer-grain selection.

We tested for spatial autocorrelation in model residuals using Moran's I correlograms (random subsets of 10,000 locations; 250m increments; 1000 bootstrapping iterations to estimate *p*-values) as implemented in the *ncf* package (Bjornstad 2020). Only one distance bin exhibited significant levels of spatial autocorrelation in residuals: 0-250m for lions at the 8-hr temporal grain (see Fig. 1.S3).

Results

For African lions, topographic slope influenced habitat selection at shorter temporal grains but became unimportant at longer temporal grains (Fig. 1.1A, Table 1.1). At the shortest grains (5-15 minutes), African lions exhibited significant avoidance of steeper slopes, but selection for slope was not significant at longer grains (≥ 1 hour). These results appear to be driven by females, with males exhibiting continued avoidance of steeper slopes at longer grains (Fig. 1.S4). Bomas influenced lion habitat selection differently between day and night. During the daytime, lions avoided locations closer to bomas across all temporal grains (Fig 1.1B). During the nighttime, lions relaxed this avoidance, and this relaxation was more pronounced for longer temporal grains, with lions switching to select locations closer to bomas at grains >4 hours (Fig. 1.1C). Responses to bomas were similar between females and males (Fig. 1.S4).

Pumas exhibited grain-dependent selection for slope that was mediated by housing density (Fig. 1.2). For short-grain movement (e.g., 5 minutes), pumas avoided steep slopes in areas without houses (0 houses/km^2, Fig 1.2A), but relaxed this avoidance in areas of higher housing density (28 houses/km^2, Fig 1.2B). For longer-grain movement (e.g., 12 hours), pumas selected shallower slopes in areas with less development but selected intermediate slopes when housing density was higher. Males avoided steeper slopes more strongly than females, but grain-dependent patterns of response to slope were similar between sexes (Fig. 1.S5). Similar to lions, pumas showed diel differences in their response to anthropogenic features. During the day, pumas avoided housing strongly across temporal grains (Fig. 1.2C). At night, pumas relaxed their avoidance of housing and even exhibited selection for areas of higher housing density at longer temporal grains (Fig. 1.2D). Responses to housing density were similar between females and males (Fig. 1.S6). Excluding the 3 pumas <2 years old did not influence our results (Fig. 1.S7 and 1.S8).

Habitat covariates significantly influenced movement behavior for both lions and pumas. Distance to boma and slope mediated lion movement (Fig. 1.3, Table 1.S2). At the 5-minute through 4-hour temporal grains, there was a significant negative interaction between slope and step length, indicating that lions selected shorter steps and moved more slowly in areas with steeper slopes (Fig. 1.3). Additionally, at the 5-minute through 4-hour temporal grains, there were significant interactions between distance to boma and step length, with lions moving faster in areas closer to bomas. Habitat covariates did not strongly impact directional persistence for lions.

For pumas, there were significant interactions between step length and slope at short temporal grains (5 minutes through 2 hours), indicating that at these grains pumas moved slower where slope was steeper (Fig. 1.3, Table 1.S3). In contrast, housing density did not significantly influence puma movement at short grains, but did mediate step length at longer grains, where pumas selected shorter steps in areas of higher housing density. In addition, pumas selected more tortuous movement with increasing cover and slope at short temporal grains, and with increasing housing density at longer temporal grains, although the interactions between habitat covariates and directional persistence were of lower magnitude than for step length. Grain-dependent patterns were largely consistent across sexes in how covariates influenced movement for both species (Fig. 1.S9 and 1.S10).

The distributions of slope, cover, and anthropogenic covariates in available locations were similar across grains (Fig. 1.S1). For each covariate, variance within matched-case groups was less than overall variance and increased with temporal grain. This pattern was most pronounced for distance to boma (Fig. 1.S2).

Discussion

Like most large carnivore species in human-dominated environments, African lions and pumas must balance high energetic demands alongside risk of anthropogenic mortality. Through a multi-scale approach to habitat selection integrating both the movement and selection processes, we showed that the relative importance of these goals in driving large carnivore movement varied with temporal grain. While lions and pumas strongly avoided anthropogenic risk during the daytime at all temporal grains, landscape features related to energetic expenditure most strongly drove selection and movement over short temporal grains and tolerance of anthropogenic risk during the nighttime was more apparent at longer grains.

Both African lions and pumas avoided steeper slopes during movement at short temporal grains. Topographic slope is a strong determinant of energetic expenditure for large carnivores and most terrestrial species (Shepard et al. 2013, Nickel et al. 2021), and the strong influence of slope at fine temporal grains indicates that energetic constraints may be stronger drivers of short-term rather than long-term selection. Similarly, both lions and pumas took shorter steps, indicating slower movement, when slopes were steeper at short temporal grains, but slope did not mediate step length at longer grains. Animals may choose slower speeds to help mitigate the energetic costs of demanding terrain (Shepard et al. 2013, Wilson et al. 2015, Halsey 2016), and here, slowing down when traversing steeper slopes likely reflects the trade-off between energetic expenditure and time. Interestingly, the Laikipia region is much flatter overall compared to the Santa Cruz Mountains, so the fact that this fine-scale avoidance of steep slopes was still seen across both systems suggests that locomotion-driven energetic concerns are an important drivers of carnivore movement even in flatter environments. For both lions and pumas, males avoided steeper slopes more strongly than females, and male lions exhibited avoidance of steeper slopes even across longer temporal grains. Males of both species engage in territorial patrol and generally range farther than females, which are associated with heightened importance of energetic constraints during locomotion (i.e., avoidance of steep slopes), and, therefore, likely drive the observed sex-specific patterns (Benhamou et al. 2014, Johansson et al. 2018, Nickel et al. 2021).

Pumas also exhibited a grain-dependent pattern in how they responded to slope in areas of higher risk from humans. Pumas avoided areas of steeper slopes across all temporal grains when housing density was low, but when risk from humans was higher, pumas did not respond to slope at fine grains and selected areas of intermediate slopes over longer-term movement. These results indicate that carnivores prioritized avoiding risk from humans over energetic constraints when faced with a trade-off between the two, consistent with previous findings (Nickel et al. 2021). Additionally, previous puma habitat selection studies have found both avoidance (Wilmers et al. 2013, Zeller et al. 2017) and selection of steeper slopes (Benson et al. 2016b, Blecha et al. 2018). Our study demonstrates that puma response to slope is dependent both on temporal grain and exposure to risk from humans, so differential results may arise from the temporal grain of analysis and level of human presence on the landscape.

Both African lions and pumas also demonstrated temporally-sensitive risk avoidance, avoiding human features during the daytime and relaxing this avoidance at night. In human-dominated systems, many species have been shown to temporally shift their activity patterns to minimize overlap with humans (Oriol-Cotterill et al.

2015a, Gaynor et al. 2018, Suraci et al. 2019b). In Laikipia and in the Santa Cruz Mountains, human activity around anthropogenic features is highest during the daytime, so daytime avoidance of these features likely functions to minimize the risk of encountering people. For both species, daytime avoidance of areas with more human influence was strong across temporal grains, underscoring that avoiding anthropogenic risk is crucial to large carnivores traversing human-dominated landscapes. Additionally, this suggests that patterns of daytime avoidance over longer periods of time resulted from the scaling-up of finer-grained responses to anthropogenic features (Boyce et al. 2017, Prokopenko et al. 2017). Notably, this pattern holds for lion responses to bomas as well as puma responses to housing, despite the fact that bomas and houses are distributed markedly differently – bomas are rare landscape features and overall boma density is very low in Laikipia, while housing development covers a wide range of densities across the Santa Cruz Mountains. Large carnivore avoidance of risk from humans may lead to broader ecological effects through changes in carnivore impacts on prey behavior, affecting space use by species across multiple trophic levels (Suraci et al. 2019a) with potential effects on primary producers (Yovovich et al. 2021).

While daytime avoidance was strong across temporal grains, the relaxation of this avoidance during the nighttime was stronger at longer temporal grains for both felids. When risky areas overlap with resource availability, animals are expected to use these areas for foraging during times of lower risk (Kronfeld-Schor and Dayan 2003). In Laikipia, bomas are located in areas of high-quality livestock forage and thus likely overlapped substantially with habitat preferred by native large ungulates, and additionally may present a source of food themselves, in the form of domestic livestock – though previous studies have shown that wild prey account for the majority of lion kills even close to bomas (Suraci et al. 2019b). A previous study demonstrated that African lion selection for habitat near bomas was driven by feeding behavior, suggesting that African lions balance costs and benefits from these risky but high-value areas by using them during less risky times (Suraci et al. 2019b). Thus, nighttime selection for bomas may have been driven by hunting opportunities and resource acquisition, and these goals may be stronger drivers of longer-term rather than short-term movements.

Pumas also exhibited nighttime selection for housing density at longer temporal grains, but the mechanism is less clear. Deer detection on camera traps is higher in more human-dominated areas, which could indicate higher deer abundance (Smith et al. 2016). This could result either from deer responses to human subsidies (e.g., landscaping and lawn irrigation) or if deer were using more developed areas as "human shields" (Hebblewhite et al. 2005, Berger 2007). However, other studies have shown that pumas avoided housing density when killing deer and deer kill sites were disproportionately located in wildlands relative to more developed areas (Wilmers et al. 2013, Nickel et al. 2021), which is contrary to what would be expected if nighttime selection for housing density was driven by pumas hunting deer in those areas. Several smaller mesocarnivore prey species are almost certainly more abundant nearer to people, but make up a much smaller percentage of puma diets (Smith et al.

2016). Thus, while it’s possible that prey availability may drive nighttime selection, more investigation is needed to resolve this issue. Alternatively, it is possible that nighttime selection for housing density was in part a function of the strong avoidance that pumas exhibited during the day. In this fragmented landscape, pumas may need to move through more developed areas as they traverse their home ranges and choose to do this during relatively safer nighttime hours to allow for stronger daytime avoidance.

Interestingly, both how anthropogenic features mediated movement as well as the grain-dependent patterns of these responses differed between lions and pumas. At short temporal grains, lions moved faster in areas closer to bomas, while pumas moved more slowly in areas of higher housing density over longer temporal grains. These different strategies may be due to the relative abundance of these features on the landscape – since bomas are fairly rare, it is possible that the optimal choice is to quickly move past them when they are encountered (Dickie et al. 2020), whereas pumas must slow down and move more tortuously to navigate carefully around areas of higher housing density that cover wide swaths of the Santa Cruz study area. A meta-analysis synthesizing human impacts on animal movement also documented mixed responses (Doherty et al. 2021), and future work looking at movement responses to anthropogenic features for other large carnivores in human-dominated landscapes could elucidate whether variations in speed responses are related to the density or distribution of risky features on the landscape. Additionally, the role of sociality may influence carnivore movement strategies around risky features –

solitary pumas may be able to effectively avoid detection around humans by moving slowly, but group living may preclude cryptic movement near human-dominated areas for social species like African lions. In this case, moving quickly through such areas may be a more effective strategy for lions to minimize the risk of detection and encounter. How animal sociality influences movement is an emerging research topic (Westley et al. 2018) and investigating these responses across other solitary and social carnivores may elucidate whether there are consistent patterns in how sociality mediates movement strategies around risky features. However, one commonality between species is that habitat covariates modified step length more strongly than directional persistence, indicating that these species modify their speeds to a greater degree than their tortuosity in relation to energetics and risk avoidance. Increased tortuosity in movement can present substantial energetic costs (Wilson et al. 2013), so an interesting future direction would be to explore the energetic costs of modifying speed versus tortuosity in response to risky features. While some broad-scale movement patterns have been identified across taxa, including generally reduced movement in more human-dominated areas and increased nocturnality (Gaynor et al. 2018, Tucker et al. 2018), variability in these patterns is still apparent across species and systems (Doherty et al. 2021) – quantifying the mechanisms behind patterns in movement and selection responses across species will be an exciting area of future research.

Alongside behavioral mechanisms, changes in characteristics of the availability domain may produce scale-dependent patterns in habitat selection (Beyer et al. 2010, Laforge et al. 2016). First, selection may be related to the mean availability of habitat features – known as a functional response (Mysterud and Ims 1998), which can arise via behavioral processes or through statistical or sampling artifacts (Beyer et al. 2010, Laforge et al. 2016, Holbrook et al. 2019). Given the distributions of covariate values were consistent across grains (Fig. 1.S1) and since we calculated selection strength relative to the same reference location across grains (in Fig. 1.1 and 1.2), these grain-dependent patterns are unlikely to have emerged primarily from functional responses. Second, a covariate that varies over large distances may exhibit minimal variation at the matched-case level over short temporal grains, hence having a reduced impact on selection at short relative to longer temporal grains. Distance to boma exhibited this pattern (Fig. 1.S2), and while lions responded more strongly to bomas at longer temporal grains at night, during the day they exhibited equivalently strong avoidance across temporal grains. Furthermore, all covariates exhibited increased within-strata variation with increasing temporal grain to some degree (Fig. 1.S2), so if spatial autocorrelation in covariates was solely responsible for grain-dependent habitat selection patterns, we would expect to see stronger responses to all covariates with increasing temporal grain. Since this is not what we observed, we do not believe that this mechanism alone drove our results.

These two potential explanations for grain-dependent patterns – scale-dependent behavioral strategies and patterns of covariate variation – are not mutually exclusive, and both likely influence how habitat selection and movement change with the temporal grain of analysis. In our case, examining selection and movement across grains (1) revealed dynamics that would not have been apparent had only one temporal grain been considered (e.g., avoidance of steeps slopes at fine grains, and nighttime selection for anthropogenic features at longer temporal grains), and (2) suggested changes in the shape of the responses with temporal grain (e.g., slope for pumas). Selecting a single temporal grain (e.g., 5-minutes or 4-hours), as is typically done in habitat selection studies, would have resulted in qualitatively different conclusions about how lions and pumas responded to these features.

By considering how habitat covariates impacted movement and selection across temporal grains, our study sheds light on how large carnivores balance multiple, sometimes conflicting goals when traversing human-dominated landscapes, providing novel insight on large carnivore behavioral ecology. Temporal grain is an important consideration in habitat selection studies, with energetic constraints driving carnivore movement over the short-term, while diel partitioning of risk and resource acquisition influenced selection more strongly at longer temporal grains. Our results also suggest that avoiding anthropogenic risk may supersede energetic concerns for large carnivores in human-dominated landscapes. Since results were consistent across two very different human-dominated landscapes (a pastoral rangeland system and a fragmented, urban-adjacent system) and for two very different species (the large, social African lion and smaller, solitary puma), these patterns may represent commonalities in large carnivore movement ecology across a variety of risky areas and landscapes of anthropogenic fear.

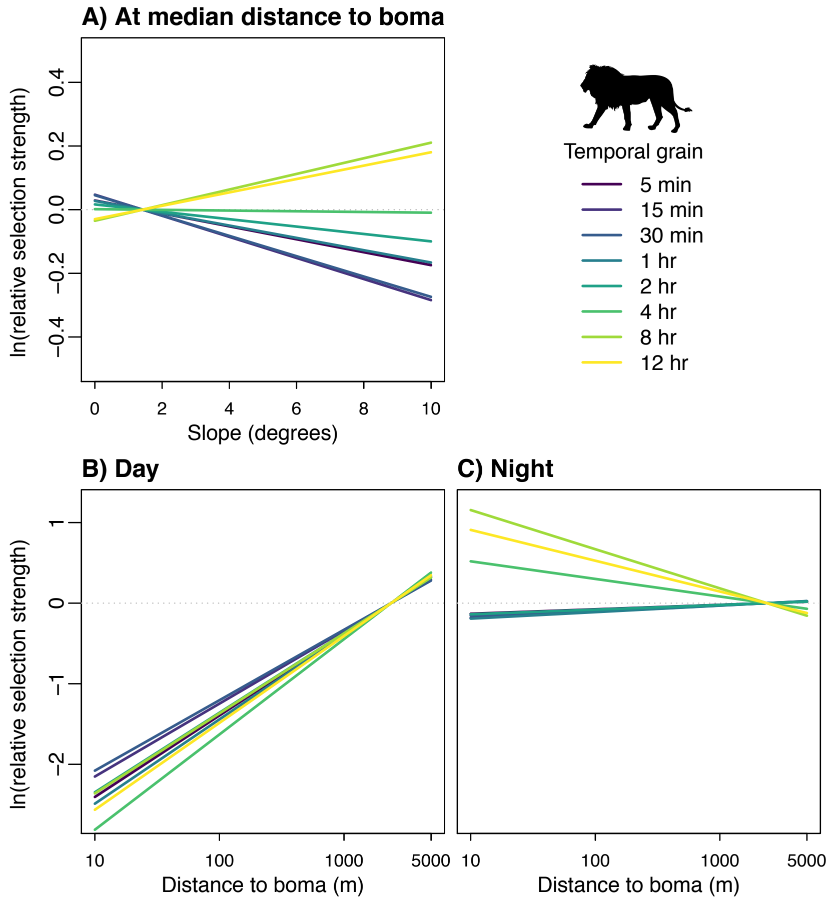

Figure 1.1. Relative selection strength of slope and distance to boma by lions across temporal grains. Selection strength was calculated relative to the same reference location across temporal grains, which had focal covariates (slope in panel A, distance to boma in panels B-C) set to their median values of 4-hour available locations (Appendix 1.S5). Non-focal covariates (distance to boma in panel A, slope in panels B-C, and cover in all panels) were set to their median values of 4-hour available locations, and movement covariates were set to their mean values for each temporal grain. Distance to boma is shown on the log scale.

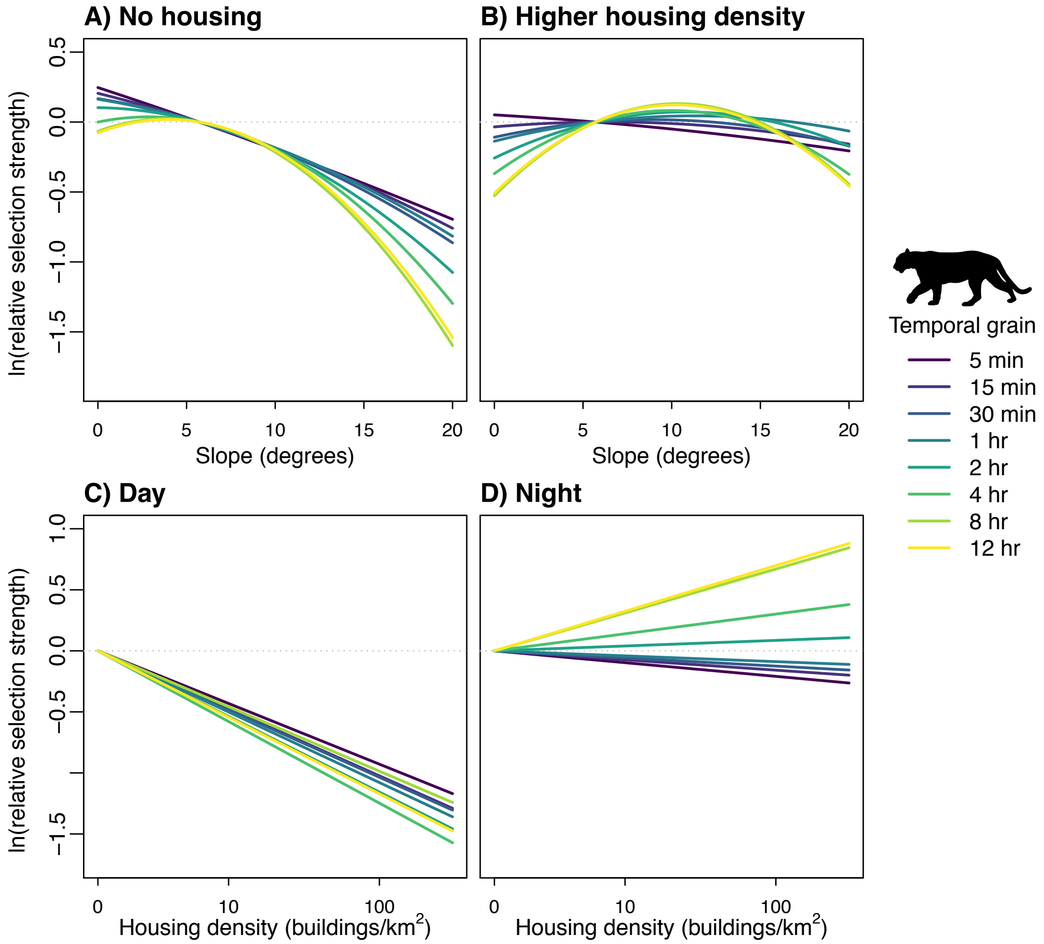

Figure 1.2. Relative selection strength of slope and housing density by pumas across temporal grains. Housing density was set at 0 and 28 houses/km^2 in panels A and B, respectively (lower and upper quartiles of 4-hour available locations). Selection strength was calculated relative to the same reference location across temporal grains, which had focal covariates (slope in A-B, housing density in C-D) set to their median values of 4-hour available locations (Appendix 1.S5). Slope in panels C-D and cover in all panels were set to their median values of 4-hour available locations, and movement covariates were set to their mean values for each temporal grain. Housing density is shown on the cube-root scale.

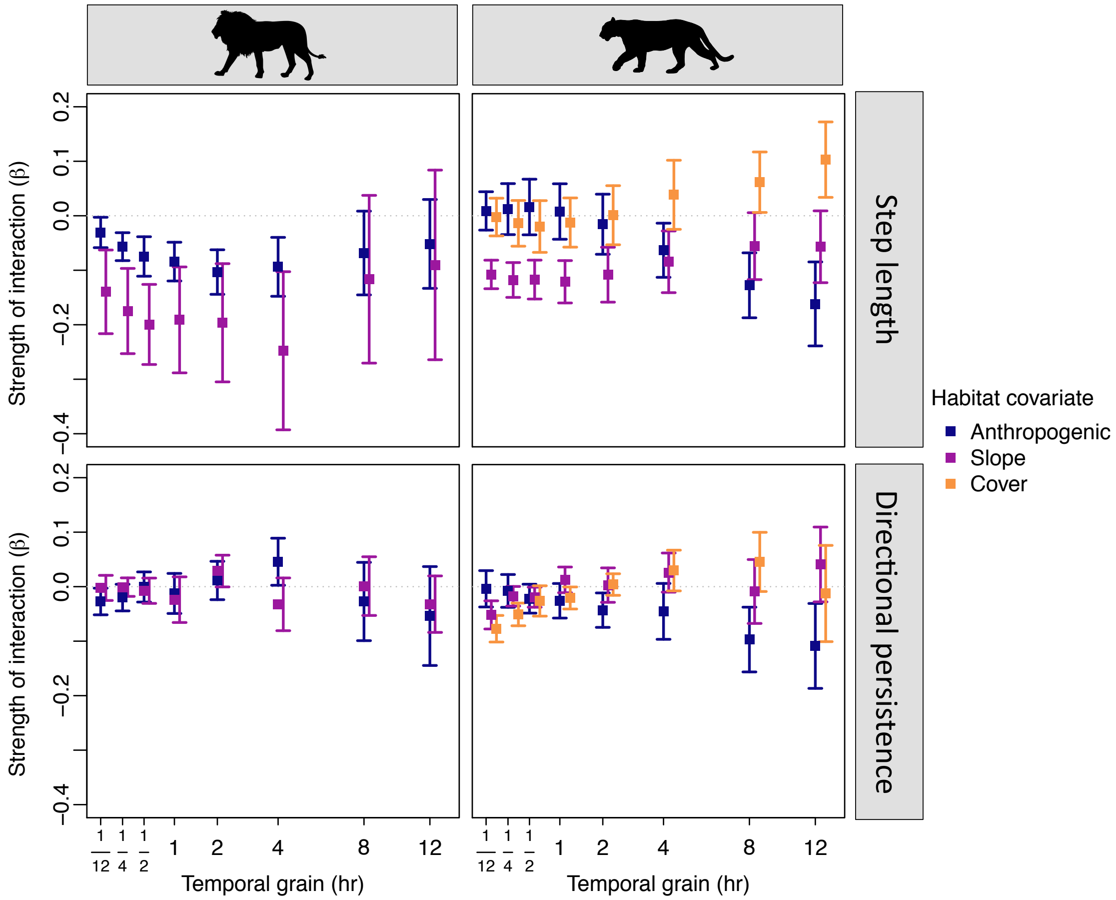

Figure 1.3. Effects of habitat covariates on lion and puma movement. For each species, the strength of interaction is the coefficient of the interaction between habitat and movement covariates multiplied by the same unit change in each habitat covariate (the standard deviation at the 4-hour dataset for each species). Temporal grain is square-root-transformed for readability.

Table 1.1. Coefficient estimates for lion iSSA. Robust standard errors are in parentheses and * and ** denote p-values <0.05 and <0.01 respectively. ΔQIC values are shown relative to best-supported model within each temporal grain (Table 1.S2).

	5 min	15 min	30 min	1 hr	2 hr	4 hr	8 hr	12 hr
Boma	0.292** (0.099)	0.265** (0.069)	0.261** (0.061)	0.301** (0.057)	0.290** (0.054)	0.336** (0.060)	0.293** (0.059)	0.337** (0.075)
Boma*Night	-0.269** (0.105)	-0.229** (0.075)	-0.222** (0.067)	-0.261** (0.064)	-0.249** (0.063)	-0.379** (0.072)	-0.393** (0.085)	-0.393** (0.095)
Boma*Slope	0.032 (0.016)	0.059 (0.019)	0.078 (0.022)	0.065 (0.026)	0.086 (0.030)	0.056 (0.035)	0.094 (0.044)	0.161 (0.058)
Slope	-0.050** (0.015)	-0.086** (0.018)	-0.088** (0.021)	-0.057 (0.024)	-0.043 (0.028)	-0.012 (0.034)	0.047 (0.041)	0.023 (0.051)
Cover	-0.001 (0.009)	0.018 (0.011)	0.032 (0.014)	0.030 (0.017)	0.051 (0.021)	0.078 (0.026)	0.046 (0.033)	0.057 (0.040)
DP	0.125** (0.008)	0.068* (0.010)	0.030 (0.012)	0.011 (0.015)	-0.016 (0.018)	-0.021 (0.024)	0.034 (0.032)	0.035 (0.038)
SL	-0.117** (0.007)	-0.111** (0.011)	-0.078 (0.013)	-0.040 (0.016)	-0.006 (0.019)	-0.004 (0.025)	0.048 (0.031)	0.105 (0.035)
Boma*DP	-0.026* (0.007)	-0.020 (0.010)	-0.001 (0.012)	-0.012 (0.016)	0.011 (0.019)	0.046* (0.025)	-0.028 (0.034)	-0.054 (0.041)
Boma*SL	-0.029* (0.006)	-0.055** (0.009)	-0.074** (0.012)	-0.084** (0.014)	-0.104** (0.018)	-0.094** (0.023)	-0.070 (0.030)	-0.052 (0.036)
Slope*DP	-0.003 (0.006)	-0.001 (0.010)	-0.008 (0.012)	-0.025 (0.015)	0.029 (0.019)	-0.032 (0.023)	0.001 (0.029)	-0.032 (0.035)
Slope*SL	-0.165** (0.009)	-0.192** (0.014)	-0.216** (0.018)	-0.198** (0.022)	-0.196** (0.027)	-0.248** (0.035)	-0.115 (0.038)	-0.090 (0.042)
DP*SL	0.437** (0.010)	0.426** (0.013)	0.321** (0.014)	0.223** (0.016)	0.115** (0.018)	0.003 (0.022)	-0.072* (0.030)	-0.060 (0.034)
ΔQIC	0.00	0.00	0.20	0.00	0.00	0.00	0.00	0.17

Table 1.2. Coefficient estimates for puma iSSA. Robust standard errors are in parentheses and * and ** denote *p*-values <0.05 and <0.01 respectively. ΔQIC values are shown relative to best-supported model within each temporal grain (Table 1.S3).

	5 min	15 min	30 min	1 hr	2 hr	4 hr	8 hr	12 hr
HD	-0.424** (0.022)	-0.481** (0.025)	-0.499** (0.028)	-0.534** (0.033)	-0.583** (0.036)	-0.657** (0.040)	-0.537** (0.043)	-0.675** (0.055)
HD*Night	0.339** (0.026)	0.420** (0.029)	0.453** (0.033)	0.505** (0.038)	0.646** (0.043)	0.834** (0.050)	0.927** (0.063)	1.088** (0.073)
HD*Slope	0.091** (0.004)	0.116** (0.006)	0.137** (0.008)	0.153** (0.011)	0.189** (0.014)	0.200** (0.019)	0.263** (0.025)	0.258** (0.029)
Slope	-0.106** (0.004)	-0.078* (0.007)	-0.056 (0.009)	-0.038 (0.012)	-0.009 (0.015)	0.031 (0.020)	0.082 (0.026)	0.096* (0.031)
Slope^2	-0.004 (0.003)	-0.012 (0.004)	-0.022 (0.006)	-0.020 (0.008)	-0.041 (0.010)	-0.065* (0.014)	-0.090** (0.019)	-0.089* (0.022)
Cover	0.166** (0.005)	0.173** (0.008)	0.189** (0.010)	0.191** (0.013)	0.200** (0.016)	0.220** (0.021)	0.248** (0.028)	0.238** (0.032)
DP	0.039 (0.003)	0.064** (0.005)	0.062** (0.007)	0.053* (0.009)	0.026 (0.012)	0.005 (0.015)	0.005 (0.020)	0.005 (0.024)
ln(SL)	-0.100** (0.003)	-0.118* (0.005)	-0.105* (0.007)	-0.071 (0.009)	-0.014 (0.012)	-0.003 (0.015)	-0.010 (0.021)	0.005 (0.025)
HD*DP	-0.004 (0.003)	-0.009 (0.005)	-0.024 (0.007)	-0.027 (0.010)	-0.045** (0.012)	-0.045 (0.017)	-0.093** (0.023)	-0.101* (0.028)
HD*ln(SL)	0.010 (0.003)	0.014 (0.005)	0.017 (0.007)	0.008 (0.010)	-0.016 (0.013)	-0.063* (0.018)	-0.123** (0.025)	-0.150** (0.030)
Slope*DP	-0.053** (0.003)	-0.018 (0.006)	-0.020* (0.007)	0.013 (0.010)	0.003 (0.013)	0.026 (0.016)	-0.009 (0.022)	0.040 (0.027)
Slope*ln(SL)	-0.111** (0.003)	-0.120** (0.006)	-0.119** (0.008)	-0.123** (0.010)	-0.108** (0.013)	-0.085** (0.017)	-0.055 (0.023)	-0.056 (0.027)
Cover*DP	-0.095** (0.004)	-0.058** (0.006)	-0.029* (0.008)	-0.022* (0.010)	0.004 (0.013)	0.030 (0.017)	0.044 (0.023)	-0.012 (0.028)
Cover*ln(SL)	-0.003 (0.003)	-0.016 (0.006)	-0.022 (0.008)	-0.013 (0.010)	0.001 (0.013)	0.038 (0.018)	0.059* (0.024)	0.097** (0.028)
DP*ln(SL)	0.528** (0.003)	0.568** (0.005)	0.546** (0.007)	0.485** (0.009)	0.387** (0.011)	0.268** (0.014)	0.169** (0.019)	0.285** (0.023)
ΔQIC	0.00	0.00	1.26	7.21	11.20	0.00	0.38	1.85

Appendix 1.S1 – Animal capture and collaring

African lions and pumas were captured and collared under Animal Use Protocols No. 191 from UC Berkeley (issued to L. G. Frank) and WilmC1402 from UC Santa Cruz (issued to C. C. Wilmers). African lions were captured by using baits and audio calls, and free darting from a vehicle. Ketamine and medetomidine were used to anesthetize lions and were reversed with atipamezole ~1 hour after darting. Pumas were captured using trained hounds or box traps and were anaesthetized with Telazol. Both African lions and pumas were fitted with GPS collars set to record a GPS location every 5 minutes (Vectronics Aerospace GPS Plus or Vertex, Berlin, Germany). High-resolution (5-minute) spatial data were collected for an average of 55 days (range: 5-135) for 14 African lions and 60.1 days (range: 13-114) for 20 pumas.

Appendix 1.S2 – Calculating percent cover

Vegetative cover has been identified as an important landscape feature for movement and hunting behaviors for several large carnivore species (Boydston et al. 2003, Ordiz et al. 2011), so we included percent vegetative cover as predictors for both African lion and puma analyses. We calculated percent cover for both species by first assigning cover or no cover indicators to vegetative data from both study systems. For Laikipia, we used the habitat layer from the Centre for Training and Integrated Research in ASAL Development for Laikipia[1], and for the Santa Cruz

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[1] www.cetrad.org

Mountains, we used California GAP Data[2]. For both data sources, we sorted habitat categories into two classes, cover and no cover, and then we conducted a focal analyses to calculate the percent cover was taken over a 90m moving window using the *raster* package (Hijmans 2019).

For lions, cover classes (0 or 1) were assigned to raster cells based on the classifications of low, medium, and high concealment described in (Suraci et al. 2019b). Medium and high concealment were considered cover (1), with low concealment considered no cover (0).

For pumas, cover classes (0 or 1) were assigned to raster grid cells with the following classifications considered "cover": Forest and woodland systems (CN Level 1); Developed (CN Level 2, within Human Use Land); Chaparral, Deciduous dominated savanna and glade, and Conifer dominated savanna (CN Level 2, within Shrubland, steppe and savanna systems; all Floodplain and riparian (CN Level 1, within Riparian and wetland systems) except for Inter-Mountain Basins Greasewood Flat and North American Warm Desert Wash (CN Level 3); and Harvested Forest - Northwestern Conifer Regeneration (CN Level 3), Recently burned forest (CN Level 3), , (CN Level 3), Recently burned forest > Introduced Upland Vegetation - Treed (CN Level 3), Introduced Riparian and Wetland Vegetation (CN Level 3).

Appendix 1.S3 – Generalized Estimating Equations

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[2] https://www.usgs.gov/core-science-systems/science-analytics-and-synthesis/gap

In step selection analyses, non-independence in the data can arise from the high temporal resolution of GPS data (i.e., temporal autocorrelation) and/or variation in habitat selection behavior across individuals (Prima et al. 2017). Generalized estimating equations (GEE) can account for both of these potential sources of non-independence through specifying clusters of data, in which data are potentially correlated within clusters but independent across clusters (Prima et al. 2017). Bias is minimized when there are ≥20 independent clusters (Prima et al. 2017). To account for variation between individuals, separate clusters can be created for each individual. However, if no substantial variation in behavior is observed across individuals, then data from the same individual can be separated into multiple clusters via destructive sampling, where some amount of data is removed between subsequent clusters from the same individual to ensure that those clusters are temporally independent. Pumas tend to exhibit individual variability in selection of housing density, so destructive sampling would have been inappropriate, and each puma was treated as a separate cluster (N = 20 clusters). For African lions, individual variability in response to bomas was minimal so for all but one individual we created two clusters of data separated by at least 3 days (N=27 clusters total), which was identified in a previous analysis to be the amount of time after which temporal autocorrelation is negligible (Fortin et al. 2005, Suraci et al. 2019b).

Appendix 1.S4 – Model selection

For both African lions and pumas, models that contained day/night interaction with the anthropogenic covariate were best-supported across all temporal grains, with models without interactions scoring >2 ΔQIC. For lions, there was support for models containing interactions between slope and distance to boma (Table 1.S1), and interactions between slope and distance to boma with movement terms (Table 1.S2). While the interaction between distance to boma and slope received support across temporal grains (Table 1.S1), this interaction was not significant at any grain (Table 1.1). For pumas, models containing a quadratic slope term and interactions between slope and housing density were best-supported, and interactions between slope, housing density, and cover with movement terms also received support across temporal grains (Table 1.S3).

Appendix 1.S5 – Relative selection strength

Relative selection strength (RSS) was calculated to visualize how slope and anthropogenic covariates impacted habitat selection at each temporal grain. RSS is calculated as the ratio of the relative probability of use of point x_2 to the relative probability of use of point x_1: $RSS(x_2, x_1) = w(x_2)/w(x_1)$ (Avgar et al. 2017). Each panel in Figures 1.1 and 1.2 show how the natural log of RSS varies across the range of a particular focal covariate for point x_2 (e.g., slope for Fig. 1.1A). In each panel, non-focal habitat covariates for both x_2 and x_1 were held constant, generally at their median value (or upper and lower quartiles for housing density in Fig. 1.2A-B), measured for 4-hour available locations. The value of the focal covariate at location

x_1 was also set to its median for 4-hour available locations. The 4-hour dataset was chosen to select constant covariate values, as it was an intermediate grain considered and one frequently used in habitat selection analyses. Movement covariates were set at their means for each temporal grain.

Thus, the RSS can be interpreted as the relative selection for a location with a particular value of the focal covariate relative to a location with the median value of that covariate at the 4-grain, with all other covariates held constant and assuming mean movement behavior for that temporal grain. Since the reference location (x_1) was identical across temporal grains, this allows for cross-grain comparisons of RSS curves.

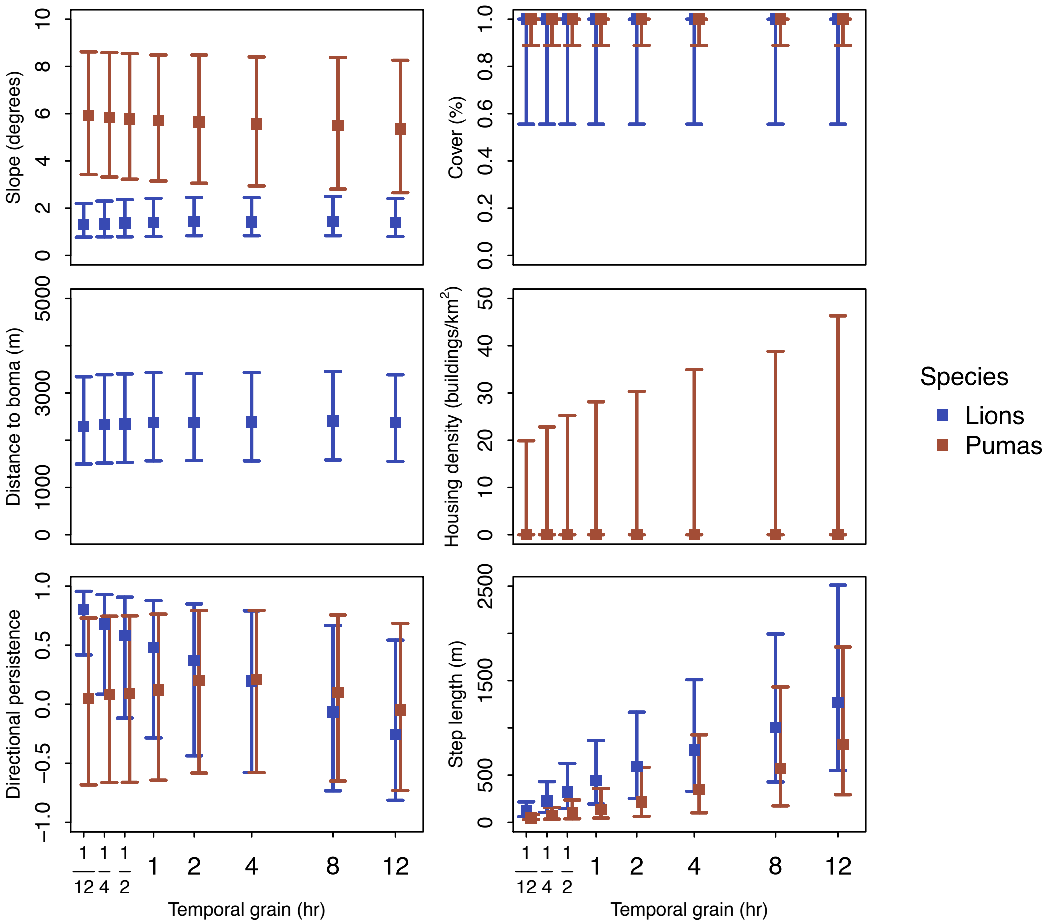

Figure 1.S1. Distributions of habitat and movement covariates across temporal grains. Point estimate shows the median value, with bars denoting upper and lower quartiles. Temporal grain is square-root-transformed for readability.

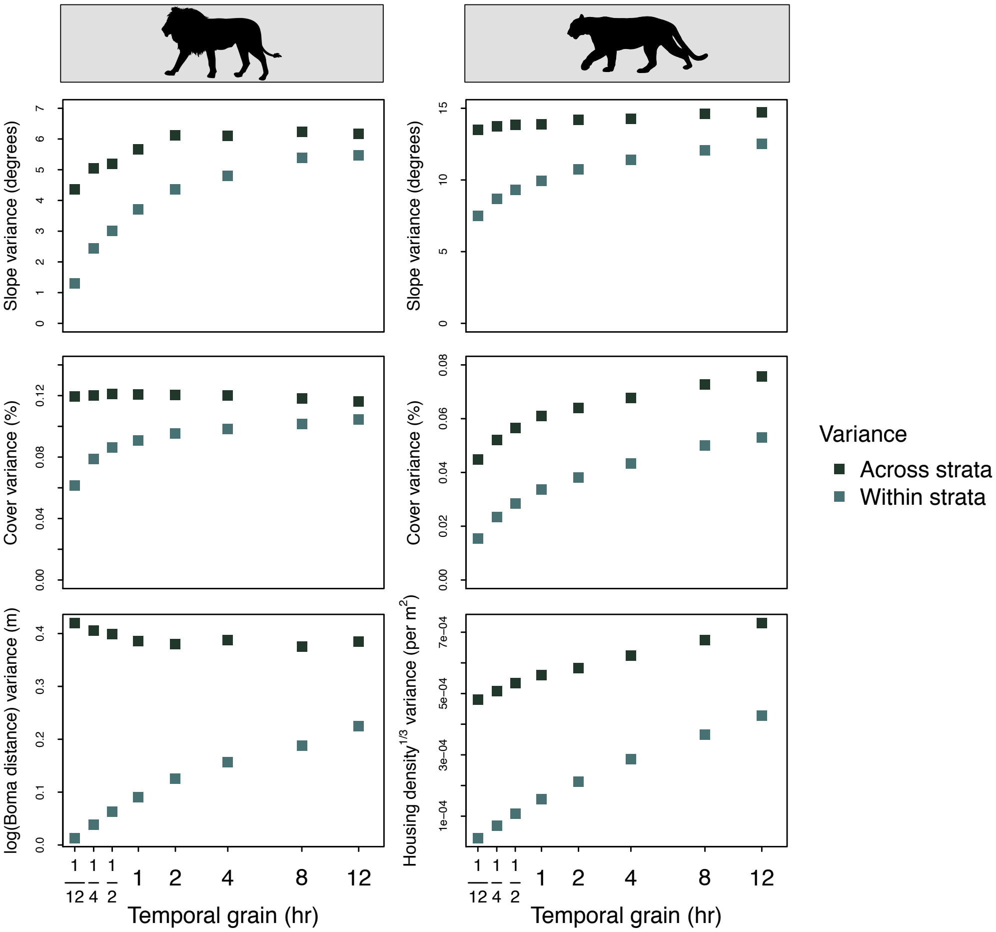

Figure 1.S2. Variance in habitat covariates within and across matched-case strata for all temporal grains. Temporal grain is square-root-transformed for readability.

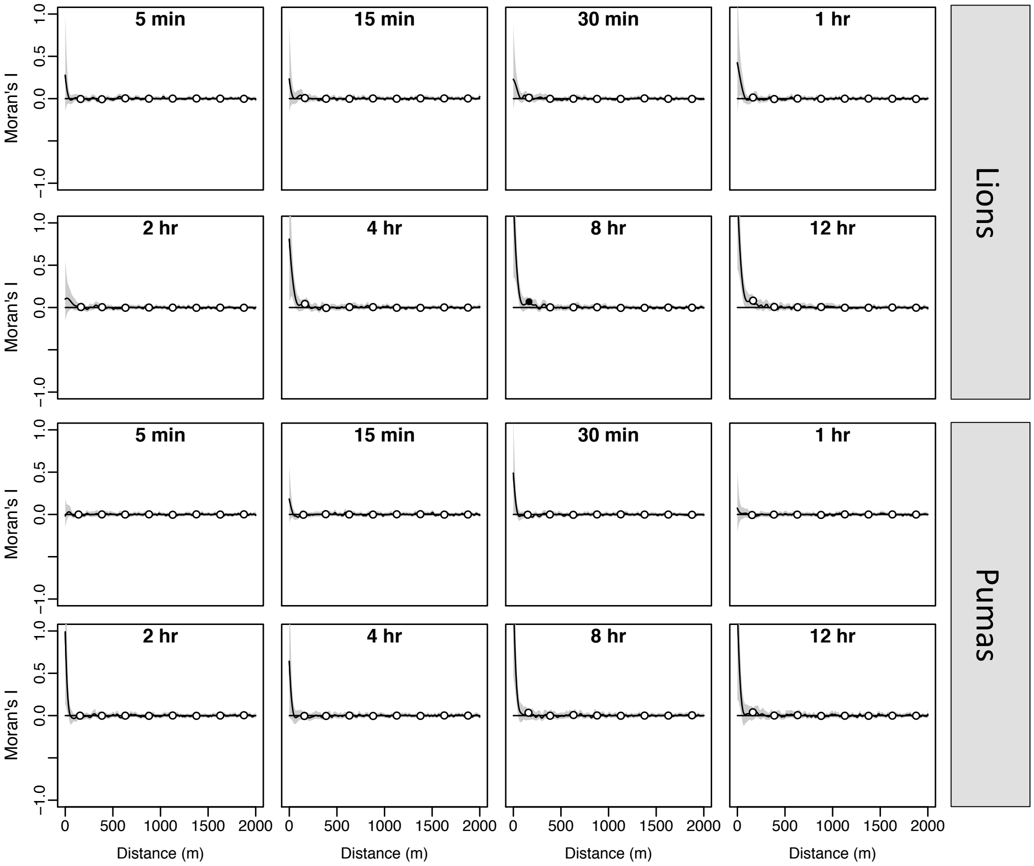

Figure 1.S3. Spline correlograms of Moran's *I* across distance for model residuals. Points denote Moran's *I* calculated in 250m bins. Black points denote $p < 0.05$ (i.e., significant spatial autocorrelation) and white points denote $p > 0.05$.

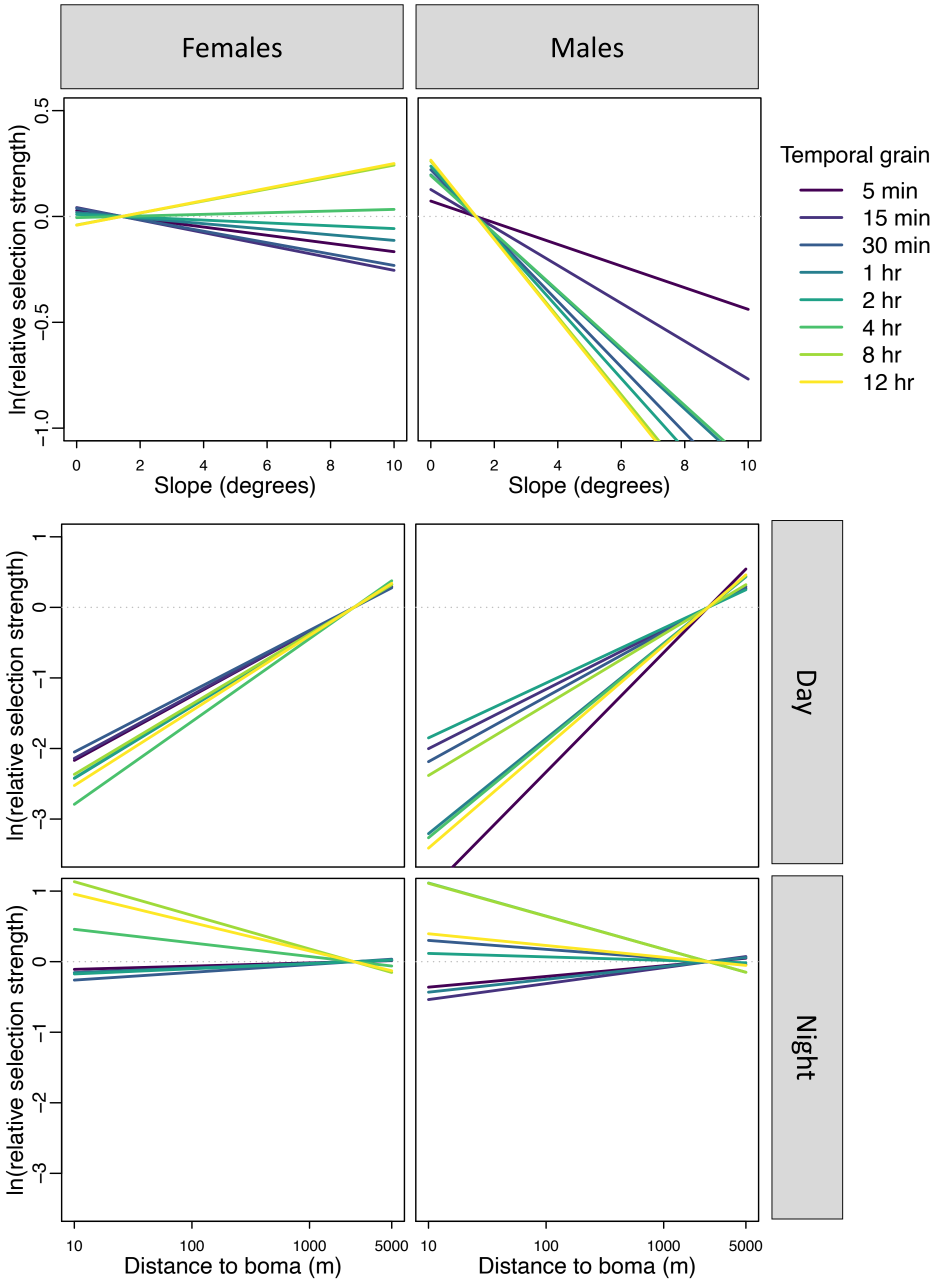

Figure 1.S4. Sex-specific relative selection strength of slope and distance to boma for lions across temporal grains. Selection strength was calculated relative to the same reference location across temporal grains as in Figure 1.1.

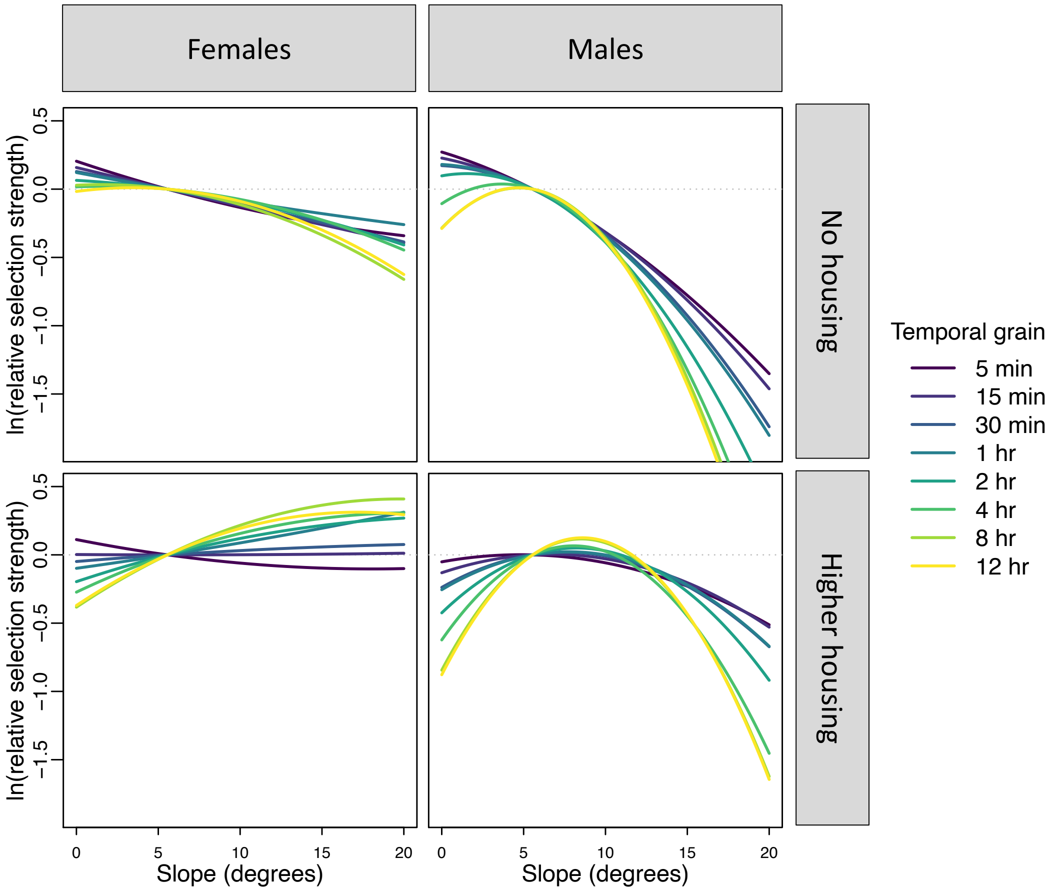

Figure 1.S5. Sex-specific relative selection strength of slope by pumas across temporal grains. Selection strength was calculated relative to the same reference location across temporal grains as in Figure 1.2.

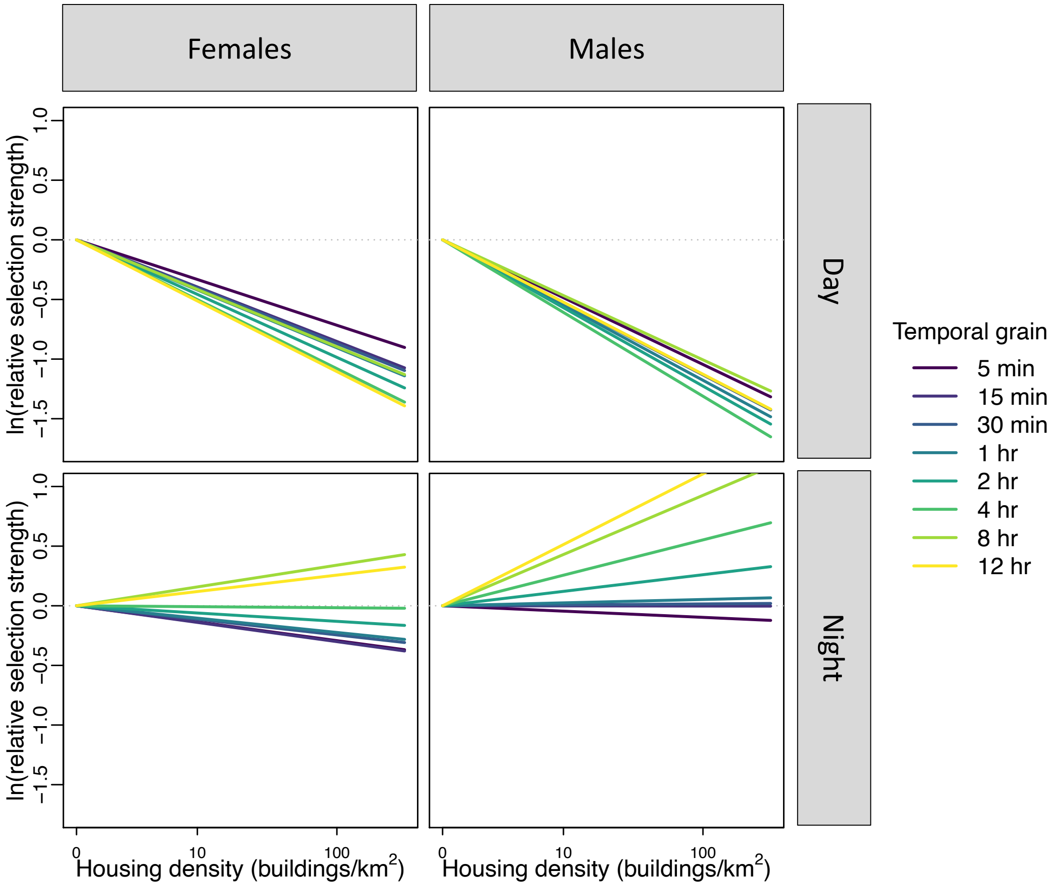

Figure 1.S6. Sex-specific relative selection strength of housing density by pumas across temporal grains. Selection strength was calculated relative to the same reference location across temporal grains as in Figure 1.2.

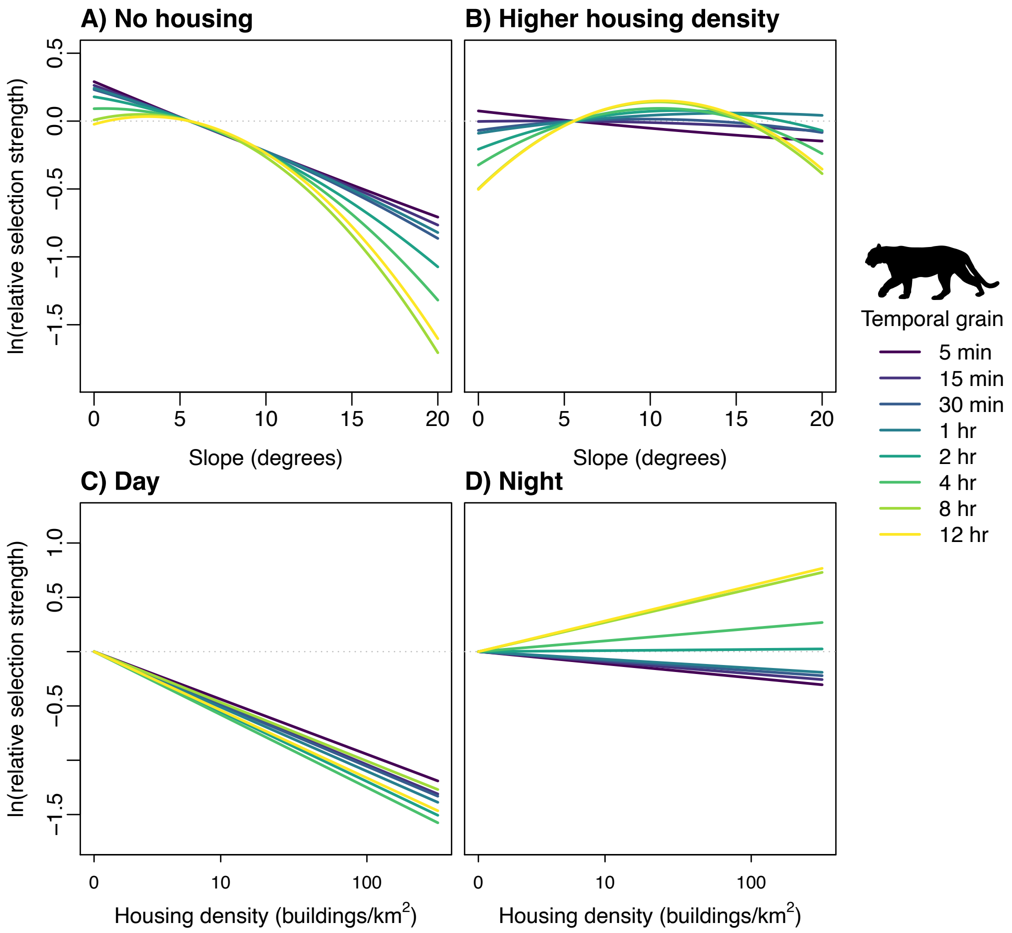

Figure 1.S7. Relative selection strength of slope and housing density for 17 pumas >2 years old across temporal grains. Selection strength was calculated relative to the same reference location across temporal grains as in Fig. 1.2.

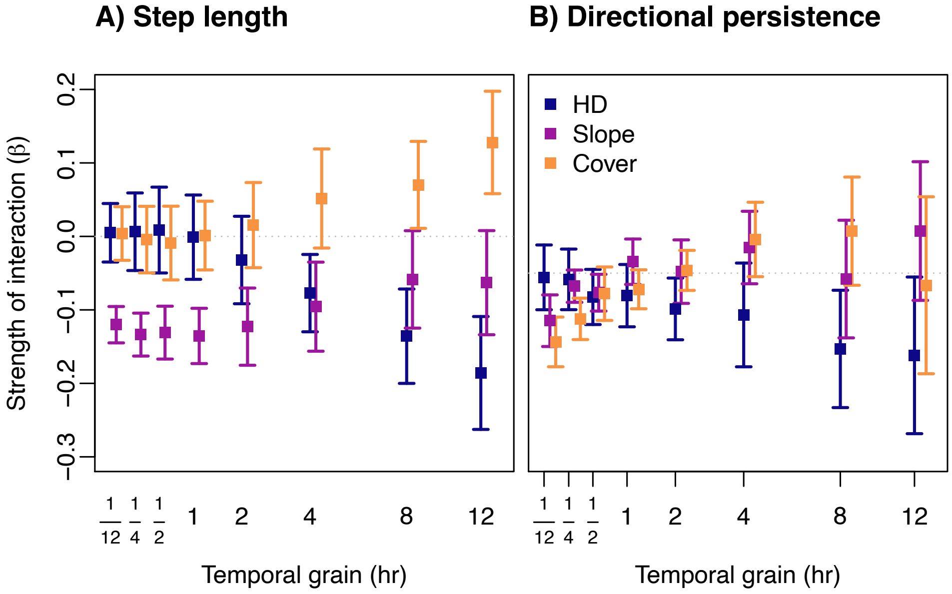

Figure 1.S8. Effects of habitat covariates on puma movement for 17 pumas >2 years old. The strength of interaction is the coefficient of the interaction between habitat and movement covariates multiplied by the same unit change in each habitat covariate as in Figure 1.3.

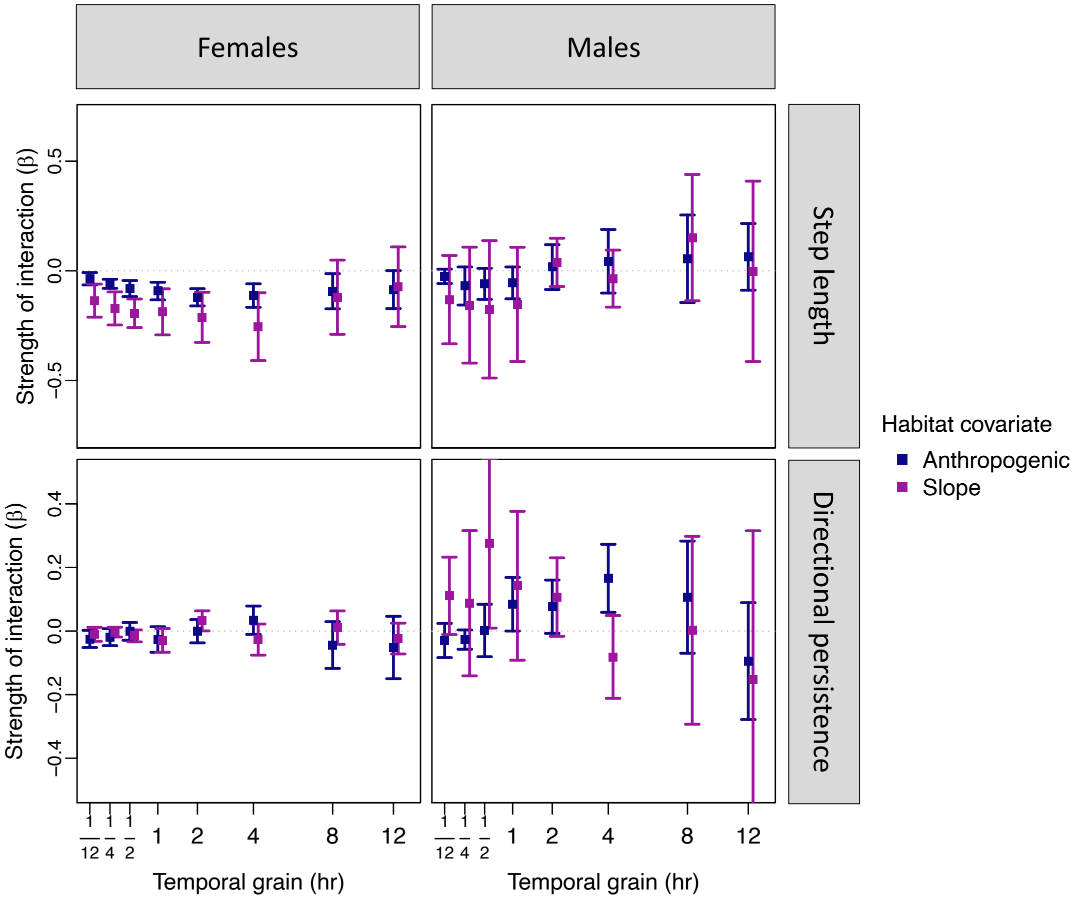

Figure 1.S9. Sex-specific effects of habitat covariates on lion movement. The strength of interaction is the coefficient of the interaction between habitat and movement covariates multiplied by the same unit change in each habitat covariate as in Figure 1.3.

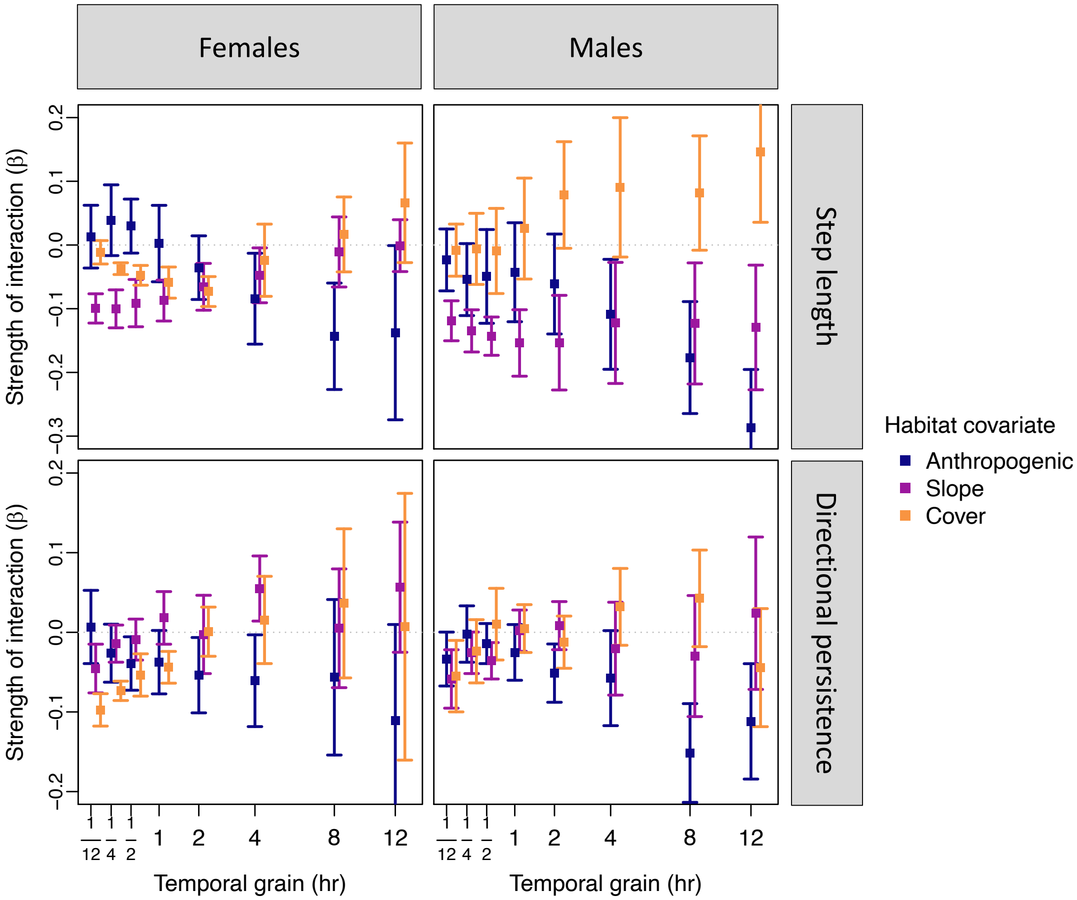

Figure 1.S10. Sex-specific effects of habitat covariates on puma movement. The strength of interaction is the coefficient of the interaction between habitat and movement covariates multiplied by the same unit change in each habitat covariate as in Figure 1.3.

Table 1.S1. Model selection for models with interactions between boma and slope and boma and cover for lions, with no interactions between habitat and movement covariates. All models also contain an interaction between boma and night.

Temporal grain	Model	ΔQIC
5 min	Boma * Slope	0.00
15 min	Boma * Slope	0.00
30 min	Boma * Slope	0.00
1 hr	Boma * Slope	0.00
	Boma * Slope + Boma * Cover	0.42
2 hr	Boma * Slope	0.00
	Boma * Slope + Boma * Cover	0.86
4 hr	Boma * Slope	0.31
	Boma * Slope + Boma * Cover	0.00
8 hr	Boma * Slope	0.00
12 hr	Boma * Slope	0.00

Table 1.S2. Model selection for models with interactions between habitat covariates (boma, slope, cover) and movement covariates (step length, directional persistence) for lions. Models also contain an interaction between boma and slope and boma and night.

Temporal grain	Model	ΔQIC
5 min	(Boma + Slope)*movement	0.00
15 min	(Boma + Slope)*movement	0.00
30 min	(Boma + Slope)*movement	0.20
	(Boma + Slope + Cover)*movement	0.00
1 hr	(Boma + Slope)*movement	0.00
2 hr	(Boma + Slope)*movement	0.00
	(Boma + Slope + Cover)*movement	1.73
4 hr	(Boma + Slope)*movement	0.00
8 hr	(Boma + Slope)*movement	0.00
12 hr	No movement interactions	0.00
	(Boma + Slope)*movement	0.17

Table 1.S3. Model selection for models with interactions between habitat covariates (housing density, slope, cover) and movement covariates (log(step length), directional persistence) for pumas. Models also contain an interaction between housing density and slope and a quadratic slope term.

Temporal grain	Model	ΔQIC
5 min	(HD + Slope + Cover)*movement	0.00
15 min	(HD + Slope + Cover)*movement	0.00
30 min	(HD + Slope)*movement	0.00
	(HD + Slope + Cover)*movement	1.26
1 hr	(HD + Slope)*movement	0.00
2 hr	(HD + Slope)*movement	0.00
4 hr	(HD + Slope)*movement	1.38
	(HD + Slope + Cover)*movement	0.00
8 hr	(HD + Cover)*movement	0.00
	(HD + Slope + Cover)*movement	0.38
12 hr	(HD + Cover)*movement	0.00
	(HD + Slope + Cover)*movement	1.85

CHAPTER 2

Unreliable human cues create an ecological trap for a large carnivore in a human-dominated landscape

Abstract

Animals' fear of people is widespread across taxa and can mitigate the risk of human-induced mortality, facilitating coexistence in human-dominated landscapes. However, humans can be unpredictable predators and anthropogenic cues that animals perceive may not be reliable indicators of the risk of being killed. In turn, unreliable habitat cues may produce ecological traps. Here, we evaluated whether behavioral responses to human cues reflect the actual risk of human-caused mortality for a large carnivore, the puma *(Puma concolor*) in the fragmented Santa Cruz Mountains, CA. Retaliatory killings following livestock depredation were the leading cause of death for this population, and we modeled habitat selection and retaliatory killing risk to evaluate whether puma avoidance of human cues reflected their risk of being killed by people. We documented a mismatch between human cues, fear responses, and actual risk. Rather than scaling directly with housing density, retaliatory killings occurred at intermediate levels of human development and at night. While pumas avoided these areas during the day, they selected for these high-risk areas at night, resulting in an ecological trap impacting 17% of the study area. We also investigated and found no evidence for the alternative hypothesis that state-dependent foraging drove depredations of livestock and subsequent killings of pumas. These results suggest that

fear responses, when decoupled from actual risk, could lead animals into an ecological trap. Because behavioral responses to humans are widespread, our findings suggest a novel mechanism by which ecological traps may impact a variety of species and systems.

Introduction

A central assumption of ecology is that animals select habitat in heterogeneous landscapes to maximize fitness (Fretwell and Lucas 1969, Rosenzweig, 1981). However, the value of a given location in terms of its influence on fitness may be impossible to assess directly, so animals often use habitat features as proxies for habitat quality (Robertson and Hutto 2006). Whether behaviors are adaptive depends in large part on how well the cues to which animals respond reflect habitat quality (Fretwell and Lucas 1969, Robertson and Hutto 2006). Rapid environmental change can disrupt relationships between cues and habitat quality, leading animals to exhibit maladaptive habitat selection, especially in human-dominated environments (Delibes et al. 2001, Sih 2013). In these cases, animals may select (or fail to avoid) low-quality areas – a phenomenon known as an ecological trap (Robertson and Hutto 2006, Robertson et al. 2013, Hale and Swearer 2016). Understanding when and where ecological traps occur is essential for conservation efforts, as traps can magnify source-sink dynamics and threaten population viability (Battin 2004). The mismatch between cues and habitat quality that drives ecological traps has been widely documented following human disturbance or alteration to the landscape (Robertson et al. 2013). However, human disturbance may not be the only mechanism that can produce ecological traps.

Many species exhibit fear responses to humans by avoiding anthropogenic features in space and time, similar to the ways in which prey respond to predators (Frid and Dill 2002, Smith et al. 2017, Gaynor et al. 2018, Suraci et al. 2019b). In some cases, these responses may facilitate coexistence or population persistence in human-dominated environments by allowing animals to avoid anthropogenic mortality (Carter and Linnell 2016). However, the cues used by animals to perceive risk may not correspond perfectly to the actual risk of being killed by people (Smith et al. 2021). Despite widespread research interest in and conservation importance of both ecological traps and the ecology of fear, little is known about the intersection of these two concepts. If anthropogenic cues and risk do not align, then behavioral responses that should function to mitigate risk from humans may be ineffective and may actually contribute to ecological traps.

Anthropogenic mortality is a key threat to many large carnivore populations (Ripple et al. 2014) with deaths from humans far outstripping mortality from any other predator (Darimont et al. 2015), and adult survival is generally the key determinant of individual fitness and population growth for longer-lived species like large carnivores (Heppell et al. 2000, Beckmann and Lackey 2008). As such, strong behavioral responses to humans – predicted as an adaptation to high levels of mortality (Houston et al. 1993, Brown 1999) – are often apparent in habitat selection patterns by large carnivores. Many large carnivore species exhibit both spatial and temporal avoidance of anthropogenic landscape features, such as buildings, roads, and other infrastructure (Wilmers et al. 2013, Abrahms et al. 2015, Milleret et al. 2018, Suraci et al. 2019b). These fear responses are widespread across large carnivore species and, when effective, they can contribute to human-carnivore coexistence (Carter and Linnell 2016, Suraci et al. 2019b). However, whether anthropogenic cues reflect the risk of being killed by people and the degree to which fear responses mitigate anthropogenic mortality remains unknown, and likely depend on characteristics of both cue and mortality source. If cues and risk do not align, these responses could result in maladaptive habitat selection.

The puma (*Puma concolor)* population in the fragmented Santa Cruz Mountains (SCM) of California presents an opportunity to explore the relationship between fear responses and ecological traps. In this population, anthropogenic killings are the leading source of mortality and pumas exhibit strong fear responses to human risk cues (Wilmers et al. 2013, Smith et al. 2017, Suraci et al. 2019a). As with many large carnivore populations (Inskip and Zimmermann 2009, Ripple et al. 2014), retaliatory killing following carnivore consumption of livestock is a common source of mortality for pumas in the SCM. Most retaliatory killings occur after pumas kill domestic livestock, primarily goats held in small numbers on rural, residential properties, rather than commercial livestock operations. While pumas avoid human infrastructure and other cues of immediate human presence, they readily use areas with lower levels of exurban development (Wilmers et al. 2013, Smith et al. 2017), where they may come into contact with livestock. Indeed, sparsely developed exurban areas may present few of the cues that pumas associate with anthropogenic risk, particularly at night when human activity is low, yet these areas may be occupied by the subset of humans most likely to come into conflict with pumas – livestock owners. Alternatively, large carnivores may kill livestock despite accurately perceiving risk from humans according to state-dependent foraging theory, which predicts that animals in depleted energetic states accept higher risk when foraging (Mangel and Clark 1986, McNamara and Houston 1987).

Here, we evaluate whether the behavioral responses of pumas to human cues mitigate or exacerbate the risk of being killed by humans in the SCM. We hypothesized that formerly adaptive behavioral responses to risk from humans can become decoupled from actual risk, resulting in maladaptive habitat selection and an ecological trap. We predicted that mortality of pumas associated with human-wildlife conflict mostly occurs in areas of lower housing density where cues used by pumas to perceive risk are low. Accordingly, we predicted that pumas spatially avoid areas of higher housing density where cues are present (but risk is low) and select areas of lower housing density where cues are scarce (but risk is higher). We also tested the alternative hypothesis that state-dependent foraging drives puma consumption of livestock and subsequent retaliatory killings. This alternative hypothesis would predict that pumas involved in depredation of livestock would be in a depleted energetic state with respect to hunger. By examining these two behavioral phenomena – the ecology of fear and ecological traps – synergistically, our work advances understanding of human-wildlife relationships in human-dominated landscapes and ways in which both human and animal behavior contribute to human-carnivore coexistence.

Methods

Study System

Our 2800 km^2 study area was located in the Santa Cruz Mountains (SCM) of California's Central Coast, just south of the cities of San Francisco and San Jose and north of the city of Santa Cruz. The SCM were a mosaic of open space preserves, large state and county parks, privately held undeveloped properties which contain large swaths of relatively undisturbed native forests, and various levels of exurban and rural residential development interspersed throughout. This created a heterogeneous environment ranging from urban, suburban and exurban areas to large tracts of intact, undeveloped habitat.

In the SCM, most livestock that are depredated by pumas are held in small numbers (e.g., <5 goats) on small, residential properties. During the time of this study, people were only permitted to kill pumas on their own property and following loss of livestock to pumas. As such, locations of retaliatory killings were driven by puma, rather than human, behavior. Typically, pumas kill a domestic animal and then are shot when they return the next night to feed on the carcass. There is not legal hunting of pumas in this system and humans do not bait pumas, use hounds, or otherwise track pumas in any capacity – they simply shoot the puma if and when it returns following livestock depredation.

Puma capture

We captured adult and subadult pumas using trained hounds or box traps and anaesthetized them with Telazol, in accordance with Animal Use Protocol WilmC1402 issued by UC Santa Cruz to C. C. Wilmers. We fit pumas with GPS collars set to record a GPS location at least every 4 hours, and those that recorded with higher frequencies were subset to 4-hour locations for all analyses. We used GPS Plus and GPS Vertex collars produced by Vectronics Aerospace (Vectronics Aerospace GPS Plus, Berlin, Germany) as well as one collar produced by Lotek (Lotek, Seattle, USA).

Quantifying an ecological trap

Three criteria must be met to demonstrate an ecological trap: there must be (A) a difference in a measure or component of fitness across habitats, (B) preference for one habitat over another or equal preference across habitats, and (C) the fitness outcome must be less in the preferred or equally preferred habitat relative to other habitat types (Robertson and Hutto 2006, Robertson et al. 2013). We first (A) quantified survival as a component of fitness as well as the magnitude of retaliatory killing relative to other sources of mortality and assessed how retaliatory killing risk varied across the gradient of housing density in the SCM. Next we (B) modeled puma habitat selection to (C) examine whether pumas selected or avoid high-risk areas. Given the inherent difficulty of quantifying lifetime reproductive success for a freeroaming large carnivore, we based our estimates of fitness on puma survival, a critical component of fitness and population dynamics for pumas, which has been used as a proxy for fitness in other large carnivore studies (e.g., Nielsen et al. 2006, Benson et al. 2015). As pumas reproduce several times throughout their life, longevity should be highly correlated with lifetime reproductive output (Pianka 1970, Beckmann and Lackey 2008). Indeed, life table studies for other large carnivores have shown that survival, rather than reproduction, determines individual fitness and even in cases where there is a trade-off between reproduction and survival, increased reproductive output does not make up for reduced adult survival in terms of population growth (Beckmann and Lackey 2008, Johnson et al. 2020). Adult survival is also the most elastic vital rate for many puma populations, highlighting its importance for population dynamics (Robinson et al. 2014, Benson et al. 2016a). Finally, while increased reproduction in high mortality risk areas could compensate for a decline in survivorship, our previous work has shown that females select against these high risk areas when raising young (Wilmers et al. 2013, Yovovich et al. 2020).

Rate of retaliatory killings

We focused on the most frequent source of mortality for pumas in our area, retaliatory killings, which we defined as legally permitted or unpermitted, confirmed retaliatory deaths following livestock consumption. We first characterized overall and cause-specific mortality rates for pumas in the SCM to evaluate the importance of retaliatory killings as a source of mortality relative to other causes of death for adult and subadult pumas in our study system. Using time-to-event data for collared pumas and censoring pumas whose collars dropped prior to their mortality on the date of their last GPS location, we estimated overall mortality rates using the Kaplan-Meier procedure with an annual recurrent timescale using the *survival* package in R version 3.6.0 (Fieberg and DelGuidice 2009, Therneau 2015). We also estimated the rate of retaliatory killing to identify the prevalence of this cause of death using the non-parametric cumulative incidence function (Heisey and Patterson 2006).

Puma habitat selection

Pumas in this system have been shown to exhibit strong fear responses to the perceived presence of people, including spatial and temporal avoidance of housing and altered movement and feeding behavior in more developed areas (Wilmers et al. 2013, Smith et al. 2015, 2017, Suraci et al. 2019a). Thus, we considered housing density as a risk cue that pumas perceived and responded to and quantified how both puma habitat selection and retaliatory killing risk varied across the gradient of housing density.

To describe puma risk perception, we quantified habitat selection in relation to housing density using step selection functions (SSFs). SSFs are movement-based resource selection analyses in which availability is defined locally by simulated steps (Fortin et al. 2005). The SSF approach thus reflects the process of animal decision-making at fine spatial and temporal scales relevant to movement through complex landscapes. The relative probability of use during movement [$w_{mvt}(\boldsymbol{x})$] takes the exponential form, $w_{mvt}(\boldsymbol{x}) = \exp(\boldsymbol{\beta x})$, where $\boldsymbol{x}$ is a vector of covariates associated with each point and covariate effects ($\boldsymbol{\beta}$) are estimated using conditional logistic regression. We generated 20 available points for each used point (at time t) by drawing random step lengths and turning angles and projecting from the previous point. Step distances were drawn from empirical distributions of pumas of the same sex as the focal individual, excluding that individual's data to avoid circularity (Fortin et al. 2005). Turning angles were drawn from a [0, 2π] uniform distribution (Forester et al. 2009).

We estimated covariate effects using conditional logistic regression using the *clogit* function from the *survival* package (Therneau 2015), and included covariates that were previously identified as being important drivers of habitat selection in this study system (Wilmers et al. 2013). We calculated housing density using Epanechnikov kernels with 500m radiuses to reflect large-scale gradients in housing density across the study area and to correspond to the scale chosen for the retaliatory killing site analysis. Housing density data was cube root transformed to improve normality. We also incorporated topographic and landscape covariates, including topographic slope, topographic position index (indicating whether a point is on a valley/ridge or mid-slope), distance to nearest perennial river or stream (National Hydrography Dataset, USGS[3]), and percent cover calculated from California GAP data (Gap Analysis Project, USGS[4]) over a 90 m x 90 m moving window calculated

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[3] https://www.usgs.gov/core-science-systems/ngp/national-hydrography

[4] https://www.usgs.gov/core-science-systems/science-analytics-and-synthesis/gap

using a focal analysis in the *raster* package (see Appendix 2.S1 for vegetative categories; Hijmans 2019). Step distance (log transformed) and directional persistence (cos[θ_t - θ_{t-1}], with θ_t - θ_{t-1} representing the difference in cardinal direction between the previous two steps) were also included as a predictors as has been recommended in previous studies (Duchesne et al. 2015, Forrester et al. 2015). All covariates were standardized, and generalized estimating equations were used for robust standard error estimation (Prima et al. 2017), with each individual puma treated as a separate cluster. We checked for collinearity by calculating Pearson's correlations between all pairs of covariates (all $|r| < 0.21$).

Because we were interested in the degree to which behavioral responses aligned with risk, we allowed habitat selection to potentially vary non-linearly with housing density and differ between day and night. We considered models that included linear and quadratic forms for the housing density term (models M1 and M2). We also considered interactions between night and housing density terms for both linear and quadratic models to allow pumas to respond differently to human risk during the nighttime compared to daytime (models M3 and M4). Thus, we built several candidate models with and without interactions and non-linear relationships and used quasilikelihood information criterion (QIC) to evaluate model support, with models <2 ΔQIC considered strongly supported (Pan 2001).

Spatial predictors of retaliatory killing events

We characterized where retaliatory killings were most likely to occur across the gradient of housing density using a resource selection function (RSF) framework, in which "used" locations were locations where retaliatory killings occurred (McLoughlin et al. 2005) and available locations were drawn from the study area as defined by merged 95% minimum convex polygons (MCPs) for collared individuals. Here, the relative probability of retaliatory killing [$w_{rk}(\boldsymbol{x})$] also takes the form $w_{rk}(\boldsymbol{x}) = \exp(\boldsymbol{\beta x})$ where $\boldsymbol{x}$ are covariates associated with GPS locations and covariate effects $\boldsymbol{\beta}$ are estimated via logistic regression (Manly et al. 2002).

Used points were locations of death for pumas killed by humans after killing and consuming livestock. To quantify retaliatory killing risk, we included data from N = 32 (9 females, 22 males, 1 unknown sex) retaliatory deaths within the SCM from 11/23/2009 to 12/31/2019. For collared animals that were killed via depredation permits (N = 8) or unpermitted but confirmed retaliatory killings (N = 4), GPS locations of death were taken from collar data. For uncollared animals killed via depredation permit, GPS points were recorded by field personnel when possible. If a GPS point had not been recorded, we used the GPS coordinates associated with the address where the retaliatory killing occurred.

Locations of death are driven both by how risk is distributed across the landscape but also by where animals choose to spend time. To account for this, we generated available locations that reflected the range of availability across the study area while accounting for the habitat selection tendencies of pumas in our system. We first sampled the study area by randomly drawing 10,000 GPS locations from the merged 95% MCPs for all collared individuals. For each of these locations, we calculated nighttime $w_{mvt}(\boldsymbol{x})$ values using our best-fit model for habitat selection (M4) that included a day/night interaction with a quadratic housing density relationship. We calculated nighttime-specific rather than time-of-day-independent relative selection because all retaliatory killings occurred at night, but our results are robust to controlling for time allocation using time-of-day-independent habitat selection (Fig. 2.S1). From those 10,000 locations, we then sampled a subset of 1000 locations weighted by $w_{mvt}(\boldsymbol{x})$ values, such that areas that were more likely to be used by pumas were more likely to be included. Thus, our final availability sample consisted of 1000 points that are distributed throughout the study area after taking into account puma time allocation through nighttime habitat selection.

To characterize how housing density is related to risk of retaliatory mortality, we considered models with linear and quadratic housing density terms. If risk of retaliatory killing increased linearly with housing density, then housing density would be a reliable risk cue, but a quadratic relationship between housing density and risk could result in a mismatch between cue and risk if risk peaked at intermediate levels. Housing density was calculated at the 500m-scale to reflect the larger-scale gradient of human use and was cube root transformed to improve normality. Additionally, vegetative cover may impede a person’s ability to see or shoot a puma. Percent cover was included to control for this possibility, and was calculated over a 510m x 510m moving window using a focal analysis in the *raster* package (Hijmans 2019) using the cover definitions as presented in Appendix 2.S1. We did not include other covariates that may influence puma habitat selection (e.g., slope) but are not likely to influence retaliatory killing risk directly, as we had already accounted for these when generating available points. We standardized both covariates, and Pearson correlation between percent cover and housing density showed that they were not collinear ($r = -0.01$).

We fit RSFs using the *glm* function and we conducted model selection using Akaike information criterion corrected for small sample size (AICc) by considering models with <2 ΔAICc to be strongly supported (Burnham and Anderson 2002). Candidate models included a model with percent cover only (model R1), models with linear and quadratic terms for housing density (models R2 and R3), and models with linear and quadratic housing density terms as well as percent cover (models R4 and R5).

We also modeled the spatial distribution of mortalities from other causes to check whether costs resulting from heightened retaliatory killing risk in some areas would be offset by higher risk of other sources of mortality elsewhere. For this analysis, used locations were the 21 locations of mortality of collared individuals from sources other than retaliatory killings. To generate available locations, we controlled for time allocation by sampling points weighted by time-of-day-independent relative probability of use ($w_{mvt}(\boldsymbol{x})$ calculated by M2). In contrast to retaliatory killing deaths, other causes of death occurred across all times of day and night so it would be inappropriate to use a habitat selection model that was specific to a particular time of day. We fit models and conducted model selection in the same way as we did for retaliatory killing mortalities.

State-dependent foraging

We used *t*-tests to compare the observed weights for pumas killed following livestock consumption with weights recorded for all animals during capture. We also calculated the time since last predicted black-tailed deer (*Odocoileus hemionus columbianus*) kill for pumas killed following livestock consumption and compared that to mean inter-kill intervals observed in this population using a kill prediction model developed for a prior study (Appendix 2.S2; Smith et al. 2015). We also used t-test to compare mean ages at death for pumas killed following livestock consumption to deaths from other causes to evaluate whether our results were driven by potentially naïve juvenile pumas.

Results

The overall mortality rate for pumas in the SCM was 0.252 (N = 33 deaths of collared pumas, 95% CI: 0.169, 0.327). Of the 33 deaths observed, 17 were from confirmed anthropogenic causes (12 retaliatory killings, 4 vehicle strikes, and 1 poaching event not related to livestock depredation). The cause-specific mortality rate for retaliatory killings was 0.090 (95% CI: 0.049, 0.131), accounting for 36% of total mortality and the majority of anthropogenic mortality.

Locations of retaliatory mortalities for both collared and uncollared pumas (N=32) were most likely to occur at intermediate housing densities ($\beta_{HD} = 1.625$, SE = 0.421, $p < 0.001$; $\beta_{HD2} = -0.785$, SE = 0.269, $p = 0.003$; Fig. 2.1A). All retaliatory killings where time of death was recorded (N = 17) occurred at night. Percent cover was negatively related to risk of retaliatory killing ($\beta_{cover} = -0.394$, SE = 0.157, $p < 0.012$) and was included in the model with the most support (Table 2.1). Other sources of mortality were distributed randomly with respect to housing density (Table 2.1, Fig. 2.2). Indeed, the null model was among the top competing models (ΔAICc = 0.56) and superior to all models including housing density (ΔAICc ≥ 1.99), suggesting no support for an influence of housing density and on risk of other causes of mortality.

During the daytime, pumas avoided areas of higher housing density and avoidance increased monotonically across the gradient of housing density (N = 65 pumas monitored from 5/2/2009 to 8/18/2019; Table 2.2, Table 2.S1). In contrast, at night pumas selected intermediate levels of housing density and avoided housing less strongly overall (Fig. 2.1B). Comparing risk and habitat selection indicated a mismatch between avoidance behavior and areas where retaliatory killings were most likely to occur (Fig. 2.1B, Fig. 2.3). At night, pumas selected levels of housing density that almost perfectly corresponded to those associated with higher risk of retaliatory killing by humans. Areas that had both high risk of retaliatory killing and that were relatively selected by pumas during the nighttime made up 17.2% of the study area (Fig. 2.3C).

There was no difference in weights of pumas killed following depredation events compared to weights observed from live pumas during captures for either females (retaliatory killing weights: 77.5 lb [SD=5.4, N=3]; capture weights: 81.9 lb [8.34, 56]; *p* = 0.30) or males (retaliatory killing weights: 108 lb [21.2, 14]; capture weights: 112 lb [21.2, 63]; *p* = 0.60). Additionally, estimates of time since last predicted deer kill for pumas consuming livestock were within the range of mean inter-kill intervals estimated for pumas during the study (Fig. 2.4). Mean kill rates were 62.1 (SE=2.87, N=29) deer/year for females and 51.8 (3.97, 33) deer/year for males, corresponding to mean inter-kill intervals of 6.27 (SE=0.06) and 8.71 (0.13) days, respectively. Mean time since last predicted deer kill for pumas killed following livestock depredation was 6.58 (SE=0.42, N=2) days for females and 7.69 (1.60, 8) days for males. Finally, there was no difference between the age at death of pumas killed following consuming livestock (mean=63.3 months, SD=26.5, N=12) versus other causes (55.0 months, SD=26.7, N=21; p=0.40).

Discussion

We demonstrated a mismatch between a human cue, the associated fear response, and anthropogenic mortality risk for pumas in the SCM, which appeared to produce an ecological trap affecting considerable portions of habitat. Retaliatory killings were the leading cause of death and largest source of anthropogenic mortality for pumas in this area, accounting for over a third of the overall annual mortality rate and the majority of anthropogenic mortality. If habitat selection were to effectively mitigate risk from humans, pumas would need to avoid areas associated with high risk of retaliatory killing. In contrast, though pumas exhibited strong behavioral responses to human cues and habitat selection varied across the housing density gradient, they did not distinguish the conditions where risk from humans was highest. Rather, pumas selected the riskiest places during the riskiest times.

The reliability of human risk cues determines whether fear responses are effective at mitigating the risk of being killed by people. Here we found that housing density as a risk cue was not monotonically related to risk from humans. Instead, retaliatory killing risk peaked at intermediate housing densities, which likely reflects the distribution of livestock ownership across the study area as residents in more remote areas are more likely to keep livestock on their properties relative to residents in denser neighborhoods. Thus, housing density is a complicated cue for actual mortality risk in the SCM, as pumas would need to exhibit avoidance across lower levels of housing density to mitigate risk effectively.

Indeed, pumas' responses to human risk cues were decoupled from risk both spatially and temporally. During the daytime, pumas strongly avoided housing, including the range of housing density associated with high risk of retaliatory killing. But at night, pumas relaxed this avoidance and even selected intermediate levels of housing density that presented the most risk (Fig. 2.1B). Relaxing avoidance during the nighttime is consistent with temporal partitioning, in which carnivores shift their activity patterns towards nighttime hours to minimize overlap with human activity (Oriol-Cotterill et al. 2015a, Gaynor et al. 2018, Suraci et al. 2019b) likely in an attempt to reduce risk (Kronfeld-Schor and Dayan 2003, Benson et al. 2015). However, all retaliatory killings occurred at night, so while exhibiting stronger avoidance in the daytime likely reduced pumas' exposure to human activity, it did not reduce their exposure to risk. Thus, the risk of retaliatory killing was high in the absence of risk cues, which rendered puma fear responses – both spatial avoidance and temporal partitioning – ineffective at mitigating risk. Instead, unreliable cues led pumas into an ecological trap in which they selected the conditions where they were most likely to be killed.

Humans can be unpredictable predators, and in this case we found that risk from humans did not easily map onto the cues pumas use to gauge anthropogenic risk and was high under conditions where risk cues were low or absent. Only a subset of people (i.e., livestock owners who have lost livestock to puma depredation) have the reason and ability to legally kill pumas in the SCM, and even among that population some choose not to request lethal permits following loss of livestock. The distribution of this relatively small subset of people with motive to kill pumas across a landscape that is characterized by high human population density and activity may be difficult or impossible for pumas to perceive. Furthermore, since retaliatory killings are decoupled from easily discernable human presence and activity cues, it might be difficult for pumas to evolve an adaptive behavioral response or learn to mitigate this risk.

Historically, however, avoidance of high-human areas during times of higher human activity likely aided pumas in avoiding being killed by people. For much of the twentieth century, pumas were heavily persecuted in California through vermin and game classifications, including a bounty system, with pumas killed for myriad reasons: opportunistically, for sport, following livestock depredation, and when they ventured into more populated areas (Dellinger and Torres 2020). Over time, attitudes among the general public began to shift and became more positive towards pumas, which was reflected in legislation and management policy. In 1990, CA voters passed a proposition imposing a permanent hunting ban on pumas in CA, and in 2013 the CA legislature voted to mandate local law enforcement to non-lethally remove pumas from densely populated areas – prior to this, they were often shot in these situations. Before these changes in attitudes and policy, mortality risk from humans almost certainly scaled directly with the intensity of human cues, and avoiding areas with more people during times of high human activity likely did allow pumas to avoid risk from humans, especially since pumas were regularly shot when entering more developed areas. Now, as our analyses show, areas of high housing density are actually less risky than areas of intermediate housing density, likely due to generally positive public attitudes towards pumas (Crook 2019), increased legal protections, and more humane management policies. It is thus likely that anthropogenic risk has only recently become decoupled from human cues in the SCM.

An alternative potential explanation for these findings is that individuals in poor body condition accept additional risk consistent with state-dependent and risk-sensitive foraging theory (Mangel and Clark 1986, McNamara and Houston 1987, Blecha et al. 2018). For example, a study in Colorado's Front Range showed that pumas relaxed avoidance of housing density when hungry to take advantage of increased hunting success for native prey that they experienced in areas closer to people (Blecha et al. 2018). Our data did not support this alternative conclusion, however, as both body condition and time since previous deer kill for pumas killed following livestock depredation in the SCM were within the range of what was observed in the general population. Thus, our results suggest that state-dependent foraging decisions did not drive pumas to kill livestock in this system. Rather, it is likely that pumas were simply not able to ascertain where they were at risk of being killed by people. This has conservation implications, as any individual, regardless of energetic state, could fall into this trap – including prime-age adults in good body condition, whose survival strongly impacts population dynamics.

One limitation of our study is that we were unable to assess true fitness via lifetime reproductive success. However, there is strong evidence both that 1) adult survival is a good proxy of fitness for pumas, and 2) accounting for other components of fitness, including reproduction, would not counteract the mortality costs associated with higher retaliatory killing risk at intermediate housing densities. First, as discussed above, survival is expected to correlate to lifetime reproductive success and thus determine individual fitness for K-selected species that reproduce multiple times over relatively long lives (Pianka 1970, Beckmann and Lackey 2008, Johnson et al. 2020), and additionally is the most important driver of large carnivore population dynamics (Heppell et al. 2000, Robinson et al. 2014, Benson et al. 2016a). As such, survival has been used as a reliable proxy for individual fitness in other large carnivore studies (e.g., Nielsen et al. 2006, Benson et al. 2015). Second, other components of fitness, including reproduction, are unlikely to produce costs or benefits along the housing density gradient that would counteract costs from retaliatory killing risk. Locations of mortality from other causes of death were distributed randomly with respect to housing density, so unlike retaliatory killings, risk of mortality from other causes did not have a strong association with a particular level of housing. It is also unlikely that the fitness costs at intermediate levels of housing were offset by fitness gains in these areas, either through reproduction or resource acquisition. Pumas strongly avoid housing while reproducing and raising young (Wilmers et al. 2013, Yovovich et al. 2020). Interestingly, even in systems where certain areas are associated with reduced survival but increased reproduction (in contrast to this system), survival is still more important for large carnivore fitness, and reproductive gains do not offset survival costs (Beckmann and Lackey 2008, Johnson et al. 2020). So while we were unable to account for reproduction, both the higher fitness contribution of survival relative to reproduction and the fact that reproduction is inversely related to housing density suggests that survival is a reasonable metric for true habitat quality for pumas. Finally, there is no evidence that intermediate or high housing density areas present increased hunting opportunities for deer in the SCM, as previous analyses have found that pumas select wildland areas, rather than places with any housing, for deer kill sites (Wilmers et al. 2013, Nickel et al. 2021), and that deer occupancy is not related to housing density (Nickel et al. 2021). Taken together, this evidence suggests that fitness costs stemming from heightened retaliatory killing risk at intermediate housing densities were not offset either by higher mortality from other sources elsewhere on the housing density gradient or by improved reproduction or resource acquisition in high-risk areas.

Previous literature has described two mechanisms that can produce ecological traps for large carnivores. First, especially near protected area boundaries, carnivores may be unable to perceive elevated risk outside of protected areas, since habitat type may be similar and there are often no risk cues associated with higher human risk outside of parks (Balme et al. 2010, Loveridge et al. 2017). These are generally equal-preference traps (Robertson and Hutto 2006), where carnivores simply do not avoid high-risk areas as they should, rather than selecting these areas (Balme et al. 2010). Secondly, especially for bear species (*Ursus* spp.), anthropogenic subsidies can create high-risk, high-reward areas, where human-associated resource inputs – for example, agricultural resources, alteration to vegetative communities producing enhanced berry growth, grain spillage and ungulate carcasses along transportation lines, and/or easier travel along linear features – can promote preference or use of habitats that have higher anthropogenic mortality risk (Nielsen et al. 2006, Northrup et al. 2012, Lamb et al. 2017, Penteriani et al. 2018, St Clair et al. 2019, Johnson et al. 2020).

Here, rather than failing to perceive risk cues or being drawn into high-risk areas by food resources, pumas in the SCM responded to unreliable human risk cues that actually put them at increased risk of being killed. While pumas were able to generally avoid humans, they were not able to successfully avoid conditions in which they were likely to be shot. Cue accuracy and reliability, along with an animal's ability to perceive these cues, are the mechanisms that underlie habitat selection and determine whether animals can behave optimally and respond to anthropogenic change (Sih 2013). In this case, anthropogenic risk has become decoupled from anthropogenic cues, rendering these human risk cues unreliable. Anthropogenic landscapes of fear are common among large carnivore species as well as other taxa (Frid and Dill 2002), so the mechanism we report here may result in traps for a range of other species and systems in cases where anthropogenic risk cues become unreliable or inaccurate.

Anthropogenic mortality is a key contributor to large carnivore decline (Ripple et al. 2014, Darimont et al. 2015) and fear responses to humans are both widespread and energetically costly (Frid and Dill 2002, Smith et al. 2017). Thus, understanding how fear responses reflect anthropogenic mortality risk will be useful in informing management especially in human-dominated areas where anthropogenic mortality rates are high. When ecological traps are identified, they can be remedied either by improving cues or improving habitat quality (Robertson and Hutto 2006). Manipulating risk cues has been accomplished for some large carnivore species and is recognized as a potentially important strategy to enable human-carnivore coexistence (Miller and Schmitz 2019, St Clair et al. 2019). In this case, improving livestock husbandry to reduce livestock losses by fully enclosing livestock in enclosures at night, especially in high-risk, lower-housing-density areas, would help reduce mortality risk for pumas in areas that they perceive as safe.

Large carnivore behavior can facilitate coexistence with humans in mixed landscapes (Carter and Linnell 2016), but here we show that even when fear responses are evident, they may not effectively mitigate mortality risk. Ecological traps involving fear responses in turn may have negative implications for carnivore conservation, especially when they impact prime-age adults. Understanding whether and when large carnivore behaviors are effective or ineffective can thus inform conservation and management actions to promote their persistence in complex, human-dominated landscapes.

Table 2.1. Model selection for retaliatory killing location RSF [$w_{rk}(\boldsymbol{x})$] and locations of mortality from other sources. HD denotes housing density.

Cause of death	Model		ΔAICc
Retaliatory killing	R5	Cover + HD + HD^2	0.00
	R3	HD + HD^2	3.67
	R4	Cover + HD	14.56
	R2	HD	20.36
	R1	Cover	21.48
	Null		25.70
Other	R1	Cover	0.00
	Null		0.56
	R4	Cover + HD	1.99
	R2	HD	2.54
	R5	Cover + HD + HD^2	3.55
	R3	HD + HD^2	4.23

Table 2.2. Model selection for population-level movement SSF [$w_{mvt}(\boldsymbol{x})$].

Model		ΔQIC
M4	Quadratic (night interaction)	0.00
M3	Linear (night interaction)	641.56
M2	Quadratic	2965.74
M1	Linear	3408.48

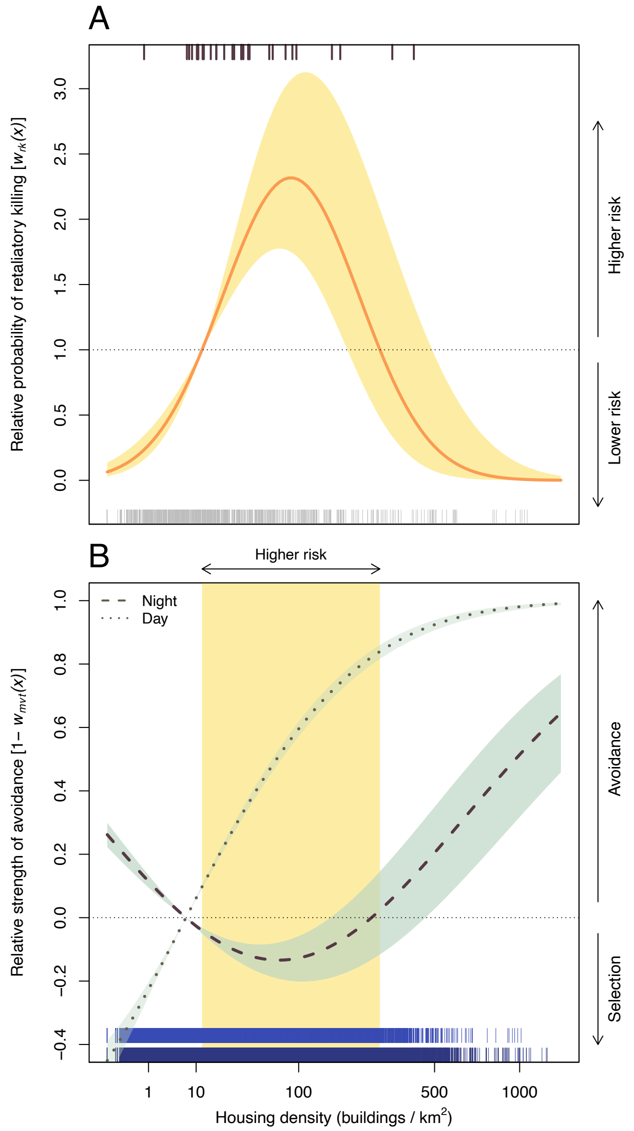

Figure 2.1. Retaliatory killing risk peaked at intermediate housing densities **(A)**, creating a mismatch between risk and puma behavior during high-risk times (i.e., nighttime; **B**). In panel **(A)**, predicted relative probability of retaliatory killing values >1 indicate that retaliatory killings are more likely than random to occur at those housing densities, and values <1 are less likely to occur than at random. Risk was predicted using coefficient estimates from model R5. Rug plots in maroon show

housing densities at retaliatory killing locations, and grey show available locations. In panel **(B)**, relative strength of avoidance during movement was calculated by subtracting the predicted relative probability of use during movement from 1, with negative values indicating selection and positive values indicating avoidance. The yellow shaded area represents the range of housing densities where retaliatory killing risk is high ($w_{rk}(x) > 1$). Rug plots in lighter blue show housing densities of used daytime points, and darker blue show used nighttime points. In both panels, shaded areas around curves are ±1 SE.

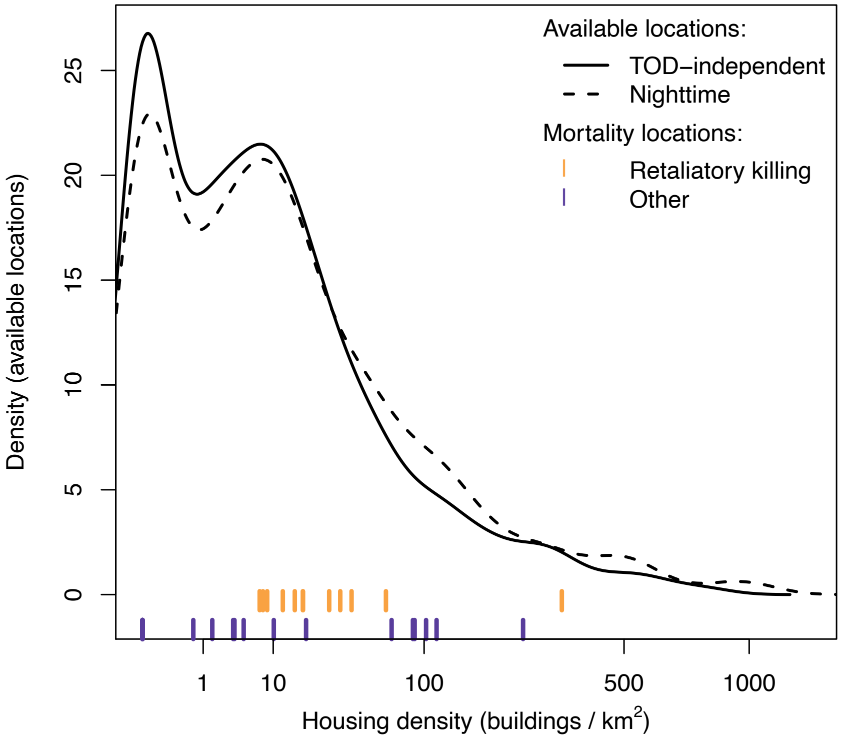

Figure 2.2. Distribution of locations of retaliatory killings and other mortalities for collared pumas across the housing density gradient (rug plots). Lines show the distribution of housing density at available locations, with time allocation controlled for using time-of-day-independent (solid) and nighttime-only (dashed) habitat selection.

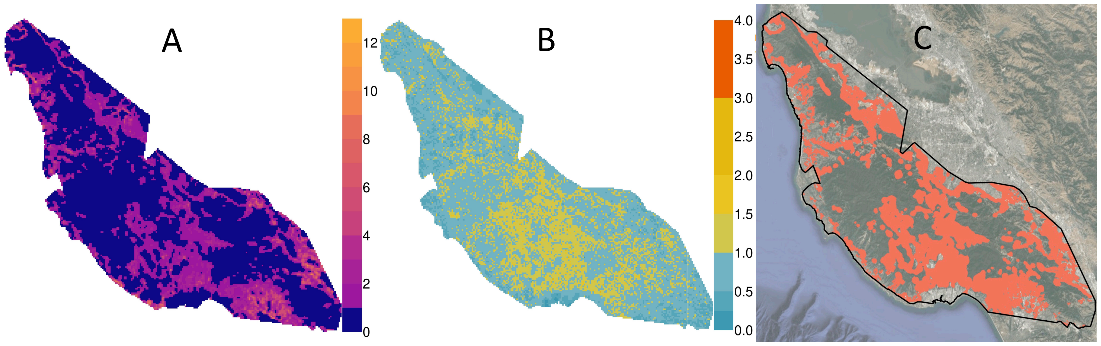

Figure 2.3. Maps showing **(A)** relative risk of retaliatory killing ($w_{rk}(\boldsymbol{x})$), **(B)** relative probability of nighttime selection ($w_{mvt}(\boldsymbol{x})$), and **(C)** ecological trap habitat across the SCM study area. In **(A)** values >1 indicate higher retaliatory killing risk than would occur at random and in **(B)** values >1 indicate selection. Trap habitats in **(C)** are defined as areas where relative risk of retaliatory killing >1 and relative probability of nighttime movement >1, and are plotted in orange. The study area boundary is outlined in black, and satellite imagery is provided by Google.

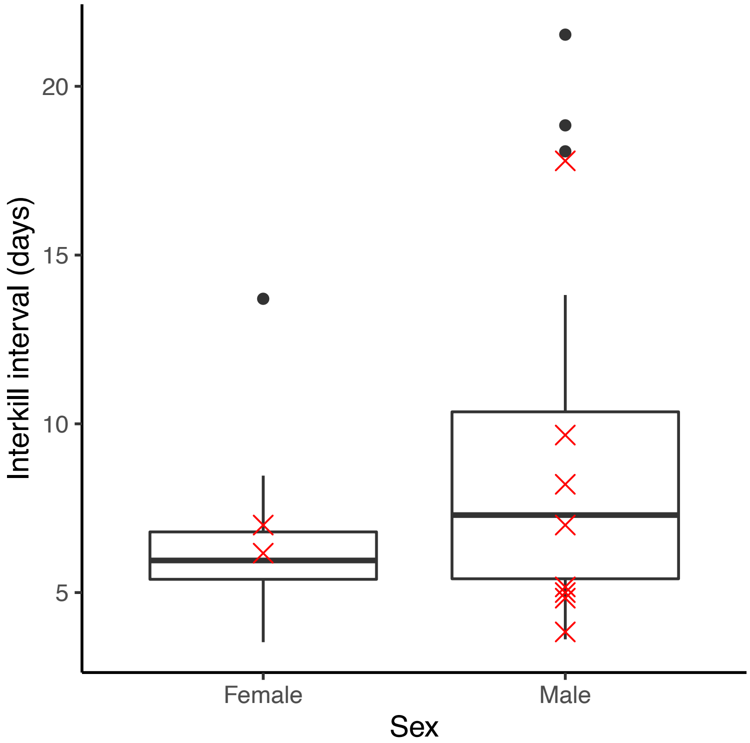

Figure 2.4. Box plots showing the inter-kill intervals for all collared pumas. Red points are time since last predicted kill for collared pumas killed after consuming livestock.

Appendix 2.S1 – Assigning cover class to vegetation categories

Cover classes (0 or 1) were assigned to raster grid cells from California GAP data. The following vegetative classes were considered cover (coded 1): Forest and woodland systems (CN Level 1); Developed (CN Level 2, within Human Use Land); Chaparral, Deciduous dominated savanna and glade, and Conifer dominated savanna (CN Level 2, within Shrubland, steppe and savanna systems; all Floodplain and riparian (CN Level 1, within Riparian and wetland systems) except for Inter-Mountain Basins Greasewood Flat and North American Warm Desert Wash (CN Level 3); and Harvested Forest - Northwestern Conifer Regeneration (CN Level 3), Recently burned forest (CN Level 3), , (CN Level 3), Recently burned forest > Introduced Upland Vegetation - Treed (CN Level 3), Introduced Riparian and Wetland Vegetation (CN Level 3).

Appendix 2.S2 – Estimating kill rates and interkill intervals

GPS locations were aggregated into clusters using a custom cluster algorithm described in (Wilmers et al. 2013, Smith et al. 2015). Characteristics of clusters, including whether the cluster lasted for >1 day, the number of nighttime locations, and the harmonic mean distance of points to cluster center, were then used to predict whether a cluster was a kill site as described in Smith et al. (2015). We calculated mean puma kill rates in the SCM for all animals whose collars recorded continuous data for > 21 days by dividing the number of predicted kills by total time monitored. We calculated inter-kill intervals as the reciprocal of kill rate. We next quantified time since last predicted kill for each depredation event for which 4-hour GPS data was recorded prior to death (N = 10). Pumas were shot at least one day after killing livestock, so we defined the date of livestock kill as one day before the puma's date of death. Time since last predicted kill was then estimated by comparing the time of livestock kill to the start date of the prior predicted kill.

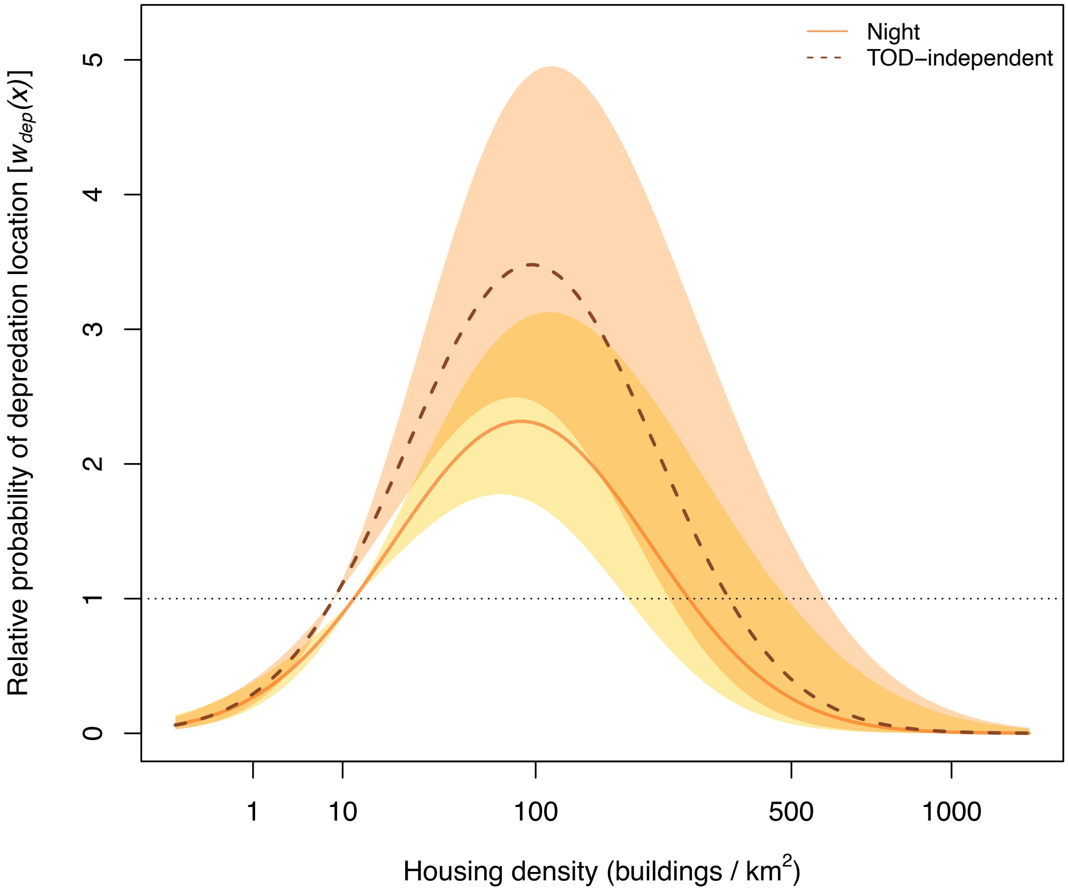

Figure 2.S1. Predicted relative probability of retaliatory killing using two time allocation controls. The orange solid line shows relative risk when the nighttime-specific time allocation control was used, and the dashed red line shows relative risk when the time-of-day-independent control was used. Dashed areas are ±1 SE.

Table 2.S1. Coefficient estimates for the best-supported puma movement SSF (model M4). Standard errors are noted in parentheses and asterisks indicate p-values <0.01.

Covariate	**Coefficient**
Slope	-0.088* (0.004)
TPI	0.158* (0.003)
Slope*TPI	-0.075* (0.003)
Cover	0.170* (0.005)
Distance to river	-0.023 (0.007)
Step distance	0.013 (0.003)
Directional persistence	0.216* (0.004)
HD:Day	-0.462* (0.011)
HD:Night	0.206* (0.009)
HD^2:Day	-0.100* (0.006)
HD^2:Night	-0.084* (0.004)

CHAPTER 3

Habitat fragmentation reduces puma survival and drives source-sink dynamics

Abstract

Conservation of large carnivore populations in fragmented, human-dominated landscapes is essential to their long-term persistence, yet living in human-dominated landscapes comes with both direct and indirect costs, including direct anthropogenic mortality and sublethal behavioral and energetic costs. How these costs impact individual fitness and population dynamics are not fully understood, due in part to the difficulty in collecting long-term demographic data for these species. Rigorous understanding of how habitat features impact population dynamics is essential for species conservation, especially in mixed-use landscapes where source-sink dynamics may be at play. Here, we analyzed a 11-year dataset on puma (*Puma concolor*) space use, mortality, and reproduction in the Santa Cruz Mountains, CA, to quantify how living in a fragmented landscape impacts individual survival and population dynamics. Long-term exposure to housing density drove mortality risk, resulting in a 20-point reduction in annual survival for individuals in exurban versus remote areas. This relationship was stronger for females, who experience higher energetic costs in more developed areas compared to males, suggesting that these costs scale up over time to negatively impact survival. While overall population growth appears stable, reduced female survival in more developed areas drove source-sink dynamics across the study area, with 42.1% of the study area exhibiting estimated population growth

rates < 1. These results underscore the importance of conserving high-quality source habitat within the Santa Cruz Mountains to support long-term population persistence. Habitat selection is often used as a proxy for habitat quality, and we also assessed whether puma habitat selection predicted true habitat quality as defined by expected population growth rate. Habitat selection modeled for daytime behavior and with the same spatial sensitivity to development as seen during reproduction best predicted true habitat quality, but habitat selection that did not account for time of day performed poorly as a proxy. Together, these results illuminate the individual and population consequences of indirect behavioral costs that large carnivores experience in human-dominated landscapes and highlight the importance of quantifying and considering source-sink dynamics in these places. As these costs are widespread across large carnivore taxa, these results can inform their conservation in similar systems.

Introduction

Effective species conservation relies on an accurate understanding of habitat quality. Habitat quality is most rigorously and reliably quantified by linking habitat features to individual fitness and population dynamics through some demographic process, such as survival or reproduction (Van Horne 1983, Pulliam 2000, Mosser et al. 2009). When habitat quality is not defined via its relationship to fitness, for example, through patterns of occupancy, distribution, or habitat selection, important ecological dynamics, such as source-sink dynamics, may be obscured (Pulliam and

Danielson 1991, Schlaepfer et al. 2002). However, for many species, quantifying the relationship between habitat features and individual fitness can be difficult due to the related issues of high data requirements, the necessity of long-term monitoring for long-lived species, and/or logistical constraints (Dias 1996, Johnson 2007) . These constraints and challenges are especially true for long-lived species, species that exist at low densities on the landscape, or species that are cryptic or otherwise difficult to study – characteristics that typify many species of conservation concern (Cardillo et al. 2005). A rigorous definition of habitat quality is particularly important in human-dominated landscapes, where species must coexist alongside humans and bear any associated costs of living alongside anthropogenic disturbance. However, despite the critical conservation importance of understanding the relationship between habitat features, animal space use, individual fitness, and population dynamics, these relationships have rarely been quantified for species in human-dominated environments.

Large carnivore decline is widespread across the globe and conservation of large carnivore populations outside of protected areas and in human-dominated landscapes is recognized as being essential for continued persistence of many of these species (Chapron et al. 2014, Ripple et al. 2014, Carter and Linnell 2016). However, living in human-dominated areas comes with a suite of direct and indirect costs. Direct anthropogenic mortality is very high for large carnivores in comparison to other taxa (Darimont et al. 2015), and is often elevated outside of protected areas due more lenient take regulations, and/or increased exposure to human hazards (e.g., Wolfe et al. 2015). Large carnivores tend to respond to humans as though they are predators, altering their movement, habitat selection, and feeding behavior to avoid the risk of encountering people (Wilmers et al. 2013, Oriol-Cotterill et al. 2015a, Suraci et al. 2019b, 2019a). These behavioral responses can carry substantial costs, including increased energetic expenditure during movement and reduced feeding times at kills (Smith et al. 2015, 2017, Nickel et al. 2021). Thus, large carnivores in human-dominated areas experience both 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. It is not known, however, whether or to what degree these indirect costs may scale up over time to impact individual survival.

In turn, impacts on survival likely have consequences for population dynamics, since adult survival most strongly determines individual fitness and population growth for many large carnivore species (Heppell et al. 2000, Beckmann and Lackey 2008, Robinson et al. 2014, Benson et al. 2016a). Understanding how habitat features are related to survival will thus enable a rigorous quantification 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 with despotic distributions 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 (Horne 1983, Pulliam and Danielson 1991, Dias 1996, O'Neil et al. 2020). Identifying source-sink dynamics is of central conservation importance, as sources must be protected and conserved in order to maintain long-term population viability (Dias 1996).

Quantifying the relationship between habitat features and habitat quality for a population of large carnivore in a human-dominated environment can also shed light on when other, more easily obtainable metrics may be appropriate proxies for habitat quality (Stephens et al. 2015). For example, 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 true habitat quality. First, following rapid environmental change, formerly adaptive behaviors may become maladaptive, resulting in ecological traps (Robertson and Hutto 2006, Robertson et al. 2013). Second, density is expected to reflect habitat quality when animals are distributed under the ideal free distribution, but territorial behavior often results in animals being distributed according to other distributions such as the despotic distribution (Mosser et al. 2009, O'Neil et al. 2020). Under both of these circumstances, habitat selection is expected to be an incomplete and potentially even misleading predictor of true habitat quality. Additionally, habitat selection is often dynamic and may change with time of day and/or behavioral state of the animal. Animals often partition their activity across the course of the day to minimize overlap with human activity, often exhibiting stronger avoidance of human development during the daytime, (Kronfeld-Schor and Dayan 2003, Oriol-Cotterill et al. 2015b, Suraci et al. 2019b) and also avoid or select features differently depending on behavior (Wilmers et al. 2013, Abrahms et al. 2015). It is thus likely that habitat selection patterns during certain times or certain behaviors will better predict true habitat quality, and understanding to what degree habitat selection reflects habitat quality could shed light on whether and how habitat selection be used as an effective proxy, despite its limitations.

The puma (*Puma concolor*) population in the Santa Cruz Mountains, CA, presents an opportunity to quantify the impacts of exposure to human development on large carnivore survival and population dynamics. The Santa Cruz Mountains consists of a mosaic of different levels of human use and residential development, including a considerable amount of exurban sprawl, which is the fastest growing land use type in the western U.S. (Theobald 2005). Pumas in this area experience direct anthropogenic mortality, primarily due to retaliatory killings following livestock loss as well as vehicle strikes (Nisi et al. Chapter 2). 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 (Wilmers et al. 2013, Smith et al. 2015, 2017, Nickel et al. 2021). The degree to which pumas exhibit these responses also varies between individuals, allowing us to investigate how individual variation in risk avoidance behavior is related to mortality risk.

Here, we analyzed 11 years of tracking and mortality data for 65 adult and subadult pumas to quantify the survival consequences of habitat fragmentation, implications for population dynamics and source-sink dynamics, and whether and how habitat selection reflects habitat quality in terms of population growth. We predicted that both long- and short-term exposure to housing density would be related to higher risk of mortality. We also investigate how puma behavior mediates the relationship between habitat fragmentation and mortality risk, hypothesizing that animals who exhibit stronger avoidance of human features will experience less mortality risk. We then parameterized a matrix population model to examine how the population growth rate varies across the landscape, as mediated by the relationship between adult survival and exposure to housing density. Here we predicted that source-sink dynamics, which occur when some areas support positive growth while others cannot, will be evident, with areas of higher housing density being population sinks. Finally, we compared habitat quality as defined by estimated population growth rate to patterns of habitat selection to ask whether and which habitat selection metric reflects true habitat quality. Here, we predicted that daytime behavior will more accurately reflect fitness compared to nighttime or time-of-day-independent habitat selection behavior.

Methods

Study System: The Santa Cruz Mountains (SCM) was a 2800 km^2 area located in California's Central Coast. 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 variegated environment ranging from urban, suburban and exurban areas to large tracts of intact, undeveloped habitat.

Puma capture and monitoring

We captured pumas using trained hounds or box traps, and we anaesthetized pumas with Telazol (Animal Use Protocol WilmC1402 issued by UC Santa Cruz to C. C. Wilmers). We fit pumas with GPS collars that recorded locations once every 4 hours. Collars were produced by Vectronics (Vectronics Aerospace GPS Plus, Berlin, Germany) as well as one Lotek collar (Lotek, Seattle, WA, USA).

Mortality events of collared pumas were investigated 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 24 hours of a collar being stationary); or 3) UHF download of GPS data indicating that a collar had been in the same spot for at least several 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".

For all mortality events, we define estimated time of death to be the first 4-hour GPS point recorded at the location of mortality. Two collars were damaged on impact during vehicle strike and did not record new locations after death, so we defined time of death as the last GPS point that the collar recorded (the last point before death). Since these collars were both on 4-hour schedules, their recorded time of death is <4 hours from their actual time of death.

Survival modeling:

We used a Cox Proportional Hazards model (Cox 1972) to relate mortality risk to spatial, behavioral, 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 (Pollock et al. 1989, Fieberg and DelGuidice 2009). For this study, we used an annual recurrent design (Fieberg and DelGuidice 2009), which allows the baseline hazard to vary over the course of the year.

The Cox Proportional Hazards model assumes that the instantaneous risk of mortality (hazard ($h_i(t)$)) for each individual i at time t is related to both the baseline hazard at time *t* ($h_0(t)$), which all animals experience, as well as covariate effects experienced by that individual. This relationship takes the form:

$$h_i(t) = h_0(t)e^{\boldsymbol{x}_i\boldsymbol{\beta}}$$

in which $\boldsymbol{x}_i$ is a vector of covariates associated with individual *i* at time *t*, $\boldsymbol{\beta}$ is a vector of coefficients that describe the effects of each covariate $\boldsymbol{x}$ on mortality risk. Because all individuals monitored at the same time experience the same baseline hazard, the hazards ratio between any two individuals under observation is constant over time. For a series of event times for mortalities from *m* monitored animals (t_1 through t_m), this property allows for covariate effects ($\boldsymbol{\beta}$) to be estimated through the following partial likelihood function (Cox 1972, Hosmer and Lemeshow 1999):

$$PL(\boldsymbol{\beta}) = \prod_{i=1}^{m} \frac{e^{\boldsymbol{x}_i\boldsymbol{\beta}}}{\sum_{j \in R_i} e^{\boldsymbol{x}_j\boldsymbol{\beta}}}$$

This partial likelihood function compares the instantaneous hazard experienced by each individual mortality event (*i* in 1 through *m)* with the hazard experienced by animals under observation at time t_i (or in the risk set, R_i) in a matched-case framework.

Here, we are interested in how exposure to housing density impacts mortality risk. As such, for each time of death t_i, we calculated housing density experienced 2 and 45 days prior to t_i for all animals in the risk set at t_i and coded start and stop times accordingly. For each death, animals in the risk set "entered" at $t_i - 1$ and "exited" at $t_i + 1$, while the animal that died "entered" at $t_i - 1$ and "exited" at t_i. Because the partial likelihood function only incorporates information from times of death, this approach allowed us to directly compare the exposure of animals in the risk set at each t_i to the animal that died without losing any information (Fieberg and DelGuidice 2009). The alternative approach would have been to regularly update exposure at regular intervals (e.g., each month), but this would result in individuals dying early- or mid-month having a different time scale of exposure than animals in the risk set. We used the *survival* package (Therneau 2015) to conduct all survival analyses.

Spatial and behavioral covariates:

Residential housing is the primary human use in the SCM, so we calculated housing density as a metric of exposure to anthropogenic impact. Exposure to housing is scale-dependent metric, and pumas in our area have been shown to respond to housing density both at longer and shorter temporal scales (Nickel et al. 2021), so we considered both short-term and long-term housing exposure. For long-term exposure, we calculated housing density (buildings/km^2) calculated within an animal's home range (number of buildings divided by home range area) calculated over the 45 days prior to each event time. We used semivariance analysis to confirm that the 45-day period was sufficient to encompass several home-range-crossing times for range-resident individuals (Fleming et al. 2014, Calabrese et al. 2016; Appendix 3.1). We calculated short-term exposure taking the mean housing kernel density over an animal's movement path 2 days prior to each event time.

We also considered different spatial scales of both short- and long-term housing exposure. For long-term exposure, we considered different home range metrics. We calculated housing density in 50% (core) and 95% (total) minimum convex polygons (MCPs) and adaptive local convex hulls (aLoCoHs) (Getz et al. 2007). MCPs tend to include more unused space by an individual, reflecting the broader landscape in which an animal was spending time, while aLoCoHs are more tightly constrained around the areas an individual actually used, minimizing Type 1 and Type 2 error to a greater degree than other estimator types (Getz et al. 2007, Laforge et al. 2016). MCPs were fit using the *adehabitatHR* package (Calenge 2006), and aLoCoHs using the *tlocoh* package (Lyons et al. 2013). For short-term exposure, we calculated housing density with different kernel extents: 150m and 500m.

Behavioral variability in habitat selection was quantified by step selection functions (SSFs) (Fortin et al. 2005). Step selection functions are a type of resource selection function, in which used points are compared to available points to estimate the relative probability of use through the exponential function, $w(\boldsymbol{x}) = \exp(\boldsymbol{\beta x})$, with $\boldsymbol{x}$ a vector of spatial covariates and coefficients ($\boldsymbol{\beta}$) (Manly et al. 2002). For step selection functions, available points are drawn via simulated steps and paired with the corresponding used point, and covariate effects ($\boldsymbol{\beta}$) are estimated via matched-case logistic regression (Fortin et al. 2005, Forester et al. 2009, Thurfjell et al. 2014). Here, 4-hour GPS locations that were > 20m from the previous point were used movement locations. Available locations were drawn via simulated steps, with step distances drawn from empirical distributions for other animals of the same sex, excluding the focal individual (Fortin et al. 2005) and turning angles drawn from a circular uniform distribution.

To describe behavioral variability in habitat selection for each individual over time, separate SSFs were fit for each individual for each 45-day period to each time of death. We included covariates that had been identified as important drivers of habitat selection in previous analyses (Wilmers et al. 2013, Nisi et al. Chapter 2), including housing density (500m kernel; cube root transformed), absolute value of topographic position index (TPI), topographic slope, the interaction between slope and TPI, step distance (log transformed), and directional persistence (cos[θ_t - θ_{t-1}], with θ_t and θ_{t-1} being the angles from the x-axis of the two previous steps; Duchesne et al. 2015, Nicosia et al. 2017). All covariates were rasterized at 30m resolution and were centered and scaled across all data (rather than within each model's dataset) to ensure that coefficient estimates were directly comparable across individuals and time periods. SSFs were fit using the *clogit* function in the *survival* package (Therneau 2015). The coefficient estimate associated with housing density (β_h) from each individual's SSF to be the degree to which that animal was selecting for or avoiding housing density during that 45-day interval. Thus, we included β_h as a predictor in Cox proportional-hazards models to assess whether the strength of selection or avoidance of housing impacts mortality risk.

Model selection

For selecting best spatial and temporal scale of housing density, we competed univariate models that included each housing density term. We used Akaike's Information Criterion corrected for small sample size (AICc; Burnham and Anderson

2002) to identify supported models, with models with ΔAICc < 2 considered well-supported. After selecting the best-supported housing density covariate, we considered models that included sex, behavioral variability, and interaction terms. Because of low sample size, no models with > 2 covariates were considered. All models included a cluster term by individual to allow for robust standard error calculation.

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:

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

Where S_k, S_j, and S_a are stage-specific survival rates for kittens, juveniles, and adults, respectively, L is mean litter size, and b is mean birth rate (number of births per year).

Vital rates were calculated from puma monitoring data. The birth rate was calculated by dividing the number of denning events by the amount of time females were wearing collars recording 4-hour GPS data. Denning events were identified visually by periods of time lasting longer than three weeks when female pumas localize to one cluster of points and make repeated excursions and returns to multiple different neighboring locations.

We investigated a subset of these denning events, making field visits to count kittens at two weeks and to collar kittens at 4 weeks. Since survival monitoring started at 4 weeks, we calculated litter size as the average number of kittens alive at the 4-week visit. We assumed a .5 sex ratio. 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.

We estimated S_k and S_j by fitting a Cox proportional hazards model with an interaction between sex and age class and calculating estimated survival rates using the *survfit* function. For S_a, we used the best-fit model that included an interaction between sex and housing density to calculate estimated survival rates at different housing densities.

We then projected this model across the study area. We created a raster of density of building points by aggregating building locations at a 1 km^2 resolution, which corresponded to the mean size of a female 50% aLoCoH calculated with 45 days of GPS data. For grid cells that had a housing density within the range of the housing densities within 50% aLoCoHs (358 houses/km^2), we calculated estimated survival rates and estimated λ. Confidence intervals for λ were calculated from parameterizing a matrix with the upper and lower 95% CI's of estimated female survival in that grid cell.

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 through step selection functions (SSFs) and then quantified the relationship between predicted relative probability of use and whether $\lambda > 1$ using logistic regression. To model habitat selection, we fit SSFs as described above but for the entire population rather than by individuals. We used generalized estimating equations (GEE) to account for temporal autocorrelation and estimate robust standard error (Prima et al. 2017). From previous work (Nisi et al. Chapter 2), the relationship between relative probability of selection and housing density is quadratic and conditional on time of day (day/night). We thus fit a model containing linear and quadratic housing density terms both interacted with day/night alongside other habitat covariates that have been shown to be important for puma movement: slope, topographic position, distance to nearest perennial stream, and percent vegetation cover. We also included step length and directional persistence as predictors, which is recommended to account for the movement process (Forrester et al. 2015, Nicosia et al. 2017). We also fit models with no time-of-day interaction with housing density. Finally, to examine how spatial grain of measuring housing density mediates this relationship, we considered these models with housing density calculated with a 150m and 500m kernels. The 150m kernel is most informative for movement behavior while larger kernels (500m) more strongly inform reproductive behaviors (Wilmers et al. 2013). Thus, we had 4 movement models: TOD-dependent and TOD-independent responses to housing density at the 150m scale (M1 and M2) and TOD-dependent and TOD-independent responses to housing density at the 500m scale (M3 and M4).

From these models, we calculated the relative probability of selection (RSS), relative to mean habitat conditions, for each 1 km^2 grid cell. For time-of-day-dependent models, RSS was calculated during the day and during the night. We next used logistic regression to relate whether or not a grid cell was expected to support population growth or decline ($\lambda > 1$ versus $\lambda < 1$) to its RSS (combined, day, and night for each spatial grain of housing density). We conducted model selection using ΔAIC and calculated area under the receiver operator characteristic curve to assess goodness of fit. All analyses were conducted in R version 3.6.0.

Results

We observed 33 mortality events from the 65 adult and subadult pumas monitored from 3/11/2009-10/19/2020. We also observed 14 deaths of the 42 kittens collared and monitored between 6/6/2009 and 3/4/2020. Sex- and age-specific survival rates are presented in Table 1. 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 births/year. The mean observed litter size was 2.24 kittens.

Long-term exposure to housing density drove mortality risk for pumas in the Santa Cruz Mountains. The best spatial scale for predicting mortality risk was housing density calculated in the 50% aLoCoH home range (Table 3.2). Short-term exposure to housing (over 2 days prior to death) was not informative, performing worse than the null model and violating the proportional-hazards assumption.

Sex mediated the relationship between housing density and mortality risk. The model interacting sex with housing density received the most support, and the only other model that received support was an additive model with sex and housing density (ΔAIC = 1.84). Females living in more developed areas exhibiting heightened risk compared to females in more remote areas, but males exhibited similar risk across the gradient of housing density (Fig. 3.1). 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 an 18.8-point reduction in annual survival relative to females in remote areas (0 buildings/km^2; Fig. 3.1). Finally, pumas exhibited variation in habitat selection behavior relative to housing density, with selection responses ranging from strong avoidance to selection (range of β_h: -3.27 to 1.22). However, this behavioral variability among animals in response to housing did not predict mortality risk, with all models containing behavior terms receiving no support (ΔAICc > 2). Adult survival was the most elastic vital rate with an elasticity of 0.581, and maternity, kitten survival, and juvenile survival all had elasticity values of 0.140.

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 Fig. 2.1, the expected population growth rate is 1.113 (95% CI: 1.040, 1.181) in remote areas (0 buildings/km^2), 1.037 (95% CI: 0.952, 1.135) in rural areas (5 buildings/km^2), and 0.945 (95% CI: 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 Santa Cruz Mountains, with 57.9% of the study area exhibiting $\lambda \geq 1$ and 42.1% exhibiting $\lambda < 1$ (including 7.1% of the study area for which housing densities were above the maximum observed housing density for a core home range; Fig. 3.2). The expected λ when adult female puma survival is set at its mean for this population (0.826, 95% CI: 0.742, 0.921) was 1.025 (95% CI: 0.950, 1.110).

Daytime habitat selection behavior was the best predictor of population growth rate (Table 3). Time-of-day-independent habitat selection performed poorly, and nighttime behavior was inversely related to population growth rate (Fig. 3.3). Additionally, habitat selection modeled with housing density calculated at the scale at which it more strongly influences reproductive behaviors (500m) better predicted population growth compared to when habitat selection was modeled at the scale that housing density impacts movement behaviors (150m).

Discussion

Long-term exposure to housing density led to reduced 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 their more remote counterparts. In turn, reduced survival rates associated with exposure to human development produced sink areas that exhibited negative population growth rates across large areas of the Santa Cruz Mountains.

Long-term exposure to housing density drove mortality risk for female pumas, but not males, which likely reflected the difference in behavioral and energetic costs that male and female pumas experience in this landscape. Previous research from this system has documented sex-specific indirect behavioral and energetic costs, with female pumas (but not males) exhibiting higher deer kill rates in areas of higher housing density (Smith et al. 2015). These higher female kill rates in more developed areas are driven by earlier carcass abandonment and less complete consumption (Smith et al. 2017) and presents significant energetic costs for females, since hunting and killing deer requires substantial energetic expenditure (Williams et al. 2014). Our finding that female pumas experienced increased mortality risk in more developed areas dovetails with this previous finding that female pumas experience much higher indirect costs of living closer to people and suggests that these indirect behavioral and energetic costs scale up over the long term to negatively impact individual fitness for female pumas. Additionally, the poor performance of short-term housing exposure relative to long-term exposure suggests that mortality risk was driven by chronic exposure to human development and its associated indirect costs. While previous work has described energetic costs associated with living near humans (Wang et al. 2017, Nickel et al. 2021), these costs have not been linked to components of individual fitness or population-level processes. Our study suggests that the energetic costs associated with living alongside people can, over time, negatively impact individual survival for females. Pumas experience energetic costs associated with avoiding humans during locomotion, which scale up to constrain long-term territory size for males (Nickel et al. 2021). Reduced home range size in more developed areas may confer fitness losses to males if they come into contact with fewer females or secure fewer breeding opportunities – however, these results suggest that these locomotory energetic costs do not negative survival outcomes for male pumas.

This reduction in female survival drove source-sink dynamics across our study area. Remote and wildland areas were associated with survival rates that result in positive population growth, while rural and exurban areas contain development that caused a reduction in survival below that which supports a stable population over time. While the overall population growth rate was stable (1.025), this indicates that further development of the Santa Cruz Mountains has the potential to expand sink habitat and threaten puma population viability, in addition to reducing habitat connectivity (Smith et al. 2019b). Low-density exurban development and rural sprawl are the leading cause of land-use change in the US and often surrounds or is adjacent to protected areas (Theobald 2001, 2005). Our work underscores that in addition to the many other environmental issues associated with exurban sprawl (Radeloff et al.

2005a, Wilson and Chakraborty 2013), low-level exurban and rural development has substantial negative consequences for the population viability of large carnivores.

Furthermore, characterizing the relationship between habitat features – namely housing density – and individual fitness allowed us to rigorously quantify habitat quality for an urban-adjacent large carnivore population, and investigate how other metrics of habitat quality that require less data but may be less reliable compare to more rigorous but less accessible metrics. Puma habitat selection differed between day and night, but only daytime behavior reflected habitat quality in terms of fitness and population growth. While daytime habitat selection behavior was directly predictive of population status, nighttime behavior was inversely related to whether an area could support positive population growth because at night pumas select areas of intermediate housing density (Nisi et al. Chapter 2). Because of the opposing responses to housing density between day and night, when time of day was not considered (combined habitat selection in Fig. 3.3), habitat selection behavior was only loosely related to habitat quality. This underscores the necessity of relating habitat characteristics directly to fitness metrics rather than inferring habitat quality by presence, use, or selection alone (Mosser et al. 2009, Gaillard et al. 2010) . 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. 2019b). Our results suggest that the increased sensitivity and spatial partitioning that animals exhibit during the daytime better reflects habitat quality in terms of fitness costs relative to their nighttime behavior, and that temporal partitioning can decouple the apparent relationship between habitat selection and habitat quality. 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 habitat quality for species that exhibit temporal partitioning of space and activity related to risk from humans.

Additionally, habitat selection models fit with housing density calculated at a broader scale (500m) better predicted population growth compared to those fit with finer-scale housing density (150m), even though finer-scale housing density performed better in predicting habitat selection when pumas move and feed (Wilmers et al. 2013). The broader scale corresponds to the scale at which pumas respond to housing during reproduction (Wilmers et al. 2013), suggesting that the scale of selection associated with sensitive behaviors that carry high fitness costs, such as reproduction, may better reflect true habitat quality compared to selection patterns at finer scales associated with movement and feeding. Broadly, our results suggest that for adaptable animals in human-dominated environments, the most predictive behaviors – such as daytime movement rather than nighttime movement, and at scales representative of reproductive versus movement behaviors – likely best reflect habitat quality in terms of population dynamics.

Despite variation in habitat selection behavior among individuals, this variation did not predict mortality risk, which could be due to several factors. First, previous research has shown a mismatch between avoidance behavior and risk of retaliatory killing, meaning that puma behavior is not effective at mitigating this mortality source (Nisi et al, Chapter 2), and this mismatch likely contributed to this relationship. Additionally, it is possible that selection of home range locations (2nd-order selection; Johnson 1980) more strongly constrains and determines individual fitness relative to selection of locations within home ranges (3rd-order selection), which was what we modeled here. In a territorial species like the puma, exclusion of conspecifics from home ranges results in deviation from the ideal free distribution whereby animals are evenly spaced out across a gradient of habitat quality (O'Neil et al. 2020). In this case, pumas occupying high-quality, remote habitat exclude others from doing so. Since long-term exposure to housing density, calculated over the time it takes to cross a home range multiple times, drove mortality risk, this suggests that locations of home ranges, rather than behavior within home ranges, is the most important factor in determining individual fitness. Put another way, where a home range is located matters most, and behaviors that pumas exhibit to further mitigate their exposure to humans, including avoiding housing density, are not sufficient to overcome the long-term energetic costs associated with living in these areas.

Compared with other puma populations, survival rates in this system are higher than those seen in heavily hunted and more urban-adjacent populations, but lower than those remote and unhunted areas. Survival rates observed here are most similar to other semi-protected populations with minimal hunting (Wolfe et al. 2015), and as well as to those found in Colorado's Front Range, which contains similar levels of exurban development (Moss et al. 2016). Populations that were more fully protected exhibited higher survival rates (Logan and Sweanor 2001b, Ruth et al. 2011), and as expected, heavily hunted populations exhibit much lower survival rates than this population (Robinson et al. 2014), although female rates observed here are similar to rates observed in some hunted populations, especially for females with exurban home ranges (Lambert et al. 2006, Robinson et al. 2008). Finally, survival rates in the SCM are much higher than what is seen in the Santa Ana and Eastern Peninsular Ranges, which are two non-hunted populations in southern California that experience substantial anthropogenic mortality through vehicle strikes and depredation mortalities, respectively (Vickers et al. 2015), but are lower than survival rates in the Santa Monica Mountains (Benson et al. 2016a).

While our study only modeled the relationship between survival and housing density, previous research suggests that puma reproduction also decreases with increasing development, which would exacerbate the negative relationship between development and population growth rate that we document here. While we lack sufficient data to quantify the relationship between reproductive output and housing, pumas strongly avoid human development when selecting den site locations (Wilmers et al. 2013, Yovovich et al. 2020). Additionally, as adult survival was the most elastic vital rate in this analysis and for other puma populations (Robinson et al. 2014, Benson et al. 2016a), we expect that the survival impacts associated with human development would be stronger than any reproduction-mediated impacts between development and puma population growth.

Overall, this work emphasizes the cryptic precarity of a population of large carnivores living within a developed and developing environment: while currently stable, further development could threaten long-term viability for pumas in the Santa Cruz Mountains by expanding population sinks and reducing population sources. Exurban development is a common and growing component of land use change in the western U.S. (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 increasingly recognized as essential for global conservation efforts (Carter and Linnell 2016), but for this to be possible, we must understand how anthropogenic features impact population vital rates such as survival, 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 alongside humans within a matrix of low-density residential development, they experience costs in doing so that reduce their individual fitness and cascade on to have population-level consequences. Because exurban sprawl is a widespread across the US, our research sheds light on mechanisms by which other large carnivore populations in many systems may be impacted by human development.

Table 3.1. Estimated annual survival rates for all sex and age classes.

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

Table 3.2. Univariate models relating housing density to mortality risk at different spatial and temporal scales.

Temporal scale	Spatial scale	Coefficient estimate	SE	*p*	ΔAICc	PH Assumption
Long term (45 days)	50% aLoCoH	0.37	0.17	0.034	0.00	Meets
	95% MCP	0.36	0.18	0.042	0.10	Meets
	50% MCP	0.34	0.17	0.052	0.85	Meets
	95% aLoCoH	0.26	0.19	0.157	2.33	Meets
Null	Null				2.57	
Short term (2 days)	150m kernel	0.06	0.25	0.814	4.60	Violates
	500m kernel	0.05	0.24	0.836	4.63	Violates

Table 3.3. Model selection for logistic models relating population status (growth or decline) to habitat selection (RSS).

Housing density	Time of day	ΔAIC
500m	Combined	1050242.46
	Night	671089.44
	Day	0.00
150m	Combined	1014797.64
	Night	1133893.71
	Day	460759.61

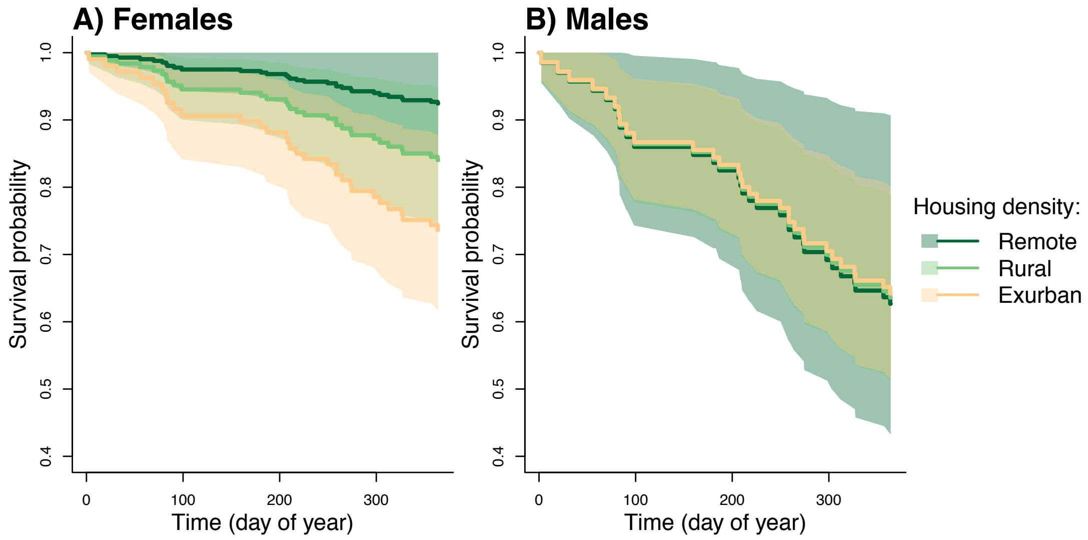

Figure 3.1. Predicted annual survival curves for (A) females and (B) males across 3 levels of housing density. Remote, rural, and exurban housing densities refer to 0, 5, and 25 buildings/km^2, respectively, in an individual's 50% aLoCoH home range. Shaded areas are 95% confidence intervals.

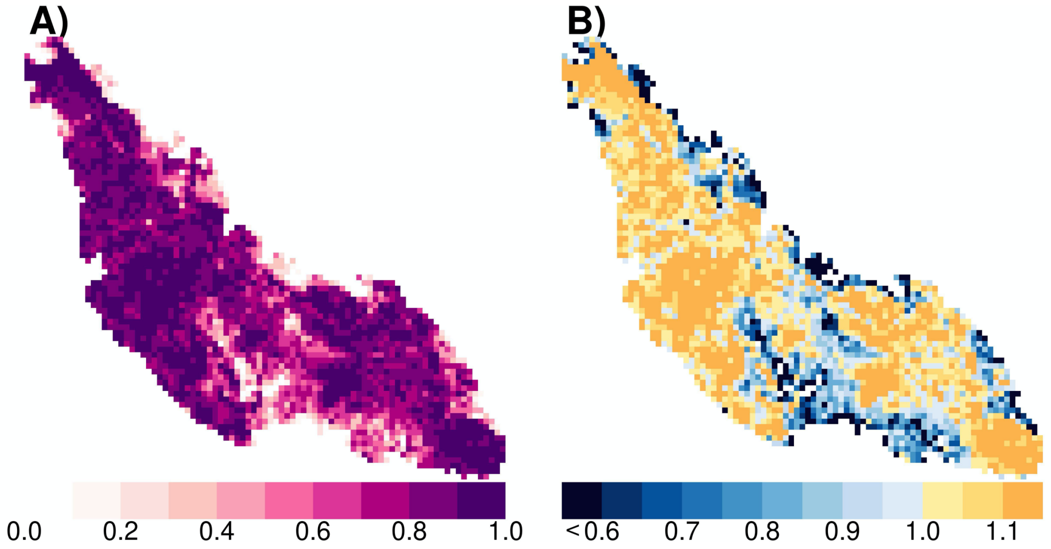

Figure 3.2. Projected (A) annual survival rates and (B) estimated population growth rate across the study area. In (B), the darkest blue color indicates all values < 0.60.

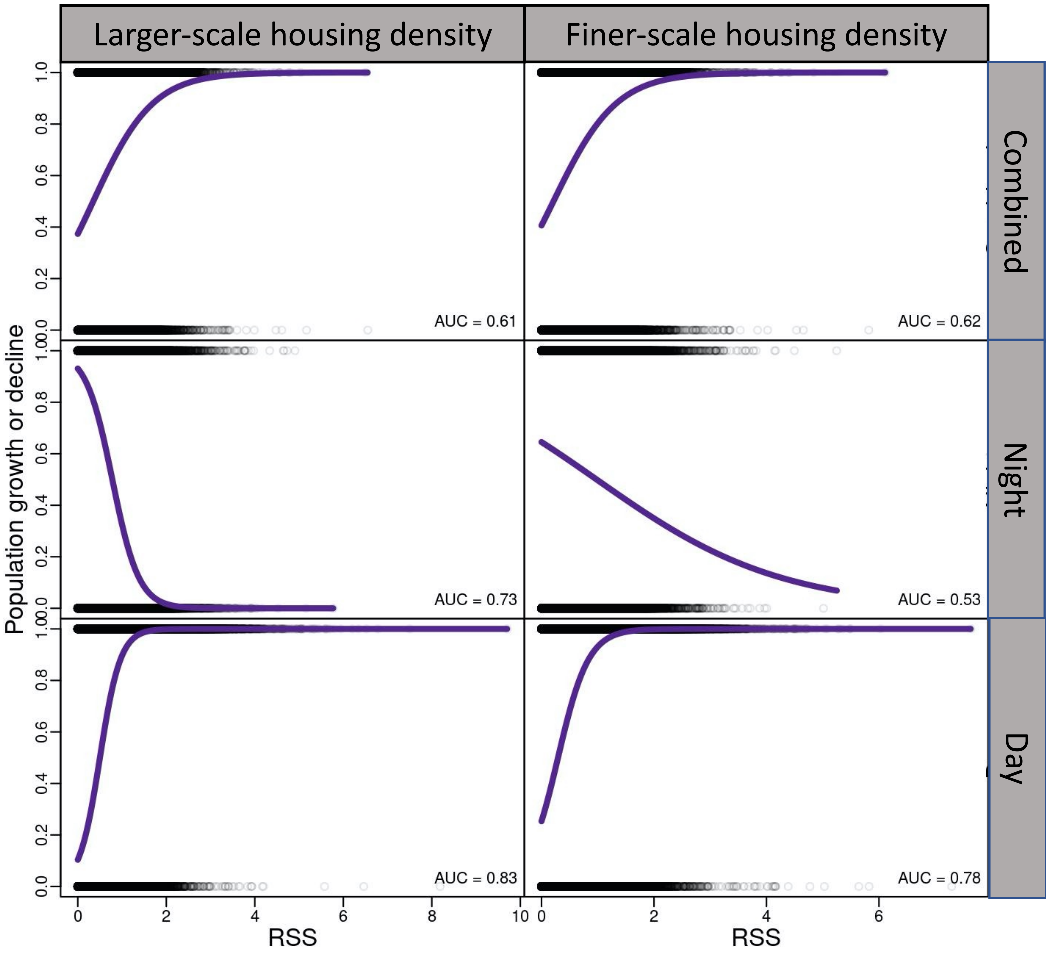

Figure 3.3. Relationship between predicted population status (growth [$\lambda > 1$] or decline [$\lambda < 1$]) and relative selection strength. Lefthand panels show results from models hta tinclude housing density calculated at a broader spatial grain (500m) and righthand panels show results from finer-grained (150m) housing density. Top panels show RSS results from time-of-day-independent models, and bottom two panels show nighttime- and daytime-specific RSS.

Appendix 3.1

Semivariance analysis

We used semivariance analysis to inform our choice of 45 day periods as long-term movement. For resident (non-dispersing) pumas that had >60 days of data, we used the *ctmm* package to fit semivariograms for each individual (Calabrese et al. 2016). Next, to characterize asymptotic behavior we fit Michaelis-Menten functions to semivariograms, which take the form $\frac{ax}{b+x}$, in which *a* represents the asymptotic semivariance (in km^2) and *b* is the half-saturation parameter, or half the time it takes to reach the asymptote. The long-term asymptote for semivariograms denotes long-term home-ranging behavior (Fleming et al. 2014, Calabrese et al. 2016), so the parameter *b* sheds light on how long it takes for an animal to traverse its home range. We calculated mean half-saturation values for resident animals, and considered mean home-range-crossing time to be twice the value of the mean half saturation value.

In our population, the mean half-saturation value was 7.80 days for females, 10.26 days for males, and 8.90 days overall. The long-term 45-day intervals thus represent >2 home range crossings for males and > 2.9 home range crossings for females.

CHAPTER 4

Wildfire vulnerability, carbon emissions, and wildlife habitat quality across the wildland-urban interface

Abstract

Land use patterns can either contribute to or mitigate many environmental issues – including climate change, wildfire risk, and habitat loss. Understanding whether and how these impacts align may shed light on land-use strategies that could confer benefits to multiple environmental problems. Here, we examined how wildfire risk, household carbon emissions, and wildlife habitat quality vary across land use categories, from sparsely developed areas to the wildland urban intermix and interface to dense, urban areas. These three environmental impacts largely aligned - sparsely developed areas were associated with high habitat quality, household emissions, and burn risk, with urban areas associated with lower levels of each. Intermix areas emerged as especially problematic, characterized by high burn risk and carbon emissions, and further development in these areas has the potential to drastically reduce habitat quality. Combined, these results highlight that low-density exurban development has negative impacts on climate change, wildfire vulnerability, and wildlife conservation, and suggest that urban infill could mitigate these three environmental impacts.

Introduction

Land use patterns related to residential development contribute to – and can either exacerbate or mitigate – key factors related to both climate change and biodiversity loss (Wilson and Chakraborty 2013, Venter et al. 2016, Jones et al. 2018, Radeloff et al. 2018). Land use decisions often come with environmental trade-offs, and in some cases, action to mitigate one environmental impact may have negative impacts on the other. For example, renewable energy infrastructure can cause mortality or habitat degradation for sensitive species (Northrup and Wittemyer 2013), and LEED-certified buildings may have higher rates of bird collisions due to higher glass area (Ocampo-Peñuela et al. 2016). In other cases, multiple environmental objectives may align and can be accomplished by the same action, for example, restoration projects may enhance both biodiversity and carbon sequestration (Dybala et al. 2019), and reducing vehicle miles traveled lowers carbon emissions while conferring co-benefits to air and water quality and reducing wildlife mortality (Fang and Volker 2017). Exurban sprawl is the fastest-growing land use category in the Western United States and is associated with myriad negative environmental impacts, including both climate change and biodiversity loss (Theobald 2005, Wilson and Chakraborty 2013). Here, we explore how three key environmental issues – greenhouse gas emissions, catastrophic wildfires, and habitat loss – are driven by land use type across rural to exurban to urban areas and whether there are alignments, synergies, or trade-offs between these impacts.

Residential development patterns strongly influence greenhouse gas emissions. Denser urban development enables wider transit options and better walkability, leading to lower automobile travel and reduced greenhouse gas emissions (Kahn 2000, Ewing and Cervero 2010) while also increasing efficiency in household energy use (Glaeser and Kahn 2010, Jones et al. 2018). Across land use types, this results in carbon footprints and greenhouse gas emissions that are highest in the suburbs and rural areas, and decline with increasing density in urban areas (Jones and Kammen 2014).

Climate change is causing an increase in frequency and severity of catastrophic wildfires across the Western U.S. and California specifically, leading to loss of life, widespread negative health impacts, and destruction of property and habitat (Abatzoglou and Williams 2016, Williams et al. 2019, Bowman et al. 2020). Wildfire risk and vulnerability are strongly driven by land use patterns and peak in the wildland-urban interface (WUI), where residential development abuts (interface WUI) or is interspersed within (intermix WUI) wildland vegetation (USDA and USDI 2001, Stewart et al. 2007). Compared to sparsely developed areas as well as denser urban areas, the wildland urban interface and intermix are most impacted by wildfire in terms of loss of life and property destruction and have the highest frequency of human-caused ignitions (Radeloff et al. 2005b, 2018). Despite the increasing danger that wildfire poses to these places (Holden et al. 2018, Goss et al. 2020), the WUI is rapidly expanding in the U.S. and California specifically, and is driven by housing expansion and development into wildland areas rather than changes in wildland vegetation patterns (Mann et al. 2014, Radeloff et al. 2018).

Habitat loss and fragmentation through conversion to development are key drivers of species decline and extinction (Newbold et al. 2015). Exurban development has negative impacts for wildlife habitat quality as it often converts remote, undisturbed areas to lower-quality, human-dominated spaces (Theobald et al. 1997, Burdett et al. 2010, Smith et al. 2019a). Large carnivore species are particularly vulnerable to this type of land use change and are at heightened risk of extinction and population declines due to their large area requirements, low population densities, and reliance on mobile and large-bodied prey (Crooks et al. 2011, Ripple et al. 2014). Because of these characteristics, many large carnivores can be considered an "umbrella species" whose protection can confer benefits to other co-occurring species with similar habitat suitability requirements (Di Minin et al. 2016, Thornton et al. 2016). Thus, understanding how exurban development impacts large carnivore habitat quality and pursuing planning strategies that conserve high-quality carnivore habitat likely will have cascading benefits to other species conservation.

Because these three environmental problems – greenhouse gas emissions, wildfire risk and vulnerability, and habitat destruction – are influenced by residential land use patterns, there is value in understanding the intersections between these issues and where new housing could be built to minimize impacts. For example, depending on how these impacts are distributed across land use types, certain policy interventions, such as urban infill, could be used to mitigate multiple impacts at once. The Santa Cruz Mountains of California and surrounding urban areas, including the Silicon Valley and the city of Santa Cruz, present an opportunity to examine the linkages and intersections between these three environmental impacts. The Santa Cruz Mountains contain widespread residential development throughout wildland areas, and there are also detailed, fine-resolution information available on estimated household carbon emissions and habitat quality for an important umbrella species, pumas (*Puma concolor*) throughout this area. Here, we ask how wildfire risk, household emissions, and puma habitat quality vary across land use types: from sparsely developed open space to the wildland urban intermix and interface to urban areas. Understanding the links and synergies between these impacts can shed light on optimal land use strategies to simultaneously mitigate multiple environmental problems.

Methods

Study area

Our 4236 km^2 study area encompasses the Santa Cruz Mountains of California (Fig. 1). Of this, 42.2% is sparsely developed, 18.8% is intermix, 13.3% is interface, and 11.7% is non-WUI urban according to the definitions of (Radeloff et al. 2005b, Stewart et al. 2007). The remaining 14%, made up of industrial areas or row-crop agriculture, was excluded from this analysis. Since 2000, a total of 471.02 km^2 was burned in this area, in 30 individual fires ranging in size from 0.027 km^2 to 350.03 km^2 (the CZU Lightning Complex Fire of 2020, which killed 1 person and destroyed

1490 structures[5]). For analyses related to puma habitat quality, a 2823 km^2 subset of this study area was considered, representing the merged 95% minimum convex polygon of all puma locations used for habitat modeling (Fig. 1). This restricted area, rather than the entire study area, was used for puma habitat quality analyses to avoid extrapolating model results beyond the range of housing densities experienced by monitored pumas. Our study area has a Mediterranean climate of wet winters and hot, dry summers. Dominant vegetation communities include redwood (*Sequoia sempervirens*) and Douglass fir *(Pseudotsuga menziesii)* forests at lower elevations and northerly aspects, mixed oak (*Quercus sp.*), conifer, and madrone (*Arbutus menzziensii*) forests at higher elevations and southerly aspects, alongside grasslands, scrub, and chaparral habitats (for more detailed description see Wilmers et al. 2013).

Spatial layers of wildfire risk, wildlife habitat quality, and household carbon footprint

We obtained land use type classifications for wildland urban interface, intermix, and sparsely developed and urban areas from[6] (Fig. 1A; Radeloff et al. 2005, Stewart et al. 2007). Unvegetated areas classified as medium and high housing density were considered urban, no- and very-low-density vegetated areas were considered sparsely developed (Mann et al. 2014). For distribution of housing density

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[5] https://www.fire.ca.gov/incidents/2020/8/16/czu-lightning-complex-including-warnella-fire/

[6] http://silvis.forest.wisc.edu/data/wui-change/

categories within each land use designation see Fig. S4. Burn perimeters from wildfires from 2000-2021 was obtained from CALFIRE[7].

We investigated climate change impacts via household carbon footprints (Fig. 1B). Mean household carbon footprints (HCF) in metric tons CO_2 equivalent (tCO_2e) in 2010 at the census block group level were obtained from[8] (Jones and Kammen 2014, Jones et al. 2018). HCF data was only available for inhabited block groups and block groups with missing HCF data were excluded. This data was modeled using consumption-based inventory methods to estimate carbon footprint at the household level - meaning that carbon footprint is calculated for all that that household consumes, incorporating the entire supply chain's emissions and including transportation, housing, food, goods, and services (Jones and Kammen 2014, Jones et al. 2018). To better understand how HCF varies across land use types we also considered how income is distributed and obtained median household income data for the year 2015 at the census block group level using the R *tidycensus* package. Data from 2010 was not available.

Puma habitat quality was used as a proxy for wildlife habitat suitability. Pumas, as a large carnivore that requires ample space and relatively undisturbed habitat, can be considered an umbrella species in coastal California, as preserving high-quality puma habitat will also likely benefit myriad other co-occurring species (Thornton et al. 2016). Habitat quality is most rigorously defined through vital rates

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[7] https://frap.fire.ca.gov/frap-projects/fire-perimeters/

[8] https://coolclimate.org/scenarios

and population dynamics, as high-quality habitat must be able to support a self-sustaining population (Van Horne 1983, Pulliam 2000, Mosser et al. 2009). A previous study modeled expected puma population growth rates across the study area (Fig. 1C; Nisi et al. Chapter 3) and found that housing density is negatively related to annual survival for female pumas, which means more developed areas exhibit lower population growth rates and reduced habitat quality. Alongside population dynamics, we also considered two other components of puma habitat suitability: human-puma conflict and puma time allocation. Human-carnivore conflict is a key threat to many carnivore species, who are often killed after consuming livestock (Inskip and Zimmermann 2009, Ripple et al. 2014). In our study area, pumas often kill goats held in small numbers on residential properties and until recently were allowed to be shot if a permit was obtained. The relative risk of retaliatory killing across the study area peaks in areas of intermediate housing density, rather than scaling directly with development intensity (Fig. 1D). For details on modeling the risk of retaliatory killing see Nisi et al., Chapter 2. Finally, habitat selection sheds light on animal occupancy and time allocation (Fig. 1E). Areas that are selected by an animal are places where they spend more time relative to places that animal avoids. For details on habitat selection modeling see Nisi et al. Chapter 2. Notably, habitat selection is not a direct metric of habitat quality, but is important alongside population-relevant metrics to understand animal occupancy and distribution across a landscape.

Statistical analysis

Wildland urban interface and intermix zones are associated with high risk of wildfire losses and high rates of wildfire ignitions (Radeloff et al. 2018). To quantify wildfire risk across land use categories in the Santa Cruz Mountains, we first extracted whether each structure had been threatened by wildfire (i.e., within a burn perimeter) since 2000, using a manually digitized satellite map of building locations across our study area (Wilmers et al. 2013). We then conducted a logistic regression relating the probability that a home was threatened by wildfire to land use category. No urban areas were within burn perimeters, so urban areas were excluded in this analysis. We present odds ratios of being in a burn perimeter for intermix and interface areas, relative to sparsely developed areas, as well as the proportion of homes within burnt areas in each land use category. To categorize the continuous relationship between housing density and burn risk, we fit logistic regressions relating whether a building was threatened by wildfire to housing density, calculated as households per area within each census block group to correspond with the scale of analysis for household emissions data. For this analysis, we included urban areas. To test for a non-linear relationship between housing density and burn risk, we also considered a quadratic relationship and competed models using Akaike information Criterion (AIC). Housing density was log-transformed for these analyses.

To assess how household carbon footprint (HCF) varied across land use types, we drew a sample of 5000 locations from all non-agricultural block groups in the study area. For each location we extracted land use category (non-WUI urban, interface, intermix, sparsely developed) and mean HCF was compared across land use types using analysis of variance (ANOVA) and Tukey post-hoc tests. We also looked at how income was distributed across land use type – this relationship varied by county, so we also investigated county-specific patterns in HCF.

To quantify how puma habitat quality varied with land use category, we extracted three components of puma habitat quality –puma population growth rate representing overall habitat quality, habitat selection representing puma time allocation, and retaliatory killing risk representing human-carnivore conflict – at 5000 random locations from within the puma study area boundary. We used ANOVA with Tukey post-hoc tests to assess whether metrics of habitat quality differed across land use categories.

To visualize how HCF and puma habitat quality change continuously with housing density, we calculated mean HCF, puma population growth rate, and retaliatory killing risk in each census block group and fit smoothing splines (5 knots) against household density (households/km^2) in each block group. Splines were fit using the *npreg* package. All analyses were conducted in R version 3.6.0, with spatial operations performed using the *sf* package (Pebesma 2018).

Results

Houses in intermix and interface areas were significantly less likely to be threatened by wildfire relative to houses in sparsely developed areas (odds ratio for intermix: 0.388 [95% CI: 0.355, 0.425]; interface: 0.00366 [0.00306, 0.00438], Fig. 2A). Intermix areas were at much higher risk of being in a burn perimeter relative to interface, and no burn perimeters entered urban areas. While homes in sparsely developed areas were at increased risk of being threatened by wildfire, intermix homes made up the majority of threatened structures: of the total buildings that were in burned areas, 70% were in intermix areas, with 24.7% in sparse development and 5.1% in interface. Burn risk declined with housing density, and the quadratic relationship was best supported (β_0=-2.12 [SE=0.098, $p < 0.001$], β_{HD}=0.377 [SE=0.069 $p<0.001$], β_{HD2}=-0.229 [SE=0.011 $p<0.001$]; Fig. 3B).

Mean household carbon footprint was lowest in urban areas compared to intermix, interface, and sparsely developed areas (Fig. S2, Fig. 3C), though between counties, this relationship depended on income. This pattern was very pronounced in Santa Clara and Santa Cruz Counties, with urban areas in both counties exhibiting significantly lower HCF compared to other land use types (Fig. 2B). In contrast, San Mateo County exhibited the opposite trend - mean HCF was actually higher in urban areas compared to sparse development and was not significantly different from intermix or interface areas. This pattern mirrors how household income, which strongly influences HCF, is distributed across land use categories in the three counties, with median household income in urban areas in San Mateo being higher than other land use types, in contrast to Santa Clara and Santa Cruz Counties (Fig. 2B). Transportation contributed the most to household carbon footprint, and transportation-related emissions were lowest in urban areas compared to other categories (Fig. S3).

Across all three metrics of puma habitat quality considered (population dynamics, time allocation, and conflict risk), intermix and interface areas were poorer-quality relative to sparsely developed areas. Puma habitat quality measured by population dynamics was better in intermix areas relative to interface, and pumas largely avoided low-quality interface and urban areas relative to sparsely developed and intermix areas (Fig. 2C, Fig. 3D). However, intermix areas exhibited higher human-carnivore conflict risk, with retaliatory killing risk highest in intermix areas (Fig. 2C, Fig. 3E).

Conclusions

Wildland urban interface and intermix habitats were associated with heightened wildfire risk and household carbon emissions relative to urban areas, and lower wildlife habitat quality relative to sparsely developed areas. This alignment of multiple environmental impacts underscores that exurban development within or near wildland vegetation contributes both to the causes and consequences of the climate crisis, as well as biodiversity loss. Together, these results suggest that land use policy that encourages development within urban areas thus can confer co-benefits to wildfire risk, carbon emissions, and wildlife conservation.

While the risk of a structure being threatened by wildfire declined with increasing housing density, the majority of threatened structures were in intermix spaces. These results are consistent with larger-scale patterns of WUI areas being associated with high structure lost and frequent wildfire ignitions, especially in

California (Kramer et al. 2018, Radeloff et al. 2018), and combined underscore the high wildfire risk and vulnerability in WUI areas, especially intermix areas, in our study system. Interestingly, a study that investigated the risk of structure destruction found that most destroyed homes in California were in interface areas (Kramer et al. 2019) – together with our results, this perhaps highlights the stochastic nature of catastrophic fires and spatial variability in their impacts even within California. Because different forms of development have drastically different outcomes for wildfire vulnerability, land use policy can help mitigate wildfire risk by encouraging growth in certain areas over others, with urban infill development resulting in reduced wildfire impacts (Syphard et al. 2013).

Similar to burn vulnerability, household carbon footprints overall were inversely related to housing density, which is expected given the improved transit options and walkability alongside increased home energy efficiency associated with higher-density living (Ewing and Cervero 2010, Glaeser and Kahn 2010, Jones et al. 2018). The county-level differences we found were driven by household income, as urban areas in San Mateo county had higher median household incomes than neighboring WUI and sparsely developed areas, driving higher urban HCFs. Wealthier households consume more goods and services and have higher home energy expenditure and transportation-related emissions (Glaeser and Kahn 2010, Jones and Kammen 2014, Jones et al. 2018), but importantly, higher-income households in urban areas have lower carbon emissions compared to if the same household were located in a suburban or rural area (Jones et al. 2018).

Alongside high wildfire risk and carbon emissions in interface and intermix areas, these places were also lower-quality habitat for pumas relative to sparsely developed areas. Interface and urban areas were largely unsuitable for and avoided by pumas, consistent with previous studies documenting the detrimental effects of development on these species (Chapter 3, Wilmers et al. 2013, Ripple et al. 2014). In contrast, intermix areas, with lower housing densities compared to interface areas (Fig S4), supported reduced population growth relative to sparsely developed areas but were not strongly avoided by pumas. Intermix areas were places where human-carnivore conflict was most prevalent, since puma depredation of livestock and subsequent retaliatory killings peaks at intermediate levels of exurban development (Fig. 3D; Chapter 2). Taken together, these results indicate the problematic nature of low-density, exurban development for pumas and other carnivores: while these areas can still support resident animals, animals that live there experience enhanced costs and threats compared to those in undeveloped areas. Thus the intermix, in addition to being a place of high wildfire risk and vulnerability, is also uniquely problematic for wildlife habitat quality.

Considering the marginal impact of further development in each land use category can shed light on policies or development strategies that can mitigate these multiple environmental impacts. For both wildfire risk and household carbon footprint, any additional home built in one area will likely experience the same wildfire risk and carbon emissions as their neighbors, assuming characteristics of the homes built are the same. Further development in urban areas, where wildfire risk and per-household emissions were lowest, would thus confer benefits for both impacts. However, pumas and many other species exhibit continuous responses to housing density such that an additional unit can alter habitat quality or connectivity (Smith et al. 2019a). Retaliatory killing risk sharply increased across the gradient of housing density in intermix areas, and population growth rates decreased across the gradient of housing density (Fig. 3E) - indicating that any additional housing constructed in sparsely developed and intermix areas carries with it increased risk of human-puma conflict and negative implications for population growth. Importantly, because urban areas are already essentially unsuitable habitat for pumas, further development within urban spaces will have minimal impact on puma population health or human-puma conflict. More generally, urban areas generally constitute lower-quality habitat in themselves for many species, but they can facilitate land-sparing and reduced overall human footprint in more remote, higher-quality areas (Venter et al. 2016).

Taken together, these results emphasize the need for urban infill development that is accessible to lower incomes. Further development in urban areas would come at reduced wildfire risk, expected household carbon emissions, and impacts on wildlife habitat relative to further development in remote, intermix, or interface areas. In the planning context, there is increasing attention on the dual benefits of urban infill development in mitigating wildfire risk and reducing greenhouse gas emissions[9], and some environmental NGOs are recognizing the links between

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[9] https://urbanland.uli.org/planning-design/planning-for-a-fire-resilient-future-in-northern-california/

sprawling development's impact on wildlife alongside efficiency and housing equity impacts[10]. These linkages are promising, and looking across academic and subject-matter silos to understand the links and relationships between several environmental impacts can inform optimal strategies to address environmental crises and foster synergies between organizations working to mitigate seemingly disparate environmental impacts.

These implications are particularly salient for much of California and the Santa Cruz area specifically. Santa Cruz is the least affordable small city in the U.S. and is currently gripped by a housing crisis forcing renters into extreme rent burden or displacement, and last year (2020) was impacted by the deadly, destructive, and terrifying CZU Lightning Complex Fire in the neighboring wildland areas that displaced many rural residents whose homes were destroyed.[11] Developing higher-density housing stock in already developed areas in Santa Cruz could help to address the housing crisis and protect residents from future wildfire threats while mitigating these other environmental impacts. While Santa Cruz is exceptionally unaffordable, many of the land use policies that created the housing crisis in Santa Cruz – including prioritizing single-family-homes and preventing higher-density development in urban areas – are common across many municipalities. In such contexts, increasing density within already developed urban areas would confer multiple environmental benefits.

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[10] https://www.sierraclub.org/sites/www.sierraclub.org/files/sce/sierra-club-california/PDFs/SCC_Housing_Policy_Report.pdf

[11] https://www.santacruzsentinel.com/2021/08/16/housing-struggles-remain-one-year-after-czu-lightning-complex-fire/

More broadly, these results highlight the intersection and alignment of these three environmental issues – wildfire risk, carbon emissions, and habitat loss – and indicates that land-use actions taken to mitigate one impact will likely carry co-benefits for others.

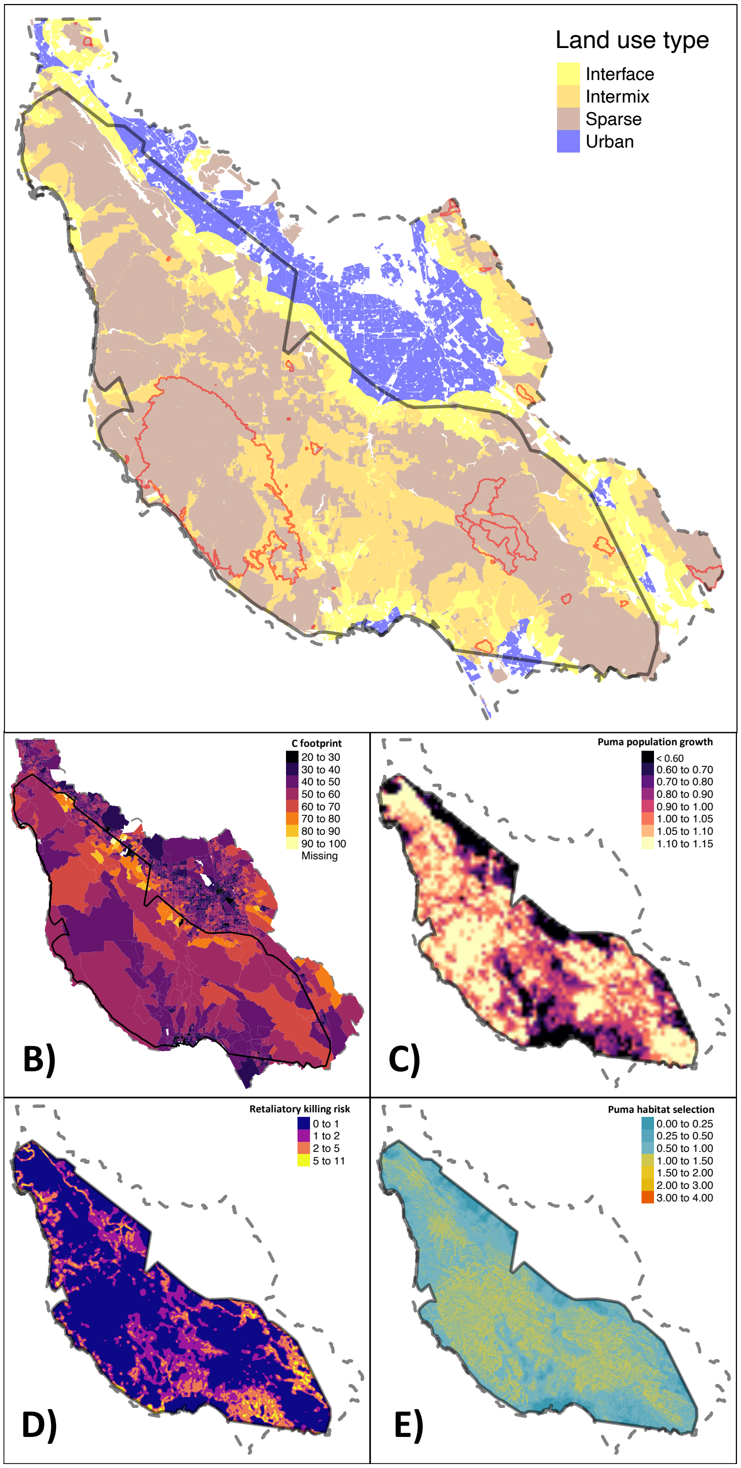

Figure 4.1. Maps of land use category, household C footprint, and puma habitat quality metrics across the study area. Panel (A) shows land use categories: sparsely developed, intermix, interface, and urban, in shaded colors alongside burned perimeters (2000-2021) outlined in red. The black solid outline is the study area

boundary for puma habitat quality metrics, and the dashed outline is the study extent for household C footprint data. Panel (B) shows mean household C footprint across census block groups, with the puma study area outlined in black. Three metrics of puma habitat quality (puma population growth rate, human-carnivore conflict represented by retaliatory killing risk, and puma time allocation represented by puma habitat selection) are shown in panels C-E.

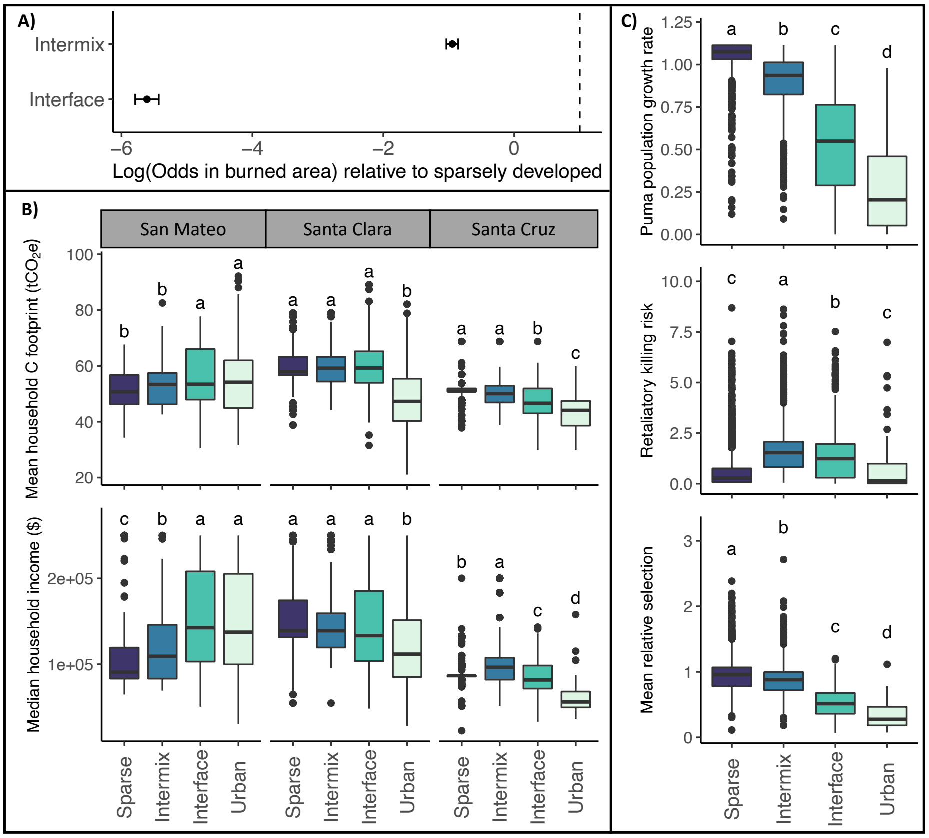

Figure 4.2. Burn risk (A), household C emissions (B), and puma habitat quality (C) across land use categories. Panel (A) shows the log odds of a housing unit being within a burn perimeter in intermix and interface areas relative to sparsely developed areas (dashed line at 1 represents if the odds of burning were equivalent to in sparse development). Urban areas were excluded as no urban homes fell within burn perimeters. Panel (B) shows mean household C footprint (in metric tons CO_2 equivalent) by county. Since C footprint is closely related to income, median household income across counties is also plotted. In panel (B), mean puma population growth rate reflects habitat quality in terms of population dynamics, retaliatory killing risk represents human-carnivore conflict, and mean relative selection shows puma time allocation (i.e., what areas they are spending more time in).

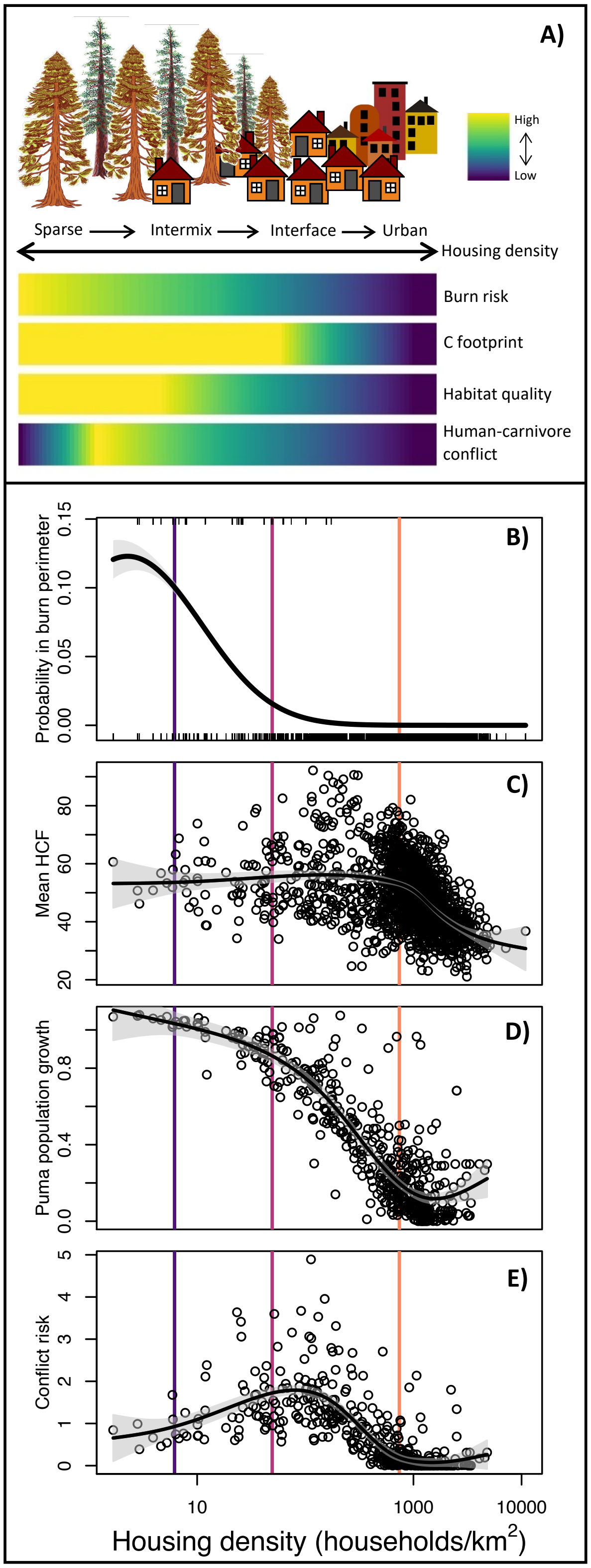
A)
High
Low
Sparse
Intermix
Interface
Urban
Housing density
Burn risk
C footprint
Habitat quality
Human-carnivore conflict
B)
Probability in burn perimeter
0.00
0.05
0.10
0.15
C)
Mean HCF
20
40
60
80
D)
Puma population growth
0.0
0.4
0.8
E)
Conflict risk
0
1
2
3
4
5
10
1000
10000
Housing density (households/km^2)

Figure 4.3. Changes in burn risk, household C footprint, and habitat quality across the gradient of housing density. Panel (A) shows a conceptual diagram with color bars showing high values in yellow and low values in blue. Panel (B) shows predicted probability of a house being within a burn perimeter from logistic regression. Panels C-E show mean household C footprint (tCO_2e), mean puma population growth rate, and mean retaliatory killing risk in each census block group against household density within that block group. Vertical lines in B-E show cutoff values between land use categories: 6.78 buildings/km^2 (purple), 49.42 buildings/km^2 (pink), and 741.31 buildings/km^2 (orange) (Fig. S3). Housing densities >6.78 (purple) can be intermix or interface areas depending on wildland vegetation characteristics- however, in our study area, intermix areas are predominantly low (6.78-49.42) while interface areas are generally medium (49.42-741.31) and high (>741.31; Fig. S4).

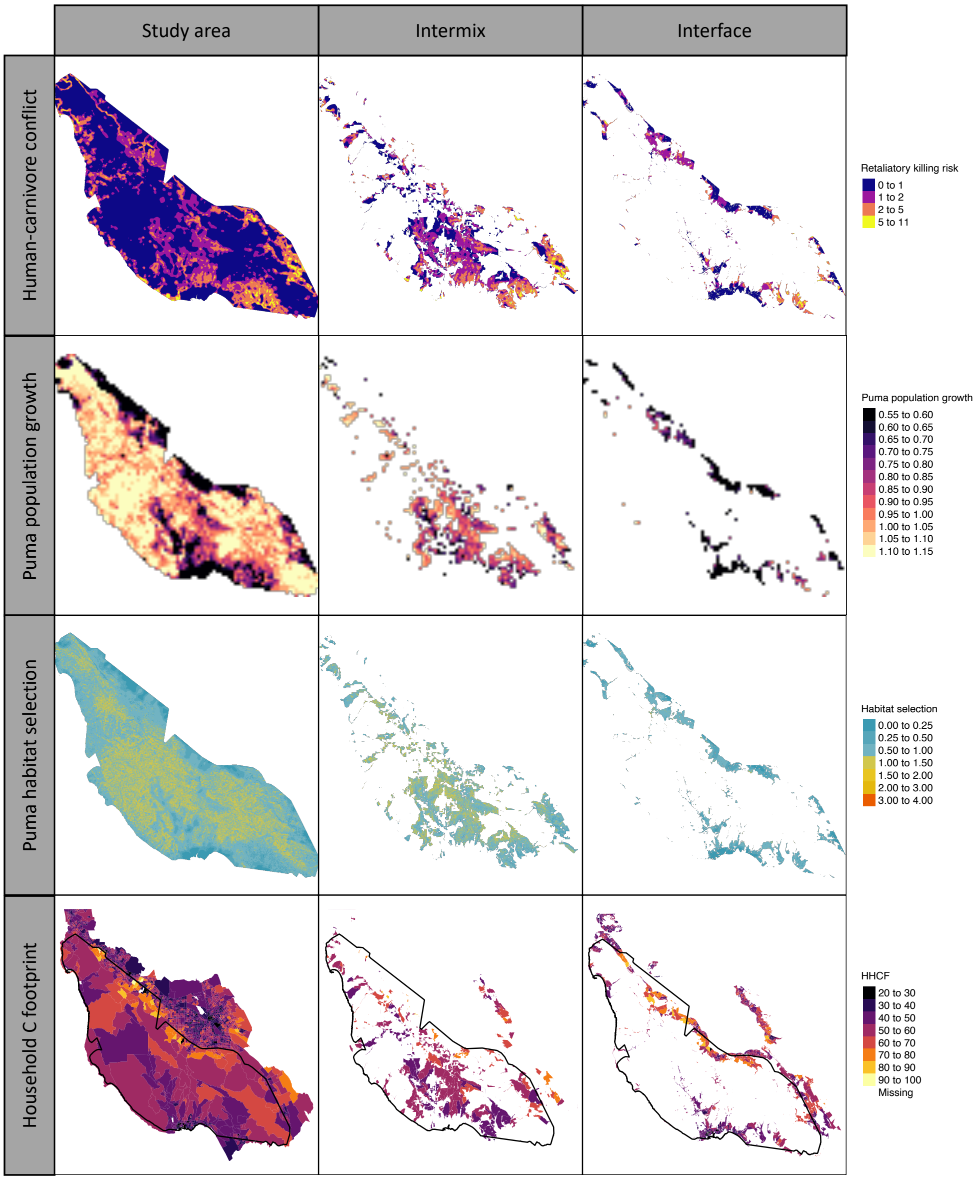

Figure 4.S1. Spatial layers for puma habitat quality and household C footprint plotted across the study area (right), in intermix areas (center) and in interface areas (left).

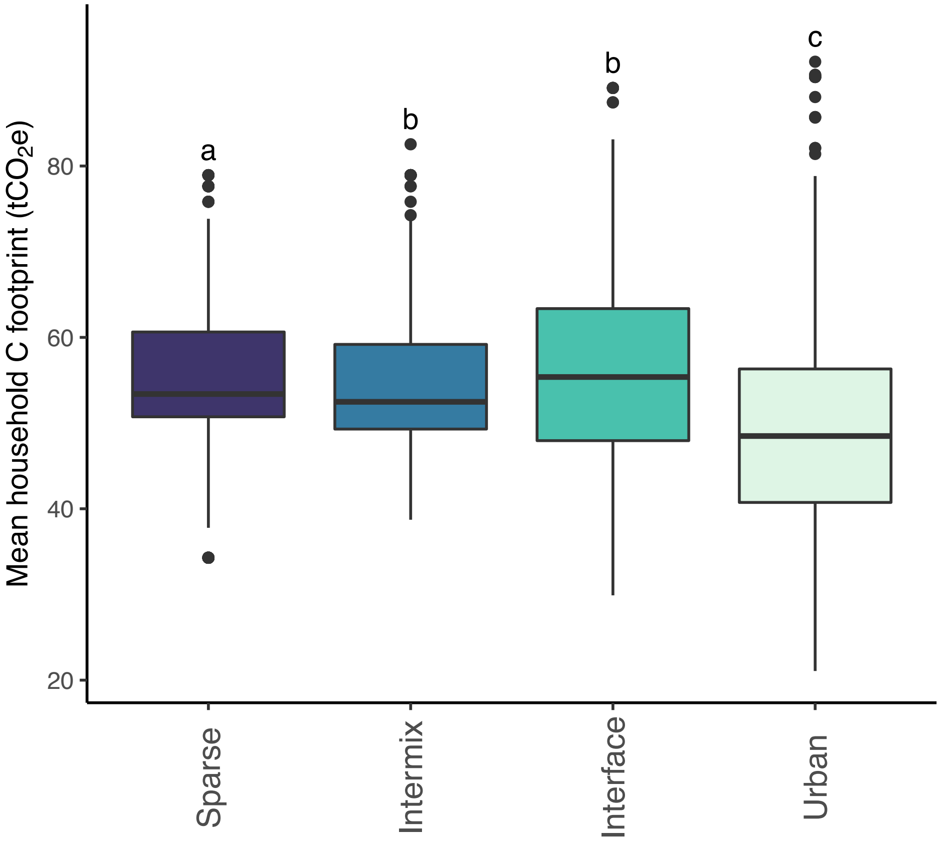

Figure 4.S2. Mean household C footprint (tCO_2e) across land use categories.

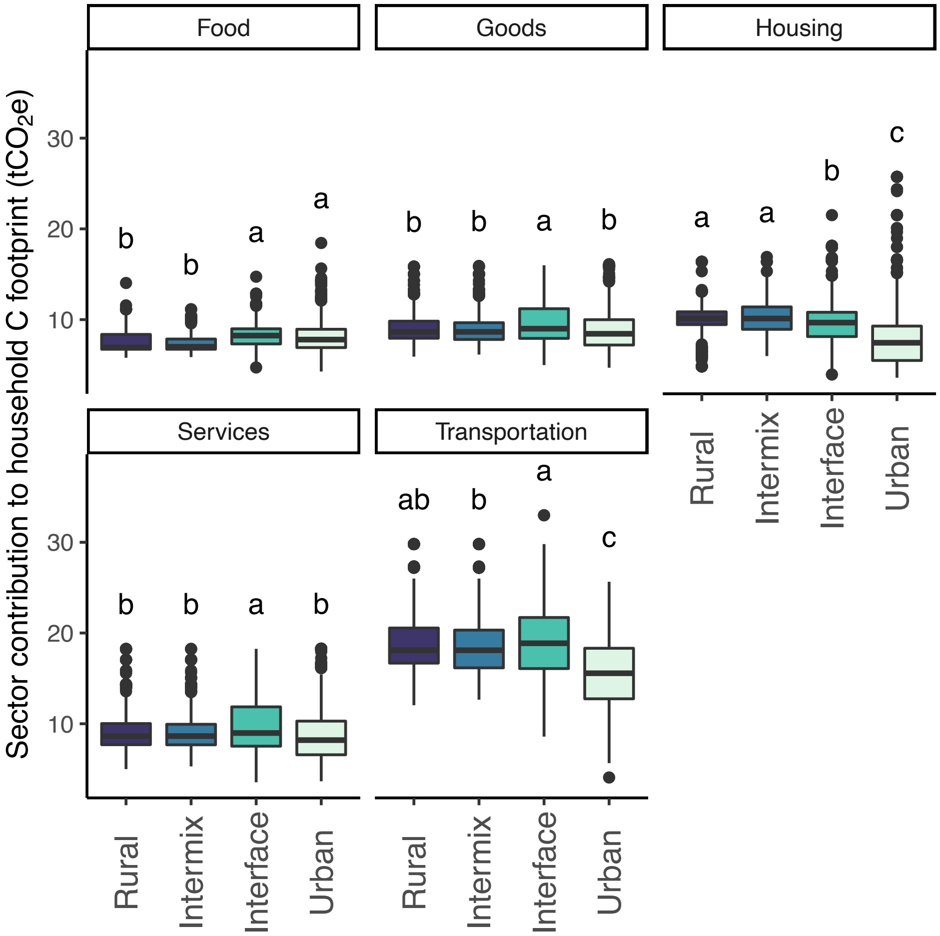

Figure 4.S3. Sector contributions to household C footprints across land use categories.

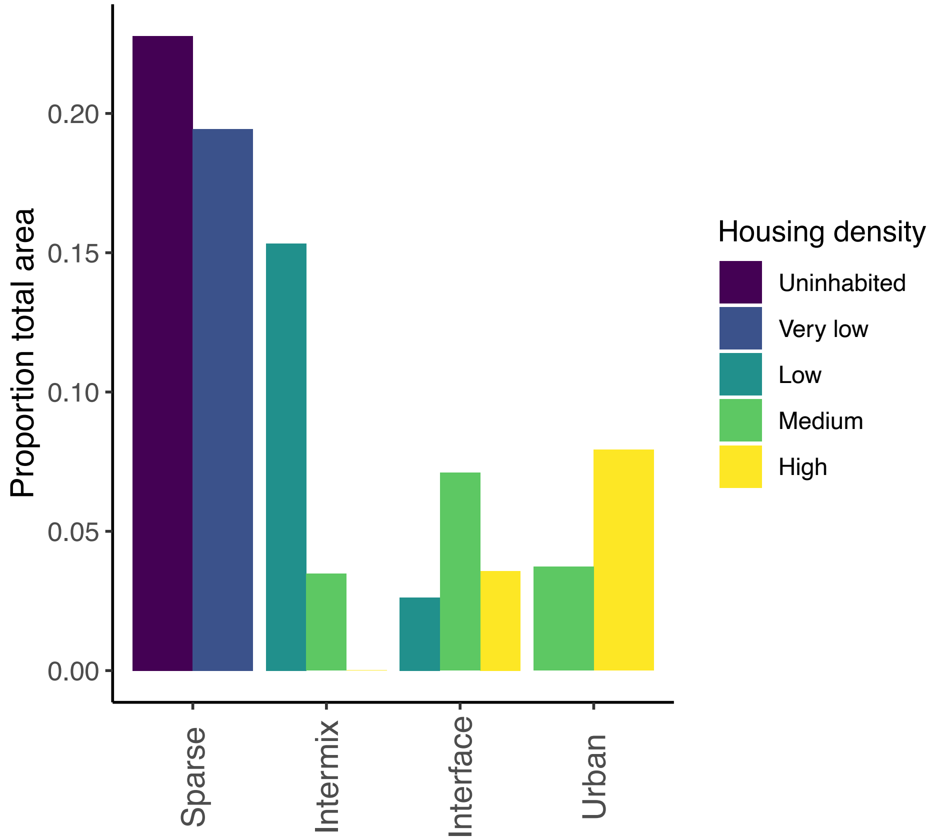

Figure 4.S4. Housing density classifications by land use category. As in Fig. 3, land use categories are very low (>0 to 6.78 houses/km^2), low (6.78-49.42), medium (49.42-741.31), and high (>741.31; Radeloff et al. 2005, Stewart et al. 2007, Mann et al. 2014).

CONCLUSION

Together, these chapters show that carnivores exhibit complex behavioral strategies in human-dominated landscapes that allow them to avoid human features spatially and human activity temporally while balancing other goals (Chapter 1). However, because humans are unpredictable predators, carnivore behavior is not always sufficient in allowing carnivores to avoid being killed by people (Chapter 2). In fact, the energetic costs associated with these behaviors may negatively impact survival for animals in more developed areas (Chapter 3). Carnivore conservation in shared landscapes requires minimizing further development in high-quality source areas as well as marginal-quality sink areas (Chapter 3). Minimizing development in wildland areas confers benefits to other environmental impacts as well, and urban infill presents a win-win strategy for habitat conservation, wildfire risk, and household carbon emissions (Chapter 4).

The Santa Cruz Mountains landscape is emblematic of a common and accelerating form of land use across California and the Western United States: low-level residential development in wildland areas. That a population of large carnivores lives here – in the backyard of Silicon Valley and several major metropolitan areas – is a testament both to the resilience of these species as well as the ability for humans and wildlife to coexist in shared landscapes. I hope that this research – in shedding light on human-carnivore coexistence as well as the broader environmental impacts of residential development in wildland areas – will be useful and applicable to the conservation of other carnivore populations in similar places.

I want to close with a brief reflection on the more abstract benefits that sharing space with carnivores – getting to glimpse one while hiking, seeing a track or scat, or just knowing that they are there – has for our own psyches (or at least for mine). Carnivore presence in human-dominated landscapes captures our imaginations and reminds us that we are connected to other species – even ones that we think of as being particularly wild, or fierce, or other. Maybe this allows us to better see the wildness and fierceness in smaller, more “mundane” beings, including ourselves. In running around and living their lives in spaces that we think of as ours, carnivores remind us that the human/nature dichotomy is a false one.

Paws travel over
crumbling slopes, redwood duff,
and sometimes concrete

En-chapparalled, just
off trail. Wild, they see us,
wild, they know us.

Our cryptic neighbors
nighttime stealth, daytime distance
moving to survive

REFERENCES

Abatzoglou, J. T., and A. P. Williams. 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proceedings of the National Academy of Sciences of the United States of America 113:11770–11775.

Abrahms, B., N. R. Jordan, K. A. Golabek, J. W. McNutt, A. M. Wilson, and J. S. Brashares. 2015. Lessons from integrating behaviour and resource selection: activity-specific responses of African wild dogs to roads. Animal Conservation 19:247–255.

Avgar, T., S. R. Lele, J. L. Keim, and M. S. Boyce. 2017. Relative Selection Strength: Quantifying effect size in habitat- and step-selection inference. Ecology and Evolution 7:5322–5330.

Avgar, T., J. R. Potts, M. A. Lewis, and M. S. Boyce. 2016. Integrated step selection analysis: Bridging the gap between resource selection and animal movement. Methods in Ecology and Evolution 7:619–630.

Balme, G. A., R. Slotow, and L. T. B. Hunter. 2010. Edge effects and the impact of non-protected areas in carnivore conservation: Leopards in the Phinda-Mkhuze Complex, South Africa. Animal Conservation 13:315–323.

Bastille-Rousseau, G., D. L. Murray, J. A. Schaefer, M. A. Lewis, S. P. Mahoney, and J. R. Potts. 2018. Spatial scales of habitat selection decisions: implications for telemetry-based movement modelling. Ecography 41:437–443.

Bastille-Rousseau, G., J. R. Potts, J. A. Schaefer, M. A. Lewis, E. H. Ellington, N. D. Rayl, S. P. Mahoney, and D. L. Murray. 2015. Unveiling trade-offs in resource selection of migratory caribou using a mechanistic movement model of availability. Ecography 38:1049–1059.

Battin, J. 2004. When good animals love bad habitats: Ecological traps and the conservation of animal populations. Conservation Biology 18:1482–1491.

Beckmann, J. P., and C. W. Lackey. 2008. Carnivores, urban landscapes, and longitudinal studies: a case history of black bears. Human-Wildlife Conflicts 2:168–174.

Benhamou, S., M. Valeix, S. Chamaillé-Jammes, D. W. Macdonald, and A. J. Loveridge. 2014. Movement-based analysis of interactions in African lions. Animal Behaviour 90:171–180.

Benson, J. F., P. J. Mahoney, and B. R. Patterson. 2015. Spatiotemporal variation in selection of roads influences mortality risk for canids in an unprotected landscape. Oikos 124:1664–1673.

Benson, J. F., P. J. Mahoney, J. A. Sikich, L. E. K. Serieys, J. P. Pollinger, H. B. Ernest, and S. P. D. Riley. 2016a. Interactions between demography, genetics, and landscape connectivity increase extinction probability for a small population of large carnivores in a major metropolitan area. Proceedings of the Royal Society B: Biological Sciences 283:20160957.

Benson, J. F., J. A. Sikich, and S. P. D. Riley. 2016b. Individual and Population Level Resource Selection Patterns of Mountain Lions Preying on Mule Deer along an Urban-Wildland Gradient. PLoS ONE 11:e0158006.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letters 3:620–623.

Beyer, H. L., D. T. Haydon, J. M. Morales, J. L. Frair, M. Hebblewhite, M. Mitchell, and J. Matthiopoulos. 2010. The interpretation of habitat preference metrics under use-availability designs. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2245–2254.

Bjornstad, O. N. 2020. ncf: Spatial Covariance Functions.

Blecha, K. A., R. B. Boone, and M. W. Alldredge. 2018. Hunger mediates apex predator's risk avoidance response in wildland–urban interface. Journal of Animal Ecology 87:609–622.

Bowman, D. M. J. S., C. A. Kolden, J. T. Abatzoglou, F. H. Johnston, G. R. van der Werf, and M. Flannigan. 2020. Vegetation fires in the Anthropocene. Nature Reviews Earth & Environment.

Boyce, M. S. 2006. Scale for resource selection functions. Diversity and Distributions 12:269–276.

Boyce, M. S., C. D. Mallory, A. T. Morehouse, C. M. Prokopenko, M. A. Scrafford, and C. H. Warbington. 2017. Defining Landscapes and Scales to Model Landscape–Organism Interactions. Current Landscape Ecology Reports 2:89–95.

Boydston, E. E., K. M. Kapheim, H. E. Watts, M. Szykman, and K. E. Holekamp. 2003. Altered behaviour in spotted hyenas associated with increased human activity. Animal Conservation 6:207–219.

Brown, J. S. 1999. Vigilance, patch use and habitat selection: Foraging under predation risk. Evolutionary Ecology Research 1:49–71.

Burdett, C. L., K. R. Crooks, D. M. Theobald, R. Kenneth, E. E. Boydston, L. M.

Lyren, R. N. Fisher, T. W. Vickers, S. A. Morrison, and W. M. Boyce. 2010. Interfacing models of wildlife habitat and human development to predict the future distribution of puma habitat. Ecosphere 1:1–21.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, NY.

Cagnacci, F., L. Boitani, R. A. Powell, and M. S. Boyce. 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2157–2162.

Calabrese, J. M., C. H. Fleming, and E. Gurarie. 2016. Ctmm: an R Package for Analyzing Animal Relocation Data As a Continuous-Time Stochastic Process. Methods in Ecology and Evolution 7:1124–1132.

Calenge, C. 2006. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Cardillo, M., G. M. Mace, K. E. Jones, J. Bielby, O. R. P. Bininda-Emonds, W. Sechrest, C. D. L. Orme, and A. Purvis. 2005. Multiple causes of high extinction risk in large mammal species. Science 309:1239–1241.

Cardillo, M., A. Purvis, W. Sechrest, J. L. Gittleman, J. Bielby, and G. M. Mace. 2004. Human population density and extinction risk in the world’s carnivores. PLoS Biology 2:909–914.

Carter, N. H., and J. D. C. Linnell. 2016. Co-Adaptation Is Key to Coexisting with Large Carnivores. Trends in Ecology and Evolution 31:575–578.

Caswell, H. 2000. Matrix Population Models: Construction, Analysis, and Interpretation. Second edition. Sinauer Associates, Inc., Sunderland, MA.

Chapron, G., P. Kaczensky, J. D. C. Linnell, M. von Arx, D. Huber, H. Andrén, J. V. López-bao, and M. Adamec. 2014. Recovery of large carnivores in Europe’s modern human-dominated landscapes. Science 346:1517–1519.

Cox, D. R. 1972. Regression Models and Life-Tables. Journal of the Royal Statistical Society. Series B (Methodological) 34:187–220.

Crook, S. E. S. 2019. Attitudes and Risk Perception Toward the Mountain Lion Bordering the Santa Cruz Mountains, California. Society & Animals 27:427–451.

Crooks, K. R., C. L. Burdett, D. M. Theobald, C. Rondinini, and L. Boitani. 2011. Global patterns of fragmentation and connectivity of mammalian carnivore habitat. Philosophical Transactions of the Royal Society B: Biological Sciences 366:2642–2651.

Darimont, C. T., C. H. Fox, H. M. Bryan, and T. E. Reimchen. 2015. The unique ecology of human predators. Science 349:858–860.

DeCesare, N. J., M. Hebblewhite, F. Schmiegelow, D. Hervieux, G. McDermid, L. Neufeld, M. Bradley, J. Whittington, K. G. Smith, L. E. Morgantini, M. Wheatley, and M. Musiani. 2012. Transcending Scale Dependence in Identifying Habitat with Resource Selection Functions. Ecological Applications 22:1068–1083.

Delibes, M., P. Gaona, and P. Ferreras. 2001. Effects of an Attractive Sink Leading into Maladaptive Habitat Selection. The American Naturalist 158:277–285.

Dellinger, J. A., and S. G. Torres. 2020. A retrospective look at mountain lion populations in California (1906-2018). California Fish and Wildlife 106:66–85.

Dias, P. C. 1996. Sources and sinks in population biology. Trends in Ecology and Evolution 11:326–330.

Dickie, M., S. R. McNay, G. D. Sutherland, M. Cody, and T. Avgar. 2020. Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species. Journal of Animal Ecology 89:623–634.

Doherty, T. S., G. C. Hays, and D. A. Driscoll. 2021. Human disturbance causes widespread disruption of animal movement. Nature Ecology and Evolution 5:513–519.

Duchesne, T., D. Fortin, and L. P. Rivest. 2015. Equivalence between step selection functions and biased correlated random walks for statistical inference on animal movement. PLoS ONE 10:e0122947.

Dybala, K. E., V. Matzek, T. Gardali, and N. E. Seavy. 2019. Carbon sequestration in riparian forests: A global synthesis and meta-analysis. Global Change Biology 25:57–67.

Ewing, R., and R. Cervero. 2010. Travel and the built environment: a synthesis. Journal of the American Planning Association 73:265–294.

Fang, K., and J. Volker. 2017. Cutting Greenhouse Gas Emissions Is Only the Beginning: A Literature Review of the Co-Benefits of Reducing Vehicle Miles

Traveled. A White Paper from the National Center for Sustainable Transportation.

Fieberg, J., and G. D. DelGuidice. 2009. What time is it? Choice of time origin and scale in extended proportional hazard models. Ecology 90:1687–1697.

Fleming, C. H., J. M. Calabrese, T. Mueller, K. A. Olson, P. Leimgruber, and W. F. Fagan. 2014. From Fine-Scale Foraging to Home Ranges : A Semivariance Approach to Identifying Movement Modes across Spatiotemporal Scales. The American Naturalist 183:E154–E167.

Forester, J. D., H. K. Im, and P. J. Rathouz. 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. Ecology 90:3554–3565.

Forrester, T. D., D. S. Casady, and H. U. Wittmer. 2015. Home sweet home: fitness consequences of site familiarity in female black-tailed deer. Behavioral Ecology and Sociobiology 69:603–612.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320–1330.

Frank, L. 2011. Living with Lions: Lessons from Laikipia. Smithsonian Contributions to Zoology:73–83.

Fretwell, S. D., and H. L. J. Lucas. 1969. On territorial behaviour and other factors influencing habitat distribution in birds. 1. Theoretical Development. Acta Biotheoretica 19:16–36.

Frid, A., and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:11.

Gaillard, J.-M., M. Hebblewhite, A. Loison, M. Fuller, R. Powell, M. Basille, and B. Van Moorter. 2010. Habitat-performance relationships: finding the right metric at a given spatial scale. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2255–2265.

Gaynor, K. M., C. E. Hojnowski, N. H. Carter, and J. S. Brashares. 2018. The influence of human disturbance on wildlife nocturnality. Science 360:1232–1235.

Getz, W. M., S. Fortmann-Roe, P. C. Cross, A. J. Lyons, S. J. Ryan, and C. C. Wilmers. 2007. LoCoH: Nonparameteric Kernel methods for constructing home ranges and utilization distributions. PLoS ONE 2.

Gilbert, S. L., K. J. Sivy, C. B. Pozzanghera, A. DuBour, K. Overduijn, M. M. Smith, J. Zhou, J. M. Little, and L. R. Prugh. 2017. Socioeconomic Benefits of Large Carnivore Recolonization Through Reduced Wildlife-Vehicle Collisions. Conservation Letters 10:430–438.

Glaeser, E. L., and M. E. Kahn. 2010. The greenness of cities: Carbon dioxide emissions and urban development. Journal of Urban Economics 67:404–418.

Gorman, M. L., M. G. Mills, J. P. Raath, and J. R. Speakman. 1998. High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. Nature 391:479–481.

Goss, M., D. L. Swain, J. T. Abatzoglou, A. Sarhadi, C. A. Kolden, A. P. Williams, and N. S. Diffenbaugh. 2020. Climate change is increasing the likelihood of extreme autumn wildfire conditions across California. Environmental Research Letters 15.

Hale, R., and S. E. Swearer. 2016. Ecological traps: Current evidence and future directions. Proceedings of the Royal Society B: Biological Sciences 283:20152647.

Halsey, L. G. 2016. Terrestrial movement energetics: current knowledge and its application to the optimising animal. The Journal of Experimental Biology 219:1424–1431.

Hebblewhite, M., and E. H. Merrill. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90:3445–3454.

Hebblewhite, M., C. A. White, C. G. Nietvelt, J. A. McKenzie, T. E. Hurd, J. M. Fryxell, S. E. Bayley, and P. C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. Ecology 86:2135–2144.

Heisey, D. D. M., and B. R. Patterson. 2006. A Review of Methods to Estimate Cause-Specific Mortality in Presence of Competing Risks. Journal of Wildlife Management 70:1544–1555.

Heppell, S. S., H. Caswell, and L. B. Crowder. 2000. Life Histories and Elasticity Patterns : Perturbation Analysis for Species with Minimal Demographic Data. Ecology 81:654–665.

Hijmans, R. J. 2019. raster: Geographic Data Analysis and Modeling.

Holbrook, J. D., L. E. Olson, N. J. Decesare, M. Hebblewhite, J. R. Squires, and R. Steenweg. 2019. Functional responses in habitat selection: clarifying hypotheses and interpretations. Ecological Applications 29:e01852.

Holden, Z. A., A. Swanson, C. H. Luce, W. M. Jolly, M. Maneta, J. W. Oyler, D. A. Warren, R. Parsons, and D. Affleck. 2018. Decreasing fire season precipitation increased recent western US forest wildfire activity. Proceedings of the National Academy of Sciences of the United States of America 115:E8349–E8357.

Van Horne, B. 1983. Density as a Misleading Indicator of Habitat Quality. Journal of Wildlife Management 47:893–901.

Horne, B. Van. 1983. Density as a Misleading Indicator of Habitat Quality. The Journal of Wildlife Management 47:893.

Hosmer, D. W., and S. Lemeshow. 1999. Applied survival analysis: regression modeling of time to event data. John Wiley & Sons Inc, New York, NY.

Houston, A. I., J. M. McNamara, and J. M. C. Hutchinson. 1993. General Results concerning the Trade-Off between Gaining Energy and Avoiding Predation. Philosophical Transactions of the Royal Society B: Biological Sciences 341:375–397.

Inskip, C., and A. Zimmermann. 2009. Human-felid conflict: A review of patterns and priorities worldwide. Oryx 43:18–34.

Johansson, Ö., G. Koehler, G. R. Rauset, G. Samelius, H. Andrén, C. Mishra, P. Lhagvasuren, T. McCarthy, and M. Low. 2018. Sex-specific seasonal variation in puma and snow leopard home range utilization. Ecosphere 9:e02371.

Johnson, D. H. 1980. The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. Ecology 61:65–71.

Johnson, H. E., D. L. Lewis, and S. W. Breck. 2020. Individual and population fitness consequences associated with large carnivore use of residential development. Ecosphere 11.

Johnson, M. D. 2007. Measuring habitat quality: A review. Condor 109:489–504.

Jones, C., and D. M. Kammen. 2014. Spatial distribution of U.S. household carbon footprints reveals suburbanization undermines greenhouse gas benefits of urban population density. Environmental Science and Technology 48:895–902.

Jones, C. M., S. M. Wheeler, and D. M. Kammen. 2018. Carbon footprint planning: Quantifying local and state mitigation opportunities for 700 California Cities. Urban Planning 3:35–51.

Kahn, M. E. 2000. The Environmental Impact of Suburbanization. Journal of Policy

Analysis and Management 19:569–586.

Kohl, M. T., D. R. Stahler, M. C. Metz, J. D. Forester, M. J. Kauffman, N. Varley, P. J. White, D. W. Smith, and D. R. MacNulty. 2018. Diel predator activity drives a dynamic landscape of fear. Ecological Monographs 88:638–652.

Kramer, H. A., M. H. Mockrin, P. M. Alexandre, and V. C. Radeloff. 2019. High wildfire damage in interface communities in California. International Journal of Wildland Fire 28:641–650.

Kramer, H. A., M. H. Mockrin, P. M. Alexandre, S. I. Stewart, and V. C. Radeloff. 2018. Where wildfires destroy buildings in the US relative to the wildland-urban interface and national fire outreach programs. International Journal of Wildland Fire 27:329–341.

Kronfeld-Schor, N., and T. Dayan. 2003. Partitioning of Time as an Ecological Resource. Annual Review of Ecology, Evolution, and Systematics 34:153–181.

Laforge, M. P., R. K. Brook, F. M. van Beest, E. M. Bayne, and P. D. McLoughlin. 2016. Grain-dependent functional responses in habitat selection. Landscape Ecology 31:855–863.

Lamb, C. T., G. Mowat, B. N. McLellan, S. E. Nielsen, and S. Boutin. 2017. Forbidden fruit: human settlement and abundant fruit create an ecological trap for an apex omnivore. Journal of Animal Ecology 86:55–65.

Lambert, C. M., R. B. Wielgus, H. S. Robinson, D. D. Katnik, H. S. Cruickshank, R. Clarke, and J. Almack. 2006. Cougar Population Dynamics and Viability in the Pacific Northwest. Journal of Wildlife Management 70:246–254.

Levi, T., a. M. Kilpatrick, M. Mangel, and C. C. Wilmers. 2012. Deer, predators, and the emergence of Lyme disease. Proceedings of the National Academy of Sciences 109:10942–10947.

Logan, K. A., and L. L. Sweanor. 2001a. Desert Puma: Evolutionary Ecology and Conservation of an Enduring Carnivore. Island Press, Washington, DC.

Logan, K. A., and L. L. Sweanor. 2001b. Mortality and Survival. Pages 115–144 Desert Puma: Evolutionary Ecology and Conservation of an Enduring Carnivore. Island Press, Washington, DC.

Loveridge, A. J., M. Valeix, N. B. Elliot, and D. W. Macdonald. 2017. The landscape of anthropogenic mortality: how African lions respond to spatial variation in risk. Journal of Applied Ecology 54:815–825.

Lyons, A. J., W. C. Turner, and W. M. Getz. 2013. Home range plus : a space-time characterization of movement over real landscapes. Movement Ecology 1:1–14.

Mangel, M., and C. Clark. 1986. Towards a Unified Foraging Theory. Ecology 67:1127–1138.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource Selection by Animals. Second edition. Kluwer Academic Publishers, Norwell, MA.

Mann, M. L., P. Berck, M. A. Moritz, E. Batllori, J. G. Baldwin, C. K. Gately, and D. R. Cameron. 2014. Modeling residential development in California from 2000 to 2050: Integrating wildfire risk, wildland and agricultural encroachment. Land Use Policy 41:438–452.

Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. Ecoscience 16:238–247.

McGarigal, K., H. Y. Wan, K. A. Zeller, B. C. Timm, and S. A. Cushman. 2016. Multi-scale habitat selection modeling: a review and outlook. Landscape Ecology 31:1161–1175.

McLoughlin, P. D., M. S. Boyce, T. Coulson, and T. Clutton-Brock. 2006. Lifetime reproductive success and density-dependent, multi-variable resource selection. Proceedings of the Royal Society B: Biological Sciences 273:1449–1454.

McLoughlin, P. D., J. S. Dunford, and S. Boutin. 2005. Relating predation mortality to broad-scale habitat selection. Journal of Animal Ecology 74:701–707.

McNamara, J. M., and A. I. Houston. 1987. Starvation and Predation as Factors Limiting Population Size. Ecology 68:1515–1519.

Miller, J. R. B., and O. J. Schmitz. 2019. Landscape of fear and human-predator coexistence: Applying spatial predator-prey interaction theory to understand and reduce carnivore-livestock conflict. Biological Conservation 236:464–473.

Milleret, C., A. Ordiz, G. Chapron, H. P. Andreassen, J. Kindberg, J. Månsson, A. Tallian, P. Wabakken, C. Wikenros, B. Zimmermann, J. E. Swenson, and H. Sand. 2018. Habitat segregation between brown bears and gray wolves in a human-dominated landscape. Ecology and Evolution 8:11450–11466.

Di Minin, E., R. Slotow, L. T. B. Hunter, F. Montesino Pouzols, T. Toivonen, P. H. Verburg, N. Leader-Williams, L. Petracca, and A. Moilanen. 2016. Global priorities for national carnivore conservation under land use change. Scientific Reports 6:1–9.

Moss, W. E., M. W. Alldredge, and J. N. Pauli. 2016. Quantifying risk and resource use for a large carnivore in an expanding urban-wildland interface. Journal of Applied Ecology 53:371–378.

Mosser, A., J. M. Fryxell, L. Eberly, and C. Packer. 2009. Serengeti real estate: Density vs. fitness-based indicators of lion habitat quality. Ecology Letters 12:1050–1060.

Mysterud, A., and R. A. Ims. 1998. Functional responses in habitat use: availability influences relative use intrade-off situations. Ecology 79:1435–1441.

Newbold, T., L. N. Hudson, S. L. L. Hill, S. Contu, I. Lysenko, R. A. Senior, L. Börger, D. J. Bennett, A. Choimes, B. Collen, J. Day, A. De Palma, S. Díaz, S. Echeverria-Londoño, M. J. Edgar, A. Feldman, M. Garon, M. L. K. Harrison, T. Alhusseini, D. J. Ingram, Y. Itescu, J. Kattge, V. Kemp, L. Kirkpatrick, M. Kleyer, D. L. P. Correia, C. D. Martin, S. Meiri, M. Novosolov, Y. Pan, H. R. P. Phillips, D. W. Purves, A. Robinson, J. Simpson, S. L. Tuck, E. Weiher, H. J. White, R. M. Ewers, G. M. MacE, J. P. W. Scharlemann, and A. Purvis. 2015. Global effects of land use on local terrestrial biodiversity. Nature 520:45–50.

Nickel, B. A., J. P. Suraci, A. C. Nisi, and C. C. Wilmers. 2021. Energetics and fear of humans constrain the spatial ecology of pumas. Proceedings of the National Academy of Sciences 118:e2004592118.

Nicosia, A., T. Duchesne, L.-P. Rivest, and D. Fortin. 2017. A Multi-State Conditional Logistic Regression Model for the Analysis of Animal Movement. The Annals of Applied Statistics 11:1537–1560.

Nielsen, S. E., G. B. Stenhouse, and M. S. Boyce. 2006. A habitat-based framework for grizzly bear conservation in Alberta. Biological Conservation 130:217–229.

Northrup, J. M., G. B. Stenhouse, and M. S. Boyce. 2012. Agricultural lands as ecological traps for grizzly bears. Animal Conservation 15:369–377.

Northrup, J. M., and G. Wittemyer. 2013. Characterising the impacts of emerging energy development on wildlife, with an eye towards mitigation. Ecology Letters 16:112–125.

O'Brien, T. G., M. F. Kinnaird, S. Ekwanga, C. Wilmers, T. Williams, A. Oriol-Cotterill, D. Rubenstein, and L. G. Frank. 2018. Resolving a conservation dilemma: Vulnerable lions eating endangered zebras. PLoS ONE 13:e0201983.

O'Neil, S. T., J. A. Vucetich, D. E. Beyer, S. R. Hoy, and J. K. Bump. 2020. Territoriality drives preemptive habitat selection in recovering wolves: Implications for carnivore conservation. Journal of Animal Ecology 89:1433–

1447.

Ocampo-Peñuela, N., R. S. Winton, C. J. Wu, E. Zambello, T. W. Wittig, and N. L. Cagle. 2016. Patterns of bird-window collisions inform mitigation on a university campus. PeerJ 2016.

Ordiz, A., O. G. Støen, M. Delibes, and J. E. Swenson. 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. Oecologia 166:59–67.

Oriol-Cotterill, A., D. W. Macdonald, M. Valeix, S. Ekwanga, and L. G. Frank. 2015a. Spatiotemporal patterns of lion space use in a human-dominated landscape. Animal Behaviour 101:27–39.

Oriol-Cotterill, A., D. W. Macdonald, M. Valeix, S. Ekwanga, and L. G. Frank. 2015b. Spatiotemporal patterns of lion space use in a human-dominated landscape. ANIMAL BEHAVIOUR 101:27–39.

Oriol-Cotterill, A., M. Valeix, L. G. Frank, C. Riginos, and D. W. Macdonald. 2015c. Landscapes of Coexistence for terrestrial carnivores: The ecological consequences of being downgraded from ultimate to penultimate predator by humans. Oikos 124:1263–1273.

Pan, W. 2001. Akaike's Information Criterion in Generalized Estimating Equations. Biometrics 57:120–125.

Pebesma, E. 2018. Simple Features for R: Standardized Support for Spatial Vector Data. The R Journal 10:439–446.

Penteriani, V., M. D. M. Delgado, M. Krofel, K. Jerina, A. Ordiz, F. Dalerum, A. Zarzo-Arias, and G. Bombieri. 2018. Evolutionary and ecological traps for brown bears Ursus arctos in human-modified landscapes. Mammal Review 48:180–193.

Pianka, E. K. 1970. On r- and K-Selection. The American Naturalist 104:592–597.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival Analysis in Telemetry Studies: The Staggered Entry Design. The Journal of Wildlife Management 53:7–15.

Prima, M.-C., T. Duchesne, and D. Fortin. 2017. Robust Inference from Conditional Logistic Regression Applied to Movement and Habitat Selection Analysis. PLoS ONE 12:e0169779.

Prokopenko, C. M., M. S. Boyce, and T. Avgar. 2017. Extent-dependent habitat selection in a migratory large herbivore: road avoidance across scales. Landscape Ecology 32:313–325.

Pulliam, H. R. 2000. On the relationship between niche and distribution. Ecology Letters 3:349–361.

Pulliam, R. H., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. The American Naturalist 137:S50–S66.

Radeloff, V. C., R. B. Hammer, and S. I. Stewart. 2005a. Rural and suburban sprawl in the U.S. Midwest from 1940 to 2000 and its relation to forest fragmentation. Conservation Biology 19:793–805.

Radeloff, V. C., R. B. Hammer, S. I. Stewart, J. S. Fried, S. S. Holcomb, and J. F. McKeefry. 2005b. The Wildland-Urban Interface in the United States. Ecological Applications 15:799–805.

Radeloff, V. C., D. P. Helmers, H. Anu Kramer, M. H. Mockrin, P. M. Alexandre, A. Bar-Massada, V. Butsic, T. J. Hawbaker, S. Martinuzzi, A. D. Syphard, and S. I. Stewart. 2018. Rapid growth of the US wildland-urban interface raises wildfire risk. Proceedings of the National Academy of Sciences of the United States of America 115:3314–3319.

Raynor, J. L., C. A. Grainger, and D. P. Parker. 2021. Wolves make roadways safer, generating large economic returns to predator conservation. Proceedings of the National Academy of Sciences of the United States of America 118:1–10.

Rettie, W. J., and F. Messier. 2000. Hierarchical Habitat Selection by Woodland Caribou: Its Relationship to Limiting Factors. Ecography 23:466–478.

Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D. Wallach, and A. J. Wirsing. 2014. Status and ecological effects of the world’s largest carnivores. Science 343:1241484.

Ripple, W. J., A. J. Wirsing, C. C. Wilmers, and M. Letnic. 2013. Widespread mesopredator effects after wolf extirpation. Biological Conservation 160:70–79.

Robertson, B. A., and R. L. Hutto. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. Ecology 87:1075–1085.

Robertson, B. A., J. S. Rehage, and A. Sih. 2013. Ecological novelty and the emergence of evolutionary traps. Trends in Ecology and Evolution 28:552–560.

Robinson, H. S., R. Desimone, C. Hartway, J. A. Gude, M. J. Thompson, M. S. Mitchell, and M. Hebblewhite. 2014. A test of the compensatory mortality hypothesis in mountain lions: A management experiment in West-Central Montana. Journal of Wildlife Management 78:791–807.

Robinson, H. S., R. B. Wielgus, H. S. Cooley, and S. W. Cooley. 2008. Sink Populations in Carnivore Management: Cougar Demography and Immigration in a Hunted Population. Ecological Applications 18:1028–1037.

Rosenzweig, M. L. 1981. A Theory of Habitat Selection. Ecology 62:327–335.

Ruth, T. K., M. A. Haroldson, K. M. Murphy, P. C. Buotte, M. G. Hornocker, and H. B. Quigley. 2011. Cougar survival and source-sink structure on Greater Yellowstone's Northern Range. Journal of Wildlife Management 75:1381–1398.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution 1:103–113.

Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. Trends in Ecology and Evolution 17:474–480.

Shepard, E. L. C., R. P. Wilson, W. G. Rees, E. Grundy, S. A. Lambertucci, and S. B. Vosper. 2013. Energy Landscapes Shape Animal Movement Ecology. American Naturalist 182:298–310.

Sih, A. 2013. Understanding variation in behavioural responses to human-induced rapid environmental change: A conceptual overview. Animal Behaviour 85:1077–1088.

Smith, J. A., T. P. Duane, and C. C. Wilmers. 2019a. Moving through the matrix: Promoting permeability for large carnivores in a human-dominated landscape. Landscape and Urban Planning 183:50–58.

Smith, J. A., T. P. Duane, and C. C. Wilmers. 2019b. Moving through the matrix: Promoting permeability for large carnivores in a human-dominated landscape. LANDSCAPE AND URBAN PLANNING 183:50–58.

Smith, J. A., K. M. Gaynor, and J. P. Suraci. 2021. Mismatch Between Risk and Response May Amplify Lethal and Non-lethal Effects of Humans on Wild Animal Populations. Frontiers in Ecology and Evolution 9:1–13.

Smith, J. A., J. P. Suraci, M. Clinchy, A. Crawford, D. Roberts, L. Y. Zanette, and C. C. Wilmers. 2017. Fear of the human 'super predator' reduces feeding time in large carnivores. Proceedings of the Royal Society B: Biological Sciences 284:20170433.

Smith, J. A., Y. Wang, and C. C. Wilmers. 2016. Spatial characteristics of residential development shift large carnivore prey habits. The Journal of Wildlife Management 80:1040–1048.

Smith, J., Y. Wang, and C. C. Wilmers. 2015. Top carnivores increase their kill rates on prey as a response to human-induced fear. Proceedings of the Royal Society B: Biological Sciences 282:20142711.

St Clair, C. C., J. Backs, A. Friesen, A. Gangadharan, P. Gilhooly, M. Murray, and S. Pollock. 2019. Animal learning may contribute to both problems and solutions for wildlife-train collisions. Philosophical Transactions of the Royal Society B: Biological Sciences 374:20180050.

Stephens, P. A., N. Pettorelli, J. Barlow, M. J. Whittingham, and M. W. Cadotte. 2015. Management by proxy? The use of indices in applied ecology. Journal of Applied Ecology 52:1–6.

Stewart, S. I., V. C. Radeloff, R. B. Hammer, and T. J. Hawbaker. 2007. Defining the wildland-urban interface. Journal of Forestry 105:201–207.

Suraci, J. P., M. Clinchy, L. Y. Zanette, and C. C. Wilmers. 2019a. Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. Ecology Letters 22:1578–1586.

Suraci, J. P., L. G. Frank, A. Oriol-Cotterill, S. Ekwanga, T. M. Williams, and C. C. Wilmers. 2019b. Behavior-specific habitat selection by African lions may promote their persistence in a human-dominated landscape. Ecology 100:e02644.

Syphard, A. D., A. Bar Massada, V. Butsic, and J. E. Keeley. 2013. Land Use Planning and Wildfire: Development Policies Influence Future Probability of Housing Loss. PLoS ONE 8:1–12.

Theobald, D. M. 2001. Land-Use Dynamics beyond the American Urban Fringe. Geographical Review 91:544.

Theobald, D. M. 2005. Landscape patterns of exurban growth in the USA from 1980 to 2020. Ecology and Society 10.

Theobald, D. M., J. R. Miller, and N. T. Hobbs. 1997. Estimating the cumulative effects of development on wildlife habitat. Landscape and Urban Planning 39:25–36.

Therneau, T. M. 2015. A Package for Survival Analysis in S.

Thornton, D., K. Zeller, C. Rondinini, L. Boitani, K. Crooks, D. Thornton, K. Zeller, C. Rondinini, L. Boitani, K. Crooks, C. Burdett, A. Rabinowitz, and H. Quigley. 2016. Assessing the umbrella value of a range-wide conservation network for jaguars (Panthera onca). Ecological Applications 26:1112–1124.

Thurfjell, H., S. Ciuti, and M. S. Boyce. 2014. Applications of step-selection functions in ecology and conservation. Movement Ecology 2:4.

Tucker, M. A., K. Böhning-gaese, W. F. Fagan, J. M. Fryxell, B. Van Moorter, S. C. Alberts, A. H. Ali, A. M. Allen, N. Attias, T. Avgar, H. Bartlam-brooks, B. Bayarbaatar, J. L. Belant, A. Bertassoni, D. Beyer, L. Bidner, F. M. Van Beest, S. Blake, N. Blaum, C. Bracis, D. Brown, P. J. N. De Bruyn, F. Cagnacci, D. Diefenbach, I. Douglas-hamilton, J. Fennessy, C. Fichtel, W. Fiedler, C. Fischer, I. Fischhoff, C. H. Fleming, A. T. Ford, S. A. Fritz, B. Gehr, J. R. Goheen, E. Gurarie, M. Hebblewhite, M. Heurich, A. J. M. Hewison, C. Hof, E. Hurme, L. A. Isbell, R. Janssen, F. Jeltsch, P. Kaczensky, A. Kane, P. M. Kappeler, M. Kauffman, R. Kays, D. Kimuyu, F. Koch, B. Kranstauber, S. Lapoint, J. Mattisson, E. P. Medici, U. Mellone, E. Merrill, T. A. Morrison, S. L. Díaz-muñoz, A. Mysterud, D. Nandintsetseg, R. Nathan, A. Niamir, J. Odden, R. B. O. Hara, L. G. R. Oliveira-santos, K. A. Olson, B. D. Patterson, R. C. De Paula, L. Pedrotti, B. Reineking, and M. Rimmler. 2018. Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. Science 359:8–11.

USDA, and USDI. 2001. Urban wildland interface communities within vicinity of Federal lands that are at high risk from wildfire. Federal Register 66:751–777.

Venter, O., E. W. Sanderson, A. Magrach, J. R. Allan, J. Beher, K. R. Jones, H. P. Possingham, W. F. Laurance, P. Wood, B. M. Fekete, M. A. Levy, and J. E. M. Watson. 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. Nature Communications 7:1–11.

Vickers, T. W., J. N. Sanchez, C. K. Johnson, S. A. Morrison, R. Botta, T. Smith, B. S. Cohen, P. R. Huber, H. B. Ernest, and W. M. Boyce. 2015. Survival and mortality of pumas (Puma concolor) in a fragmented, urbanizing landscape. PLoS ONE 10:1–18.

Wang, Y., J. A. Smith, and C. C. Wilmers. 2017. Residential development alters behavior, movement, and energetics in a top carnivore. PLoS ONE 12:e0184687.

Westley, P. A. H., A. M. Berdahl, C. J. Torney, and D. Biro. 2018. Collective movement in ecology: From emerging technologies to conservation and management. Philosophical Transactions of the Royal Society B: Biological Sciences 373.

Wheatley, M., and C. Johnson. 2009. Factors limiting our understanding of ecological scale. Ecological Complexity 6:150–159.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Williams, A. P., J. T. Abatzoglou, A. Gershunov, J. Guzman-Morales, D. A. Bishop, J. K. Balch, and D. P. Lettenmaier. 2019. Observed Impacts of Anthropogenic Climate Change on Wildfire in California. Earth's Future 7:892–910.

Williams, T. M., L. Wolfe, T. Davis, T. Kendall, B. Richter, Y. Wang, C. Bryce, G. H. Elkaim, and C. C. Wilmers. 2014. Instantaneous energetics of cougar kills reveals advantage of felid sneak attacks. Science 346:81–85.

Wilmers, C. C., A. C. Nisi, and N. Ranc. 2021. COVID-19 suppression of human mobility releases mountain lions from a landscape of fear. Current Biology 31:3952-3955.e3.

Wilmers, C. C., Y. Wang, B. Nickel, P. Houghtaling, Y. Shakeri, M. L. Allen, J. Kermish-Wells, V. Yovovich, and T. Williams. 2013. Scale Dependent Behavioral Responses to Human Development by a Large Predator, the Puma. PLoS ONE 8:e60590.

Wilson, B., and A. Chakraborty. 2013. The environmental impacts of sprawl: Emergent themes from the past decade of planning research. Sustainability 5:3302–3327.

Wilson, R. P., I. W. Griffiths, P. A. Legg, M. I. Friswell, O. R. Bidder, L. G. Halsey, S. A. Lambertucci, and E. L. C. Shepard. 2013. Turn costs change the value of animal search paths. Ecology Letters 16:1145–1150.

Wilson, R. S., J. F. Husak, L. G. Halsey, and C. J. Clemente. 2015. Predicting the Movement Speeds of Animals in Natural Environments. Integrative and Comparative Biology 55:1125–1141.

Wolfe, M. L., D. N. Koons, D. C. Stoner, P. Terletzky, E. M. Gese, D. M. Choate, and L. M. Aubry. 2015. Is anthropogenic cougar mortality compensated by changes in natural mortality in Utah? Insight from long-term studies. Biological Conservation 182:187–196.

Yovovich, V., M. L. Allen, L. T. Macaulay, and C. C. Wilmers. 2020. Using spatial characteristics of apex carnivore communication and reproductive behaviors to predict responses to future human development. Biodiversity and Conservation 29:2589–2603.

Yovovich, V., M. Thomsen, and C. C. Wilmers. 2021. Pumas' fear of humans precipitates changes in plant architecture. Ecosphere 12.

Zeller, K. A., T. W. Vickers, H. B. Ernest, and W. M. Boyce. 2017. Multi-level, multi-scale resource selection functions and resistance surfaces for conservation planning: Pumas as a case study. PLoS ONE 12:e0179570.