

Research

Puma responses to unreliable human cues suggest an ecological trap in a fragmented landscape

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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 these cases, animal fear responses may be ineffective and may even exacerbate the risk of anthropogenic mortality. Here, we explore these questions using a 10-year dataset of movement and mortality events for the puma *Puma concolor* population in the fragmented Santa Cruz Mountains of California, for whom the leading cause of death was retaliatory killings by people following livestock loss. We modeled retaliatory killing risk and puma habitat selection relative to residential housing density to evaluate whether puma avoidance of human cues reflected their risk of being killed. 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. Pumas avoided these areas during the day but selected for these high-risk areas at night, resulting in a mismatch between cue and risk impacting 17% of the study area. These results are unlikely to be driven by puma hunting behavior: livestock constitute a very small proportion of puma diets, and we found no evidence for the alternative hypothesis that state-dependent foraging drove depredation of livestock and subsequent retaliatory killings. Our findings indicate that puma responses to human cues are not sufficient to enable human–carnivore coexistence in this area and suggest that reducing risk from humans in places with few perceptible human cues would facilitate carnivore conservation in human-dominated landscapes. Furthermore, a mismatch between human cues and responses by carnivores can lead to selection rather than avoidance of risky areas, which could result in an ecological trap.

Keywords: ecological trap, ecology of fear, habitat fragmentation, habitat selection, human-dominated landscape, *Puma concolor*

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 components of fitness, including survival and reproduction, may be impossible for an animal 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). Relationships between habitat cue and habitat quality are often disrupted in human-dominated environments (Delibes et al. 2001, Sih 2013), and may produce ecological traps, which occur when animals select low-quality areas (Schlaepfer et al. 2002, Robertson and Hutto 2006, Robertson et al. 2013, Hale and Swearer 2016). Understanding when and where ecological traps occur as well as the mechanisms that produce them is essential for conservation efforts, as traps can magnify source–sink dynamics and threaten population viability (Battin 2004).

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. 2019a). 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. Mismatches between cue and risk can result in suboptimal behavior strategies and lead to both lethal and non-lethal effects, amplifying the costs associated with living alongside humans (Smith et al. 2021). Mismatches between cue and risk, and more broadly between habitat cue and habitat quality, are of conservation importance: if anthropogenic cues and risk do not align, then behavioral responses that should function to mitigate risk from humans may be ineffective and could 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). 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. 2019a). 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. 2019a). However, whether anthropogenic cues reflect the risk of being killed by people and the degree to which fear responses mitigate anthropogenic mortality remain 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 degree to which carnivore fear responses align with actual risk from humans. 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, 2021, Smith et al. 2017, Suraci et al. 2019b). 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 retaliatory killings are an important source of mortality, livestock are not an important prey item for pumas, making up a very small portion of their diets (4%; Smith et al. 2016). Pumas avoid human infrastructure and other cues of immediate human presence but 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 puma behavioral responses to human cues are decoupled from actual risk. 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 whether and how carnivore fear responses enable avoidance of anthropogenic risk, 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 km² 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 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 from 2009 to 2019 using trained hounds or box traps and anaesthetized them with Telazol. We fit pumas with GPS collars set to record a GPS location at least every 4 h, and those that recorded with higher frequencies were subset to 4-h locations for all analyses. We used GPS Plus and GPS Vertex collars produced by Vectronics Aerospace as well as one collar produced by Lotek. Data from the Lotek collar was just used to identify that individual's mortality location and was not included in habitat selection analyses.

Rate of retaliatory killings

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. Retaliatory killings are defined as legally permitted or unpermitted, confirmed retaliatory deaths following livestock consumption. We estimated overall mortality rates using the Kaplan–Meier procedure fit with the survival package in R ver. 3.6.0 (Fieberg and DelGuidice 2009, Therneau 2015). We 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). These analyses were fit to time-to-event data from all collared pumas in an annual-recurrent study design. Pumas entered the study on the first day that they were collared, and pumas whose collars dropped prior to their death were right-censored on the date of their last GPS location.

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. 2019b). While carnivore avoidance of human features could reflect poor habitat quality for other reasons, experimental work in our system has demonstrated that pumas fear humans (Smith et al. 2017, Suraci et al. 2019b). 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 responses to human cues, 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 ($w_{mov}(\mathbf{x})$, for movement locations > 20 m from the previous location) takes the exponential form, $w_{mov}(\mathbf{x}) = \exp(\boldsymbol{\beta}\mathbf{x})$, where \mathbf{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 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 $[0, 2\pi]$ uniform distribution (Forester et al. 2009). To determine the appropriate number of available steps to include for each used location, we varied the number of available locations drawn (between 1 and 50) and determined when coefficient estimates stabilized (Northrup et al. 2013, Thurfjell et al. 2014, Fieberg et al. 2021). This analysis revealed that drawing 20 available locations for each used location was sufficient to produce unbiased coefficient estimates (Supporting information).

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 500 m 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 were right skewed and pumas spent much of their time at low housing densities, so we cube root transformed these data so that standardized coefficients better reflected the range of housing density experienced by pumas. 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, <www.usgs.gov/core-science-systems/ngp/national-hydrography>), and percent cover calculated from California GAP data (Gap Analysis Project, USGS, <www.usgs.gov/core-science-systems/science-analytics-and-synthesis/gap>) over a 90×90 m moving window calculated using a focal analysis in the raster package (Hijmans 2019). Step distance (log transformed) and directional persistence ($\cos[\theta_i - \theta_{i-1}]$, with $\theta_i - \theta_{i-1}$ representing the difference in cardinal direction between the previous two steps) were also included as predictors as has been recommended in previous studies (Duchesne et al. 2015, Forrester et al. 2015). All spatial covariates were rasterized at 30×30 m resolution and were standardized, and did not change over the course of the study. Generalized estimating equations (GEE) 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 (model 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 (model M3 and M4). Thus, we built several candidate models with and without interactions and non-linear relationships and used quasi-likelihood information criterion (QIC), suggested for use with GEE-based analyses, to evaluate model support, with models $< 2 \Delta QIC$ compared to the top model considered strongly supported (Pan 2001). We tested for spatial autocorrelation using Moran's I correlograms in model residuals against distance, using a random subset of 10 000 locations and 1000 bootstrapping iterations in the ncf package, and no distance bins exhibited significant levels of spatial autocorrelation (Supporting information).

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). Here, the relative probability of retaliatory killing ($w_{rk}(\mathbf{x})$) also takes the form $w_{rk}(\mathbf{x}) = \exp(\boldsymbol{\beta}\mathbf{x})$

where \mathbf{x} are covariates associated with GPS locations and covariate effects $\boldsymbol{\beta}$ are estimated via logistic regression (Manly et al. 2002). Available locations were drawn from the study area as defined by merged 95% minimum convex polygons (MCPs) for collared individuals. This provided an inclusive measure of availability on the landscape which would include the ranges of both collared and uncollared pumas. To ensure that habitat types were represented in proportion to their use, however, we then weighted available locations by the relative probability of use of those areas by pumas from our habitat selection analyses.

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 23 November 2009 to 31 December 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 $w_{mr}(\mathbf{x})$ 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 (Supporting information). From those 10 000 locations, we then sampled a subset of 1000 locations weighted by $w_{mr}(\mathbf{x})$ 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 500 m-scale to reflect the larger-scale gradient of human use and was cube root transformed. 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 510×510 m moving window using a focal analysis in the raster package (Hijmans 2019) using the cover definitions as presented in the Supporting information. 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 $< 2 \Delta\text{AICc}$ to be strongly supported (Burnham and Anderson 2002). Candidate models included a model with percent cover only (model R1), a linear relationship between housing density and risk (model R2), a quadratic relationship between housing density and risk (model R3) and models with linear and quadratic housing density relationships along with percent cover (model 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 ($w_{\text{mvt}}(\mathbf{x})$) 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. A previous study (Smith et al. 2015) developed a logistic regression that related characteristics of clusters of puma GPS locations to whether those clusters were kill sites. Using that model, we identified predicted kill sites for pumas to estimate time since last predicted deer kill (Supporting information). We also used t-tests 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 annual mortality rate for pumas in the SCM was 0.252 (95% CI [0.169, 0.327]). Of the 33 deaths observed

from 65 collared individuals, 17 were from confirmed anthropogenic causes (12 retaliatory killings, 4 vehicle strikes and 1 poaching event not related to livestock depredation). The cause-specific annual mortality rate for retaliatory killings was 0.090 (95% CI [0.049, 0.131]), and retaliatory killings accounted for 36% of total mortality and the majority of anthropogenic mortality.

Locations of retaliatory killings for both collared and uncollared pumas ($n = 32$) were most likely to occur at intermediate housing densities ($\beta_{\text{HD}} = 1.625$, 95% CI [0.799, 2.451]; $\beta_{\text{HD}^2} = -0.785$, 95% CI [-1.313, -0.258]; Fig. 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 ($\beta_{\text{cover}} = -0.394$, 95% CI [-0.702, -0.086]) and was included in the model with the most support (Table 1). Other sources of mortality were distributed randomly with respect to housing density (Table 1, Fig. 2). Indeed, the null model was among the top competing models ($\Delta\text{AICc} = 0.56$) and superior to all models including housing density ($\Delta\text{AICc} \geq 1.99$), suggesting no support for an influence of housing density on the combined risk of mortality from other causes.

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 2 May 2009 to 18 August 2019; Table 2, Supporting information). In contrast, at night pumas selected intermediate levels of housing density and avoided housing less strongly overall (Fig. 1B). Comparing risk and habitat selection indicated a mismatch between avoidance behavior and areas where retaliatory killings were most likely to occur (Fig. 1B, 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. 3C).

There was no difference in mean weights of pumas killed following depredation events compared to weights observed from live pumas during captures for either females (retaliatory killing weights: 35.2 kg, SD = 2.5 kg, $n = 3$; capture weights: 37.1 kg, SD = 3.8 kg, $n = 56$; $p = 0.30$) or males (retaliatory killing weights: 49.0 kg, SD = 9.6 kg, $n = 14$; capture weights: 50.8 kg, SD = 9.6 kg, $n = 63$; $p = 0.60$). 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. 4). Mean kill rates were 62.1 (SD = 15.7, $n = 29$) deer year⁻¹ for females and 51.8 (SD = 22.8, $n = 33$) deer year⁻¹ for males, corresponding to mean inter-kill intervals of 6.27 (SD = 1.88) and 8.71 (SD = 4.45) days, respectively. Mean time since last predicted deer kill for pumas killed following livestock depredation was 6.58 (SD = 0.590, $n = 2$) days for females and 7.69 (SD = 4.52, $n = 8$) 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 (mean = 55.0 months, SD = 26.7, $n = 21$; $p = 0.40$).

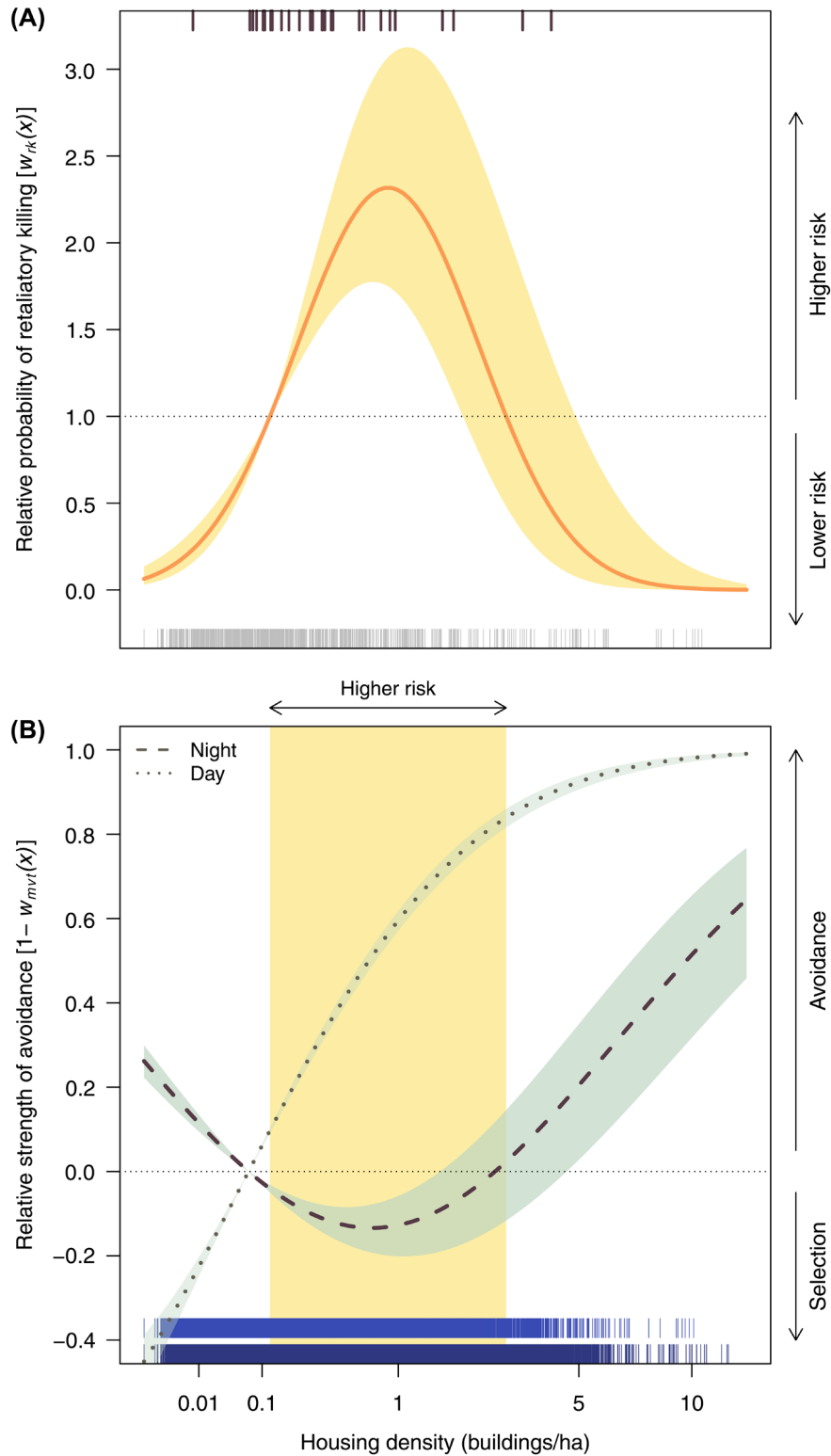


Figure 1. Retaliatory killing risk peaked at intermediate housing densities (A), creating a mismatch between risk and puma behavior during high-risk times (i.e. nighttime; B). In (A), predicted relative probability of retaliatory killing values > 1 indicate that retaliatory killings are more likely than 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 black (top) show housing densities at retaliatory killing locations, and grey (bottom) show available locations. In (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.

Table 1. Model selection for analyses of retaliatory killing locations and locations of mortality from other sources for pumas in the Santa Cruz Mountains. The AICc value for the top model for retaliatory killings was 261.61 and for other mortalities was 206.13, and ΔAICc are the difference in AICc between each model and the top model. Model numbers correspond to model descriptions in the Methods section, and HD denotes housing density.

Cause of death		Model	Deviance	Log likelihood	ΔAICc	Model weight
Retaliatory killing	R5	Cover + HD + HD ²	253.57	-126.78	0.00	0.86
	R3	HD + HD ²	259.26	-129.63	3.67	0.14
	R4	Cover + HD	270.15	-135.07	14.56	< 0.001
	R2	HD	277.95	-138.98	20.36	< 0.001
	R1	Cover	279.08	-139.54	21.48	< 0.001
	Null		285.30	-142.65	25.70	< 0.001
Other	R1	Cover	202.12	-101.06	0.00	0.37
	Null		204.69	-102.35	0.56	0.28
	R4	Cover + HD	202.10	-101.05	1.99	0.14
	R2	HD	204.66	-102.33	2.54	0.10
	R5	Cover + HD + HD ²	201.65	-100.82	3.55	0.06
	R3	HD + HD ²	204.34	-102.17	4.23	0.04

Discussion

We demonstrated a spatially widespread mismatch between human cues, the associated fear response and the risk of the leading cause of anthropogenic mortality for pumas in the SCM. 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, they did not successfully distinguish the conditions where risk from humans was highest. Rather, in terms of retaliatory killings, 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

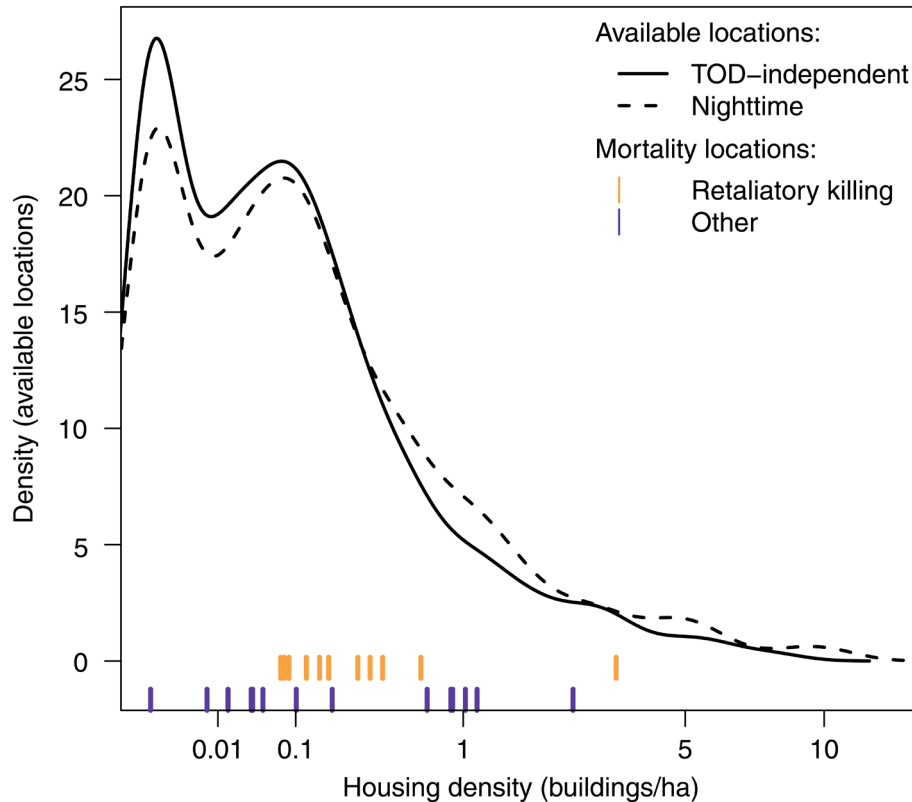


Figure 2. Distribution of locations of retaliatory killings and other mortalities for collared pumas across the housing density gradient (rug plots). Lines show the distribution of housing density at available locations, with time allocation controlled for using time-of-day-independent (solid) and nighttime-only (dashed) habitat selection.

Table 2. Model selection for step selection functions describing puma habitat selection in the Santa Cruz Mountains. The QIC value for the best fit model was 652491.11 and ΔQIC are the difference in QIC between each model and the top model. Model numbers correspond to model descriptions in the Methods section.

	Model	Log likelihood	ΔQIC	Model weights
M4	Quadratic (night interaction)	-325 977.72	0.00	1.00
M3	Linear (night interaction)	-326 332.42	641.56	0.00
M2	Quadratic	-327 487.11	2965.74	0.00
M1	Linear	-327 731.72	3408.48	0.00

people. Here we found that housing density as a risk cue was not monotonically related to the main source of 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 effectively mitigate retaliatory killing risk.

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. 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. 2015, Gaynor et al. 2018, Suraci et al. 2019a) 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 that risk. Instead, unreliable cues led pumas to select the conditions where they were most likely to be killed.

Humans can be unpredictable predators, and in this case we found that risk of the leading cause of anthropogenic mortality 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. While historically, puma persecution by people was widespread, now 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 that do 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.

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). However, our data did not support this alternative conclusion, as both body condition

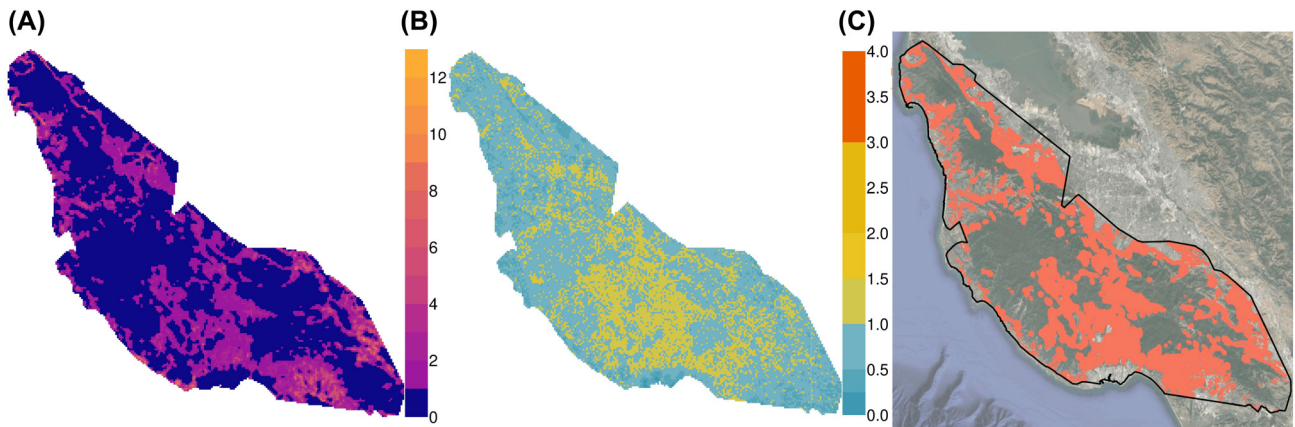


Figure 3. Maps showing (A) relative risk of retaliatory killing ($w_{rk}(x)$), (B) relative probability of nighttime selection ($w_{mnt}(x)$) and (C) mismatched fear responses across the SCM study area. In (A) values > 1 indicate higher retaliatory killing risk than would occur at random and in (B) values > 1 indicate selection. Mismatches 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.

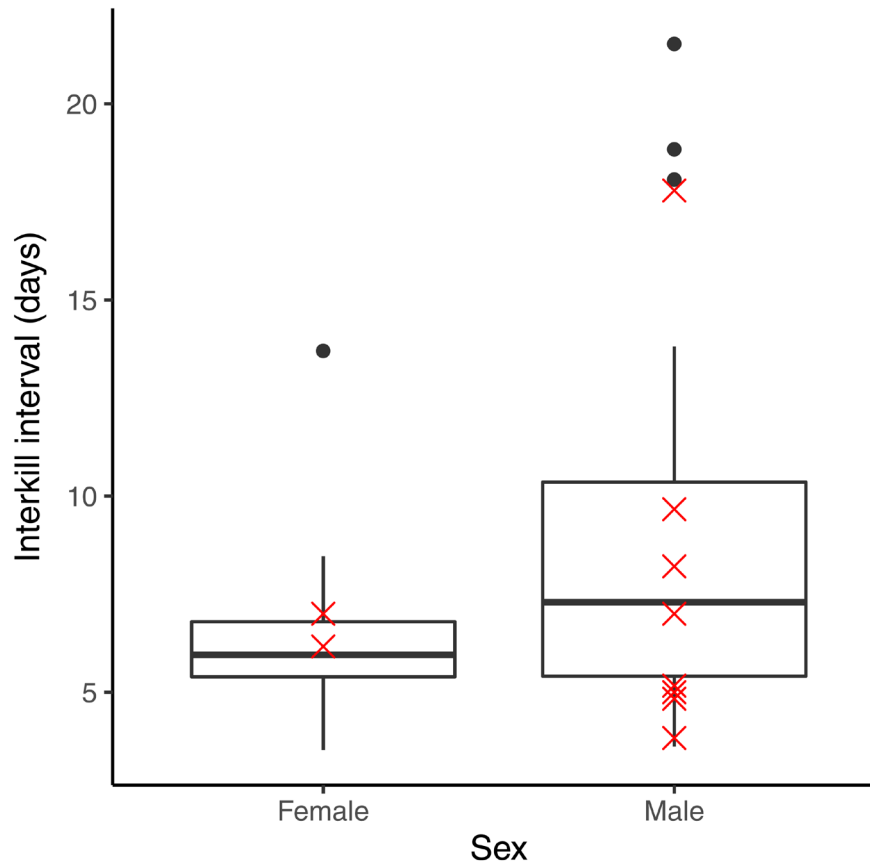


Figure 4. Box plots showing the inter-kill intervals for all collared pumas. Red points are time since last predicted kill for collared pumas killed after consuming livestock.

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. Additionally, domestic livestock represent a very small portion of puma diets in the Santa Cruz Mountains – black-tailed deer make up 90.0% of puma diet by biomass, with livestock representing only 4.1% (Smith et al. 2016). While domestic livestock present substantial risk to pumas via the threat of retaliatory killings, they do not constitute a major food resource or subsidy. 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.

It is possible that a mismatch between unreliable anthropogenic cues and animal fear responses could lead to an ecological trap. Here, we document pumas selecting, rather than avoiding, areas that present high levels of risk for the leading cause of death for this population, suggesting that habitat selection and habitat quality may be misaligned. For a trap to definitively be demonstrated, fitness must be quantified across habitats (Robertson and Hutto 2006, Robertson et al.

2013) and our study presents information on only one factor of fitness (survival), rather than overall fitness. However, there is evidence that accounting for other components of fitness would not counteract the mortality costs associated with higher retaliatory killing risk at intermediate housing densities. Survival, rather than reproduction, is expected to drive fitness for large carnivores: survival correlates to lifetime reproductive success for K-selected species (Pianka 1970, Beckmann and Lackey 2008, Johnson et al. 2020), is the most important driver of population dynamics of pumas and other large carnivores (Heppell et al. 2000, Robinson et al. 2014, Benson et al. 2016), and has been used as a reliable proxy for individual fitness in other large carnivore studies (Nielsen et al. 2006, Benson et al. 2015). As the leading cause of death for this population, retaliatory killings are an important component of overall survival, and by extension fitness. Retaliatory killings also constituted the majority of deaths caused by humans: we observed three times as many retaliatory killing deaths than vehicle collisions for collared pumas. Additionally, 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 survival costs at intermediate levels of housing were offset by

fitness gains in these areas, either through reproduction or resource acquisition. Reproduction has a lower fitness contribution than survival for large carnivores (Beckmann and Lackey 2008, Johnson et al. 2020), and pumas strongly avoid housing while reproducing and raising young, including areas of intermediate housing density (Wilmers et al. 2013, Yovovich et al. 2020). There is also 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 areas of higher housing density, 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). While it is unclear why pumas select intermediate housing densities at night, it is possible that pumas simply must move through these areas since development is so widespread throughout the landscape and choose to do so when humans are less active (Nisi et al. 2022a). 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). Second, especially for bear species (*Ursus* spp.), anthropogenic subsidies can create high-risk, high-reward areas, where human-associated resource inputs promote preference or use of habitats that have higher anthropogenic mortality risk (Nielsen et al. 2006, Lamb et al. 2017, Penteriani et al. 2018, St Clair et al. 2019, Johnson et al. 2020). As anthropogenic landscapes of fear are common among large carnivore species as well as other taxa (Frid and Dill 2002), the purported mechanism we describe here, whereby a mismatch between human cue and animal response might result in an ecological trap, has the potential to be taxonomically and geographically widespread. Thus, depending on whether and how the mismatch impacts individual fitness, ecological traps arising via this mechanism could impact a variety of species and systems.

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 cue/behavior mismatches are identified, they can be remedied either by improving the reliability of cues or improving habitat quality (Robertson and Hutto 2006, Smith et al. 2021). 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. Mismatched fear responses 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.

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Author contributions

Anna C. Nisi: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **John F. Benson:** Writing – review and editing (equal). **Christopher C. Wilmers:** Conceptualization (equal); Data curation (equal); Funding acquisition (lead); Project administration (lead); Resources (equal); Supervision (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.7291/D1JT30>> (Nisi et al. 2022b).

Supporting information

The supporting information associated with this article is available from the online version.

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