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**SHOULD I STAY OR SHOULD I GO? IMPACTS OF PEOPLE ON
PREDATORS LIVING IN A HUMAN-DOMINATED LANDSCAPE**

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ENVIRONMENTAL STUDIES

by

Barry A. Nickel

September 2019

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ABSTRACT

SHOULD I STAY OR SHOULD I GO? IMPACTS OF PEOPLE ON PREDATORS LIVING IN A HUMAN-DOMINATED LANDSCAPE

Barry Nickel

In many of the world's natural areas, humans now play, work, or live alongside wildlife with measurable effects on their physiology, behavior, and ecology. In particular, there is growing evidence of human-induced changes in the energetics, movement, and space use of many wildlife species, including large bodied predators, suggesting that fear of humans is a common phenomenon. For large carnivores, movement can be energetically expensive such that slight variations in the physical landscape can have profound impacts on the energy cost of movement. Large carnivores also face significant mortality risk from the human "super predator", and resulting fear-based changes in space use may exert energetic costs by affecting how, where, and to what extent carnivores move when in proximity to humans.

In this dissertation, I integrate these two factors to understand how competing demands around energy and risk shape the behavior and spatial ecology of free-ranging pumas (*Puma concolor*). In particular, I quantify the joint effect of the physical and risk landscapes on the fine-scale movement of pumas and evaluate whether short-term costs drive landscape-level patterns of space use. I also examine whether pumas optimize energy economy when traveling on challenging terrain and the degree to which they cope with increased movement costs near humans. Results

show that the combination of the physical and risk landscapes drives short-term movement costs for pumas, and that short-term costs, particularly those stemming from human-induced risk, scale up to influence long-term space use at the landscape scale. Further, pumas use energetically efficient movement pathways where possible, however, in areas of increasing risk from humans they adopt energetically sub-optimal paths characterized by high energy but low efficiency movement behavior. This pattern reflects a trade-off between risk avoidance and the energy costs of movement that results in a constriction of overall space use for individuals experiencing consistently high movement costs. These findings demonstrate that, along with physical terrain, predation risk plays a primary role in shaping an animal's "energy landscape" and suggests that fear of humans may be a major factor affecting wildlife movements worldwide.

In addition, I evaluate the concurrent effects of the human footprint (development) and presence (activity) on wildlife behavior as well as model where and when the immediate presence of people, and thus disturbance, is likely to be greatest outside developed areas. Results demonstrate that, for many species, human presence and human footprint are not equivalent in their impacts on wildlife habitat use and behavior, with these two forms of anthropogenic disturbance in many cases having opposing effects on occupancy and/or activity. In particular, several carnivores, including pumas, avoided developed areas but were more likely to occupy sites with high human presence (potentially due to increased access to trails) by increasing nocturnality. By contrast, synanthropic species were more likely to

occupy sites with higher building density, consistent with use of anthropogenic resources, but were substantially less detectable in areas with high human presence. Further, I found that human presence beyond developed areas to be extensive and concentrated in protected areas suggesting human impacts on wildlife may be more widespread in the region than anticipated. Given the prevalence of development and human activity in wildlands, complete avoidance of people is likely impossible for many species in the region and thus negative impacts on wildlife from human disturbance is likely high.

The research presented in this dissertation provides an important extension of recent attempts to quantify the effects of the landscape on animal movement costs by highlighting that, without accounting for predation risk, “energetic landscapes” may overlook much of the energetic cost of navigating complex environments, especially those dominated by humans. In addition, human activity is increasing in most natural ecosystems, and this work underscores the need to rigorously quantify human activity and clarify its effects on wildlife behavior in landscapes where presence of people is widespread.

To the memory of Donald Nickel,

(1936 – 2015)

a kind and gentle father whose light
brought love and laughs to us all.

You are a true inspiration and will be forever missed.

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CHAPTER 1

Introduction

A major challenge facing modern conservation is the expanding human footprint, with growing evidence that the behavior of wildlife in human-dominated landscapes are fundamentally changing in response to the presence of people (Hoffmann et al. 2010, Dirzo et al. 2014, Gaynor et al. 2018, Tucker et al. 2018). While landscape modification, habitat fragmentation, and overexploitation by humans continue to pose a significant threat to wildlife (Hoffmann et al. 2010, Butchart et al. 2010, Dirzo et al. 2014), fear of the human “super predator” (Darimont et al. 2015) correspondingly impacts wildlife by generating landscapes of fear analogous to those documented in natural predator-prey systems (Frid and Dill 2002, Laundré et al. 2010, Ciuti et al. 2012, Zanette et al. 2014). That is, wildlife perceive and respond to humans as threats similar to natural predators and thus should avoid times and places of elevated risk where possible (Frid and Dill 2002, Dröge et al. 2017). Yet, in human-dominated habitat total avoidance of humans is likely impossible thus wildlife in these areas must manage the negative effects of disturbance in order to co-exist with humans (Frid and Dill 2002, Carter et al. 2012, Gaynor et al. 2018, Tucker et al. 2018). Indeed, accumulating evidence suggests that human disturbance is significantly altering the ecology of wildlife worldwide and that the fear induced by humans is likely a common phenomenon among many species (Larson et al. 2016, Gaynor et al. 2018, Tucker et al. 2018).

For large mammalian carnivores, direct loss of habitat, persecution, and prey depletion precipitated by humans and human activity has resulted in major declines in population sizes and geographic ranges of many species (Estes et al. 2011, Crooks et al. 2011, Ripple et al. 2014). Additionally, humans as a perceived source of risk trigger a strong fear response in many carnivores that can disrupt natural patterns of activity (Wang et al. 2017, Gaynor et al. 2018), interfere with predator-prey interactions (Haswell et al. 2017, Smith et al. 2017), and alter habitat and space use dynamics (Oriol-Cotterill et al. 2015a, Loveridge et al. 2017, Tucker et al. 2018, Suraci et al. 2019b). However, several species of large carnivores are seemingly adaptable to living in human dominated landscapes, (Elfström et al. 2014, Knopff et al. 2014, Ripple et al. 2014), yet little is known about the fitness consequences of persistent exposure to humans and products of human activity (e.g. disturbance) in such species (Oriol-Cotterill et al. 2015b). As a far-ranging carnivore that often occupies areas dominated by humans and fears people (Smith et al. 2017), the puma (*Puma concolor*) provides a distinct opportunity for quantifying how the fear of humans shape the behavior and ecology of a large terrestrial carnivore inhabiting a predominately human-dominated landscape.

The pumas extensive space and prey requirements make the impact of human development particularly acute as individual lions can traverse a large gradient of anthropogenic threats resulting in significant shifts in behavior, time, or habitat (Kertson and Spencer 2011, Wilmers et al. 2013, Smith et al. 2015, 2017, Wang et al. 2017). Moreover, the cost of locomotion for pumas can be substantial (Williams et al.

2014, Bryce et al. 2017) and fear-based changes in space use (Wilmers et al. 2013, Wang et al. 2017) may also exert energetic costs by affecting how, where, and to what extent pumas move when in proximity to humans. Despite growing evidence that pumas fear humans (Smith et al. 2015, 2017), our understanding of how pumas cope with living in human-dominated landscapes, the strategies employed by pumas to coexist with humans, and the ultimate role risk plays in their ecology remains limited. Given that much of the natural world has been modified by humans, investigations into fine-scale physiological and behavioral response of pumas to human disturbance should also be relevant to questions regarding the persistence of many large carnivores in natural areas used regularly by people.

In this dissertation, I seek to advance the growing body of literature linking fear-based changes in carnivore ecology to spatial and temporal variation in human use of the landscape. Specifically, I investigate how competing demands around energy and human-induced fear shape the spatial ecology of free-ranging pumas in the Santa Cruz Mountains. Further, I assess the degree to which pumas optimize the energy economy of travel when traversing human-modified landscapes and quantify any corresponding trade-offs associated with short-term changes in movement due to fear. Finally, I examine the overlap between people and carnivores to disentangle the effect of the human footprint and human activity on wildlife behavior and subsequently quantify the broad-scale dynamics of human presence on the landscape beyond developed areas.

In Chapter 2, I quantify the joint effect of the physical landscape and predation risk on the fine-scale movement of pumas and evaluate whether short-term movement costs scale up to determine landscape-level patterns of space use. I show that the combination of the physical and risk landscapes drives short-term movement costs for pumas, and that short-term costs, particularly those stemming from human-induced risk, scale up to influence long-term space use at the landscape scale. This work demonstrates that, along with physical terrain, predation risk plays a primary role in shaping an animal's "energy landscape" and suggests that fear of humans may be a major factor affecting wildlife movements worldwide.

In Chapter 3, I examine whether pumas optimize energy economy when traveling on challenging terrain and the degree to which they cope with increased movement costs near humans due to sub-optimal travel. Results indicate that pumas traveling in environments with highly variable movement costs use energetically efficient movement pathways, however, as their exposure to human development and thus perceived risk increases their use of energetically sub-optimal paths become more prevalent. Despite the extra costs associated with sub-optimal travel, pumas still seek to optimize energy by moving as efficiently through the landscape where possible. These results suggest that pumas dynamically integrate both the energy and risk landscape when evaluating the cost of moving through different environments and highlight the synergistic nature of the energy and fear landscapes (Gallagher et al. 2016) in driving animal movement.

Finally, Chapter 4 evaluates the concurrent impact of the human footprint (development) and presence (activity) on wildlife habitat use and activity patterns. Both human presence and human footprint may simultaneously influence wildlife behavior, however our ability to disentangle these two classes of anthropogenic disturbance in their effects on wildlife remains limited, as does our capacity to predict the spatial extent of human presence independently of human footprint and thus to determine where on the landscape this disturbance type is likely to operate. Results demonstrate that human footprint and human presence have non-equivalent, and in some cases opposing, effects on the occupancy and activity patterns of wildlife. Further, the impacts of human presence extend well beyond the spatial footprint of developed regions and are particularly concentrated in protected areas with high recreational potential. Moreover, the intensity of human presence can be predicted from landscape-level variables allowing for the estimation of human impacts on wildlife even in wilderness areas. These results refine our understanding of how both human activity and development drive changes in wildlife behavior and underscore the importance of integrating multiple sources of disturbance when evaluating the degree to which human-derived risk affects wildlife.

In the final chapter (Chapter 5), I synthesize the findings from all three data chapters and discuss how this dissertation improves our understanding of the role human-induced risks plays in shaping the ecology of wildlife living in natural landscapes shared with humans. I conclude by highlighting the novel approaches developed for measuring human use and its impacts on wildlife behavior, in

particular, the focus on the energetic consequences of human disturbance, clarification of disturbance effects, and the quantification of the intensity and spatial distribution of human presence in wildland areas. Together, this work provides an important extension of recent attempts to quantify the effects of the landscape on animal movement and should provide new insights regarding human-caused disturbance of wildlife.

CHAPTER 2

Energetics and fear of humans constrain the spatial ecology of pumas

ABSTRACT

Energetic demands and fear of predators are considered primary factors shaping animal behavior, and both are likely drivers of movement decisions that ultimately determine the spatial ecology of wildlife. Yet energetic constraints on movement imposed by the physical landscape have only been considered separately from those imposed by risk avoidance, limiting our understanding of how short-term movement decisions scale up to affect long-term space use. Here, I integrate the costs of both physical terrain and predation risk into a common currency, energy, and then compare their effects on the short-term movement and long-term spatial ecology of a large carnivore living in a human-dominated landscape. Using high-resolution GPS and accelerometer data from collared pumas (*Puma concolor*), I calculated the short-term (i.e., five-minute) energetic costs of navigating both rugged physical terrain and a landscape of risk from humans (major sources of both mortality and fear for this study population). Both the physical and risk landscapes affected puma short-term movement costs, with risk having a relatively greater impact by inducing high energy but low efficiency movement behavior. The cumulative effects of short-term movement costs lead to constraints on both daily travel distances and total home range area. For male pumas, these constraints on long-term space use were predominantly driven by the energetic costs of human-induced risk. This work demonstrates that, along with physical terrain, predation risk plays a primary role in

shaping an animal's "energetic landscape" and suggests that fear of humans may be a major factor affecting wildlife movements worldwide.

INTRODUCTION

Despite broad recognition that both energetic demands and avoidance of risk from predators shape animal decision making across contexts, these factors have traditionally been examined separately when considering wildlife movement behavior and space use. Animal movement is an energetically expensive activity (Taylor et al. 1982, Garland 1983, Karasov 1992) that also plays a primary role in risk avoidance (Vanak et al. 2013, Suraci et al. 2019b). Yet the recently popularized "energy landscape", which describes the effects of the physical environment on energetic costs of movement (Wilson et al. 2012, Shepard et al. 2013, Halsey 2016), has yet to be integrated with the "landscape of fear", defined as spatial variation in perceived risk from predators (Laundré et al. 2001, Gaynor et al. 2019). Combining fear and energetic costs of movement in a common currency across broad spatial scales may dramatically improve our ability to predict space use in free-living wildlife.

Integrating these two constraints on movement may be particularly crucial for understanding space use by large carnivores living in human-dominated landscapes. The cost of locomotion for these highly mobile species can be substantial, such that slight variations in the physical landscape can have profound impacts on movement costs and path choice (Gorman et al. 1998, Williams et al. 2014, Pagano et al. 2018). Large carnivores also face significant mortality risk from the human "super predator"

(Darimont et al. 2015), and resulting fear-based changes in space use (Wilmers et al. 2013, Oriol-Cotterill et al. 2015a, Loveridge et al. 2017, Tucker et al. 2018) may also exert energetic costs by affecting the areas selected (e.g., for safety) and how carnivores move (e.g., travel speed, locomotion strategy) when in proximity to humans.

At the smallest scales, movement reflects immediate behavioral responses to internal states or external cues (Nathan et al. 2008, Morales et al. 2010), which, when integrated over longer time periods, lead to large-scale patterns of space use, including home range formation (Van Moorter et al. 2009, 2015). Thus, physical (e.g., topographic) and risk-based constraints on fine-scale movement may scale up to determine landscape-level patterns of large carnivore space use, including home range size (Fig. 1). However, the relative importance of such physical vs. ecological constraints on both the small- and large-scale spatial ecology of large carnivores remains unknown.

As a far-ranging carnivore that often occupies rugged terrain and is known to fear humans (Smith et al. 2017), the puma (*Puma concolor*) provides a distinct opportunity to quantify how the energetic costs of the physical landscape and risk avoidance shape large-scale patterns of space use. Despite incurring large transport costs due to their natural history, large body size, and low aerobic capacity (McNab 2000, Williams et al. 2014, 2015, Bryce et al. 2017), pumas persist in what would appear to be energetically challenging habitats (Williams et al. 2014, Wang et al. 2017), including areas dominated by humans (Smith et al. 2015, 2017), whose

presence may exacerbate the costs of challenging physical terrain. This study uses high temporal and spatial resolution GPS and tri-axial accelerometer data to understand how the physical and risk landscapes interact to shape the movement ecology of free-ranging pumas through their effects on energy. I hypothesize that changes in the energetic costs of travel attributable to landscape features and human-derived risk affect puma movement capacity at the step level, with ultimate impacts on the overall extent of space use at the landscape scale.

MATERIAL AND METHODS

1. Study area

This research was conducted in the Santa Cruz Mountains (37° 10.00' N, 122° 3.00' W), which lie in the Central Coast region of California (Fig. 1). In the study area, pumas primarily feed on black-tailed deer (*Odocoileus hemionus columbianus*) but occasionally on other species, including wild boars (*Sus scrofa*), raccoons (*Procyon lotor*) and domestic cats (Smith et al. 2016). The 1,700 km² study area is bisected by a large freeway and further crisscrossed by numerous smaller roads providing access to rural houses and developments.

2. Data collection

Starting in 2015, wild pumas were captured using trailing hounds or cage traps, as described in Wilmers et al. (2013). Each animal was tranquilized using Telazol and sexed, weighed, aged, and fitted with a commercial off-the-shelf

GPS/VHF collar (Vectronics Aerospace GPS PLUS) combined with an archival tri-axis accelerometer tag. Each collar was programmed to acquire a GPS fix every 5 minutes and tri-axial acceleration at a frequency of 16-32 Hz for a duration of 2 months. The GPS sampling interval was chosen to maximize relocations while ensuring that each animal could traverse their home range multiple times before the collar battery died.

I recorded 247,110 GPS locations for 13 pumas (5 females, 8 males, see Fig.2 for distribution) for a mean (\pm se) of 19,009 (\pm 753) locations per animal. The mean (\pm se) number of days that location data was recorded for each puma was 66 (\pm 3) days. The GPS fix success rate ranged from 98.2% to 99.9% with a mean (\pm se) of 99.2% (\pm 0.2) across all collars.

3. Derivation of energetic cost

The instantaneous energetic cost (kJ) and mass specific cost of transport ($\text{J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}$) was computed using an equation for converting accelerometer-derived activity into energetic costs, developed in lab trials with pumas (Williams et al. 2014). To account for the complexities of traversing a variable landscape over each 5-minute inter-location interval, I treated sampled observations as the straight-line path between successive geographic locations, s_t and s_{t+1} , as opposed to the instantaneous geographic location at time t , s_t . As such, movement costs here are distinguished from instantaneous energetic costs by calculating the mean metabolic rate ($\text{kJ}\cdot\text{min}^{-1}$)

and mean mass specific cost of transport ($\text{J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}\cdot\text{min}^{-1}$), referred to above as the landscape cost of transport (LCOT), for each five-minute interval.

4. Derivation of movement modes

I fit a three-state Hidden Markov Model (HMM) using the combined GPS and accelerometer data to distinguish between three behavioral classes: stationary, meandering, and directed movement (Wilmers et al. 2017). The stationary state represents behaviors such as resting, feeding, and grooming while the meandering and directed states are often associated with searching and foraging behaviors or transit and territorial patrol, respectively. Using the R package *momentuHMM* (McClintock and Michelot 2018) the movement of each individual was classified into one of three underlying states by characterization of the distributions of travel distances, turning angles, and metabolic rate ($\text{kJ}\cdot\text{min}^{-1}$) between consecutive locations. Travel distance is calculated as the Euclidean distance between the locations (x_t, y_t) and (x_{t+1}, y_{t+1}) , and turning angle is calculated as the change in bearing ($b_t = \text{atan2}((y_{t+1} - y_t), (x_{t+1} - x_t))$) between the intervals $[t - 1, t]$ and $[t, t + 1]$. For this HMM, Gamma distributions were used to describe travel distances and metabolic rates, a von Mises distribution described the turning angles, and the Viterbi algorithm was used to estimate the most likely sequence of movement states to have generated the observations (Langrock et al. 2012).

I began with the assumptions that resting behavior was characterized by very short travel distances, sharp turning angles, and low energy expenditure; meandering

movement by moderate travel distances, sharp turning angles, and moderate energy expenditure; and directed movement by longer travel distances, small turning angles, and higher energy expenditure. Therefore, initial state-dependent probability distribution parameters for travel distance were set at 10 (± 5) m when pumas were resting, 50 (± 25) m when meandering, and 125 (± 50) m when engaged in directed movement. Initial parameters for turn angles were set at $\pi/2$ radians when resting or meandering and 0 radians when directly moving. Angle concentration for each state was initially set at 1. For mean metabolic rate, initial parameters were set at 10 (± 5) $\text{kJ}\cdot\text{min}^{-1}$, 25 (± 5) $\text{kJ}\cdot\text{min}^{-1}$, and 35 (± 5) $\text{kJ}\cdot\text{min}^{-1}$ for resting, meandering, and directed movement, respectively.

Data from periods of relative inactivity (e.g., resting) can appear similar to those from periods of meandering behavior due to bias from GPS measurement error (Hurford 2009). Thus, to better distinguish between these behaviors I also characterized clusters of GPS locations that were potential kill sites, day beds, or short term stops during travel. I developed a custom program using the Python programming language (v. 2.7.9; Python Software Foundation, Wilmington, DE, USA) to define clusters as groups of ≥ 3 locations in which each location was within 25 meters of the cluster centroid and 1 hour of another GPS location of the same individual puma. Identified clusters representing resting behavior were then assigned as known states within the HMM framework. Since I did not intend to model the energetics of stationary behavior, subsequent analysis focused only on the predicted movement-based behaviors, meandering and directed travel.

Results of the three-state movement model identified resting as the most common behavioral state for all animals with only 20.7% (± 1.7) of the locations attributed to one of the movement-based behaviors, meandering and directed. When engaged in movement-based behavior, both states were predicted at roughly equal proportions and occurred predominately at night with a mean ($\pm se$) of 73.6% (± 1.7) of locations occurring between local sunrise and sunset.

5. Natural and anthropogenic landscape covariates

I included land cover, topographic and risk-related covariates to assess the role habitat complexity and potential risk plays in modulating energy cost and acquisition. I divided land cover into agriculture, grassland, shrub, forest, and wetland using USGS GAP Land Cover data (US Geological Survey, Gap Analysis Program (GAP). May 2011. National Land Cover, Version 2). Intact forest and forest edge are considered to be important puma habitat (Holmes and Laundré 2006, Kertson and Spencer 2011, Knopff et al. 2014) so I calculated forest core and edge based on the proportion of forest within a moving window derived from the average distance traveled between subsequent locations. For each location I also calculated topographic measures that could impact the cost of travel including local slope, ruggedness, and topographic position from a digital elevation model (DEM; US Geological Survey 2011). Ruggedness was calculated based on the vector ruggedness measure (VRM) developed by Sappington et al., (2007). Topographic position (TPI) represents position on the landscape relative to local ridges or valleys and was

calculated as the absolute difference between elevation at a location and the mean elevation within a given distance away (Wilson and Gallant 2000). Since VRM and TPI are both scale-dependent measures of landscape morphology, I incorporated each metric derived from multiple scales varying from 100-1000 meters into the statistical models and used model selection criteria to choose the best fitting bandwidth to the nearest 100m.

In order to test whether pumas either avoid areas or experience increased energetic demands in close proximity to risky human-modified habitat, I included covariates derived from housing structures and roads. To develop a spatial map of landscape risk, I included the distance to the nearest commuter road of each estimated spatial location and housing density as outlined in Wilmers et al., (2013). Similar to VRM and TPI, I incorporated housing densities derived from multiple values of bandwidths varying from 100-2000 meters into the statistical models and used model selection criteria to choose the best fitting bandwidth to the nearest 100m. All covariates were rasterized with a 30 meter x 30 meter pixel size and mean (continuous) and percent (categorical) values calculated for each linear segment between consecutive GPS locations along an individual's movement path.

All land cover covariates and distance to road were excluded from all top models based on AICc model selection (see below), and I therefore restrict my discussion of landscape impacts on puma movement costs to terrain characteristics and housing density.

6. Spatial drivers of metabolic effort at the local scale

To evaluate the local influence of the physical and risk landscapes on the relative energetic cost of movement, I regressed \log_{10} mean metabolic rate ($\text{kJ}\cdot\text{min}^{-1}$) and the \log_{10} LCOT ($\text{J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}\cdot\text{min}^{-1}$) per five-minute interval against the land cover, terrain, and risk covariates using a linear mixed effects regression model (LMM), hereinafter referred to as the MR-LMM or LCOT-LMM model, respectively. To explicitly account for any bias from spatio-temporal autocorrelation due to a high sampling rate, I adopted a spatio-temporal filtering framework that captures latent spatio-temporal structure in a dataset as a set of eigenvectors extracted from a connectivity matrix expressing spatial and temporal relationships among observation units (Dray et al. 2006, Griffith and Peres-Neto 2006). In this implementation, I generated eigenvectors based on a binary spatial weighting matrix with neighbor relationships constructed by connecting all points within a fixed space and time distance threshold. Thresholds were based on the intercept of correlograms for residuals from non-spatial mixed effects models. To account for inter-individual variation in energetic expenditure due to behavior-specific differences, I used a linear mixed effects model with the combination of individual and movement mode (i.e., “meandering” or “directed”) as a random effect. The resulting model for the vector y of either metabolic rate or LCOT at each movement segment is given (in matrix form) by,

$$y = X\beta + E\varphi + Z\gamma + \varepsilon \quad (1)$$

where β is the vector of fixed coefficients for the matrix of covariates X , φ the vector of fixed coefficients for the matrix of spatio-temporal eigenvectors E , γ the random coefficients for the matrix of covariates Z , and ε the vector of random errors. I fit models with multiple combinations of the predictor variables and chose the best models as those that minimize the AICc. The scales of housing density, TPI, and VRM that best fit the data were selected by finding the combination of covariates and scale for each scale-dependent covariate which minimized the AICc. All covariates were normalized (mean centered and scaled by one standard deviation) to improve model convergence and to facilitate comparison of model coefficients among covariates (Bolker et al. 2008). I also made sure that no candidate models had covariates exhibiting high levels of collinearity ($r > 0.7$).

7. Effect of metabolic effort, risk and terrain on spatial ecology at the landscape scale

To assess whether metabolic ecology drives long-term patterns of space use, I regressed individual mean daily travel distance (km) and home range area (km²) on the mean LCOT using standard ordinary least squares regression. To evaluate the influence of potential risk from humans and terrain on individual space use at a longer time scale, I also regressed individual mean daily travel distance (km) and home range area (km²) on the average housing density, slope, ruggedness, and TPI along movement paths. Given the limited sample size, each model was grouped by sex and analyzed separately to account for any life history differences in space use. Mean

distance traveled per day was calculated by the sum of individual path distances in a day and LCOT, housing density, slope, ruggedness, and TPI as defined previously. Data for each individual was averaged across the collar deployment to obtain a single mean daily travel distance, mean LCOT, and mean housing density, mean slope, mean ruggedness, and mean TPI value for each individual. Home ranges were obtained using a fixed local convex hull (k-LOCOH) home range estimator, where the 95% isopleth represented the home range boundary (Getz and Wilmers 2004, Getz et al. 2007, Downs et al. 2012).

All statistical analyses were performed using the language R (v. 3.4.2; R Development Core Team, 2010) with the lme4 (Bates et al. 2015) and lmerTest (Kuznetsova 2017) package for linear mixed effects models, the spdep (Bivand 2019) package for spatial autocorrelation modeling, AICc scores with the AICcmodavg (Mazerolle 2019) package, and the adehabitatHR (Calenge 2006) package for home range estimation.

RESULTS AND DISCUSSION

I deployed combined GPS/accelerometer collars on 13 adult pumas (5 females, 8 males; Fig. 2) living the Santa Cruz Mountains of central California, a rugged, 1700-km² study area ranging from dense urban development to large tracts of relatively undisturbed native forest. I used accelerometer-derived activity (collected at 16-32 Hz) to calculate mean metabolic rate (kJ·min⁻¹) and the landscape cost of transport (LCOT; J·kg⁻¹·m⁻¹·min⁻¹) for each five-minute interval between GPS fixes. LCOT is

a novel metric, distinguished from the commonly used “cost of transport” by the incorporation of time, which permits estimation of the efficiency with which an animal moves across the landscape. The LCOT of moving between two points on the landscape will tend to increase as efficiency decreases, i.e., as an animal moves more slowly or with a less directed movement path. The energetic costs of movement may also depend on the specific movement behavior adopted (Wilson et al. 2013), and I therefore classified all puma GPS locations corresponding to movement as either “meandering” or “directed” using a Hidden Markov Model fit to GPS and accelerometer data (GPS locations classified as stationary were excluded from the analysis; see Methods).

Previous experimental work confirms that pumas in the study area fear humans (Smith et al. 2017) and that this fear impacts puma movement behavior (Suraci et al. *in review*). Fear of humans may therefore exert an energetic cost that varies with human induced risk across the landscape, analogous to variation in costs of traversing rugged physical terrain (Wall et al. 2006, Pagano et al. 2018). I compared the energetic costs of moving through both the physical and risk landscapes (Fig. 1) by modeling puma metabolic rate and LCOT at short time scales (i.e., using values for each 5-minute GPS location) using linear mixed effects models while accounting for movement behavior (meandering or directed movement) and individual puma ID with random effects (see Methods). Predictor variables included a suite of terrain characteristics that may influence the cost of travel, and housing density, which

effectively captures spatial variation in human-induced risk for pumas (Wilmers et al. 2013, Smith et al. 2015).

At the 5-minute scale, puma movement costs were influenced by both physical terrain and risk from humans (Table 1). Overall, routes on less rugged, gently sloped terrain were found to be energetically cheaper per unit distance traveled and thus more efficient pathways on the landscape for free-ranging pumas. Metabolic rate and LCOT increased with increasing ruggedness ($\beta_{MR} = 0.15$, $p < 0.01$; $\beta_{LCOT} = 0.003$, $p < 0.001$) and slope ($\beta_{MR} = 0.12$, $p < 0.001$; $\beta_{LCOT} = 0.003$, $p < 0.001$), while increasing topographic position (indicative of areas closer to local valleys or ridgelines, see Methods) led to increased metabolic rate ($\beta_{MR} = 0.005$, $p < 0.001$) but decreased LCOT ($\beta_{LCOT} = -0.007$, $p < 0.001$). This latter result indicates that travel speeds and thus efficiency of movement are highest along easy-to-traverse valleys and ridges, suggesting that previously observed selection by pumas for such topographic features (Dickson et al. 2005, Dickson and Beier 2006) is motivated by reduced locomotion costs.

Housing density also had a positive effect on both short-term metabolic rate ($\beta_{MR} = 0.01$, $p < 0.001$; Fig. 3a) and LCOT ($\beta_{LCOT} = 0.008$, $p < 0.001$; Fig. 3b), indicating that pumas experience increased energetic demands and decreased movement efficiency as their exposure to human development increases. Examination of random effects revealed that these impacts of human-induced risk are mediated by puma behavior (Fig. 1). Across individuals, housing density had a strong positive effect on metabolic rate regardless of whether pumas were meandering or moving directly (β_{id}

movement class: $\sigma^2 = 0.0003$, $\rho = 0.46$; Fig. 3a), evidence that pumas are consistently engaging in more energetically demanding movements (i.e., moving more quickly, stopping less) in areas of higher perceived risk from humans. However, the positive effect of housing density on LCOT was only apparent when pumas were meandering ($\beta_{\text{id} | \text{movement class}}: \sigma^2 = 0.0003$, $\rho = -0.07$; Fig. 3b), suggesting that, despite exerting more energy on sustained movements, the net distances traveled across the landscape are lower in human-dominated areas because pumas are forced to take more circuitous movement paths (Fig. S1). Previous work confirms that, when moving through human-dominated landscapes, pumas alter travel speeds (Dickson et al. 2005, Buderman et al. 2018) and transition between behavioral states (Wang et al. 2017), and here I show that such behavioral changes increase short-term energetic costs while decreasing movement efficiency. Overall, the energetic costs of movement rose much more rapidly with increasing risk from humans than with increasing difficulty of the terrain (standardized effect sizes for housing density were two to ten times greater than those for slope and ruggedness; Table 1), suggesting a greater impact of risk relative to physical landscape on puma movement at short time scales mediated by high energy but low efficiency movement behavior.

Despite considerable attention paid to the relationship between energetic physiology and space use across species (Reiss 1988, Jetz et al. 2004, Tamburello et al. 2015) the degree to which energetic constraints drive differences in space use patterns within a species (i.e., at the individual level) remains unclear (Rosten et al. 2016). I found that, for pumas, the short-term energetic costs of moving through the

physical and/or risk landscapes scale up to impose metabolic constraints on long-term space use. For individual pumas of both sexes, the average distance traveled per day (Fig 4a; Linear regression: $\beta = -5.7$, Adjusted $R^2 = 0.727$, $F(1,11) = 32.53$, $p < 0.001$) and home range area (Fig 4b; $\beta = -18.9$, $R^2 = 0.756$, $F(1,11) = 38.2$, $p < 0.001$) decreased sharply with increasing mean daily LCOT (i.e., averaged across each puma's collar deployment), suggesting that pumas are forced to compensate for consistently high movement costs at the step level by reducing overall vagility and home range size (Fig. 1).

For male pumas, energetic constraints on daily and long-term (i.e., home range scale) space use appear to be driven predominantly by human-induced risk, consistent with the overall greater impact of risk on movement at short time scales. The average housing density experienced by an individual along its movement path was an important predictor of mean LCOT for males (Fig 5a; $\beta = 0.02$, $R^2 = 0.575$, $F(1,6) = 10.47$, $p = 0.02$) and correspondingly had a strong, negative effect on both daily distance traveled (Fig 5b; $\beta = -0.03$, $R^2 = 0.677$, $F(1,6) = 15.69$, $p = 0.007$) and home range area (Fig 5c; $\beta = -0.68$, $R^2 = 0.71$, $F(1,6) = 17.7$, $p = 0.005$). Thus, the energetic costs associated with increasing risk from humans results in restricted space use by male pumas at both the daily and home range scales. Despite measurable costs of slope and ruggedness on short-term movement (Table 1), I did not detect comparable effects of physical terrain on any longer-term measures of spatial ecology for male pumas (Table S1, Fig. S1), suggesting that any effects of physical terrain on space use at the landscape scale are overwhelmed by the costs of risk.

Female pumas did not exhibit a comparable relationship between housing density and longer-term space use patterns (mean daily LCOT: $\beta = 0.002$, $p = 0.73$; mean daily travel distance: $\beta = 0.0006$, $p = 0.97$; home range area: $\beta = -0.03$, $p = 0.86$; Table S1), which could reflect the somewhat lower sample size for females in this study (5 females vs. 8 males), but may in fact be driven by real differences between males and females in the cumulative impacts of risk on space use. To maximize mating opportunities, male pumas must maintain large territories through near constant patrolling, and thus often have home ranges that are several times the size of (and overlap with multiple) female home ranges (Dickson and Beier 2002). This requirement to maintain large mating territories likely places a substantially higher premium on energetically efficient movement for male pumas than for females, who's home ranges only need to be large enough to provide sufficient hunting opportunities (Pierce et al. 2000, Hornocker and Negri 2010). The impact of human-induced risk on movement efficiency at short timescales (Fig. 3) may therefore result in greater cumulative costs for males at the landscape level, constraining space use where overlap with humans is high (Fig. 5).

By integrating the costs of both challenging physical terrain and risk from predators into a common currency (i.e., energy), these results reveal a novel framework linking step-level movement behavior to landscape-scale patterns of space use (Fig. 1). I show that the combination of the physical and risk landscapes drives short-term movement costs for pumas, and that such short-term costs, particularly those stemming from human-induced risk, scale up to influence long-term movement

patterns, constricting overall space use for individuals experiencing consistently high costs at the step level (Fig. 1). This work provides an important extension of recent attempts to quantify the effects of the landscape on animal movement costs and pathways (Wall et al. 2006, Wilson et al. 2012, Shepard et al. 2013) by highlighting that, without accounting for predation risk, such “energetic landscapes” may overlook much of the energetic cost of navigating a complex environment.

Indeed, these results demonstrate that risk from humans plays a primary role in driving puma energetic costs, which, at least for males, must be compensated for by reduced vagility and space use at the landscape scale. A recent global analysis shows that a wide range of mammal species exhibit lower vagility with increasing human footprint on the landscape, which the authors attribute to movement barriers or changes in resource availability (Tucker et al. 2018). I suggest that the energetic costs of avoiding risk from humans may itself lead to reduced long-term space use for many wildlife species living in human-dominated landscapes, potentially contributing to the global trend of diminished movements near people. My findings demonstrate that behavioral changes induced by the fear of humans can put considerable strain on an animal’s energy budget, in this case exacerbating the already high energetic demands of a large carnivore (Gittleman and Harvey 1982, McNab 2000, Carbone et al. 2007, 2011, Williams et al. 2014). Managing risk from people may therefore come at the cost of reductions in a range of other crucial behaviors, including long-range movements and territorial defense.

Table 2.1. Fixed effects terms from the best-supported model predicting (A) metabolic rate ($\log_{10}(\text{kJ}\cdot\text{min}^{-1})$) and (B) landscape cost of transport (LCOT; $\log_{10}(\text{J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}\cdot\text{min}^{-1})$) at the 5-minute timescale.

Model Parameter	β	SE	t	p
(A) Metabolic rate				
Topographic Position (TPI)	0.005	0.0007	6.52	< 0.001
Topographic Ruggedness	0.001	0.0004	2.17	0.03
Slope	0.002	0.0005	4.09	< 0.001
Day (1)/Night (0)	-0.008	0.001	-7.77	< 0.001
Housing Density	0.01	0.004	3.95	0.002
TPI x Slope	0.002	0.0004	5.17	< 0.001
(B) LCOT				
Topographic Position (TPI)	-0.007	0.0004	-14.49	< 0.001
Topographic Ruggedness	0.003	0.0004	9.4	< 0.001
Slope	0.003	0.0003	12.01	< 0.001
Day (1)/Night (0)	0.006	0.0006	9.74	< 0.001
Housing Density	0.008	0.002	4.75	0.001
TPI x Slope	-0.001	0.0003	-3.19	0.001

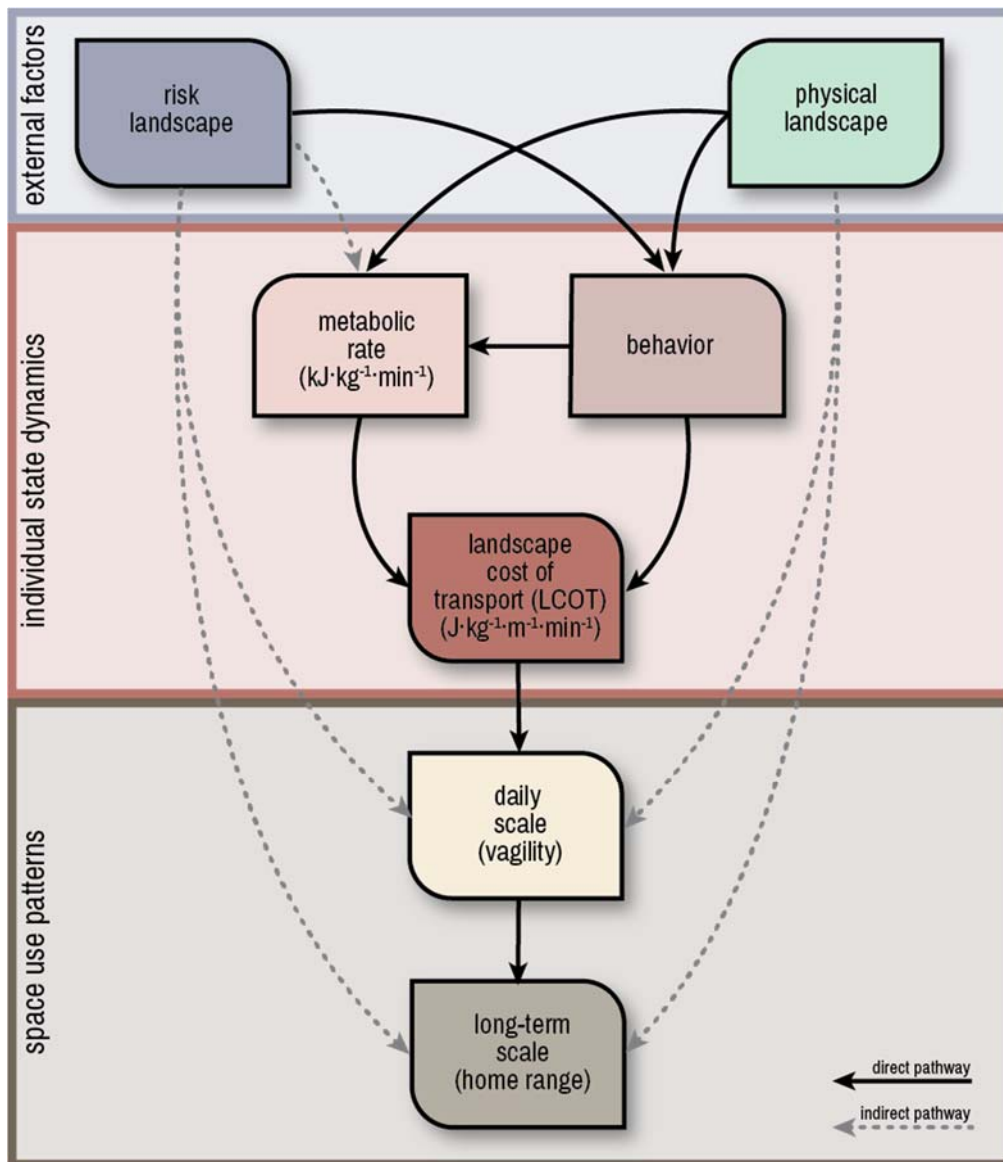


Figure 2.1. A conceptual framework illustrating the basic components and pathways linking the physical, risk, and energy landscapes to patterns of space use. The physical characteristics of the landscape (e.g. terrain) and spatial variation in risk from predators (e.g. humans) interact to modify the energy costs of movement which in turn raises or lowers an animal's energy landscape (e.g. metabolic rate or transport costs). The energy landscape provides the basis for how an animal traverses its habitats with route choice expected to favor the lowest cost pathways. Thus, movement behavior at large and small spatiotemporal scales should reflect variations in the energy landscape with changes in space use related to external factors affecting the energy economy of travel. Arrows indicate the direct (solid lines) and indirect (dotted lines) relationships among components.

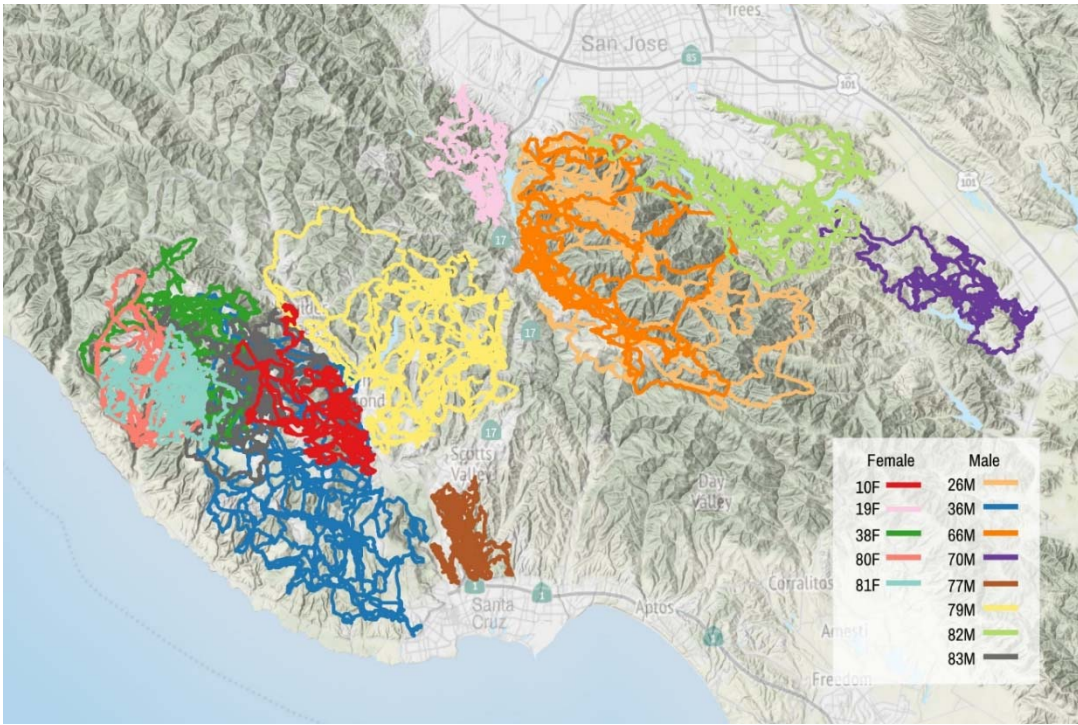


Figure 2.2. Study area showing 5-minute movement paths of 13 pumas.

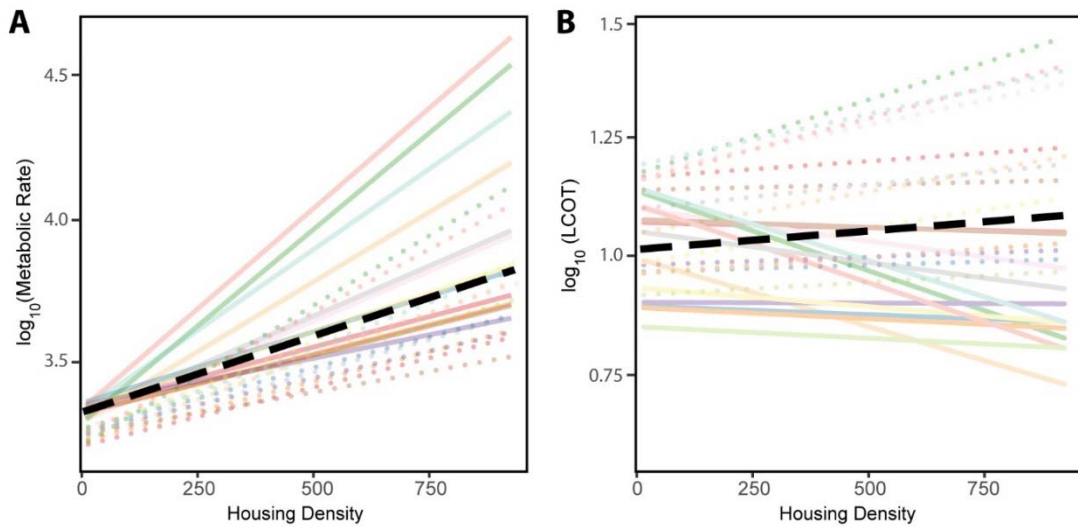


Figure 2.3. Predicted lines relating the (A) metabolic rate ($\log_{10}(\text{kJ} \cdot \text{min}^{-1})$) and (B) landscape cost of transport (LCOT; $\log_{10}(\text{J} \cdot \text{kg}^{-1} \cdot \text{m}^{-1} \cdot \text{min}^{-1})$) between 5-minute movement paths and the average housing density (200 m scale) at the population (black dashed) and individual (transparent color) level. Predictions by individual movement class is also shown as directed travel (solid) and meandering (dotted).

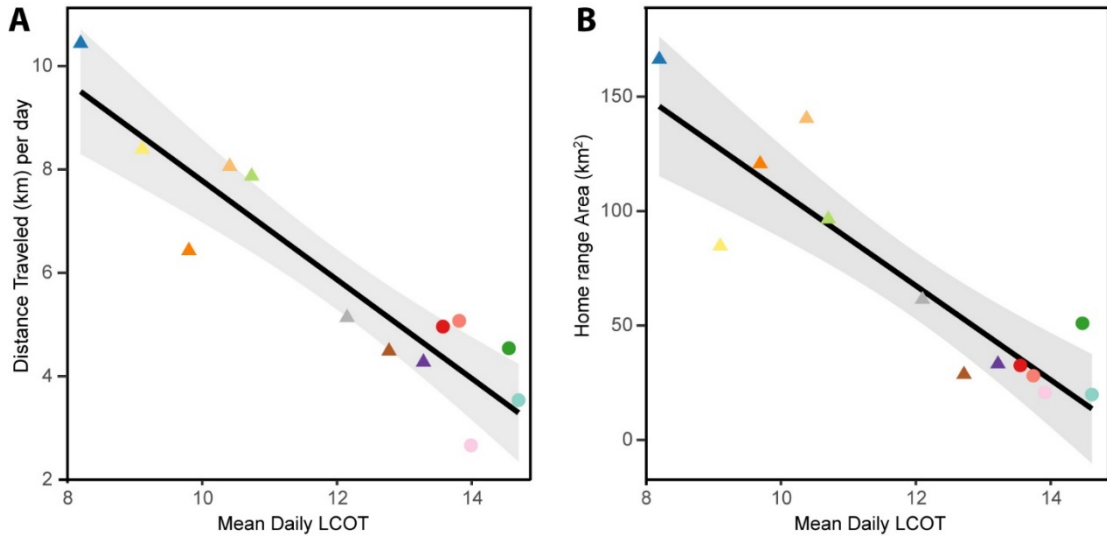


Figure 2.4. The effect of average daily landscape cost of transport (LCOT) on (a) mean daily travel distance (km) and (b) home range area (km²). The data are symbolized by individual (color) and sex, i.e. female (circle) and male (triangle). Solid lines represent results of the regression and grey areas enclose the 95% confidence interval of each regression.

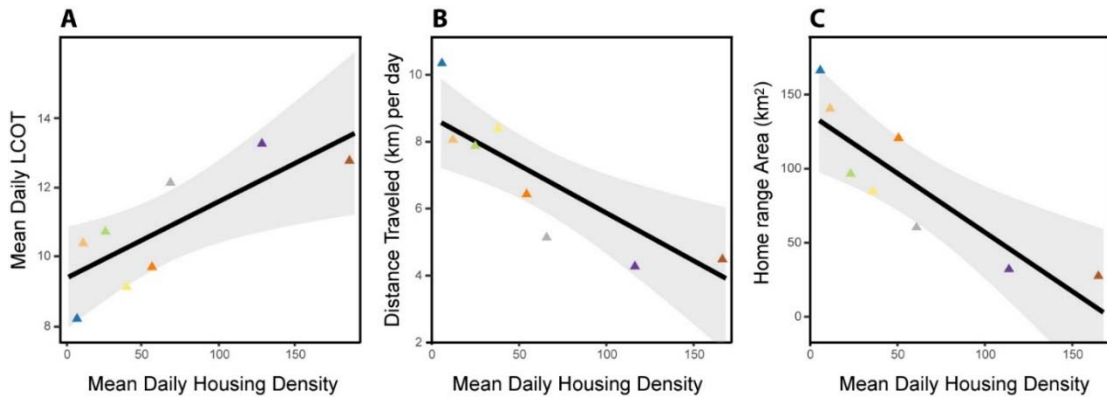


Figure 2.5. Effect of mean daily housing density on (a) mean daily travel distance (km), (b) home range area (km²), and (c) mean daily landscape cost of transport (LCOT) for male pumas. The data are symbolized by individual (color). Solid lines represent results of the regression and grey areas enclose the 95% confidence interval of each regression.

Table S2.1. P-values from linear regression models testing for the effects of human-induced risk (housing density) or physical terrain features (slope, ruggedness, and TPI) on puma longer-term space use. Analyses were run separately for males and females.

	Male	Female
<i>Daily distance traveled</i>		
Housing Density	0.007	0.971
Topographic Position (TPI)	0.934	0.254
Slope	0.871	0.310
Topographic Ruggedness	0.627	0.742
<i>Home range area</i>		
Housing Density	0.005	0.865
Topographic Position (TPI)	0.474	0.479
Slope	0.495	0.211
Topographic Ruggedness	0.396	0.335

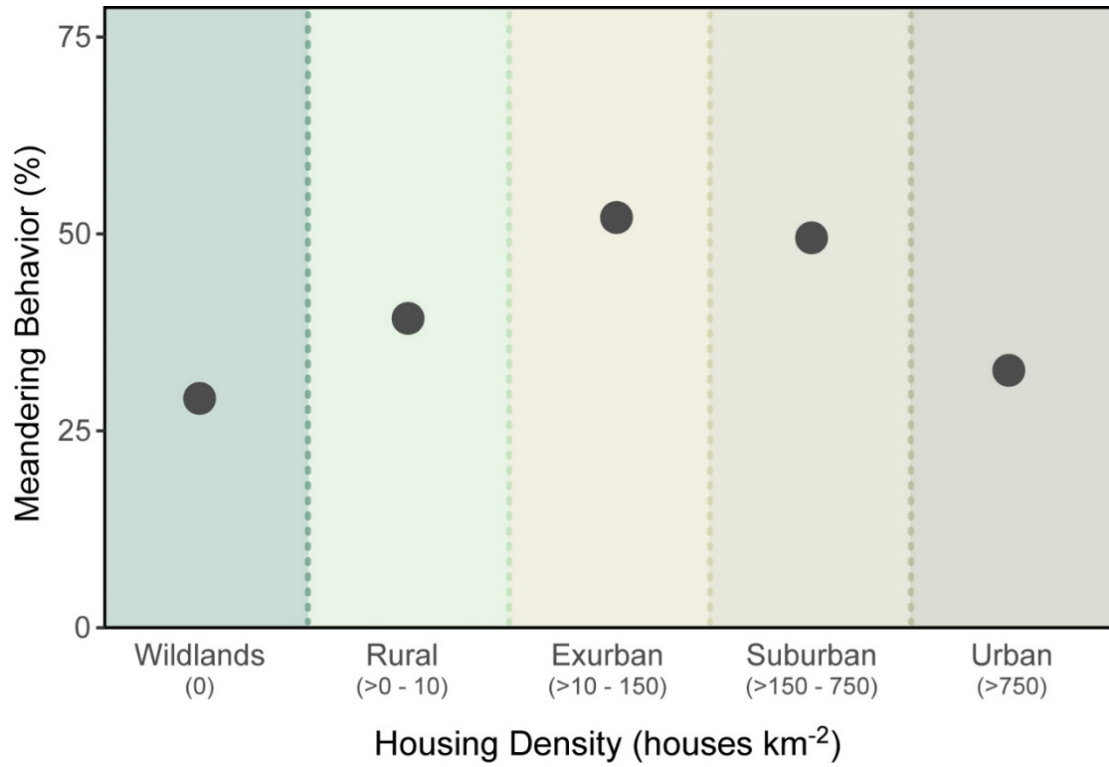


Figure S2.1. Proportion of meandering behavior relative to the intensity of housing density on the landscape. The data are categorized into five levels of housing density: wildlands (no housing), rural (greater than 0.0 and up to 10 houses per km²), exurban (greater than 10 and up to 150 houses per km²), suburban (greater than 150 and up to 750 houses per km²), and urban (greater than 750 houses per km²) (Theobald 2005).

CHAPTER 3

Assessing optimal strategies of movement in response to human-derived risk

ABSTRACT

Despite broad recognition that both energetic demands and avoidance of risk from predators shape animal decision making across contexts, these factors have traditionally been examined separately when considering wildlife movement behavior and space use. For large carnivores, movement can be energetically expensive such that slight variations in the physical landscape can have profound impacts on the energy cost of movement. Large carnivores also fear humans and resulting fear-based changes in space use may exert energetic costs by affecting path choice when in proximity to humans. Consequently, any evaluation of decision-making around movement in carnivores should include the interaction between the landscapes of energy and risk under a common currency (i.e. energy). Here, I examine whether the puma (*Puma concolor*) optimizes energy economy when traveling on challenging terrain and the degree to which individuals cope with increased movement costs near humans due to sub-optimal travel. Results indicate that pumas traveling in environments with highly variable movement costs use energetically efficient movement pathways, however, as exposure to human development and thus perceived risk increases their use of energetically sub-optimal paths become more prevalent. Despite the considerable costs associated with sub-optimal travel, pumas still seek to optimize energy by moving as efficiently through the landscape where possible. These results suggest that pumas dynamically integrate both the energy and

risk landscape when evaluating the cost of moving through different environments and highlight the synergistic nature of the energy and fear landscapes in driving animal movement. In addition, these findings demonstrate the potential for using energy landscapes in cost-based corridor modeling, however, constraints such as risk should be considered when developing cost surfaces under this framework.

INTRODUCTION

Movement is fundamental to most behaviors with the energetic costs of locomotion key in influencing whether, where, and to what extent an animal moves through its environment (Shepard et al. 2013, Wilson et al. 2015b, Halsey 2016, Halsey and White 2016). Maintaining energetic balance is vital to survival and thus the decision to move is inextricably linked to trade-offs between energy expenditure and other related currencies (Mangel and Clark 1986, Shepard et al. 2013, Halsey 2016). Movement described under such a framework can be cast in terms of cost of transport (COT), expressed as the energy per unit distance for an animal to move itself (Schmidt-Nielsen 1972), which placed into the proper spatial context defines the ‘energy landscape’ (Wilson et al. 2012, Shepard et al. 2013, Halsey 2016), that is, spatial variation in the energy costs of movement. While the energy landscape provides a compelling framework for determining how and why an animal moves it overlooks other ecological constraints on movement, such as risk avoidance (Gallagher et al. 2016, Halsey 2016). The ‘landscape of fear’, defined as spatial variation in perceived predation risk, similarly structures how animals use their

environments (Laundré et al. 2010, Gaynor et al. 2019) but fails to consider movement costs as a significant driver of animal space use (Gallagher et al. 2016). Consequently, any evaluation of decision-making around movement in wild animals should include the interaction between the landscapes of energy and risk under a common currency thereby enhancing our understanding of the selective path of movement. However, rarely have studies on free-ranging animals measured movement in these terms (Gallagher et al. 2016), in part due to the difficulties of measuring both risk and an animal's travel costs over heterogeneous landscapes, couched under one currency (energy).

For large carnivores, locomotion can be energetically expensive and represent a considerable part of the daily energy budget (Taylor et al. 1982, Garland 1983, Karasov 1992). In particular, the characteristics of the physical landscape, such as terrain, can have profound impacts on the energy cost of movement and thus path choice in carnivores (Gorman et al. 1998, Williams et al. 2014, Wilson et al. 2015a, Pagano et al. 2018). Large carnivores also face significant mortality risk from the human "super predator" (Darimont et al. 2015) that can exert additional costs by affecting where and how carnivores move when in proximity to humans (Oriol-Cotterill et al. 2015a, Loveridge et al. 2017, Tucker et al. 2018, Suraci et al. 2019b). As such, the joint costs of physical and risk-based constraints on movement should determine the relative efficiency of the geographical paths taken and their cumulative costs over time. However, the degree to which energy and human-derived fear interact to affect optimality in carnivore movement has not been investigated to date.

Filling such a gap would provide for a more mechanistic understanding of how large carnivores navigate different landscapes, particularly those that are disturbed, and why they choose to move the way they do.

Due to their persistence in energetically challenging habitats (Williams et al. 2014, Wang et al. 2017), including areas of greater perceived risk from humans (Smith et al. 2015, 2017), the puma (*Puma concolor*) provides a unique opportunity for evaluating how competing demands around energy and risk shape movement behavior in a large carnivore. Pumas are assumed to incur high transport costs largely due to their natural history, large body size, and low aerobic capacity (McNab 2000, Carbone et al. 2007, 2011, Williams et al. 2014, 2015, Bryce et al. 2017), thus it is expected that they should be judicious with respect to energy expenditure and select routes that afford minimal travel costs. However, pumas fear humans (Smith et al. 2015, 2017) such that human disturbance is expected to change the energy economy of travel by inducing non-optimal movement in areas used by humans (Fahrig 2007). For instance, previous work on puma behavior has shown the selective use of low cost topographic features when moving, e.g. ridges, valleys and gentle slopes (Dickson et al. 2005, Dickson and Beier 2006, Wilmers et al. 2013, Chapter 2), however, in human dominated areas they shift to marginal habitat, e.g. steep slopes (Wilmers et al. 2013), alter travel speeds (Dickson et al. 2005, Suraci et al. 2019a), and transition behaviors (Wang et al. 2017) all of which can elevate energy costs. Pumas thus represent a good model to test short-term optimality in movement and

quantify the energetic trade-offs made by pumas when traversing complex and/or disturbed landscapes.

Building on previous work examining movement energetics in puma (Chapter 2), this study seeks to understand the degree to which puma movement reflects optimal travel and the potential for human-derived risk to promote sub-optimal movement. Assuming that pumas move with a goal of minimizing energy, I hypothesize that pumas should favor “low energy” pathways and thus observed paths will align with the energetically optimal route where possible. In contrast, I expect that as human presence on the landscape increases, thus increasing perceived risk to puma, pumas will be less judicious with respect to energy and take higher cost but lower risk pathways in response. In turn, pumas will deviate farther from the optimal route and experience elevated movement costs relative to routes expected in the absence of human risk. While the focus here is on puma movement, I also discuss the broader application of this work to conservation planning, including corridor connectivity and the design of habitat linkages (Sawyer et al. 2011, Zeller et al. 2012).

MATERIAL AND METHODS

1. Study area

This research was conducted in the Santa Cruz Mountains (37° 10.00' N, 122° 3.00' W), which lie in the Central Coast region of California (Fig. 1). The 1,700 km² study area encompasses a diverse landscape ranging from dense, urban development

to large tracts of intact and relatively undisturbed native vegetation (see Wang et al. 2015). The area contains part of the California Coast Ranges, a northwest-trending series of mountain ranges with terrain varying from gently rolling hills to steep, rugged ridges separated by narrow canyons; altitudes range from sea level to 1,500 m. It is bisected by a large freeway and further crisscrossed by numerous smaller roads providing access to rural houses and developments.

2. Data collection and movement path generation

Starting in 2015, wild pumas were captured and fitted with a commercial off-the-shelf GPS/VHF collar (Vectronics Aerospace GPS PLUS) combined with an archival tri-axis accelerometer tag. Each collar was programmed to acquire a GPS fix every 5 minutes and tri-axial acceleration at a frequency of 16-32 Hz for a duration of 2 months. To isolate only those locations that relate to movement, I used the results from a three-state Hidden Markov Model (HMM) fit to the combined GPS and accelerometer data for individual pumas (see Chapter 2). A movement path was defined as any continuous temporal series of fixes that was at least 1 hour in duration and started and terminated at identified clusters representing stationary behavior, i.e. a kill or rest site. Each continuous trajectory represents a single realization of a path to be used for comparison against the hypothetically optimal path.

3. Physical and risk landscape covariates

I included spatial covariates based on results of the linear mixed effects model outlined in Chapter 2 to derive surfaces of the metabolic costs of movement (LCOT), i.e. energy landscapes. Physical landscape variables included were downhill slope, ruggedness, and topographic position calculated from a digital elevation model (DEM; US Geological Survey 2011). Ruggedness was calculated based on the vector ruggedness measure developed by Sappington et al., (2007). Topographic position represents position on the landscape relative to local ridges or valleys and was calculated as the absolute difference between elevation at a location and the mean elevation within a given distance away (Wilson and Gallant 2000). Spatial variation in risk was represented by the density of human development on the landscape as outlined in Wilmers et al., (2013). All covariates were rasterized with a 30 meter x 30 meter pixel size.

4. Derivation of energy landscapes and optimal paths

The energy landscape represents the energetic cost of traversing different landscape attributes and is derived by predicting, on a cell-by-cell basis, the LCOT (expressed in $\text{J}\cdot\text{kg}^{-1}\cdot\text{m}^{-1}\cdot\text{min}^{-1}$) using the individual-level parameter estimates from the best-fit linear mixed effects regression model in Chapter 2. To evaluate the relative impact of risk on optimal path choice, I generated two energy landscapes per individual that (1) assumed travel costs based solely on the physical landscape, i.e. no risk effect, and (2) included the joint effect of the physical and risk landscape hereinafter referred to as the “physical” and “physical + risk” energy landscapes,

respectively. Each derived energy landscape was used as the basis to compare observed movement paths to the hypothetically optimal path, in a least cost sense.

Least cost path analysis (LCPA) was used to derive estimates of the theoretically optimal path each individual puma should use when traversing each energy landscape. LCPA evaluates potential animal movement routes across the landscape based on the cumulative cost of movement (Adriaensen et al. 2003, Chetkiewicz et al. 2006, Sawyer et al. 2011), in this case defined by minimizing the sum of the LCOT values between two locations on the energy landscape. Source and destination locations are required to establish optimum paths via LCPA, however, movement decisions by animals occur along a time-scale continuum and therefore decisions to move with respect to the energy landscape may vary between temporal scales. Thus, least-cost paths were generated based upon source and destination points from temporally subsampled movement segments using a moving window of varying temporal widths ($\tau = 0.5 - 4$ hrs by increments of 0.5 hr). For each location X_i along an observed path, a temporal subset of locations representing the scale τ was isolated between the location X_i and all possible next locations up to location $X_{i+\tau}$ and the least-cost path generated using X_i and $X_{i+\tau}$ as the source and destination points.

I generated least cost paths for both the “physical” and “physical + risk” energy landscapes and for each path measured the maximum distance an observed path deviated away from the optimum ($\Delta DIST$) and the average difference in LCOT between the observed and optimal path ($\Delta LCOT$). The relative impact of risk on path choice was represented by the average difference in housing development between

the observed and optimal path ($\Delta RISK$). To account for any costs attributed to the physical landscape due to sub-optimal movement, I also calculated the average difference in topographic position (ΔTPI), ruggedness (ΔVRM), and downhill slope ($\Delta SLOPE$) between the observed and optimal path.

5. Data Analysis

To identify the scale at which idealized least cost paths aligned closest with observed movement, I used a mixed-effects ANOVA to test for differences in the maximum deviation of the observed path from that of the least cost path ($\Delta DIST$) between each temporal scale (τ) used to subsample movement paths. I used least cost paths derived from the “physical + risk” energy landscape, i.e. assuming the joint effects of the physical and risk landscapes on cost of travel, as this best reflects the environment pumas in the wild were circumnavigating. I applied a Box-Cox transformation on the $\Delta DIST$ variable to improve model fit. Individual puma was included as a random factor to account for inter-individual variation. Tukey’s honestly significant difference (HSD) was used to test for differences among time scales. The time scale where $\Delta DIST$ was lowest and differed significantly from the next higher order scale best replicated paths taken by pumas and thus represented the characteristic scale (τ^*) used for subsequent analyses.

To isolate the effect of risk avoidance on travel costs and evaluate the degree to which human-induced fear promotes non-optimal movement, I used a linear mixed effects model based on optimal paths derived from the “physical” energy landscape

only. I tested for the fixed effects of human development ($\Delta RISK$), distance from optimum ($\Delta DIST$), and terrain covariates (ΔTPI , ΔVRM , $\Delta SLOPE$) on the change in landscape cost of travel ($\Delta LCOT$). Additionally, to test whether path deviation due to risk avoidance alters the costs attributable to terrain and risk, I included 2-way interactions between $\Delta DIST$ and all other covariates. I applied a Box-Cox transformation on the $\Delta DIST$ variable to account for non-linearity and $\Delta LCOT$ was \log_{10} -transformed to improve model fit. I included the identity of each puma as a random intercept to account for inter-individual variation. All covariates were normalized (mean centered and scaled by one standard deviation) to improve model convergence and to facilitate comparison of model coefficients among covariates (Bolker et al. 2008). I also made sure that no candidate models had covariates exhibiting high levels of collinearity ($r > 0.7$). I fit models with multiple combinations of the predictor variables and chose the best models as those that minimize the AICc.

Assuming pumas move to maintain low energy pathways while traversing the risk landscape where possible, I also evaluated to what degree observed paths aligned with optimal paths derived from the “physical + risk” compared to that of the “physical” energy landscapes. I used mixed-effects ANOVA to test for differences in the distance from optimum ($\Delta DIST$) and change in travel costs ($\Delta LCOT$) between paths derived from each energy landscape. I applied a Box-Cox transformation on the $\Delta DIST$ variable to improve model fit. Individual puma was included as a random factor to account for inter-individual variation.

All analyses were performed using the language R (v. 3.4.2; R Development Core Team, 2010) with the lme4 (Bates et al. 2015) and lmerTest (Kuznetsova 2017) package for mixed effects models and AICc and marginal R^2 with the MuMIn (Bartoń 2018) package. All GIS analyses were performed using the Python programming language (v. 2.7.9; Python Software Foundation, Wilmington, DE, USA) and ArcGIS for Desktop (v. 10.6.1; ESRI Inc., Redlands, CA, USA).

RESULTS

My criteria for identifying continuous movement paths resulted in 1,252 paths across 13 pumas (5 females, 8 males, see Fig. 2 for distribution) for a mean (\pm se) of 96 (\pm 5) routes per animal. Comparison of temporal scales for subsampling paths indicated that scales equal to and greater than 1 hour were significantly different in terms of observed and predicted track alignment (mixed-effects ANOVA: $F_{7,5666} = 452.2$, $p < 0.001$). In such cases, as the temporal subsampling increased the accordance of least cost pathways with observed movement became less common (Fig. 3). However, there were no significant differences detected below 1 hour and paths subsampled at this interval aligned more closely with predicted paths compared to all other scales. Consequently, for these data, observed trajectories were best replicated when subsampled using a 1 hour interval and thus served as the characteristic time scale (τ^*) for subsequent analyses.

Linear mixed effects models predicting the effect of risk on travel costs revealed that the change in LCOT relative to the optimal path ($\Delta LCOT$) showed a

significant relationship with both physical and risk related landscape attributes (Table 1). Observed paths incurred greater travel costs ($\Delta LCOT$) compared to that of the optimal path as the distance from the optimal path ($\beta = 0.04$, $p < 0.001$), degree of risk from human development ($\beta = 0.04$, $p < 0.001$), slope ($\beta = 0.06$, $p < 0.001$), topographic position ($\beta = 0.06$, $p < 0.001$), and ruggedness ($\beta = 0.02$, $p < 0.001$). However, the farther a path deviated from the optimal path the lower the relative impact of risk ($\beta = -0.02$, $p < 0.001$), slope ($\beta = -0.008$, $p < 0.05$), topographic position ($\beta = 0.01$, $p < 0.05$), and ruggedness ($\beta = -0.009$, $p < 0.05$) on travel costs.

In addition, mixed effects ANOVA indicated that pumas strive to maintain lower energy pathways where possible, even when faced with additional costs attributable to risk avoidance. Observed paths aligned more closely (mixed-effects ANOVA: $F_{1,2395} = 953.4$, $p < 0.001$; 57.9 ± 30.9 vs 161.7 ± 115.9) and incurred lower travel costs relative to (mixed-effects ANOVA: $F_{1,2395} = 7179.8$, $p < 0.001$; 0.56 ± 0.35 vs 3.5 ± 1.2) optimal paths based on the “physical + risk” landscape compared to those predicted on the “physical” landscape alone (Fig. 5).

DISCUSSION

Here I demonstrate the joint impact of the physical and risk landscapes on movement costs and, consequently, path choice in free-ranging pumas. Pumas have been shown to adjust behavior in response to human-derived disturbances, primarily through temporal and spatial shifts in activity (Burdett et al. 2010, Kertson and Spencer 2011, Wilmers et al. 2013, Knopff et al. 2014, Wang et al. 2015b, Tucker et

al. 2018, Suraci et al. 2019a), however the energy cost of such adjustments remains relatively unmeasured. This approach allowed me to estimate the cost of risk avoidance by comparing the energy costs of travel between observed paths and optimal paths derived from a landscape assuming no risk. Results show that pumas deviate substantially from pathways predicted to be energetically optimal as a means to avoid risk from humans but at the cost of greater energy loss. Indeed, pumas avoiding risky areas increased the effective distance required to travel between two locations by $48\% \pm 1.4$ and incurred up to a $25\% \pm 0.7$ increase in travel costs in comparison to pathways expected on 'physical' landscapes (see Fig. 6 for an example). These additional costs suggest that fear-based changes in space use amplify movement costs due to sub-optimal travel on the energy landscape and give some measure of the importance of risk in affecting path choice.

My results demonstrate that the elevated energy costs associated with risk avoidance can, in part, be attributed to increased travel on rugged terrains. Pumas naturally incur large transport costs due to their life history (Williams et al. 2014, Bryce et al. 2017) and thus slight variations in the physical landscape can impact movement costs greatly (Chapter 2). Previous studies have shown that pumas commonly favor less rugged, gently sloped valleys and ridgelines when traveling (Dickson et al. 2005, Dickson and Beier 2006), likely due to reduced locomotion costs on these topographic features (Chapter 2). However in areas dominated by human presence and thus greater perceived risk (Smith et al. 2015, 2017) pumas alter their use of habitat, including use of steep, rugged terrain, in response (Kertson and

Spencer 2011, Wilmers et al. 2013). Since human activity and development tend to cluster on flatter terrain, pumas must travel on uneven terrain and steep inclines to avoid these areas on the landscape. Locomotion on inclined terrain is known to be relatively costly for a wide variety of animals (Halsey and White 2017), including pumas (Chapter 2), thus a puma moving with little regard to terrain when avoiding humans is sacrificing energy economy for safety. Repeated use of energetically expensive terrain may be detrimental in the long term if pumas are unable to take advantage of alternative strategies for optimizing the energy economy of travel.

My data reveal that pumas exhibit some degree of flexibility in their movement choices as a means to minimize the energy costs sustained while avoiding riskier areas. While movement near humans is shown to be energetically sub-optimal, pumas appear to seek paths that remain the lowest cost in terms of energy, risk, or both where possible. The two-way interaction terms involving distance, slope, topographic position, ruggedness, and risk (Table 1) suggest that despite an overall increase in energetic costs the impact of these factors on energy attenuates as pumas move away from higher risk areas. In this case, fear-based changes in movement raise the energy costs of travel (Gallagher et al. 2016) but pumas attempt to minimize the impact by other means, e.g. adjusting speeds of movement, traverse angles, or aligning with alternative low cost paths (Shepard et al. 2013, Halsey 2016). Indeed, I found that puma movement aligned more closely with the paths predicted to be optimal on the “physical + risk” energy landscape, i.e. including fear and terrain, compared to those predicted on an energy landscape assuming no risk (Fig. 5). These

results suggest that a puma's realized energy landscape assimilates risk such that "peaks" on the landscape of fear translate to "peaks", perceived or otherwise, on the energy landscape. Consequently, a puma optimizing energy should adjust route selection accordingly and realign pathways, where possible, to alternate low cost options on their risk-integrated energy landscape. My results are consistent with this notion and indicate that pumas accept extra travel costs due to sub-optimal travel near humans but still seek to optimize energy by moving as efficiently through the landscape as possible.

Movement patterns are inherently scale dependent (Nathan et al. 2008, Avgar et al. 2013) and consequently it is expected that an animal's response to its underlying energy and risk landscape should exhibit a similar dependence on scale. The current analysis was conducted at the path level, defined as a continuous trajectory of 1 hour in duration, and thus reflects a puma's behavioral response at this scale relative to a step (e.g. minutes) or home range (e.g. months) level response. However, recent work on puma movement energetics has shown that both short and long-term movement in pumas are comparably influenced by the landscapes of energy and risk. For example, the energy costs of short-term movement (e.g. minutes) increase when pumas traverse both rugged terrain and areas of greater perceived risk on the landscape (Chapter 2). Further, movement patterns over the long-term (e.g. days, months) are driven by the cumulative experience of short-term movement costs whereby higher cumulative costs, including those due to risk, result in reduced vagility and smaller home range size (Chapter 2). Thus, scale-dependent adjustments in a puma's response to energy,

fear, or both shape its movement behavior and subsequent use of space at all scales (short, long, and intermediate) which, in turn, promotes or limits its ability to optimally navigate complex and/or disturbed landscapes.

While the focus of this study has been on puma movement, it is worth mentioning the broader implications of these results on conservation planning, especially examinations of corridor connectivity and the design of habitat linkages (Sawyer et al. 2011, Abrahms et al. 2016, Zeller et al. 2017). The most widely used technique to assess corridor connectivity is based on estimating landscape resistance to movement, or resistance surfaces, representing hypothetical ‘movement costs’ on the landscape (LaRue and Nielsen 2008, Sawyer et al. 2011, Zeller et al. 2012). Shepard (2013) recently proposed that the energy landscape could provide more realistic values for resistance surfaces, rather than resistance to habitat selection which is most commonly assumed (Zeller et al. 2012). These results demonstrate the potential for using energy landscapes in cost-based corridor modeling given that hypothetical least cost pathways adhered well to observed movement pathways of pumas (Fig. 5). However, I point out that paths were best predicted on energy landscapes integrating risk compared to those based solely on the physical landscape suggesting that constraints beyond energy should also be considered when developing cost surfaces under this framework. Further, this approach may be limited to specific scales of movement given accordance between predicted and observed pathways decreased as the duration of travel modeled increased (Fig. 3). Nonetheless, integrating the energy and risk landscape into resistance surfaces shows promise and,

albeit a challenging standard, should improve cost-based corridor models by producing more realistic estimates of landscape resistance to animal corridor use. More research is warranted to determine the efficacy and value of this approach to connectivity conservation planning.

The present study shows the extent to which the energy and risk landscapes interact to affect optimal path choice and provides insights into the mechanistic basis of decision-making and the movement process in wild pumas. Movement costs certainly drive movement and space use in pumas (Chapter 2) and are important in terms of optimizing strategies where trade-offs between risk avoidance and energy expenses due to movement play together to produce observed pathways. My findings indicate pumas traveling in environments with highly variable movement costs align with low cost pathways, however, as their exposure to human development and thus perceived risk increases their use of energetically sub-optimal paths become more prevalent. The energetic cost difference between the optimal and observed pathways is indicative of the extent to which risk affects movement patterns beyond that of the energy landscape. Despite these costs, pumas move to maintain low energy pathways where possible suggesting they dynamically integrate both the energy and risk landscape when evaluating the cost of moving through different environments. These results highlight the complementary aspects of the energy and fear landscape paradigms (Gallagher et al. 2016) and illustrate the utility of deriving least cost pathways within these landscapes for quantifying and understanding the various drivers of movement (Lempidakis et al. 2018).

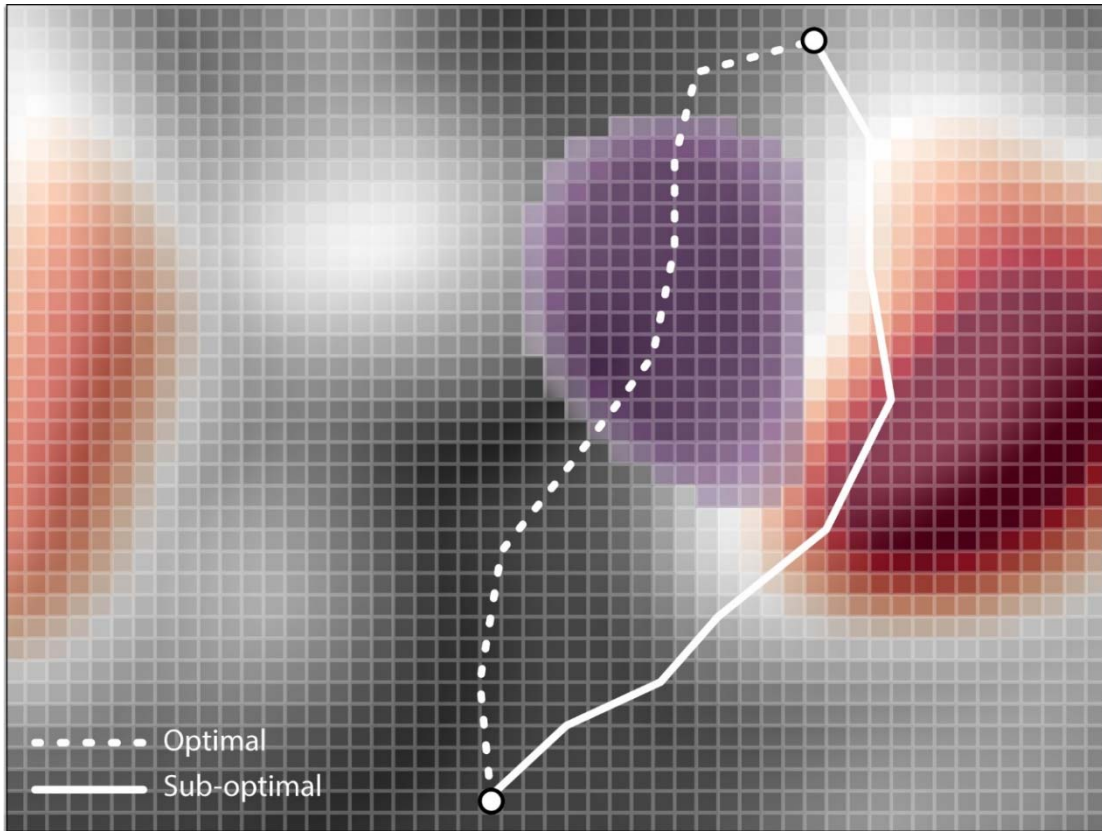


Figure 3.1. Conceptual diagram illustrating the impact of the energy and risk landscapes on optimal path choice. The grid denotes the energy landscape with each cell representing the cost of transport (COT). An animal moving to minimize energy costs should follow low-cost (dark grey) cells and avoid high-cost (red) cells where possible, e.g. the dotted pathway. However, the risk landscape induces sub-optimal movement, e.g. the solid trajectory, due to the animal’s need to circumnavigate high risk areas (purple) at the expense of energy economy. The extent of the deviation from the low-cost (optimal) path is indicative of the additional energy costs that the animal must incur due to risk avoidance.

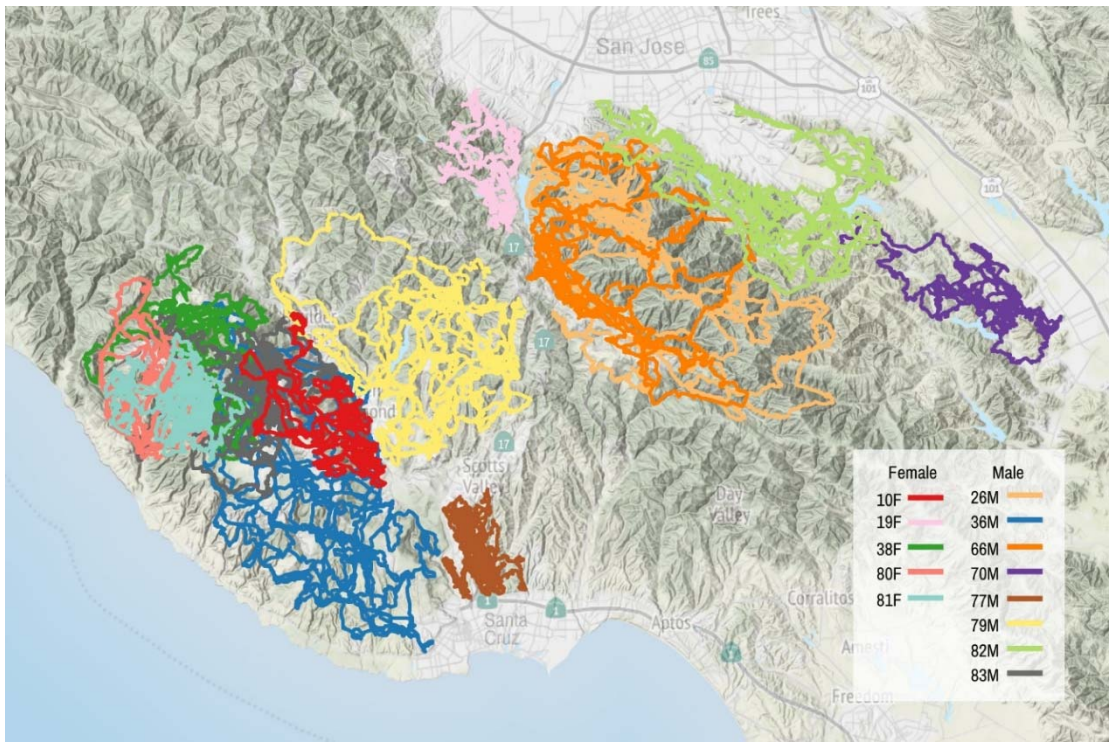


Figure 3.2. Study area showing movement paths of 13 pumas.

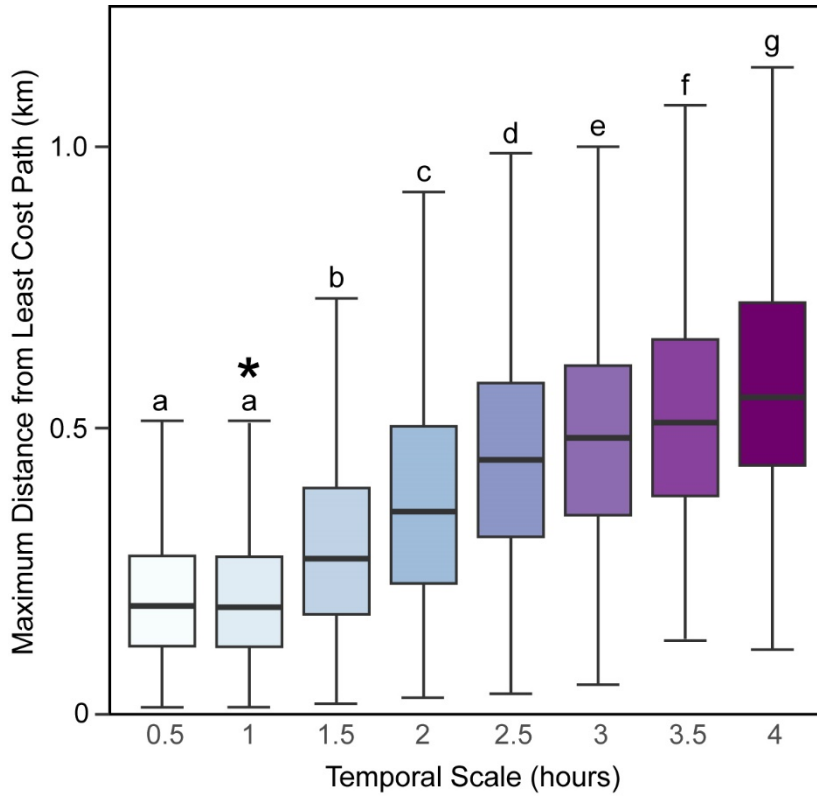


Figure 3.3. Maximum distance of observed paths from the least cost path calculated at different time scales. The bottom, middle, and upper lines of the box plots correspond to the 25th, 50th, and 75th percentiles, respectively. The whiskers extend to the extreme values within 1.5 times the interquartile range. Pairwise comparisons from Tukey’s HSD tests reported in superscripts, where different letters represent a statistically significant difference. Asterisk denotes the time scale (τ^*) used for subsequent analyses.

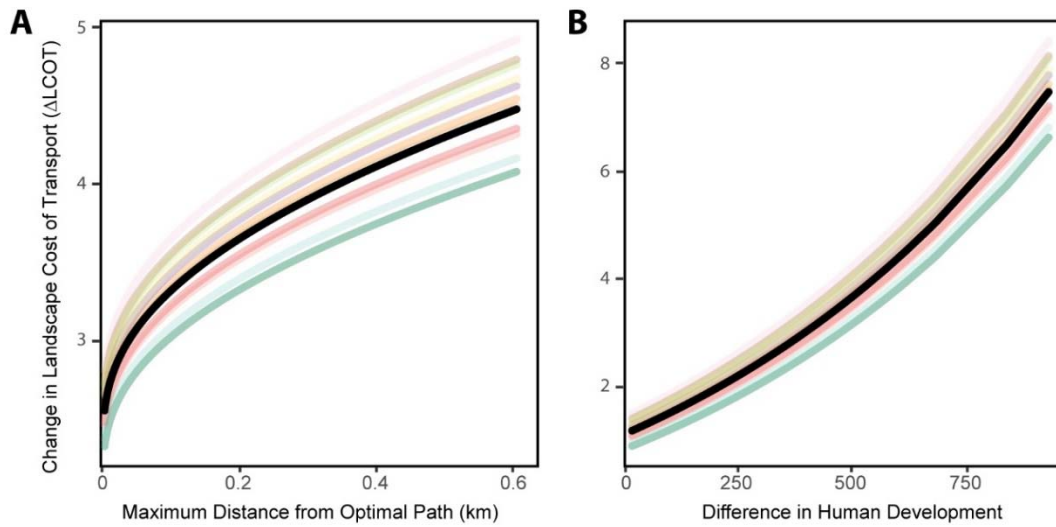


Figure 3.4. Predicted lines relating the change in landscape cost of transport between observed and optimal paths to the (a) maximum deviation from the optimal path and (b) difference in the human development along the least cost path at the population (black) and individual (transparent color) level.

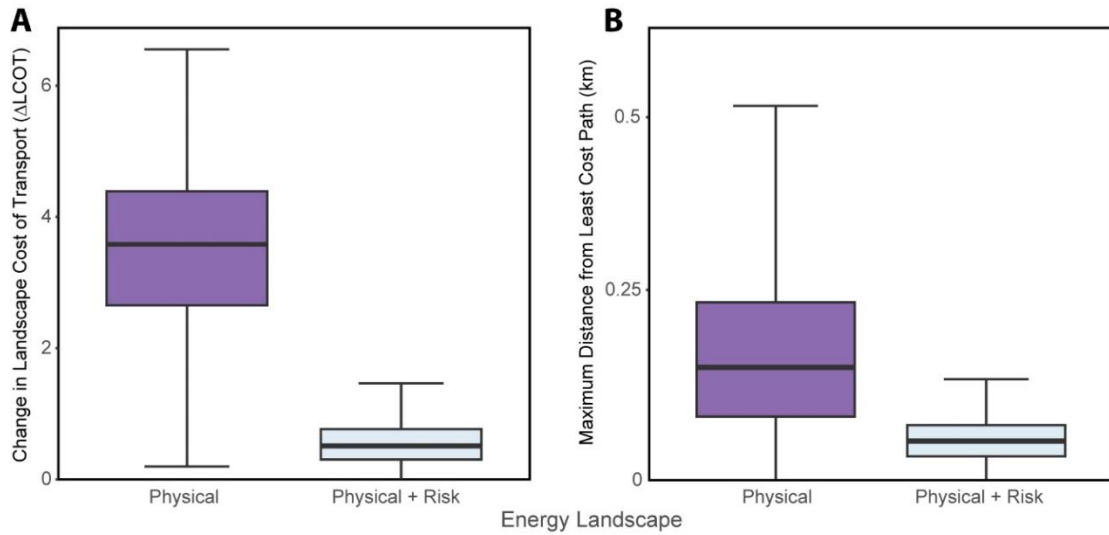


Figure 3.5. The difference between optimal and observed pathways based on the physical landscape and combined physical and risk energy landscapes in terms of (A) change in landscape cost of transport and (B) maximum deviation from the optimal path. The bottom, middle, and upper lines of the box plots correspond to the 25th, 50th, and 75th percentiles, respectively. The whiskers extend to the extreme values within 1.5 times the interquartile range.

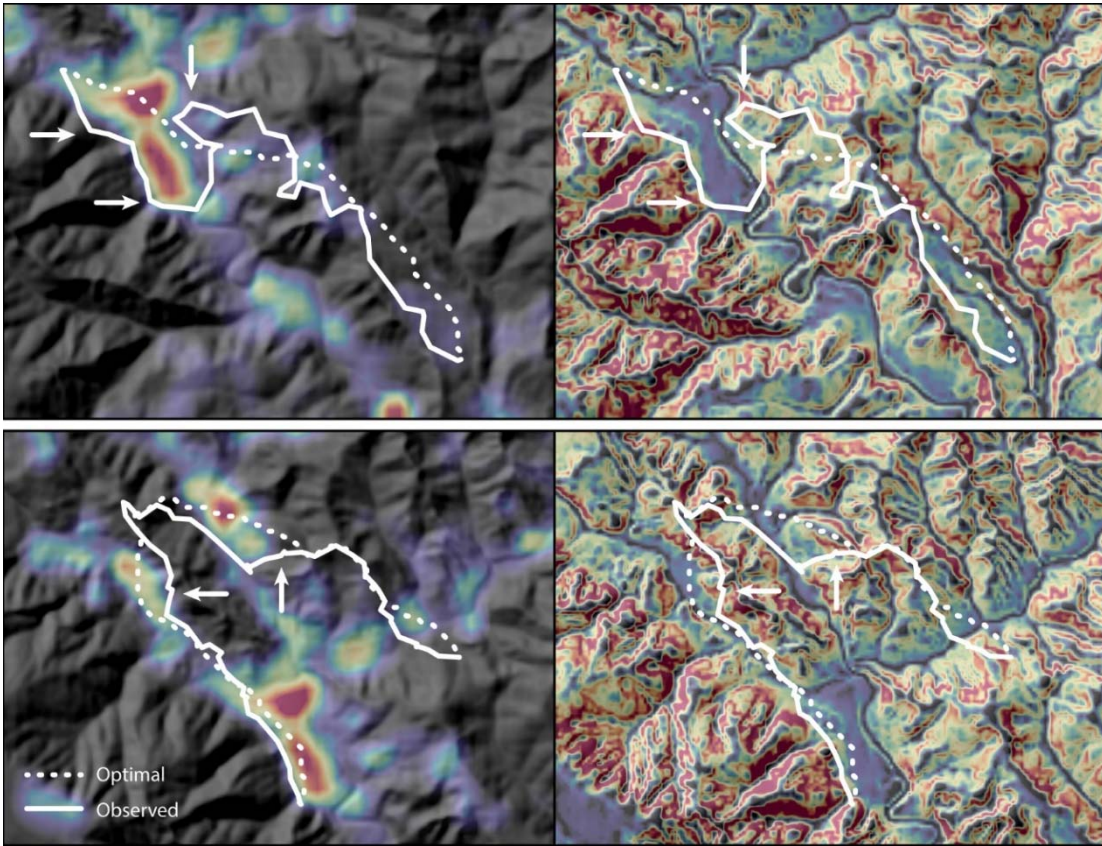


Figure 3.6. Example of the effects of the energy (right panel) and risk (left panel) landscapes on observed paths relative to the energetically optimal path. The dotted trajectory is the optimal path based on the physical landscape only while the solid trajectory is the observed path. Arrows correspond to regions of greater travel cost on the energy landscape (red regions in the right panel) that pumas must traverse when avoiding areas of higher relative risk (color regions in the left panel).

Table 3.1. Fixed effects terms from the best-supported model for predicting the change in landscape cost of transport ($\log_{10}(\Delta\text{LCOT})$).

Model Parameter	β	SE	t	p
<i>(A) Change in landscape cost of transport</i>		<i>Marginal R² = 0.53</i>		
ΔDIST	0.035	0.004	7.53	< 0.001
ΔRISK	0.037	0.006	5.73	< 0.001
ΔSLOPE	0.059	0.004	14.64	< 0.001
ΔTPI	0.055	0.004	12.92	< 0.001
ΔVRM	0.019	0.004	4.89	< 0.001
$\Delta\text{DIST} : \Delta\text{RISK}$	-0.024	0.005	-4.68	< 0.001
$\Delta\text{DIST} : \Delta\text{SLOPE}$	-0.008	0.004	-2.12	0.03
$\Delta\text{DIST} : \Delta\text{TPI}$	-0.011	0.004	-2.43	0.01
$\Delta\text{DIST} : \Delta\text{VRM}$	-0.009	0.004	-2.21	0.02

Chapter 4

Human presence and human footprint have non-equivalent effects on wildlife habitat use

ABSTRACT

Human activity can substantially impact wildlife, altering the distribution and behavior of species across terrestrial communities. These impacts stem from both the human footprint on the landscape (e.g., development) as well as the immediate presence of people in wildlife habitat (e.g., recreation), which elicits fear responses in many wildlife species. Anthropogenic effects on wildlife are not exclusively negative, however, with many “synanthropic” species using developed areas to exploit resource subsidies. Thus, both human presence and human footprint may simultaneously influence wildlife behavior, potentially in opposition. However, our ability to disentangle these two classes of anthropogenic disturbance in their effects on wildlife remains limited, as does our capacity to predict the spatial extent of human presence independently of human footprint and thus to determine where on the landscape this disturbance type is likely to operate. I used camera trap data from a grid spanning the Santa Cruz Mountains, a mixed-use landscape in central California, to (i) compare the effects of human presence (detections of people on camera) and human footprint (building density) on behavior and habitat use of mammalian predators (large carnivore and mesopredators), and (ii) to develop a model predicting the spatial extent of human presence and its impacts outside of developed areas. Multi-species occupancy models and analysis of temporal activity showed that human presence and footprint had non-equivalent and often opposing effects on wildlife,

revealing predictable patterns of either spatial or temporal avoidance of humans based on disturbance type and species life history. Spatial modeling indicated that intensity of human presence is high throughout the study region, including in relatively remote protected providing otherwise high-quality wildlife habitat. This work highlights the need to integrate multiple sources of disturbance and information on the extent of human presence across the landscape when evaluating the degree to which human activity impacts wildlife.

INTRODUCTION

The expanding influence of humans has greatly impacted wildlife by disrupting the distribution and activity patterns of animals globally (Hoffmann et al. 2010, Dirzo et al. 2014, Gaynor et al. 2018, Tucker et al. 2018). The increasing human footprint on the landscape (i.e., urbanization, land use change) is a key threat to wildlife across virtually all taxonomic groups, not only through habitat loss and fragmentation (Hansen et al. 2005, Radeloff et al. 2005b, Fischer and Lindenmayer 2007), but also because urbanized areas represent concentrations of anthropogenic “disturbance” (i.e., real or perceived threats that elicit antipredator responses; Frid and Dill 2002), which may be actively avoided by wildlife. However, human impacts are not restricted to developed areas only, as the mere presence of humans has been shown to impact wildlife behavior and activity patterns even in wildland areas (Suraci et al. 2019a) The latter is particularly salient given the rapid expansion of outdoor recreation into previously undisturbed landscapes (Cordell et al. 2008, Balmford et al.

2009, Cordell 2012) and its potential negative effect on many wildlife species (Larson et al. 2016). Wildlife responses to humans are therefore likely to be impacted by multiple forms of human influence.

Wildlife species respond to human activities in complex ways, ranging from acute behavioral changes to chronic distributional effects, which may depend on the type, intensity, and frequency of disturbance (Larson et al. 2016, Tablado and Jenni 2017, Gaynor et al. 2018, Tucker et al. 2018). Humans are a major source of mortality for many wildlife species, particularly mammalian carnivores (Darimont et al. 2009, 2015), and recent experimental work confirms that many species therefore exhibit strong fear responses to human presence just as many prey respond fearfully to the presence of their predators (Clinchy et al. 2016, Smith et al. 2017, Suraci et al. 2019a). The fear induced by human presence has correspondingly been shown to affect behavior and activity patterns of wildlife at the landscape scale (Suraci et al. 2019a), and likely mediates many of the impacts associated with recreational activity in wildland areas (Larson et al. 2016, Tablado and Jenni 2017). When compared to the relatively transient presence (and associated fear) of humans during recreation, sustained and high-intensity disturbance associated with long-term land use changes (e.g., housing development) may be expected to exert even greater impacts on wildlife habitat use. Yet many synanthropic species (e.g., mesopredators like skunks and opossums) appear to benefit from increased human footprint on the landscape, taking advantage of resource subsidies such as food waste (Ordeñana et al. 2010, Wang et al. 2015a) and/or decreased risk from other predators where human activity

is high (the “human shield” effect) (Muhly et al. 2011, Steyaert et al. 2016). Indeed, multiple anthropogenic influences may simultaneously affect wildlife, potentially in opposition, if for instance some species avoid risky interactions with people but take advantage of resources concentrated near development (Beckmann and Berger 2003, Bateman and Fleming 2012, Suraci et al. 2019a).

An animal’s response to a particular anthropogenic disturbance may additionally depend upon the relative constancy or regularity of the disturbance type in space and time and thus the animal’s ability to predict when and where potential threats from humans are likely to occur. Predator-prey theory suggests that long-term, consistent spatial variation in risk should lead to outright avoidance and thus changes in prey space use (the “risky places hypothesis”) (Creel et al. 2008, Dröge et al. 2017). Alternatively, predation risk that is more spatially variable but exhibits regular temporal fluctuations (e.g., due to the predator’s daily activity cycle; Kohl et al. 2018) may lead to temporal partitioning, where prey avoid predators in time by increasing activity at times of day when the predator is less active (Suraci et al. 2019b). Thus, it is possible that human development as a long-term, spatially constant source of risk may be more likely to induce spatial displacement and altered habitat use (i.e., avoidance of risky places) (Frid and Dill 2002, Tucker et al. 2018), while human presence in wildlife habitat, which is less constant and largely restricted to diurnal periods, may prompt shifts in temporal activity (Gaynor et al. 2018).

Despite ample reason to expect that human footprint and human presence will differ in their impacts on wildlife behavior and habitat use, ambiguity exists in how wildlife species respond to these two categories of anthropogenic disturbance. One reason for such ambiguity is that human footprint is often used as a proxy for multiple forms of anthropogenic disturbance, due in part to the ease of acquiring landscape level data on, e.g., land cover, human population density, and built infrastructure (e.g. Venter et al. 2016). However, such variables may be poor predictors of human presence across the landscape, particularly in wildland areas where outdoor recreation is growing (Cordell et al. 2008, Cordell 2012, Balmford et al. 2015). Using the human footprint as a proxy for human presence may therefore conflate the effects of different types of human disturbance on wildlife (Tablado and Jenni 2017).

An additional challenge lies in measuring the spatial extent of human presence outside of developed areas, and thus the area over which human activity is likely to impact wildlife. Studies of human presence in wildland areas typically rely on the localized deployment of sensors (e.g., camera traps) in the environment, a site-specific approach that may not be representative of landscape-scale patterns human presence (Larson et al. 2016, Gutzwiller et al. 2017). In particular, efforts to scale up existing research to broader spatial extents are limited and have the potential to overlook human disturbance and its impacts in parts of the landscape not directly covered by camera trapping surveys (Monz et al. 2013). As such, landscape-scale assessments quantifying where non-consumptive activity is expected to be greatest would be valuable for understanding the extent of human disturbance on wildlife

beyond developed areas (Gutzwiller et al. 2017). Specifically, there is a need to predict human presence in wildland areas from readily available landscape-level variables, allowing estimation of broad-scale spatial patterns of human activity and associated impacts on wildlife beyond sites at which on-the-ground surveys have been conducted.

Here I use an extensive network of camera-traps deployed across a gradient of human recreational use and development in the Santa Cruz Mountains of California to quantify the effects of both human footprint (building density) and actual human presence (occurrence of people on camera traps) on wildlife behavior and habitat use. I then model where and when the observed impacts of human presence are likely to be greatest on the landscape using a suite of spatial predictors of human activity. I focus my analysis of wildlife on large and medium-sized mammalian predators, which experience the highest per capita risk of human-caused mortality (Darimont et al. 2015) and are correspondingly known to exhibit strong behavioral responses to the immediate presence of people (Clinchy et al. 2016, Smith et al. 2017, Suraci et al. 2019a), but which also represent a range of responses to human development, from reclusive large carnivores to synanthropic mesopredators. This work was conducted in areas of the Santa Cruz Mountains ranging from undeveloped tracks of forest to moderately developed rural and exurban areas, thus typifying the mosaic of wildlife habitat and human development characteristic of the wildland-urban interface (WUI) (Radeloff et al. 2005a, 2010, Leu et al. 2008, Wade and Theobald 2010, Bar-Massada et al. 2014). I show that human footprint and human presence have non-equivalent,

and in some cases opposite, effects on habitat use and activity patterns, with observed differences between species likely driven by species-specific tradeoffs between the costs and benefits of sharing habitat with humans. I further show that the intensity of human presence across the landscape (including in wildland areas) can be predicted from landscape-level variables, allowing estimation of human impacts on wildlife even outside of developed areas. This research underscores the importance of integrating multiple sources of disturbance and demonstrates that solely focusing on one or the other disturbance may lead to erroneous conclusions regarding the way human-derived risk affects wildlife.

METHODS

Study area

The Santa Cruz Mountains (37° 10.00' N, 122° 3.00' W) encompasses a diverse landscape comprised of large tracts of relatively undisturbed native vegetation intermixed with low- and intermediate-density development that are surrounded by heavily developed areas along the fringe. The region has a legacy of preserving large tracts of open space, with 24% of the surrounding San Francisco Bay Area held in some form of public land trust or conservation easement (Rissman and Merenlender 2008). Many large private landholdings are managed for resource extraction and a significant portion of the public lands are available for a wide variety of recreational activities (e.g. biking, hiking, dog walking). However, development comprises 76%

of all anthropogenic land-use in the region (Riordan and Rundel 2014) with one-third of the landscape falling within the wildland-urban interface (Martinuzzi et al. 2015). The study area is crisscrossed by several highways and numerous smaller roads providing access to rural houses and developments. The region thus provides marked gradients of development and human recreational pressures that allow for concurrently evaluating wildlife response to multiple forms of human disturbance.

Camera trap study design

As part of a long-term wildlife monitoring program in the Santa Cruz Mountains, I used a camera trap grid covering the entire region, but focused on undeveloped and moderately developed areas that still provide substantial wildlife habitat. A grid of 100 cameras, with a spacing between cameras of 4 km, was created across a mosaic of public and private land. Each grid point was visited and searched for fine-scale landscape features to maximize detections of carnivores (O'Connell et al. 2011), placing each camera trap within 400 m (10% of the diameter of the grid cell) of the original grid point. Twelve cameras were unable to be placed due to land access or safety issues, leading to a total of 88 cameras deployed. Camera traps were placed using standardized procedures (i.e., camera trap height and orientation) and programmed to take a series of 3 photos each time they detected motion with 1 min between trigger events.

Camera traps were deployed for five to seven weeks during three separate study periods: Spring 2015 (10 March to 13 April), Autumn 2015 (23 August to 10 October), and Spring 2016 (4 March to 21 April). During each study period, camera traps were deployed and collected on a rolling basis, and the date ranges noted above correspond to the weeks when at least 80% of the 88 camera traps were active. I scored all camera trap images for the presence of mammalian predators species including the sole large carnivore in the Santa Cruz Mountains, the puma (*Puma concolor*) and a suite of mammalian mesopredators (coyote *Canis latrans*, bobcats *Lynx rufus*, gray fox *Urocyon cinereoargenteus*, northern raccoon *Procyon lotor*, striped skunks *Mephitis mephitis*, and Virginia opossum *Didelphis virginiana*). I also scored all detections of humans on camera traps and included information on the presence of domestic dogs and bicycles. All images of the same species on the same camera were considered independent occurrences if they were separated by at least 30 min from all other occurrences of the same species. This is likely to be conservative for many species, particularly humans, which were typically moving along trails when detected on camera and thus unlikely to remain in the vicinity of the camera trap.

Anthropogenic and habitat covariates

For each camera site, I measured several anthropogenic and habitat covariates that could potentially affect both human and wildlife activity including building

density (BUILDING), road density (ROAD), trail density (TRAIL), distance to urban area (URBAN), distance to public open space (i.e., state and local parks and other outdoor recreation areas; OPEN), distance to parking lot and camp sites (a proxy for human accessibility of wildland areas; ACCESS), proportion of forest cover (FOREST), elevation gradient (ELEV), proportion of visible landscape (i.e. vista opportunities; VIEW), and average ruggedness (RUGGED) in a 1 km radius around each camera trap. As outlined in Wilmers et al. (2013), building and road density were derived from spatial data representing the location of every structure and commuter road in the study area, respectively. To classify areas of wildlife-urban interface across the region I combined a database of assessor parcels with buildings to categorize parcels into housing density levels as defined by Wade and Theobald (2010): wildland (no housing), rural (greater than 0.0 and up to 0.062 houses per hectare), exurban (greater than 0.062 and up to 1.45 houses ha⁻¹), suburban (greater than 1.45 and up to 4.12 houses ha⁻¹) and urban parcels (greater than 4.12 houses ha⁻¹). Exurban parcels intersecting a 1 km radius of a camera site represented areas of surrounding wildland-urban interface. To identify the impact of trails and parking lots, I used a compilation of recreational trail networks and access points maintained by municipal, county, and state agencies further augmented by crowd-sourced data extracted from OpenStreetMap (2017) where necessary. BUILDING, ROAD, and TRAIL were measured as the total number (buildings) or distance (road, trail) of each in a 1 km radius around each camera trap. ACCESS was defined as the Euclidean distance from the camera to the nearest parking lot associated with a recreational area.

Data on the locations of protected open space (public and private) were extracted from the California Protected Areas Database (GreenInfo Network 2017). I defined OPEN as the Euclidean distance from the camera to the nearest public open space. URBAN was measured as the Euclidean distance from the camera to the nearest medium to high density urban areas based on the WUI (Martinuzzi et al. 2015). Forest cover was extracted from the USGS GAP Land Cover data (US Geological Survey, Gap Analysis Program (GAP). 2011. National Land Cover, Version 2) with FOREST defined as the percent area of forest in a 1 km radius around each camera trap. Ruggedness, elevation gradient, and vista opportunities were calculated from a digital elevation model (DEM; US Geological Survey 2011). RUGGED was calculated based on the vector ruggedness measure developed by Sappington et al., (2007). Elevation gradient (ELEV) was calculated as the difference between the maximum and minimum elevation within 1 km of a camera. Scenic potential, i.e. vista opportunity (VIEW), was measured as the proportion of visible landscape within 1 km of a camera based on viewshed analysis (Baerenklau et al. 2010). All GIS analyses were performed using the Python programming language (v. 2.7.9; Python Software Foundation, Wilmington, DE, USA) and ArcGIS for Desktop (v. 10.6.1; ESRI Inc., Redlands, CA, USA).

Comparing the effects of human presence and human footprint on wildlife habitat use

For each camera trap, I derived estimates of human presence at both the daily and study period (i.e., Spring, 2015, Autumn 2015, and Spring 2016) levels from images of humans recorded on camera traps. Daily estimates were simply the total number of independent human detections during each calendar day on a given camera trap (humans per day, or HPD). Study period-level estimates were the number of humans detected per day on a given camera averaged across each study period (meanHPD). I used building density (i.e., BUILDING, described above) as our estimate of human footprint at each camera site.

To estimate the effects of the two forms of human disturbance on wildlife habitat use and behavior, I fit multi-species occupancy models (Burton et al. 2012, Broms et al. 2016) to camera trap data on detections of the seven mammalian predators (pumas, coyotes, bobcats, foxes, raccoons, skunks, and opossum). Occupancy models estimate two parameters that could both be affected by human disturbance: (i) site occupancy, an estimate of whether or not a species occurs at a given site, and (ii) detection probability, which is driven (at least in part) by animal behavior, with decreased activity levels or increased cryptic behavior leading to lower detection probability. As all of the target wildlife species are at least partially nocturnal, particularly where humans are present (Wang et al. 2015a), I defined each night that a camera trap was active as a survey (Burton et al. 2012), and recorded whether a given species was detected (1) or not (0) over a 24-hour period spanning each night (from noon to noon). Estimates of wildlife species detection were therefore offset (by 12 hours) from the daily estimates of human activity on camera

such that detection of a wildlife species during a given nocturnal period could be modeled as a function of the number of humans present during the immediately preceding diurnal period.

I formulated the occupancy models as hierarchical zero-inflated binomial models, with separate binomial submodels describing occupancy and detection probability (MacKenzie et al. 2002, Royle and Dorazio 2008). I fit two occupancy models varying only in the type of human disturbance used to model occupancy and detection probability, i.e., human footprint (building density) or human presence (HPD and meanHPD for detection probability and occupancy respectively). Each model also included environmental covariates that could affect occupancy and detection probability at camera sites (i.e., FOREST, RUGGED, and TPI). While the relatively small number of study periods for which I had camera trap data (three) meant that estimating occupancy dynamics (i.e., site colonization and extinction) using multi-season models (MacKenzie et al. 2003) was not worthwhile, I did allow occupancy to vary between study periods to ensure that the closure assumption was not violated. The occupancy state (1 or 0) of species i at site j during study period t (z_{ijt}) was therefore modeled as

$$z_{ijt} \sim \text{Bernoulli}(\psi_{ijt})$$

where ψ_{ijt} is the probability that species i occurs at site j during study period t . ψ_{ijt} was modeled as a function of several site-level (j) and/or period-level (t) covariates as

$$\begin{aligned} \text{logit}(\psi_{ijt}) = & \alpha_{0,i} + \alpha_{1,i} \text{disturbance} + \alpha_{2,i} \text{FOREST}_j + \alpha_{3,i} \text{TPI}_j \\ & + \alpha_{4,i} \text{RUGGED}_j + \alpha_{5,i} \text{FOREST}_j * \text{disturbance} \end{aligned}$$

where *disturbance* is either *BUILDING_j* for the human footprint model or *meanHPD_{jt}* for the human presence model, and α is a vector of parameter estimates for species *i*.

Detection (y_{ijkt}) of species *i* at site *j* during daily survey *k* is conditional on occupancy of species *i* at site *j* during the study period *t* during which survey *k* occurred, and was modeled as

$$y_{ijkt} \sim \text{Bernoulli}(z_{ijt} * p_{ijk})$$

$$\begin{aligned} \text{logit}(p_{ijk}) = & \beta_{0,i} + \beta_{1,i} \text{disturbance} + \beta_{2,i} \text{FOREST}_j + \beta_{3,i} \text{TPI}_j \\ & + \beta_{4,i} \text{RUGGED}_j + \beta_{5,i} \text{FOREST}_j * \text{disturbance} \end{aligned}$$

where p_{ijk} is the probability of detecting species *i* on camera *j* during survey *k*. *disturbance* in this case is either *BUILDING_j* or *HPD_{jk}*, the latter varying between daily surveys. β is a vector of parameter estimates for species *i*. I included an interaction between forest cover and human disturbance in both the occupancy and detection submodels because the presence of protective cover may affect how responsive a species is to human disturbance and thus alter the effect of disturbance on site use and/or activity.

Species-level parameter estimates for both the occupancy (α_i) and detection probability (β_i) submodels were drawn from distributions governed by community-level hyperparameters (Burton et al. 2012, Broms et al. 2016) as follows

$$\alpha_i \sim \text{Normal}(\mu_\alpha, \sigma_\alpha)$$

$$\beta_i \sim \text{Normal}(\mu_\beta, \sigma_\beta)$$

where μ and σ are vectors of means and standard deviations.

I analyzed the occupancy models in a Bayesian framework, using the JAGS (Plummer 2003) language called through the package R2jags (Su and Yajima 2015) in R (v. 3.4.2; R Development Core Team, 2010). For each model, I ran three Markov Chain Monte Carlo (MCMC) chains of 20,000 iterations each and make inference from 1,000 samples from the posterior distribution of each chain after a burn in of 15,000 and a thinning rate of 5. I chose vague priors for all random variables and random starting values for all chains. Convergence of MCMC chains was confirmed by visual inspection of trace plots, and via the Gelman-Rubin statistic (\hat{R}) (Hobbs and Hooten 2015). To test model fit, I calculated Freeman-Tukey (Conn et al. 2018) and chi-squared statistics (Royle and Dorazio 2008) for both observed data and expected values derived from the fitted model and compared these statistics using Bayesian p-values (Hobbs and Hooten 2015). In describing the effect of model covariates on occupancy and detection probability below, I report the posterior probability that the

coefficient estimate for a given covariate is more extreme (greater or less than) zero (hereafter, ‘posterior probability’).

Comparing the effects of human presence and human footprint on wildlife nocturnality

I estimated the degree to which wildlife activity was concentrated during nocturnal hours by calculating the time difference in hours between noon and each detection of a wildlife species on camera. The absolute value of this “hours to noon” estimate was taken as a measure of nocturnality such that detections occurring farther from noon (i.e., closer to the middle of the night) were considered to exhibit greater nocturnality. I then calculated the average nocturnality value for each species at each camera site, as well as the total number of independent detections of the species at each site. I used linear regression to compare the effects of human presence and human footprint on species nocturnality. Camera site-level human presence was estimated as human detections per week (HPW), averaged across all three study periods (see above) at a site, and site-level human footprint was estimated from building density (BUILDING) as described above. Both HPW and BUILDING were centered and scaled to permit direct comparison of coefficient estimates, and log transformed to deal with heterogeneity of variances (for most species, there were large numbers of observations at very low levels of HPW and BUILDING, with fewer observations at higher levels). For each wildlife species, I fit a single, weighted

linear regression model including both HPW and BUILDING as covariates and total detections of the species as a weighting term. Model fit was confirmed by inspecting residual vs. fitted value and quantile-quantile plots.

Predicting the intensity of human presence across the landscape

I evaluated landscape scale predictors of human activity to determine where and when human presence would be concentrated on the landscape beyond developed areas. I estimated camera site-level human presence based on daily counts of humans detected at each camera, as described above. I expected temporal variation in human activity due to a “day-of-the-week effect” (WEEKEND), given that outdoor activity is typically greater on weekends when recreational opportunities are greatest (Nix et al. 2018). I therefore summed human counts for each camera site based on day of the week, creating two estimates per site corresponding to expected low and high human activity, i.e., counts during the 5 days in the middle of the week (Monday - Friday; low activity) and those during the 2 days on the weekend (Saturday and Sunday; high activity). To account for uneven sampling effort between level of activity (weekday versus weekend), I included the total number of weekday or weekend days a camera was active as an offset in models described below, resulting in a response of humans per day (HPD). HPD was modeled based on landscape attributes that I hypothesized were proxies of the intensity of human activity and best characterized the potential for nature-based recreation (Neuvonen et al. 2010, Sen et al. 2014, Weyland and Laterra

2014). Recreational use in an area has been shown to increase with adjacency to development due to lower travel demand and accessibility (Spinney and Millward 2013, Rossi et al. 2015) thus the following variables representing spatial demand were included in the model: ROAD, BUILD, URBAN, and WUI . In addition, I included the TRAIL, VIEW, OPEN, and ACCESS variables since the availability of recreation services are considered important determinants of visitation to and human activity in an area (Hill and Courtney 2006, Ode and Fry 2006). Natural features, such as tree vegetation and rough reliefs, can generate high scenic value and recreational opportunities (hiking, biking, etc.) therefore I also included FOREST, RUGGED, ELEV and VIEW variables. To evaluate whether any landscape characteristics associated with human activity varied between weekends versus weekdays, I included a 2-way interaction between WEEKEND and all other covariates. All covariates were normalized (mean centered and scaled by two standard deviations) to improve model convergence and to facilitate comparison of model coefficients among covariates (Gelman 2008). I also made sure that no candidate models had covariates exhibiting high levels of collinearity ($r > 0.7$). Based on Vuong closeness tests (Vuong 1989), I formulated the model as a zero-inflated Poisson (ZIP) model as data were skewed towards counts of zero humans per camera day. All analyses were performed using the language R (v. 3.4.2; R Development Core Team, 2010) with the zero-inflated Poisson model and Vuong closeness tests fit using the R package pscl (Zeileis et al. 2008) and AICc calculated using the MuMIn (Bartoń 2018) package.

RESULTS

Effects of human presence and human footprint on wildlife habitat use

Both human presence and human footprint occupancy models exhibited successful convergence ($\hat{R} < 1.1$ for all model terms) and excellent fit (Bayesian p-values: $0.445 \leq p \leq 0.499$). These models revealed that human presence and human footprint are not equivalent in their effects on wildlife habitat use (Fig. 2, Tables S1, S2, S3 and S4). The intensity and sign of the effect of each human disturbance type varied substantially between species. Several species (pumas, bobcats, and foxes) exhibited a significant positive association between occupancy probability and average human activity at a camera site (posterior probability for all species ≥ 0.99 ; Table S1). Interestingly, none of the species analyzed exhibited a negative association between occupancy and human activity. By contrast, fox occupancy probability was strongly negatively associated with building density (posterior probability = 1; Fig. 2, Table S3), while several well-known synanthropic species (coyotes, skunks, and opossums) exhibited relatively strong positive associations between occupancy probability and building density (posterior probability: coyote = 0.99, skunk = 0.96, opossum = 0.92).

Human presence and building density had similarly non-equivalent effects on wildlife detection probability. The number of human detections in the immediately preceding diurnal period had a strong negative effect on skunk and opossum detection

probability (posterior probability = 0.99 and 0.97, respectively), with bobcats and foxes showing the opposite effect (posterior probability = 1 for both species; Fig. 2, Table S2). Pumas (0.97), bobcats (0.99), and foxes (1.0) were all less likely to be detected with increasing building density, while common synanthropic species showed increasing detection probability with increasing building density (skunk and raccoon, posterior probability = 1.0 for both species; Fig. 2, Table S4).

For several species, the effects of human presence on habitat use were mediated by the availability of forest cover. Both foxes and opossums were more likely to occupy sites with high human presence if high forest cover was also available (Fig. 3a,b; Table S1). Coyotes similarly exhibited increased occupancy probability at high building density sites where high forest cover was available, while bobcats showed the opposite pattern, though with substantial variability (Fig. 3c,d; Table S3). Full results of the human presence and human footprint occupancy models, including main effects of forest cover, topographic position, and ruggedness, are presented in Tables S1, S2, S3, and S4.

Effects of human presence and human footprint on wildlife nocturnality

Several wildlife species exhibited significant temporal shifts in their diel activity patterns across the gradients of human presence and/or building density. Pumas (weighted linear regression: $F_{1,67} = 17.22$, $p < 0.001$), bobcats ($F_{1,67} = 3.81$, $p = 0.054$), and coyotes ($F_{1,67} = 8.47$, $p = 0.007$) exhibited increased nocturnality as

human presence at a site increased. Bobcats also exhibited increased nocturnality with increasing building density ($F_{1,67} = 9.51, p = 0.003$) while foxes were moderately less nocturnal at increasing levels of building density ($F_{1,67} = 8.38, p = 0.005$; Fig. 4, Table S3).

Predicting the intensity of human presence across the landscape

The zero-inflated Poisson regression model predicting landscape scale variation in human activity was statistically significant ($\chi_{11,176} = 1163, p < 0.001$; Pseudo $R^2 = 0.63$) and revealed that variables representing spatial demand, recreational services, and natural features were strong predictors of the intensity of human activity at a camera location, i.e. humans per day (HPD). As expected, human activity varied depending on the time of the week with increased activity on weekends ($\beta_{\text{WEEKEND}} = 0.29, p < 0.001$) relative to weekday use. HPD also increased significantly in areas with greater opportunities for recreational activities, including proximity to public open space ($\beta_{\text{OPEN}} = -0.77, p < 0.001$), higher trail density ($\beta_{\text{TRAIL}} = 0.99, p < 0.001$), greater proportion of vista opportunities ($\beta_{\text{VIEW}} = 0.10, p < 0.001$), and adjacency to recreational access points ($\beta_{\text{ACCESS}} = -0.89, p < 0.001$). Additionally, HPD was greater in proximity to highly developed urban areas ($\beta_{\text{URBAN}} = -0.16, p = 0.04$) as well as those dominated by exurban expansion into rural landscapes ($\beta_{\text{WUI}} = 0.11, p < 0.001$). However, an interaction with weekend ($\beta_{\text{URBAN:WEEKEND}} = 0.46, p < 0.001$) suggests activity is more prevalent in areas farther away from developed areas

on the weekend, with use localized to areas near development during weekdays. The surrounding natural characteristics of a site also influenced HPD with decreased activity in more rugged landscapes ($\beta_{\text{RUGGED}} = -0.14$, $p < 0.001$), though human use of rugged areas increased on weekends ($\beta_{\text{RUGGED:WEEKEND}} = 0.2$, $p = 0.004$). I did not find significant correlations for the remainder of the variables. The Vuong test suggested that the zero-inflated model was a significant improvement over a standard Poisson regression model ($p < 0.0001$).

DISCUSSION

Although a growing body of research demonstrates that both the human footprint and human presence (including recreation) can have negative impacts on wildlife (Larson et al. 2016, Gaynor et al. 2018, Tucker et al. 2018), studies aimed at disentangling the concurrent effect of both forms of disturbance on wildlife behavior are surprisingly rare. These results demonstrate that human footprint and human presence have differential effects on the occupancy and activity patterns of wildlife in the region. I further show that human presence beyond developed areas is more extensive in the region than anticipated, particularly in protected areas with high recreation potential. Moreover, I was able to predict the intensity of human presence from landscape-level variables allowing estimation of human impacts on wildlife even in wilderness areas. Together, these results refine our understanding of how both human activity and development drive changes in wildlife behavior and underscore

the importance of integrating multiple sources of disturbance when evaluating the degree to which human-derived risk affects wildlife.

Contrasting effects of human presence and human footprint on wildlife habitat use and behavior

These results demonstrate that human presence and human footprint are not equivalent in their impacts on wildlife habitat use and behavior, with these two forms of anthropogenic disturbance in many cases having opposing effects on occupancy and/or detection probability. Building density and other forms of development represent long-term and spatially constant sources of disturbance, and several sensitive wildlife species have been shown to avoid these risky places (Riley 2006, Ordeñana et al. 2010), including pumas in the study area (Wilmers et al. 2013, Wang et al. 2015a). I correspondingly found negative effects of building density on the habitat use of several carnivores, including pumas and bobcats, which were less detectable in areas of high building density, indicative of reduced overall activity levels in areas of consistent human disturbance (Fig 2). Grey foxes appeared to be particularly sensitive to human footprint, with building density having a strong negative effect on fox occupancy and detection probability for this species (Fig. 2).

By contrast, these same three carnivores (and to a lesser extent, coyotes) exhibited increased occupancy and/or detection probability with increasing human presence, despite growing experimental evidence that several large and medium-sized

carnivore species (including pumas and bobcats) exhibit strong fear responses to humans (Clinchy et al. 2016, Smith et al. 2017, Suraci et al. 2019a). Spatial modeling results (Fig. 5) revealed that human presence is relatively high throughout many of the protected areas in the Santa Cruz Mountains, and thus likely overlaps with high-quality habitat for many species potentially making the outright avoidance of human presence in wildland areas overly costly. Additionally, highly mobile species such as pumas, bobcats, and coyotes, may be positively associated with areas of high human presence because, like humans, these species are attracted to trails through wooded areas (Kays et al. 2017), which provide energetically efficient movement pathways across relatively large home ranges. These results indicate that, instead of avoiding humans in space, these species take advantage of the high temporal predictability of human activity to avoid humans in time, becoming increasingly nocturnal as human presence increases (Fig. 4). Increased wildlife nocturnality with increasing human disturbance has been demonstrated for a large number of species globally (Gaynor et al. 2018) and has been associated with both human footprint on the landscape (e.g., residential development, urbanization, agriculture; Beckmann and Berger 2003, Graham et al. 2009, Díaz-Ruiz et al. 2016) and high human presence (e.g., recreation) in wildland areas (e.g., Coleman et al. 2013, Wang et al. 2015, Reilly et al. 2017). Restricting activity to nocturnal hours may involve substantial costs for some wildlife species, e.g., by interfering with foraging behavior or increasing overlap with predators or competitors (Gaynor et al. 2018, Smith et al. 2018), but may nonetheless

promote coexistence by allowing humans and wildlife to use the same habitat (Carter et al. 2012, Suraci et al. 2019b).

Human presence and human footprint also had opposing effects on habitat use by skunks and opossums, synanthropic species which commonly take advantage of human resource subsidies (e.g., food waste) in developed areas (Bateman and Fleming 2012). Recent experimental work demonstrates that, despite their strong association with human development, these species are nonetheless fearful of immediate human presence, reducing activity and foraging behavior when perceived human presence was experimentally increased (Suraci et al. 2019a). The present study confirms that these experimental results are relevant at the regional scale. Despite exhibiting increased occupancy (skunks and opossums) and detection probability (skunks) with increasing building density, both skunks and opossums were substantially less detectable in areas with high human presence, consistent with reduced activity levels in the presence of people. Taken together, these findings suggest that, even for synanthropic species, human presence is potentially costly, and that the benefits of exploiting anthropogenic environments (e.g., resources subsidies) must be traded off against the risks of a potentially dangerous direct encounter with humans.

For several carnivore species, occupancy of habitats with either high human presence (foxes and opossums) or high human footprint (coyotes) increased with increasing forest cover, indicating that the availability of protective cover reduces the

risk that some wildlife species perceive from humans. Previous studies have similarly demonstrated increased use of human-dominated landscapes by carnivores when the availability of protective cover is high (Boydston et al. 2003, Ordiz et al. 2011, Suraci et al. 2019b), suggesting that cover availability plays a key role in mediating coexistence between humans and carnivores by reducing the impacts of anthropogenic disturbance on carnivore behavior.

Predicting the intensity of human presence across the landscape

Human presence beyond heavily developed areas varied widely across the region with the most important drivers of use related to variation in recreation potential and demand. In particular, human presence was higher in conserved lands with built capital providing access to recreational opportunities. Proximity to public open space, vehicle access, and trail density were the strongest predictors of human presence at a site, consistent with previous findings suggesting that access to dense trail networks is correlated with significantly higher visitation rates (McKinney 2005, Reed and Merenlender 2008, 2011, Neuvonen et al. 2010, Kienast et al. 2012, Beeco et al. 2014, Taczanowska et al. 2014, Larson et al. 2018). Similarly, ruggedness and the scenic potential of a site were positively associated with human use (Ode and Fry 2006, Termansen et al. 2013, Kellner et al. 2017). As such, human presence is likely more regular and widespread than expected in protected areas with greater recreation potential and where recreation infrastructure is well-developed. Given that protected

lands often overlap with high-quality habitat for many species, elevated human activity in these areas likely leads to substantial, yet unintended, impacts on wildlife from disturbance.

While the supply of recreational opportunities influences the level of human activity outside developed areas, human presence is also affected by the surrounding demand for recreation (Hill and Courtney 2006, Rossi et al. 2015). My modeling results are consistent with other studies showing that distance or travel time from population centers is a significant predictor of visitation rates to open spaces (Humpel et al. 2002, Hill and Courtney 2006, Ode and Fry 2006, Rossi et al. 2015, Larson et al. 2018). I found higher levels of human presence at sites adjacent to urban development as well as those dominated by exurban expansion (Hanink and White 1999, Rossi et al. 2015, Patten and Burger 2018, Larson et al. 2018). This pattern is particularly significant for urban-adjacent reserves as the potential for human-wildlife interactions and thus negative impacts is likely greatest given the already elevated presence of humans in protected areas of the region. However, I detected a significant interaction between distance to urban center and weekend (Table 1), indicating that human presence in protected areas shifted depending on the day of the week with greater concentrations of activity at sites further away from developed areas on weekends, potentially due to time-dependent constraints on recreation (Arnberger 2006, Degenhardt et al. 2011, Fredman et al. 2011, Rossi et al. 2015, Larson et al. 2018). For instance, frequent but short-term recreational use in nearby open spaces has been shown to be more prevalent during workdays when discretionary time is

limited (Hanink and White 1999, Rossi et al. 2015) while, weekend recreation is characterized by longer stays at more distant locales, especially larger regional and national parks, where greater recreational opportunities, e.g. challenging trails or higher scenic value, are more available but difficult to access during weekdays (Hanink and White 1999, Rossi et al. 2015). This shift in human activity depending on day of the week meant that even relatively remote areas of the Santa Cruz Mountains were exposed to substantial human presence during some time periods.

My approach to modeling human presence and evaluating species response to human activity can be used to guide future research and inform guidelines for the management of non-consumptive recreation in wilderness areas. For example, landscape level measures of the human footprint, such as land cover, population density, and built infrastructure, are well developed and readily available (e.g. Venter et al. 2016), however spatially explicit data on human presence outside of developed areas are notably absent (but see Gutzwiller et al. 2017). This approach helps address this gap and demonstrates that the intensity of human presence on the landscape (including in wildland areas) can be predicted from landscape-level variables, allowing estimation of human impacts on wildlife even outside of developed areas. Further, I show that modeling human presence is possible using increasingly available sources of spatial data (e.g., parcels, elevation, trails) allowing for projecting or forecasting the intensity of human activity at the landscape scale (Fig. 5). Predictive models of this nature could be used to improve landscape-wide management of non-consumptive forms of human disturbance and suggest practical management actions

for reducing impacts on wildlife or evaluating the effectiveness of alternative management decisions. For example, when planning for future recreation uses of an area, land-use managers could estimate human activity, and thus disturbance potential, in newly acquired land or under varying use or development scenarios that alter recreational potential or demand.

Management Implications

Taken together, this research demonstrates that in many cases the human footprint on the landscape is unlikely to be an adequate predictor of total anthropogenic impacts on wildlife communities given that (i) human presence and development differ in their effects on wildlife behavior and habitat use (Fig. 1), and (ii) the potential impacts of human presence extend well beyond the spatial footprint of developed areas (Fig. 4). This work underscores the need to better understand the complex, non-linear response of wildlife to human disturbance as well as the diverse factors likely to promote human activity in wildland areas. Occupancy modelling results revealed that several wildlife species avoided human development overall, meaning that projected increases in development (Smith et al. 2019) will only increase the importance of protected areas in providing wildlife habitat. However, as development intensifies so will human activity and the associated costs to wildlife in terms of changes in behavior and activity patterns, posing serious challenges for landscape management and conservation. This is especially true in and around

protected areas where recreation activity is often greatest but not always compatible with conservation objectives (Larson et al. 2016). Conservation planning should thus take into account not only wildlife distributions but also the spatial extent of human activities, including recreational demand, and its compatibility with conservation goals and other land-management objectives.



Figure 4.1. The study area in the Santa Cruz Mountains, California, including the network of cameras traps (black dots) used as part of this study.

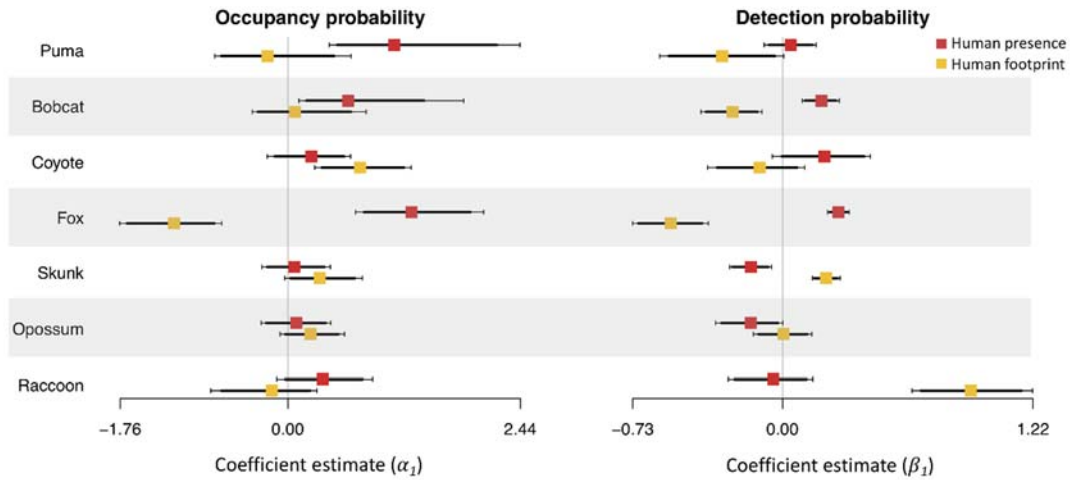


Figure 4.2. Coefficient estimates from the multispecies occupancy models showing the effect of human detections (red) and building density (yellow) on occupancy and detection probabilities for each wildlife species. Symbols to the right of zero (vertical line) indicate a positive effect of the human disturbance metric on occupancy or detection probability, and symbols to the left of zero indicate a negative effect. Thick horizontal lines are 90% Bayesian credible intervals, and thin horizontal lines are 95% credible intervals.

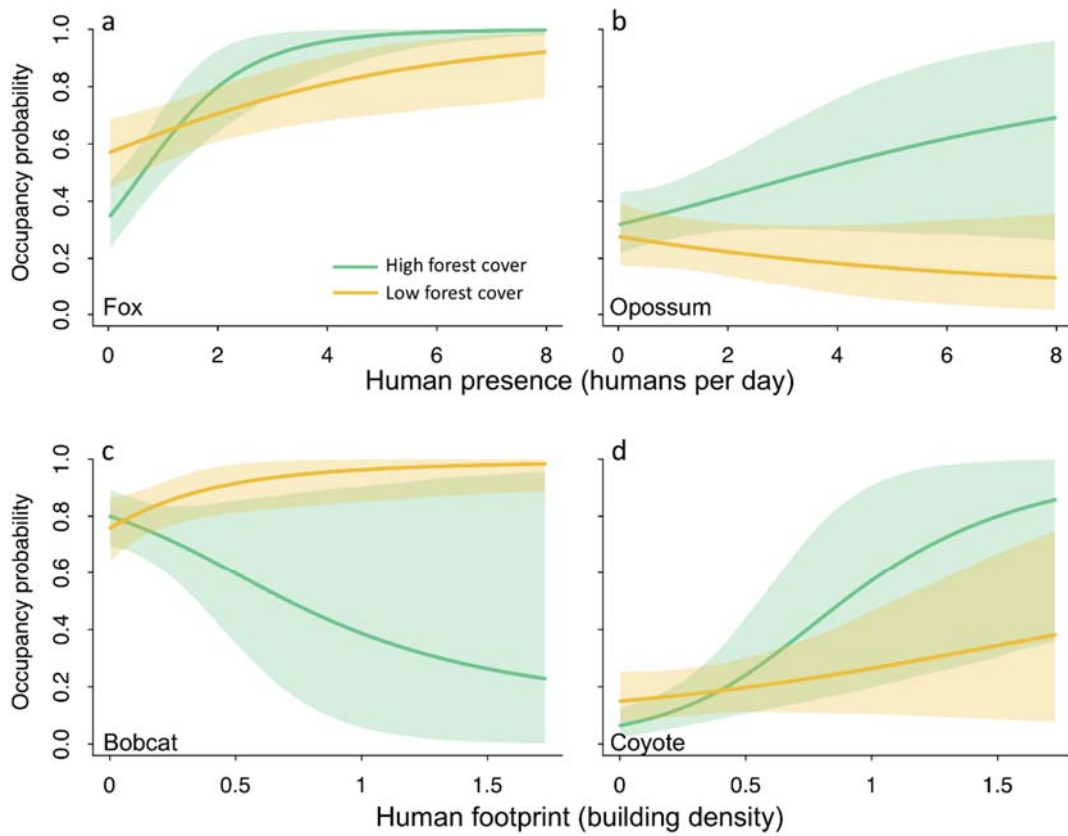


Figure 4.3. Human disturbance interacts with forest cover to affect wildlife species occupancy probability. The effect of human detections (a,b) and building density (c,d) on occupancy probability are shown for (a) foxes, (b) opossums, (c) bobcats, and (d) coyotes at both low (yellow) and high (green) levels of forest cover. Low and high forest cover are here defined as the 20% and 80% quantiles, respectively, of forest cover across all camera sites. Lines and shaded areas are predictions and 95% credible intervals from the multi-species occupancy model.

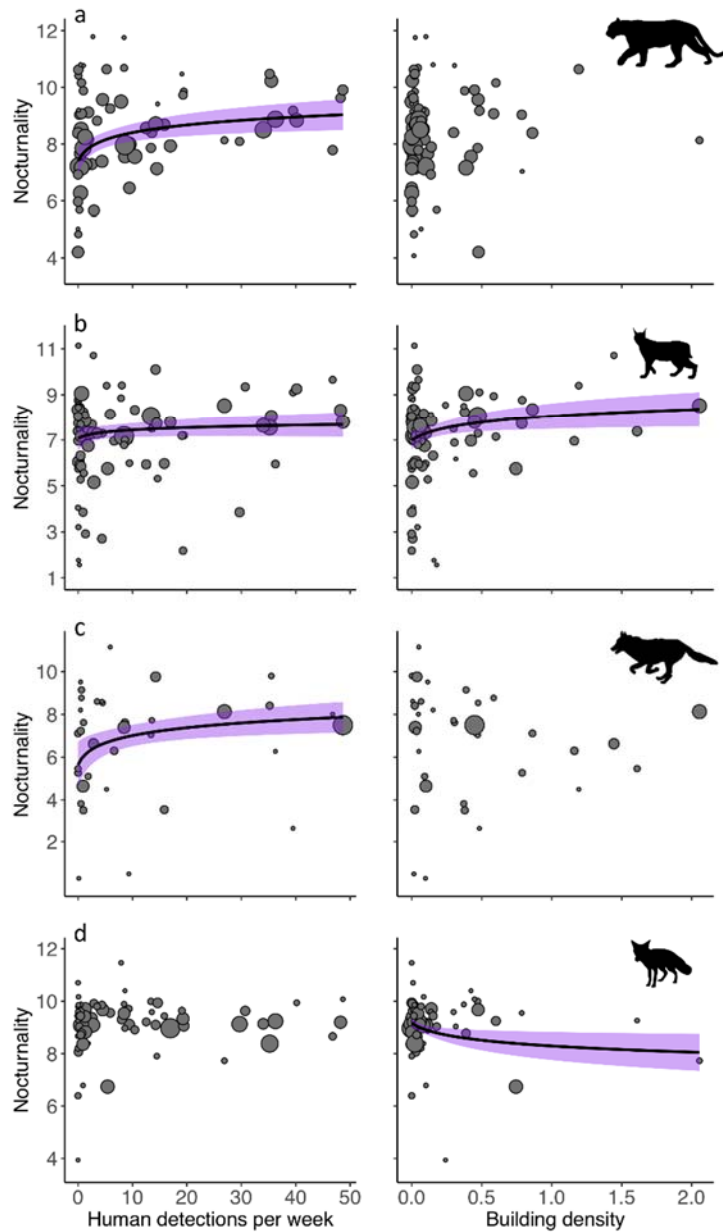


Figure 4.4. The effect of human disturbance on wildlife nocturnality. Nocturnality estimates (i.e., average time of detections on camera expressed as hours from noon) at a given camera site are plotted against human detections per week and building density at that camera site for (a) pumas, (b) bobcats, (c) coyotes, and (d) foxes. Fitted lines and shaded areas represent the predicted effect, \pm 95% confidence intervals, of human disturbance on nocturnality. Absence of a fitted line indicates no significant effect of disturbance on nocturnality. Only those wildlife species for which at least one human disturbance type significantly affected nocturnality are shown.

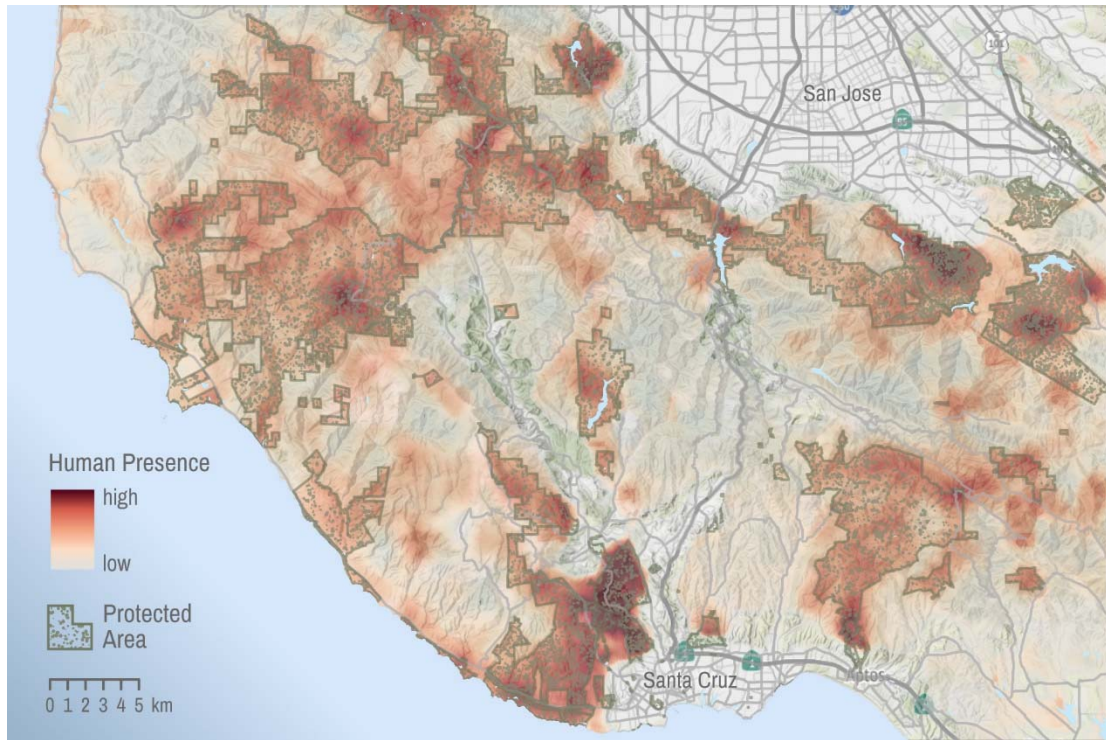


Figure 4.5. Landscape level prediction of human activity in the region based on the modeling results (Table 4.1) using publicly available sources of spatial data (e.g., protected areas, parcels, elevation, trails). Levels of human presence outside developed areas range from low (pink) to high (dark red) in relation to protected (green stipple) and urban areas across the region.

Table 4.1. Fixed effects terms from the best-supported model for predicting human presence on the landscape.

Model Parameter	β	SE	t	p
<i>Marginal R² = 0.63</i>				
TRAIL	0.99	0.004	7.53	< 0.001
ACCESS	-0.89	0.006	5.73	< 0.001
OPEN	-0.77	0.004	14.64	< 0.001
WEEKEND	0.29	0.004	12.92	< 0.001
RUGGED	-0.14	0.004	4.89	< 0.001
WUI	0.11	0.005	-4.68	< 0.001
VIEW	0.10	0.004	-2.21	0.05
URBAN	-0.16	0.004	-2.12	0.03
URBAN : WEEKEND	0.46	0.004	-2.43	0.004
RUGGED : WEEKEND	0.20	0.004	-2.21	0.02

Table S4.1. Full results of the human presence multispecies occupancy model, showing coefficient estimates ($\pm 95\%$ credible intervals) for all covariates hypothesized to affect species occupancy probability at a camera site. Bolded and italicized estimates are those for which the 95% credible interval does not cross zero.

	Puma	Bobcat	Coyote	Fox	Skunk	Opossum	Raccoon
<i>Occupancy probability</i>							
Intercept (a_0)	0.49 (-0.02, 1.15)	1.45 (1.05, 2.05)	-1.85 (-2.31, -1.41)	0.6 (0.24, 1.02)	0.53 (0.24, 0.83)	-0.82 (-1.13, -0.52)	-1.84 (-2.38, -1.23)
Humans per day (a_1)	<i>1.2</i> (0.44, 2.44)	<i>0.71</i> (0.12, 1.85)	0.24 (-0.22, 0.66)	<i>1.32</i> (0.71, 2.05)	0.07 (-0.27, 0.45)	0.09 (-0.28, 0.45)	0.37 (-0.12, 0.89)
Forest cover (a_2)	<i>0.45</i> (0.04, 0.93)	-0.17 (-0.57, 0.23)	-0.12 (-0.53, 0.27)	-0.03 (-0.35, 0.31)	<i>0.5</i> (0.21, 0.81)	0.29 (-0.02, 0.61)	-0.28 (-0.75, 0.13)
Topographic position (a_3)	-0.01 (-0.49, 0.37)	0.08 (-0.23, 0.39)	0.17 (-0.17, 0.57)	0.19 (-0.08, 0.5)	0.11 (-0.16, 0.38)	-0.17 (-0.5, 0.12)	-0.07 (-0.52, 0.35)
Ruggedness (a_4)	0.09 (-0.34, 0.58)	-0.26 (-0.6, 0.09)	-0.36 (-0.83, 0.07)	<i>0.82</i> (0.45, 1.22)	-0.27 (-0.56, 0)	<i>-0.56</i> (-0.93, -0.23)	-0.12 (-0.57, 0.29)
Forest x HPD (a_5)	0.36 (-0.14, 1.09)	0 (-0.54, 0.46)	-0.02 (-0.37, 0.31)	<i>0.65</i> (0.22, 1.15)	0.25 (-0.03, 0.56)	<i>0.32</i> (0.01, 0.65)	0.09 (-0.36, 0.44)

Table S4.2. Full results of the human presence multispecies occupancy model, showing coefficient estimates ($\pm 95\%$ credible intervals) for all covariates hypothesized to affect species detection probability at a camera site. Bolded and italicized estimates are those for which the 95% credible interval does not cross zero.

	Puma	Bobcat	Coyote	Fox	Skunk	Opossum	Raccoon
<i>Detection probability</i>							
Intercept (β_0)	-3.15 (-3.32, -2.98)	-2.41 (-2.5, -2.31)	-2.85 (-3.15, -2.57)	-1.21 (-1.28, -1.14)	-2.07 (-2.15, -1.98)	-2.39 (-2.54, -2.24)	-2.98 (-3.5, -2.56)
Humans per day (β_1)	0.04 (-0.09, 0.16)	0.19 (0.1, 0.28)	0.2 (-0.05, 0.43)	0.27 (0.22, 0.33)	-0.16 (-0.26, -0.05)	-0.16 (-0.33, 0)	-0.05 (-0.27, 0.15)
Forest cover (β_2)	0.01 (-0.15, 0.18)	-0.39 (-0.48, -0.31)	-0.27 (-0.52, -0.03)	-0.05 (-0.12, 0.02)	-0.04 (-0.13, 0.05)	-0.14 (-0.28, 0)	0.1 (-0.12, 0.34)
Topographic position (β_3)	0.2 (-0.01, 0.41)	-0.06 (-0.14, 0.03)	-0.36 (-0.63, -0.1)	0.41 (0.35, 0.47)	-0.07 (-0.16, 0.02)	-0.08 (-0.25, 0.1)	-0.82 (-1.35, -0.38)
Ruggedness (β_4)	-0.23 (-0.41, -0.05)	-0.12 (-0.22, -0.03)	-0.19 (-0.41, 0.02)	0.21 (0.14, 0.27)	-0.11 (-0.19, -0.02)	0 (-0.17, 0.16)	-0.21 (-0.45, 0)
Forest x HPD (β_5)	0.04 (-0.07, 0.16)	-0.05 (-0.11, 0.01)	-0.09 (-0.28, 0.08)	0.15 (0.1, 0.2)	0.07 (-0.03, 0.18)	-0.01 (-0.14, 0.13)	0.26 (0.09, 0.44)

Table S4.3. Full results of the human footprint multispecies occupancy model, showing coefficient estimates ($\pm 95\%$ credible intervals) for all covariates hypothesized to affect species occupancy probability at a camera site. Bolded and italicized estimates are those for which the 95% credible interval does not cross zero.

	Puma	Bobcat	Coyote	Fox	Skunk	Opossum	Raccoon
<i>Occupancy probability</i>							
Intercept (a_0)	0.4 (-0.08, 1.14)	1.37 (0.98, 1.81)	-1.83 (-2.31, -1.35)	0.21 (-0.14, 0.55)	0.55 (0.24, 0.86)	-0.89 (-1.23, -0.58)	-1.78 (-2.37, -1.14)
Building density (a_1)	-0.17 (-0.77, 0.66)	0.11 (-0.37, 0.82)	0.77 (0.28, 1.29)	-1.2 (-1.76, -0.69)	0.35 (-0.03, 0.78)	0.24 (-0.08, 0.6)	-0.19 (-0.81, 0.31)
Forest cover (a_2)	0.27 (-0.15, 0.76)	-0.39 (-0.88, 0.05)	-0.19 (-0.59, 0.23)	-0.41 (-0.77, -0.07)	0.59 (0.29, 0.9)	0.3 (-0.01, 0.64)	-0.43 (-0.91, 0.01)
Topographic position (a_3)	-0.14 (-1.01, 0.31)	0.24 (-0.07, 0.59)	0.25 (-0.11, 0.69)	0.22 (-0.06, 0.52)	0.12 (-0.14, 0.39)	-0.12 (-0.46, 0.19)	0.06 (-0.4, 0.54)
Ruggedness (a_4)	0.04 (-0.43, 0.64)	-0.21 (-0.56, 0.15)	-0.21 (-0.71, 0.24)	0.68 (0.3, 1.06)	-0.2 (-0.49, 0.1)	-0.41 (-0.76, -0.08)	0.01 (-0.42, 0.45)
Forest x Building (a_5)	0.27 (-0.46, 0.99)	-0.84 (-1.8, -0.1)	0.43 (0.02, 0.92)	-0.06 (-0.57, 0.47)	0.3 (-0.05, 0.69)	-0.26 (-0.61, 0.08)	-0.42 (-0.94, 0.04)

Table S4.4. Full results of the human footprint multispecies occupancy model, showing coefficient estimates ($\pm 95\%$ credible intervals) for all covariates hypothesized to affect species detection probability at a camera site. Bolded and italicized estimates are those for which the 95% credible interval does not cross zero.

	Puma	Bobcat	Coyote	Fox	Skunk	Opossum	Raccoon
<i>Detection probability</i>							
Intercept (β_0)	-3.25 (-3.47, -3.04)	-2.4 (-2.51, -2.31)	-2.77 (-3.08, -2.48)	-1.35 (-1.45, -1.25)	-2.09 (-2.18, -2)	-2.48 (-2.65, -2.31)	-3.18 (-3.83, -2.64)
Building density (β_1)	-0.3 (-0.6, 0.01)	-0.25 (-0.4 , -0.1)	-0.12 (-0.37, 0.11)	-0.55 (-0.73 , -0.36)	0.21 (0.15 , 0.28)	0 (-0.14, 0.14)	0.92 (0.63 , 1.22)
Forest cover (β_2)	-0.07 (-0.28, 0.15)	-0.5 (-0.59 , -0.41)	-0.37 (-0.64 , -0.13)	-0.21 (-0.34 , -0.07)	-0.02 (-0.11, 0.08)	-0.06 (-0.23, 0.11)	0.58 (0.29 , 0.91)
Topographic position (β_3)	0.29 (0.04 , 0.54)	-0.08 (-0.17, 0.01)	-0.44 (-0.67, -0.22)	0.44 (0.38 , 0.5)	-0.09 (-0.18, 0)	-0.12 (-0.31, 0.06)	-0.9 (-1.55 , -0.34)
Ruggedness (β_4)	-0.27 (-0.47 , -0.08)	-0.21 (-0.29 , -0.12)	-0.24 (-0.46 , -0.02)	0.14 (0.07 , 0.2)	-0.08 (-0.17, 0.01)	0.01 (-0.16, 0.18)	-0.37 (-0.68 , -0.11)
Forest x Building (β_5)	-0.25 (-0.61, 0.15)	-0.02 (-0.13, 0.09)	-0.36 (-0.6 , -0.13)	-0.43 (-0.69 , -0.18)	0.04 (-0.05, 0.13)	-0.15 (-0.25 , -0.06)	0.45 (0.24 , 0.65)

Table S4.5. Results of linear regression models comparing the effects of human detections per week (HPW) and building density (Building) on wildlife nocturnality. Human disturbance covariates were centered and scaled.

	Estimate	Standard error	p-value
<i>Puma</i>			
HPW	0.597	0.144	< 0.001
Building	0.291	0.179	0.109
<i>Bobcat</i>			
HPW	0.280	0.144	0.054
Building	0.425	0.138	0.003
<i>Coyote</i>			
HPW	0.733	0.252	0.007
Building	0.062	0.231	0.790
<i>Fox</i>			
HPW	-0.071	0.088	0.421
Building	-0.347	0.120	0.005
<i>Skunk</i>			
HPW	0.003	0.072	0.971
Building	-0.099	0.057	0.086
<i>Opossum</i>			
HPW	0.144	0.102	0.166
Building	-0.062	0.078	0.431
<i>Raccoon</i>			
HPW	0.150	0.190	0.436
Building	-0.327	0.187	0.089

CHAPTER 5

CONCLUDING REMARKS

Understanding the impact of humans on wildlife is an important component to their effective conservation and management. As the human footprint continues to expand, natural landscapes are more likely to be shared between wildlife and people further precipitating the negative impacts of human activity on wildlife. While it is well established that these impacts are complex and vary among species (Hoffmann et al. 2010, Dirzo et al. 2014, Gaynor et al. 2018, Tucker et al. 2018), humans have a particularly unique impact on large carnivores (Estes et al. 2011, Crooks et al. 2011, Ripple et al. 2014). This is due in part to their high trophic position, low population densities and reproductive rates, large spatial and prey requirements, and propensity to conflict with humans (Woodroffe and Ginsberg 1998, Woodroffe 2000, Brashares et al. 2001, Cardillo et al. 2004, Nielsen et al. 2004, Creel et al. 2013, Rosenblatt et al. 2014). However, there is limited empirical work about how carnivores co-exist with humans and the extent to which, if any, risk plays a role in their dynamics.

This research focuses, in part, on the effects of human-induced risk on the energetic and behavioral ecology of pumas providing for a more mechanistic understanding of how large carnivores navigate complex, natural landscapes shared with humans. Specifically, I demonstrate that the fear of humans exerts an energetic cost comparable to that of physical terrain and their combined costs drive where and to what extent pumas move across the landscape. For example, pumas elect to use

energetically efficient movement pathways where possible, however, in areas of increasing risk from humans they adopt energetically sub-optimal paths. This pattern reflects a trade-off between risk avoidance and the energy costs of movement that results in a constriction of overall space use for individuals experiencing consistently high movement costs. As such behavioral changes induced by the fear of humans may put considerable strain on a puma's energy budget and therefore come at the cost of reductions in key behaviors, including long-range movements and territorial defense.

In addition, this research demonstrates that the human footprint and human presence have non-equivalent, and in some cases opposite, effects on the habitat use and activity patterns of wildlife. In most cases, wildlife adjusted their behavior in areas of high overlap between wildlife and people becoming more active when human presence was lower and generally avoiding developed areas where possible. Further, human presence beyond developed areas is extensive and concentrated in protected areas suggesting human impacts on wildlife may be more widespread in the region than anticipated. Given that both human development and activity are prevalent, complete avoidance of people is likely impossible for many species and thus the likelihood of negative impacts from human disturbance correspondingly high in the region. As such, conservation planning should take into account not only wildlife distributions in relation to human development but also the spatial extent of human activities, including recreation, when evaluating the degree to which human-derived risk affects wildlife.

Taken together, this dissertation provides an important extension of recent attempts to quantify the effects of the landscape on animal movement (Shepard et al. 2013, Halsey 2016) and provides new insights regarding human-mediated disturbance of wildlife (Larson et al. 2016, Gaynor et al. 2018, Tucker et al. 2018). Novel approaches like those presented here also advance how we measure sources of human disturbance and improves our ability to assess their impact on wildlife physiology, behavior, and ecology. In particular, integration of the energy landscapes and landscapes of fear under the common currency of energy (Gallagher et al. 2016) provides important insights into the mechanistic understanding of wildlife behavior in landscapes shared with people. Further, combining data obtained from animal-borne and remote sensors offers the opportunity to test hypotheses about the role of energetics in the ecology of wildlife at a scale that has previously been impossible (Wilmers et al. 2015). Doing so offers an avenue to bring a more mechanistic, process-based foundation to research on wildlife responses to human disturbance. Ultimately, I expect that the rigorous quantification of human activity and clarification of its effects on wildlife ecology outlined in this dissertation will prove to be a valuable framework for researchers and managers seeking to conserve wildlife in human-dominated landscapes.

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