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SANTA CRUZ

**DIRECT AND INDIRECT EFFECTS OF HUMAN-INDUCED FEAR IN A
CARNIVORE COMMUNITY**

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

DOCTOR OF PHILOSOPHY

in

ENVIRONMENTAL STUDIES

by

Justine A. Smith

June 2017

The Dissertation of Justine A. Smith
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Vice Provost and Dean of Graduate Studies

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ABSTRACT

DIRECT AND INDIRECT EFFECTS OF HUMAN-INDUCED FEAR IN A CARNIVORE COMMUNITY

Justine A. Smith

Human-induced fear in wildlife has the potential to impact animal behavior, survival, and species interactions through both direct and indirect effects. Risk-avoidance responses to fear can alter the way animals use space and resources, directly influencing their individual success and role in their ecological community. To understand ecological dynamics in systems increasingly modified and dominated by humans, a richer understanding is needed regarding the magnitude of human-induced fear in wildlife and the extent of its cascading effects.

Large carnivores act as keystone predators in many ecosystems by limiting populations of large herbivores and mesocarnivores. The loss of large carnivores can trigger trophic cascades that restructure ecological communities. However, maintaining populations of large carnivores may not be enough if human disturbances restrict the ability for carnivores to continue their functional roles. Optimal coexistence scenarios between humans and carnivores should include minimizing behavioral impacts on carnivores and preserving species interactions.

In this dissertation, I examine the nature and magnitude of human disturbances on carnivore behavior and the indirect effects of their human-induced fear. In particular, I investigate puma risk-foraging tradeoffs and their relationship to prey species on a gradient of human disturbance. I also explore the impacts of human-

induced activity shifts in mesocarnivores on dietary niche partitioning. Finally, I apply my understanding of puma movement behavior and human risk-avoidance to prioritize developable lands for conservation. In conducting this work, I used or developed novel methods in citizen science, DNA metabarcoding, playback experiments, spatial analysis, and conservation planning.

The results of my work indicate that humans can cause substantial risk-foraging tradeoffs in pumas, both at the immediate and landscape scale. This causes pumas to kill more deer per year when exposed to greater disturbance, but preferably consume smaller prey when actually adjacent to development. I also found that mesocarnivores increase diet overlap when they are disturbed by human activity and become more nocturnal. I developed a new approach to prioritizing conservation acquisitions based on puma movement potential and identified high quality land parcels that could be protected by local land trusts or county planners.

My dissertation begins to explore the diversity of pathways that humans can alter animal communities by influencing the behavior of carnivores. Future work should evaluate the extent of human-induced behavioral cascades in ecosystems and determine the long-term outcomes of pervasive anthropogenic disturbance.

DEDICATION

To my parents

*For instilling in me a love for the natural world and
inspiring me to have the determination and tenacity to protect it*

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their kill rates on prey as a response to human-induced fear. *Proceedings of the Royal Society Biological Sciences* 282 (1802):20142711; Smith, J. A., Y. Wang, and C. C. Wilmers. 2016. Spatial characteristics of residential development shift large carnivore prey composition. *Journal of Wildlife Management* 80(6):1040–1048. I conceived of each of these studies, carried out the research, and wrote the manuscripts, with advisory input from my coauthors.

INTRODUCTION

Fear is an emotion that humans viscerally understand; we have evolved in a dangerous world and developed physical, social, and mental adaptations to manage the threats we face (Cosmides and Tooby 2000). Similar adaptations are employed by wildlife, helping them to avoid risk while not wasting energy or opportunities to obtain resources (McNamara and Houston 1992). Until recently, the fear landscape experienced by wildlife was often dynamic but adaptable, as predator and prey co-evolved in a persistent evolutionary arms race that resulted in few extinction events (Dawkins and Krebs 1979, Marrow and Cannings 1993). Only in the last 50,000 years did culturally modern *Homo sapiens* enter the scene and dramatically alter the exposure and susceptibility of wildlife to perceived risk.

Humans have become a “super predator” on many taxa of animals by exploiting them at rates orders of magnitude higher than those killed by natural predators (Darimont et al. 2015). The extensive lethal power of humans alters animal communities directly, often by fully extirpating keystone species (Estes et al. 2011). However, there are also behavioral costs to the domination of humans over our ecosystems globally. Wildlife fear humans, and extend their risk-avoidance behaviors to us (Frid and Dill 2002). Human-associated perceived risk is influenced by elements of actual lethal risk (e.g. use of projectile weapons, habitat destruction, industrialization, and invasive predators, competitors, and pathogens; Churchill 1993, Alroy 2001, Steffen et al. 2007, McNeill 2011) and responsiveness by wildlife to non-

lethal cues associated with risk (e.g. noise and visual disturbances; Frid and Dill 2002, Beale and Monaghan 2004, Sih et al. 2011).

Humans are one of the most common vertebrates on the planet, exacerbating problems associated with human-induced risk-avoidance behaviors in wildlife. The high exposure of wildlife to human activity is known to impact animal space use (Hebblewhite et al. 2005), feeding behavior (Kerley et al. 2002), and species interactions (Francis et al. 2009). Fear of predation in animal populations has been linked to cascading effects on reproductive success (Zanette et al. 2011), plant community composition (Beckerman et al. 1997), and even nutrient cycling (Hawlena and Schmitz 2010). The ability for humans to stimulate fear in wildlife suggests that indirect effects of fear should also be apparent in human-dominated systems, potentially driving animal community dynamics.

Humans have a particularly unique impact on large carnivores, many of which have no natural enemies aside from conspecifics. Humans have extirpated large carnivore populations across the planet, and continue to persecute them on a global scale (Ripple et al. 2014). Large carnivores are highly sensitive to human antagonism due to their generally low density and reproductive rates and large space and prey requirements. Although some large carnivores do coexist with humans (Carter and Linnell 2016), they face threats associated with adopting novel risk-avoidance behaviors that could impact their demography, resource use, and interactions with the human environment. Because of the regulatory role of large carnivores as keystone

predators in many ecosystems, human-induced fear in carnivores has the potential to have dramatic and far-reaching effects in human-modified landscapes.

This dissertation investigates the impacts of human-induced fear on carnivores, both direct and indirect, and possible landscape planning strategies to mitigate the impacts of humans on carnivores. My work was conducted in the Santa Cruz Mountains of California on native large- and mesocarnivores. I examine direct relationships between humans and carnivores, as well as indirect effects of humans on predation and competition in carnivores.

In Chapter 1, I experimentally test the nature and magnitude of fear responses to humans in a large carnivore, the puma (*Puma concolor*). I exposed pumas to the sounds of conversational human speaking and a control sound, vocalizations of the locally common Pacific chorus frog, at kill sites where pumas were still actively feeding. I found that pumas flee much more often in response to human sounds, and that this behavior results in less time spent feeding on their kill post-exposure. This work substantiates the notion that pumas perceive humans as a top predator, and that human cues can trigger a strong risk-foraging tradeoff in a large carnivore.

Chapter 2 explores the landscape-level consequences of puma fear of humans and the relationship with their prey. I examined puma spatial and temporal behaviors at kill sites on a housing density gradient, and further explored if human-induced behavioral shifts could explain patterns of resource use for individual pumas. My results indicate that pumas exhibit myriad risk-avoidance strategies to avoid utilizing kills during periods of increased human activity in high housing density areas.

Collectively, these strategies drastically reduce time spent at kills by pumas in high housing density areas. Furthermore, pumas appear to mitigate energetic losses caused by risk-avoidance behaviors by increasing their kill rates linearly with exposure to housing. This chapter suggests that risk-foraging tradeoffs caused by human-induced fear can directly impact predator-prey interactions.

In Chapter 3, I examine the relationship between spatial characteristics of residential development and prey use by pumas. In particular, I tested the impact of housing density, clustering, and proximity on prey size class. I found that the use of small prey, which comprises mostly synanthropic species such as raccoons and house cats, is predicted best by housing density alone, at both local and regional scales. However, relative detection probability of large prey increases with housing density, indicating that shifts in prey use are likely not explained by availability alone. My results suggest that pumas alter their diet both due to increased small prey availability and reduced preference for large prey in risky residential habitats.

Chapter 4 expands on the concept of how humans indirectly impact animal communities by analyzing realized niche partitioning in a mesocarnivore guild. In this study, I compare diet composition and overlap among coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and gray foxes (*Urocyon cinereoargenteus*) in open space preserves with relatively high and low human activity. Because all of these species become or remain highly nocturnal when exposed to high human activity to avoid disturbance, I expected that diet overlap would increase as a function of human-induced temporal niche constraints. In preserves with high human activity, all three

pairs of mesocarnivore experience increased overlap, in part because coyotes, the dominant of the three species, show increased consumption of nocturnal prey. This study provides evidence that human-induced behavioral change can inhibit niche partitioning among competing carnivores.

In Chapter 5, I apply ecological understanding about carnivore sensitivity to human disturbances to conservation recommendations for land use planners. I determined the housing density at which pumas avoid moving through, and then identified developable parcels that were at risk of developing above that housing density threshold if all allowable development were to occur in Santa Cruz County. I also ranked parcels based on their conservation value and risk of development to help planners prioritize conservation acquisitions. My study demonstrates the value of maintaining permeability through partially developed regions rather than focusing only on optimal movement paths.

The human footprint has spread to 83% of the planet, and few ecosystems are devoid of anthropogenic disturbances (Sanderson et al. 2002). If we are to preserve what biodiversity remains, we must maintain animal behaviors and interactions as much as possible. Even where carnivore populations persist, behavior change resulting from increased risk-avoidance may have long-term repercussions on animal community structure and function. My dissertation begins to explore how human-induced fear can impact carnivores and the species with which they interact. It also utilizes behavioral data to inform conservation planning to retain landscape permeability for sensitive carnivores. In a world of rapid global change,

understanding and mitigating the complex ways humans impact wildlife is necessary for the conservation of all life on Earth.

Chapter 1

Fear of the human “super predator” reduces feeding time in large carnivores

Abstract

Large carnivores’ fear of the human “super predator” has the potential to alter their feeding behavior and result in human-induced trophic cascades. However, it has yet to be experimentally tested if large carnivores perceive humans as predators and react strongly enough to have cascading effects on their prey. We conducted a predator playback experiment exposing pumas to predator (human) and non-predator control (frog) sounds at puma feeding sites to measure immediate fear responses to humans and the subsequent impacts on feeding. We found that pumas fled more frequently, took longer to return, and reduced their overall feeding time by more than half in response to hearing the human “super predator”. Combined with our previous work showing higher kill rates of deer in more urbanized landscapes, this study reveals that fear is the mechanism driving an ecological cascade from humans to increased puma predation on deer. By demonstrating that the fear of humans can cause a strong reduction in feeding by pumas, our results support that non-consumptive forms of human disturbance may alter the ecological role of large carnivores.

Introduction

Humans have assumed the role of “super predator” in animal communities globally, killing terrestrial carnivores at rates as much as nine times higher than their natural predators (Darimont et al. 2015). In addition to directly killing large carnivores, humans might also elicit fear responses in these species as they do in other wildlife taxa that experience human-caused mortality (Frid and Dill 2002, Clinchy et al. 2016). Indeed, correlative evidence of human-induced changes in large carnivore space use and movement suggests that fear of humans is a common phenomenon among top predators (Ordiz et al. 2011, Wilmers et al. 2013, et al. 2015, Oriol-Cotterill et al. 2015, Smith et al. 2015). However, it has yet to be experimentally tested if large carnivores perceive humans as predators and whether changes in large carnivore behavior caused by fear of humans affects ecological communities.

It is increasingly recognized that, even in the absence of direct mortality, fear of predators can itself drive cascading changes across food webs (Schmitz et al. 2004, Suraci et al. 2016). Human-induced fear in large carnivores is likely to have similar cascading effects because of the well-documented top-down effects of large carnivores on their prey and competitors (Estes et al. 2011, Ripple et al. 2014, Kuijper et al. 2016). However, different outcomes of human-induced fear in carnivores on prey populations might be expected depending on the nature of the carnivore response. One potential outcome of large carnivore fear of humans is the human shield effect, whereby prey find refuge in human-dominated habitats and are released from top-down forces because carnivores spatially avoid human disturbance (Berger

2007, Muhly et al. 2011). However, human disturbance could have the opposite effect on the regulatory role of large carnivores if carnivores persist in human-dominated habitat by instead avoiding humans temporally. This counterintuitive response may actually increase predation pressure on prey by altering carnivore hunting behavior to accommodate an enhanced risk-foraging tradeoff; temporal avoidance could lead to reduced total feeding time at a kill, which would require increased kill rates to compensate for lost energetic return from each kill. As land is increasingly transformed by anthropogenic development, quantifying how the fear of humans affects interactions between large carnivores and their prey is essential to understanding novel ecological dynamics emerging in human-dominated landscapes (Sih et al. 2011, Oriol-Cotterill et al. 2015, et al. 2016)

We previously reported that pumas (*Puma concolor*) in the Santa Cruz Mountains of Central California spent less time at kill sites in more residential areas and increased kill rates of prey (Smith et al. 2015). This increased kill rate could potentially be explained by altered prey communities in human-dominated habitats (either from a perceived human shield or access to anthropogenic food subsidies) leading to more vulnerable (Williams et al. 2014) or available (Smith et al. 2016) prey. However, if reduced time at kill sites near residential development is fear-induced, it could also result in increased kill rates to compensate for reduced energy gained per individual predation event. Here, we experimentally test whether pumas exhibit fear responses to the human “super predator” and whether changes in puma feeding behavior in response to human-induced fear can explain our previously

reported differences in puma feeding time and kill rate between areas of high and low human presence in the Santa Cruz Mountains (Smith et al. 2015). To our knowledge this is the first direct experimental test of whether large carnivores respond fearfully to human presence, and whether this response has measurable ecological consequences.

To test the relationship between fear of humans and feeding behavior, we executed a playback experiment on wild pumas. Predator playback experiments have been used to substantiate fundamental ecological relationships (Hettena et al. 2014), including that the fear of predation reduces reproductive success in birds (Zanette et al. 2011), that fear can have cascading impacts on animal communities (Suraci et al. 2016), and that mesocarnivores exhibit heightened fear responses to human “super predators” relative to non-human predators (Clinchy et al. 2016). However, no study has linked the fear of humans to feeding behavior in large carnivores. Our study builds on protocols used in over 200 studies employing playback experiments (Hettena et al. 2014) while advancing methodologies with a novel Automated Behavioral Response (ABR) system that links a camera to a playback speaker system (Schmitz et al. 2004, Suraci et al. 2016a). Our experimental approach allows us to make direct inferences on the consequences of anthropogenic disturbance on risk-foraging tradeoffs in a large carnivore. Combined with our previous work (Smith et al. 2015) our study reveals an ecological cascade from humans to increased predation on deer mediated by fear.

Methods

Our experiment was part of a long-term study on puma ecology in the Santa Cruz Mountains of central California, USA (Wilmer et al. 2013, Smith et al. 2015). The region has a Mediterranean climate characterized by a rainy season in winter and dry season in summer. Habitat types include mixed hardwood forest, redwood forest, chaparral, and grassland. The Santa Cruz Mountains are heavily impacted by human use, particularly residential development and outdoor recreation. Puma exposure to humans here is thus commonplace; all pumas in this study have housing developments in their home range (mean: 21.7 houses/km²) and kill and cache prey as close to 5 m from people's homes (Smith et al. 2015). Pumas have a good reason to be fearful of humans in this region, as they were bounty hunted in California for decades and even today humans are their primary source of mortality in the Santa Cruz Mountains, accounting for 84% of confirmed adult deaths (Wilmer unpublished data).

We conducted a playback experiment on pumas at their active kill sites. We first located puma kill sites from recent GPS tracks of collared individuals (IACUC no. WILMC1011). We downloaded recent GPS locations successfully transmitted through GSM or Iridium technologies and identified potential fresh kill sites as clusters of locations within 100 m of one another that occurred between sunset and sunrise. We field-investigated potential kill sites that were no more than three days old and at which the puma was present the previous night. If a fresh kill was found, we tied the carcass down so it could not be dragged out of the view of our cameras.

Any behavioral effects of tying down the carcass were experienced for both control and experimental playback treatments, therefore baseline disturbance levels should not influence the relative difference in response between treatments.

To test whether pumas fear humans and quantify the cost of this fear, we broadcast predator (human) or non-predator (Pacific tree frog, *Pseudacris regilla*) playbacks at puma kill sites following well-established experimental methods (Zanette et al. 2011, Hettena et al. 2014, Suraci et al. 2016a). Tree frog vocalizations provide an ideal control – like humans, tree frogs occur throughout the study area, but unlike humans they are neither predators, prey, nor competitors of pumas, and thus represent an equally familiar but benign stimulus. Tree frog vocalizations further provide an ideal control because they may naturally be heard both night and day, whenever pumas are active. Controls in other playback studies testing for fear responses in wildlife include running water (study organism: moose; (Berger et al. 2001)), seals (study organism: raccoon; (Suraci et al. 2016a)), sheep (study organism: European badger; (Clinchy et al. 2016)), and assorted non-threatening birds (study organism: song sparrow; (Zanette et al. 2011)).

We recorded puma responses to playbacks using a video-enabled camera trap linked to a playback unit triggered by the camera's activation (Suraci et al. 2016b). We deployed the playback speaker 400-450 cm from the center of the carcass. Videos were 30 s long, the playback being broadcast for 10 s in the middle of the video. If the puma repeatedly triggered the camera it could hear the playback as often as twice per minute. We used seven exemplars of each playback type (Kroodsma et al. 2001), the

human exemplars all consisting of a single individual speaking conversationally. We edited all exemplars for consistency in amplitude and quality using Audacity® (version 2.1.0, Audacity Team 2014), and broadcast the playbacks at a consistent peak sound pressure level of 80 dB at 1 m (measured using Radioshack 33-2055 Digital Sound Level Meter set to fast response and C weighting). This volume was chosen to mimic the natural volume of human conversation. Using these exemplars we composed 30 min playlists of each treatment. The playlists alternated between frogs and humans every 30 min; which treatment the puma heard first being determined by when it triggered the camera, and was thus effectively random. An individual puma might be exposed to either or both treatments over 24 hours, depending upon its reaction. For pumas that heard both treatments, there was no significant difference in the proportion of each treatment first heard ($Z = 1.63$, $P = 0.103$). Pumas received each treatment a maximum of one time.

We tested for the fear response of pumas and its ecological cost as follows: 1) We examined the puma's initial response to the playbacks by quantifying whether the puma fled (ran away) upon first hearing a treatment. We tested for significant differences in fleeing using Fisher's exact test. 2) We assessed recovery time following their initial exposure to each playback as the time difference between their first exposure to a playback treatment and the next video in which they subsequently appeared (hereafter, 'latency to return time'). We ranked the latency to return time for each trial, assigning the highest rank to individuals who did not return. We tested for a treatment effect by applying a Mann-Whitney U test to the ranked return times. 3)

We measured the aggregate effect of hearing a playback treatment on feeding time by calculating the total time a puma was observed feeding during each treatment over the course of 24 hours. We Box-Cox transformed these data to meet normality assumptions and tested for differences using ANOVA. Because some pumas were exposed to both treatments, we included individual puma as a random effect in the feeding analysis (the only parametric test), but because the random effect did not improve model fit, we report results from the univariate fixed-effects model.

Results

We successfully conducted 29 experimental trials in which 12 pumas were exposed to predator (human) playbacks and 17 pumas were exposed to non-predator (frog) playbacks. All 12 pumas exposed to humans were also exposed to frogs, whereas 5 pumas only heard the frog treatment. Pumas fled in the majority of cases (83 %) upon first hearing humans and only once upon first hearing frogs (6 %; Fig. 1 A; Fisher's exact $P < 0.001$). The latency to return time after pumas first heard a treatment was significantly greater in response to human playbacks (Fig. 1B; M-W $U_{12,17} = 151.5$, $P = 0.028$) because pumas returned to the carcass less often following their first hearing of a human playback (42 % of trials) than following their first hearing of a non-predator (frog) playback (18 %), or if they did return, they took longer to do so after first hearing humans (median = 20 min, range = 0-257) than after first hearing frogs (median = 2 min, range = 0-40). Feeding time was significantly less for the human treatment than the non-predator (frog) treatment ($F_{1,27} = 5.74$, $p =$

0.024; Fig. 1C). Over the course of 24 hours, pumas fed for less than half as long when exposed to humans (4.6 ± 2.9 SE min; median = 0.03 min) as when exposed to frogs (10.4 ± 3.1 SE min; median = 4.5 min).

Discussion

Our results experimentally demonstrate that fear of the human “super predator” induces substantial behavioral changes in pumas, ultimately leading to significant reductions in time spent feeding. We observed almost unanimous fleeing behavior in response to the human playback treatment, directly tying a strong fear response to subsequent declines in feeding. Our previous work showed that pumas nearly halve their feeding time of deer in suburban areas compared to areas with less housing (Smith et al. 2015). The halving of feeding time during human trials compared to non-predator trials that we observed in this study suggests that this difference in puma behavior at kills based on nearby housing densities can be fully accounted for by fear, and that this consequently causes pumas to increase their kill rates by 42% (Smith et al. 2015). In a previous study we found that deer occupancy was not influenced by housing density, therefore it is unlikely that relative deer availability explains observed changes in kill rate (Smith et al. 2016). Our results support the conclusion that increased kill rates in residential areas are driven by a top-down mechanism (fear of humans), rather than a bottom-up mechanism (availability of prey). Thus, non-consumptive forms of human disturbance may alter the ecological

role of large carnivores by affecting the link between these top predators and their prey.

The experiment presented here simulates only one form of human disturbance, the sound of conversational human speech. We chose this element of human disturbance for our experiment to test if pumas exhibit risk-avoidance behaviors to the perceived presence of humans alone, rather than specific human activities. However, in disturbed landscapes, many other unnatural stimuli are also likely to disturb wildlife, including sounds of vehicles and dogs, anthropogenic lighting, and many olfactory cues. In our previous work, we have found that pumas can use disturbed landscapes for hunting and moving (Wilmers et al. 2013, Smith et al. 2016), but display risk-foraging tradeoffs when and where humans are most active (Smith et al. 2015). The results of this study substantiate these relationships; although cumulative disturbance cues appear to limit spatial distribution of certain reproductive behaviors (Wilmers et al. 2013), feeding behaviors seem to be most closely related to direct human activity.

Our results are consistent with theoretical predictions made from other playback experiments that have demonstrated the ability for humans to cause fear responses in wildlife (Clinchy et al. 2016) and for fear responses in carnivores to cascade to lower trophic levels (Suraci et al. 2016a). We have combined these concepts in context of large carnivores due to their important regulatory role and susceptibility to disproportionately high mortality rates via the human “super predator” (Darimont et al. 2015). Our results show that large carnivores are not

exempt from human-induced fear, and that human impacts on their feeding behavior might have surprising cascading effects due to temporal avoidance strategies for mitigating risk.

In this study, we implemented a novel ABR playback experiment (Suraci et al. 2016b) to quantify a large carnivore's behavioral response to humans. Such direct testing of human disturbance has not previously been done on a large carnivore due to the challenge of observing these animals in the wild. Our use of recent puma kill sites accompanied by the integrated ABR technology allowed us to make inferences on humans as a driver of risk-foraging tradeoffs in a large carnivore. Similar methods could be executed on other elusive species to investigate a diversity of risk responses to invasive predators, extirpated predators, or competing predators.

Overlap between large carnivores and humans is increasing in regions where continued agricultural and residential development coincides with the recovery of large carnivore populations (Chapron et al. 2014, Gompper et al. 2015). Although the coadaptation of humans and carnivores can lead to coexistence in human-dominated landscapes (Carter and Linnell 2016), carnivore behavioral adaptations might result in unintended indirect effects on other species (Kuijper et al. 2016). Our work suggests that fear-induced trophic cascades instigated by the human "super predator" are likely to contribute to altered ecological dynamics in human-dominated landscapes. As the habitats used by wildlife and humans are increasingly shared, additional work is needed on the extent to which fear in top predators cascades through ecosystems.

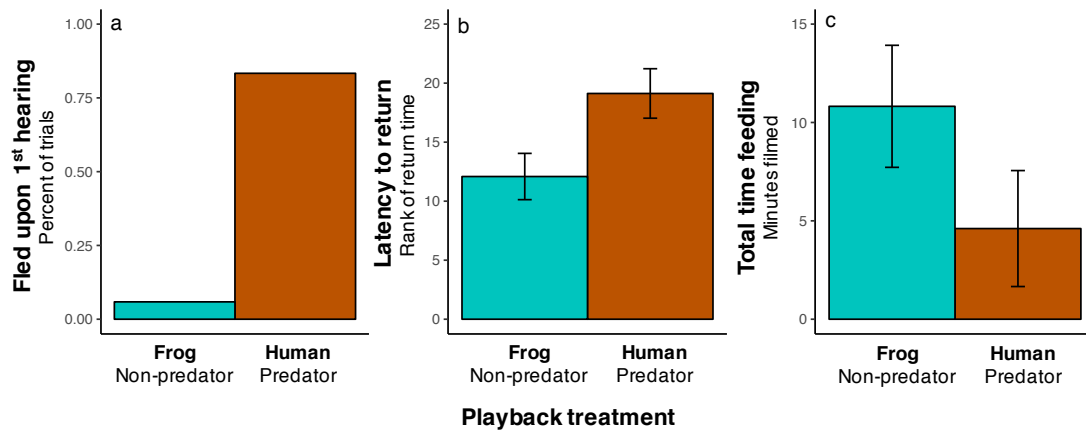


Figure 1. Responses of pumas to predator (human) and non-predator (frog) playbacks at puma feeding sites. (a) Proportion of pumas that fled following their first exposure to frog or human playbacks. (b) Latency in time to return (rank) after initial playback exposure. (c) Total time spent feeding during the first 24 hours of playback treatment.

Chapter 2

Top carnivores increase their kill rates on prey as a response to human-induced fear

Abstract

The fear induced by predators on their prey is well known to cause behavioral adjustments by prey that can ripple through food webs. Little is known, however, about the analogous impacts of humans as perceived top predators on the foraging behavior of carnivores. Here, we investigate the influence of human-induced fear on puma foraging behavior using location and prey consumption data from 30 tagged individuals living along a gradient of human development. We observed strong behavioral responses by female pumas to human development, whereby their fidelity to kill sites and overall consumption time of prey declined with increasing housing density by 36 and 42% respectively. Females responded to this decline in prey consumption time by increasing the number of deer they killed in high housing density areas by 36% over what they killed in areas with little residential development. The loss of food from declines in prey consumption time paired with increases in energetic costs associated with killing more prey may have consequences for puma populations, particularly with regard to reproductive success. In addition, greater carcass availability is likely to alter community dynamics by augmenting food resources for scavengers. In light of the extensive and growing impact of habitat modification, our study emphasizes that knowledge of the indirect effects of human

activity on animal behavior is a necessary component in understanding anthropogenic impacts on community dynamics and food web function.

Introduction

Anthropogenic disturbance can cause shifts in biotic community dynamics, generally through the loss of native species, introduction of novel species, or artificially enhanced populations of native generalists (McKinney 2006)]. These changes are characterized most often by quantifying the population size or presence of particular species. However, behavior-mediated interactions are predicted to have equal or greater impacts on animal populations than purely numerical mechanisms (Peacor and Werner 2001, Schmitz et al. 2004, Preisser et al. 2005). Animal behavioral responses to anthropogenic disturbances have the potential to be cryptic but powerful drivers of ecological change in modified habitats (Blumstein 2004).

Large carnivores are widely recognized to be sensitive to human disturbances due to slow life cycles, large space requirements, direct persecution by humans, and avoidance of human dominated areas, often resulting in their decline or extirpation. Reduced large carnivore density and occupancy in some developed areas has resulted in both mesopredator release (Crooks and Soulé 1999, Ripple et al. 2013) and overpopulation of primary consumers (Estes and Palmisano 1974, Terborgh et al. 2001). Yet some large carnivores do persist in modified landscapes, but alter their behavior to reduce interactions with humans (Wilmers et al. 2013, Knopff et al. 2014). Due to the strong regulatory influence large carnivores can exert on their

competitors and prey, changes in their behavior are likely to contribute to whole community responses to anthropogenic disturbances (Railsback and Harvey 2012).

Hunting and foraging are costly behaviors for carnivores, but are often assumed to be optimized so that individuals gain the most energy (or other limiting nutrients) for the least effort (Stephens and Krebs 1986). Animals that choose to expend more energy than what is perceived to be optimal may be responding to risks that increase the long-term payoff of certain energy-expensive behaviors through decreased chance of non-starvation mortality (McNamara and Houston 1990). Hunting in high-risk habitats can therefore create a risk-foraging tradeoff in which animals sacrifice efficient foraging to compensate for increased vigilance and risk-avoidance. Giving-up density studies support that an animal's perceived risk is inversely correlated with food intake, suggesting that time spent consuming a food item reflects the fear experienced by forager (Brown 1988).

Top carnivores generally kill large-bodied prey species, which require a high initial energetic cost during the hunting stage (Williams et al. 2014), but provide high energy gain during consumption. However, because carnivores are constrained by gut capacity, solitary carnivores can only maximize their caloric yield by repeatedly returning to feed on a prey carcass. In developed habitats, carnivores can be particularly vulnerable to risk-foraging tradeoffs because disturbance-induced carcass abandonment can result in food loss due to scavenging (Elbroch and Wittmer 2013) or decomposition (Bauer et al. 2005). Prey consumption time can therefore be limited by external forces that reduce their access to a carcass. Anthropogenic disturbances can

ultimately reduce the net caloric gain carnivores receive from consuming large prey (Kerley et al. 2002) by displacing carnivores from kill sites and decreasing their prey consumption time at kills. If perceived risk increases with human disturbance, the magnitude of human impact should be a predictor of foraging efficiency and consumption time.

We examined puma (*Puma concolor*) behavioral changes associated with perceived risk at kill sites with increasing housing density levels and investigated the relationship between risk-avoidance behaviors and kill rates in disturbed areas. We hypothesized that disturbance would displace pumas more often in highly developed areas, reducing overall prey consumption time and increasing kill rates. In the long term, we anticipate that more frequent risk-avoidance behaviors will increase puma kill rate and subsequently alter interactions with prey, competitors, and scavengers.

Methods

Our research was conducted in the Santa Cruz Mountains, which lie in the Central Coast region of California. We captured 30 pumas from 2008-2013 and fitted them with GPS/radio telemetry collars (Model GPS Plus 1or 2 D, Vectronics Aerospace, Berlin, Germany). Collars were programmed to record locations every 4 hours, and location data were downloaded remotely via UHF once a month. We used a custom cluster generation algorithm integrated in the Geographical Information Systems program ArcGIS (v.10; ESRI, 2010) using the programming languages R (v.2.1.3.1; R Development Core Team, 2010) and Python (v. 2.6; Python Software

Foundation, 2010) to identify groups of locations in which each location was within 100 m and 6 days of another location in the cluster (for full details on the algorithm, see Wilmers et al. 2013). We field-investigated clusters in reverse chronological order from their time of formation using the most recently downloaded GPS data. Clusters were investigated within 30 days of their first recorded locations. At investigated clusters, we recorded whether a kill was present, and if so, the species, age, and sex of the kill (if identifiable).

We constructed a mixed-effects binomial logistic regression model to predict deer kill sites from all generated clusters. We chose to only use deer kills because deer are the preferred prey in our study area. In addition, small prey cannot be predicted accurately from location data in our study area due to high variability in puma behaviors at small kill sites. The variables used to fit the model were behavioral characteristics associated with clusters, including number of night locations (NIGHT), a binary variable indicating greater than 1 day duration (BINARY), the harmonic mean distance of locations from the cluster center within the cluster (HMDIST), the proportion of locations occurring at night (P.NIGHT), site fidelity measured by the proportion of points occurring within the cluster over the cluster duration (P.ACTIVE), and the farthest distance traveled during a cluster period (DIST). Total duration of a cluster (DUR) was excluded due to high correlation ($r > 0.7$) with variables already used in the model. We allowed for random slopes and intercepts for individual pumas when fitting the best model. We also constructed a truncated model without behavioral variables that we expected to correlate with

housing density in order to allow inference on behavioral influences on kill rates. This model excluded P.NIGHT, P.ACTIVE, and DIST. We compared the truncated model and best-fit model to assess if we could confidently use the truncated model. We constructed ROC curves for both full and truncated models and calculated the area under the curve (AUC) to ensure that both models were similar in their predictive abilities. The AUC for the full model (AUC = 0.818) and the truncated model (AUC = 0.820) were nearly identical, and both support good discriminative ability (Swets 1988). We assigned each generated cluster as a deer kill or not a deer kill by applying the truncated model to all generated clusters.

We first investigated puma behavioral responses at the population level at four levels of housing density within 150 m of predicted kill sites: no housing, rural (greater than 0.0 and up to 0.062 houses per hectare), exurban (greater than 0.062 and up to 1.236 houses per hectare), and suburban (greater than 1.236 and up to 9.884 houses/hectare; Theobald 2005). Due to the discrete nature of housing count data, each housing class was rounded up to the nearest number of houses, resulting in housing classes within 150 m of a cluster to be defined as 0 houses for no housing, 1 house for rural, 2-9 houses for exurban, and greater than 9 houses for suburban. We used the 150 m buffer because this is the scale of development found to most impact puma hunting in our study area (Wilmer et al. 2013). We constrained the response variables to only include behaviors we expected to be associated with risk aversion, which were narrowed down to P.NIGHT, P.ACTIVE, DUR, DIST, and a final measure of prey consumption time (P.C.TIME) which was calculated as $P.ACTIVE *$

DUR. We added the prey consumption time measure because it best reflects the energetic gain an animal receives from a kill. We tested the differences in behaviors at all predicted kill sites in different housing density categories using an ANOVA test, and examined pairwise comparisons with Tukey's HSD test for all behaviors found to vary significantly with housing density.

To determine kill rates, we calculated the total number of deer predicted to be killed by each puma from the output of the deer kill prediction model using all generated GPS clusters. We divided the predicted number of kills by the total time each puma was actively collecting GPS data to obtain annual deer kill rates. We investigated sex-specific relationships between kill rates and average values for P.NIGHT, P.ACTIVE, DIST, DUR, and P.C.TIME for individual pumas using univariate linear regressions due to high correlation values ($r > 0.7$) among variables.

In order to assess the impact of housing on individual pumas, we calculated housing density within each puma home range. Puma home ranges were obtained using a LOCOH home range estimator, where the 95% isopleth represented the home range boundary (Getz et al. 2007, Downs et al. 2012). All housing points in the Santa Cruz Mountains were manually digitized from high-resolution satellite imagery. We calculated puma home range housing density as the number of houses per km². We tested for the relationship between individual puma kill rates and home range housing densities using univariate linear regression.

Results

Behavioral shifts

Of 703 field-investigated clusters, 208 were classified as deer kill sites. The other remaining clusters included 66 non-deer kills (e.g. raccoons and house cats) and 429 non-kills (often bed sites). Our best-fit binomial logistic regression model to predict deer kills included NIGHT (number of night locations), BINARY (greater than one day), HMDIST (distance of points from center), P.NIGHT (proportion night points), AND P.ACTIVE (proportion of points at kill). The truncated model included NIGHT, BINARY, and HMDIST. Neither the random intercept nor a random slope was included in the best-fit full model or the best-fit truncated model. We used the truncated model to predict 1537 deer kills from 8523 generated clusters (Fig. 1).

At predicted kill sites, females had lower P.ACTIVE ($F = 67.7, p << 0.001$), higher DIST ($F = 16.0, p < 0.001$), and shorter P.C.TIME ($F = 44.2, p << 0.001$) as housing density increased (Fig. 2; example shown in Fig. 1). In suburban habitat, female P.ACTIVE was 36% lower, DIST was 31% higher, and P.C.TIME was 42% lower than in no housing areas. Both males ($F = 19.3, p < 0.001$) and females ($F = 144.4, p << 0.001$) were more nocturnal (higher P.NIGHT) with increasing housing density at kill sites. Males did not show any responses to housing density concerning time spent at kill sites. Identical analyses using only confirmed kills supported each of the reported trends for predicted kills.

Deer Kill Rates

Male average home range size was 163.0 ± 7.7 SE km² with 15.6 ± 0.8 SE houses/km². Female average home range size was 53.8 ± 2.1 SE km² with 25.5 ± 1.3 SE houses/km². Males had an average deer kill rate of 43.7 deer/year, whereas females killed on average 67.3 deer/year. Male deer kill rates were not correlated with any of our variables of interest (P.ACTIVE, P.NIGHT, DIST, DUR, or P.C.TIME), nor with home range housing density ($p = 0.9$, $R^2 = 0.005$; Fig. 3). Conversely, female deer kill rates showed a strong positive and linear correlation with home range housing density within its observed range ($p = 0.0003$, $R^2 = 0.745$; Fig. 3). Females with home ranges in the top quartile of housing density killed 36% more deer/year (81.2) than females in the bottom quartile of housing density (59.7). Female kill rates were also negatively correlated with average fidelity to kill sites (P.ACTIVE; $p = 0.05$, $R^2 = 0.322$).

Discussion

Our estimate of average male kill rates (43.7 kills/year) stayed constant across housing densities and was comparable to previously reported values described by Knopff et al. (2010; 35 ungulates/year) and Anderson and Lindzey (2003; 47 kills/year). However, female kill rates increased positively, strongly, and linearly with housing density. Although female kill rates in lower housing density areas (59.7 kills/year) were comparable to previously estimated mule deer kill rates for solitary adult females (52.5 kills/year; Anderson and Lindzey 2003) and females with kittens (62.4 kills/year, Cooley et al. 2008); 68.1 kills/year, Anderson and Lindzey 2003;

57.2 kills/year, Knopff et al. 2010), female kill rates in the highest quartile of home range housing densities were substantially higher (81.2 kills/year). This 36% increase in kill rates between the top and bottom quartiles indicates that development may exert a significant energetic cost associated with hunting behavior.

Hunting deer requires large energetic investments in the stalking, subduing, and killing stages for pumas (Williams et al. 2014). We have documented a sizable increase in female kill rates that we expect represents higher energetic costs for females in developed landscapes. Although these costs do not appear to influence adult survival (Wilmers *unpublished data*), impacts on reproductive success possibly make development-interface zones sinks for the puma population. Anecdotally, we have observed that the tagged female living in the most developed habitat in our study area has lost at least three litters in the last three years, one of which was confirmed as abandonment (Wilmers *unpublished data*). The three other females living in less developed portions of our study area for which we have also documented at least three dens have had the majority of their litters survive. Although there are many stressors in a developed landscape that might influence kitten survival, we expect that higher energetic costs from increased hunting may contribute to this pattern.

Males did not alter their kill rates or prey consumption time at kills with increasing housing density. Because male life histories are constrained by requirements to defend much larger territories (Logan and Sweanor 2001), this is perhaps not surprising. We found that male pumas have home ranges that are approximately three times as large as female home ranges on average. Male pumas

are also known to spend significantly more time performing scent-marking behaviors than females (Logan and Sweanor 2001). We found that males have lower total cluster duration (DUR) at kills than females by 7.2 hours on average (males = 2.86 days $\pm$ 0.06 SE, females = 2.56 days $\pm$ 0.05 SE; $t = 3.83$, $df = 1000$, $p < 0.001$), likely due to their need to patrol and defend their home range boundaries from encroaching males. Therefore, because males already tend to leave their kills early, they may be less influenced by chronic disturbance. In addition, male home ranges are characterized by much lower overall housing densities, indicating that males may exhibit risk-avoidance behaviors at the landscape scale rather than at the kill site scale.

Higher deer kill rates by females in response to increased housing density appear to be driven by a behavioral shift to a lower proportion of time spent at kill sites over the consumption period. Although females did not alter their total duration spent at clusters, their overall prey consumption times declined due to a lower proportion of time spent at kills, indicating reduced utilization of carcasses at higher housing densities. Other possible explanations for female increase in deer kill rate are not supported by our understanding of puma energetics and reproduction. Deer in our study have lower detection rates in more developed habitats (Wilmers *unpublished data*), therefore variation in deer activity or abundance is unlikely to explain these patterns. In addition, it is unlikely that increased kill rate could be a result of greater reproductive activity in high housing density areas because females in our study area avoid anthropogenic development when denning (Wilmers et al. 2013). We conclude

that behavioral risk avoidance is a substantial contributor to female prey consumption time and hence hunting patterns, due to our observation that housing density is associated with decreased prey consumption time. Both food loss and increased movement as a result of these behavioral shifts may contribute to observed increased kill rate in human-modified habitats.

An increase in ungulate carcasses left by female pumas may impact the biotic community by providing additional carrion subsidies to scavengers. By leaving their kills for longer periods of time in more developed areas, female pumas might create greater opportunity for scavenging by mesopredators and birds. Subordinate predators often scavenge kills of apex predators when kills are abandoned or not guarded (Wilmers et al. 2003), and carrion can form a large proportion of their diets (Prugh 2005). Pumas are known to be important sources of food subsidies to mesopredators through carcass abandonment (Allen et al. 2014). Our results suggest that mesopredator release may occur not only through the well-documented pathway of apex predator extirpations, but also via behavior changes in extant apex predators leading to increased food provisioning. The presence of scavengers can exacerbate this pattern by reducing apex predator prey consumption time via food loss (Elbroch and Wittmer 2013).

Conclusion

The results presented here have bearing on human-modified systems globally. Behavioral responses are often overlooked as ecosystem drivers in modified systems,

overshadowed by population declines and extirpations. However, many species are able to persist in developing landscapes, but in an altered behavioral state. Our findings suggest a strong, perceivable impact of observed human-induced behavioral change on species interactions instigated by the presence of development. Risk aversion behaviors that result from anthropogenic disturbances are likely to restructure predator-prey interactions in a variety of contexts, given the large effects risk has been shown to have on foraging across taxa. Behavior-mediated interactions are powerful forces in biotic systems, often playing an even more impactful role than consumptive interactions. A greater focus on behavior-mediated effects of habitat alteration can further expand our understanding of community-level processes in human-modified systems.

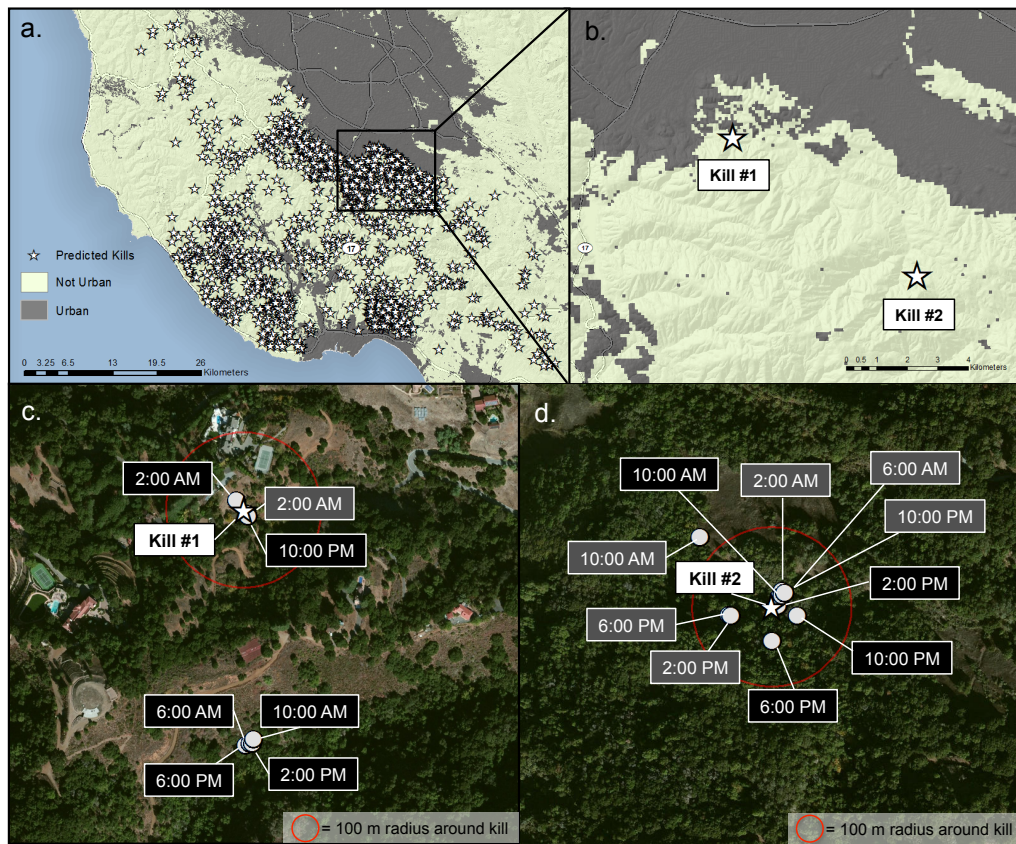


Figure 2.1. (a) Study area and predicted kill sites in relation to housing density. Box shows area (b) in which kill site examples (c) and (d) are shown. Kill site 1 (c) belongs to puma 13F, whose home range is in the top quartile of housing densities among female pumas. Kill site 2 (d) belongs to 28F, whose home range is in the bottom quartile of housing densities among female pumas. Grey labels depict the first day at the kill site and black labels depict the second day. Note that at kill site 1, the puma has made a kill close to development but spends the majority of time away from the kill, whereas at kill site 2, which has no nearby development, the puma stays within the vicinity of the kill.

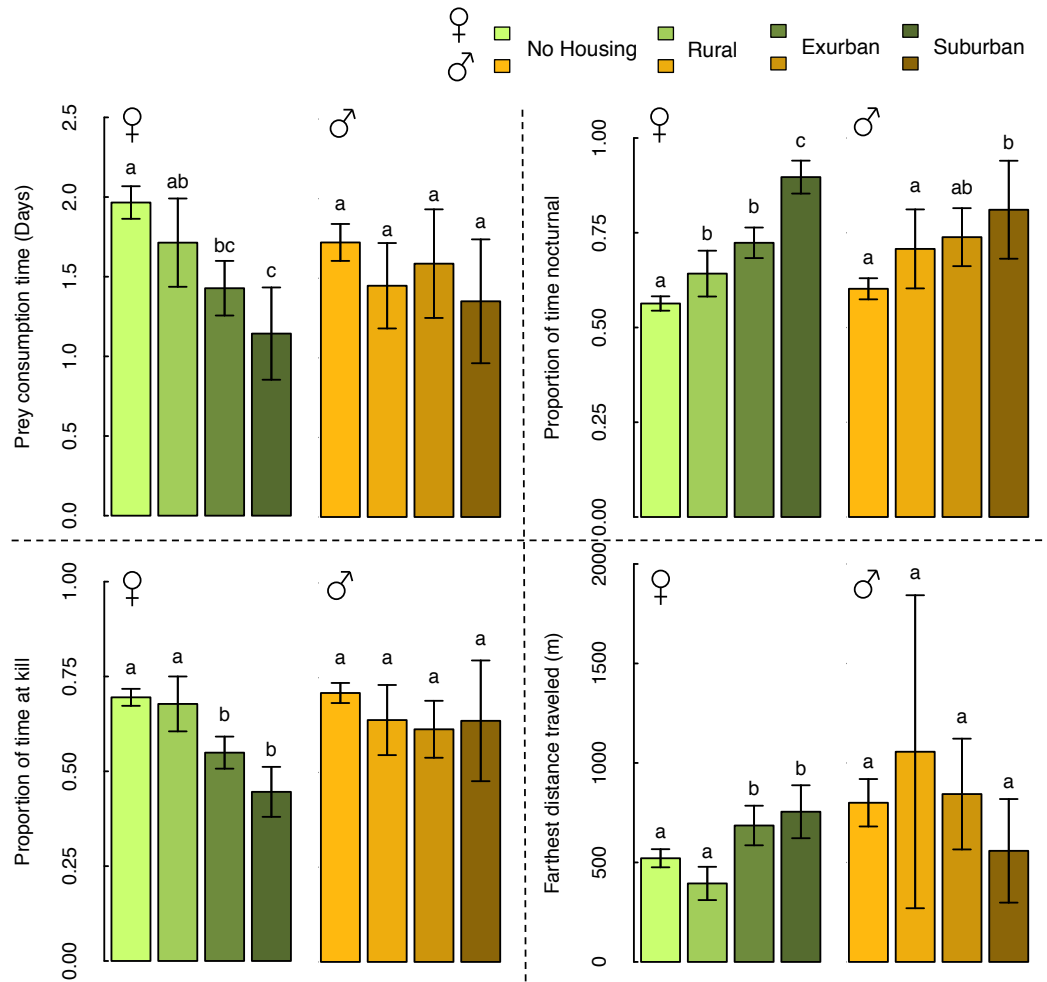


Figure 2.2. Behaviors that vary with housing density at predicted kill sites. Pairwise comparisons from Tukey's HSD tests reported in superscripts, where different letters represent a statistically significant difference. Error bars represent two standard errors from the mean. Sample sizes of housing classes at female kills are: no housing, 719; rural, 83; exurban, 186; suburban, 71. Sample sizes of housing classes at male kill sites are: no housing, 389; rural, 32; exurban, 42; suburban, 15.

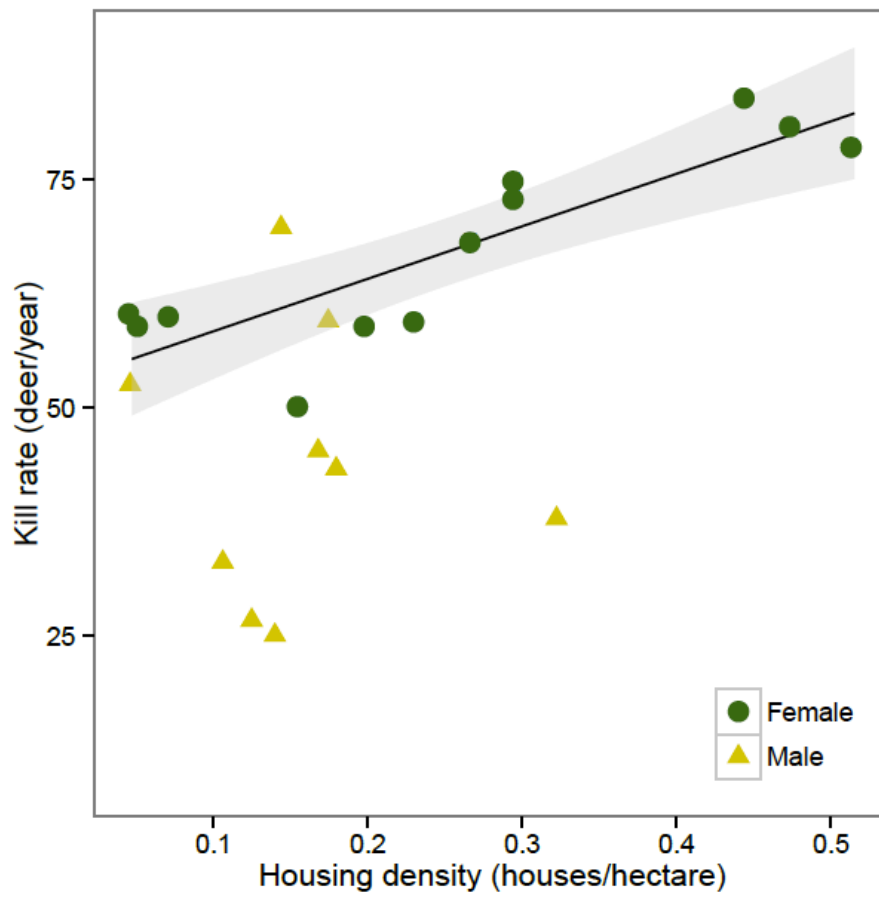


Figure 2.3. Kill rates of individual male and female pumas in response to housing density per hectare within their 95% LOCOH home range. Regression line and 95% confidence intervals for female kill rates in relation to housing density are shown.

Housing density coefficient $\beta_1 = 91.4$.

Chapter 3

Spatial characteristics of residential development shift

large carnivore prey habits

Abstract

Understanding how anthropogenic development affects food webs is essential to implementing sustainable growth measures, yet little is known about how the spatial configuration of residential development affects the foraging behavior and prey habits of top predators. We examined the influence of the spatial characteristics of residential development on prey composition in the puma (*Puma concolor*). We located the prey remains of kills from 32 pumas fitted with global positioning system (GPS) satellite collars to determine the housing characteristics most influencing prey size and species composition. We examined how differences in housing density, proximity, and clustering influenced puma prey size and diversity. We found that at both local (150 m) and regional (1km) spatial scales surrounding puma kill sites, housing density (but not the clustering of housing) was the greatest contributor to puma consumption of small prey (<20 kg), which primarily comprised human commensals or pets. The species-specific relationships between housing density and prey occupancy and detection rates assessed using camera traps were not always similar to those between housing density and proportions of diet, suggesting that pumas may exercise some diet selectivity. The influence of development on puma diet may affect puma disease risk, energetics, and demographics because of altered

species interactions and prey-specific profiles of energetic gain and cost. Our results can help guide future land-use planners seeking to minimize the impacts of development on wild species interactions and community dynamics.

Introduction

Habitat loss, conversion, and modification are the largest global influences on species extinction and declines globally (Pimm and Raven 2000), a trend which is expected to continue throughout the 21st century (Sala et al. 2000). In addition, residential development growth rates in the United States outpace population growth by 25%, further increasing the human footprint (Theobald 2005). These patterns are influenced by extensive development that occurs at low densities adjacent to or embedded within wildland areas. Altogether, exurban developments encompass >7 times the land area of urban development.

As development continues to transform wild areas, attention has been drawn to the spatial characteristics of new developments and how smart growth can assuage environmental impacts (Theobald et al. 2005, Baldwin et al. 2007). The spatial attributes of housing developments can be more important than the overall density of structures on the landscape in regard to providing habitat for sensitive species (Theobald et al. 1997), yet housing density is regularly provided as the only measure of development in ecological studies through use of the urban-rural gradient framework (Hansen et al. 2005). Not all patterns of anthropogenic development are expected to affect biotic communities equally, and the behavior and ecology of

species persisting in modified habitats are likely influenced by the spatial configuration of development. Although a preserve abutting an urban interface might support many native animal populations, landscapes comprising low-density development have been reported to decrease species diversity because of the widespread and diffuse nature of human disturbances (Merenlender et al. 2009). Adding nuance to urban-rural gradient research by incorporating animal responses to spatial characteristics of development enhances the ability to predict and understand the ecological ramifications of different development types and guide future land-use planning.

Habitat loss and fragmentation disproportionately affect large carnivores because they have large home ranges and a history of conflict with humans (Ripple et al. 2014); on average, individual carnivore species have lost approximately 50% of high-quality habitat globally (Crooks et al. 2011). Anthropogenic disturbances change the composition of animal communities by extirpating sensitive species and promoting generalists (McKinney 2006), which subsequently affects animal resource use and diet in modified habitats globally (Newsome et al. 2014). Carnivores may be expected to alter their prey habits in these sub-optimal, human-modified habitats in response to changes in prey availability. Large carnivores sometimes take advantage of human-associated prey; there are numerous accounts of carnivores consuming livestock and other anthropogenic food (Bateman and Fleming 2012). Leopards (*Panthera pardus*; Athreya et al. 2014) and hyenas (*Crocuta crocuta*; Abay et al. 2011) have been documented to consume synanthropic prey almost exclusively in

developed areas. Changes in prey size and composition affect carnivores because consuming larger-sized prey is often more energetically efficient and can increase survival probability (Bartoń and Hovestadt 2012). Although many large carnivores, particularly felids, are obligate carnivores and therefore unlikely to directly consume anthropogenic subsidies (e.g., garbage, pet food, bird seed), they can hunt species that do directly exploit these subsidies. These synanthropic prey species alter spatial patterns of prey availability and subsequently the profitability and catchability of the prey available within a carnivore's territory or home range in relation to existing human developments.

Pumas (*Puma concolor*) behaviorally respond to anthropogenic disturbances, primarily in regard to temporal activity patterns and space use (Kertson et al. 2011, Wilmers et al. 2013, Lewis et al. 2015, Smith et al. 2015, Wang et al. 2015). Although pumas in North America primarily consume large ungulate prey (Villepique et al. 2011), they are generalist predators and also consume a diversity of other species (Knopff et al. 2010, Moss et al. 2015). In exurban habitats, alternative and synanthropic prey species of pumas are often much smaller than the dominant prey species, consisting largely of mesopredators (Moss et al. 2015). A reduction in average prey size in residential areas is likely to influence puma handling time and hunting strategies, ultimately altering puma energetics, movement, and space use. We examined the patterns of use of alternative prey for pumas in the Central Coast region of California. In California, exurban (or low-density) development is projected be the greatest contributor to habitat loss through 2050, amounting to 52,000 km² (12.9

million acres) of land in the state (Mann et al. 2014); therefore, understanding changes in puma resource use in this state is essential for their management.

We investigated the magnitude and nature of the relationship between anthropogenic development and puma prey habits. We examined patterns of prey composition across an urban-rural gradient at 2 spatial scales representing the local and regional conditions surrounding a kill site. We predicted that increased hunting of small prey (<20 kg) would increase overall prey diversity and increase use of synanthropic prey species, but that this relationship would be strongest at the smaller scale representing the immediate environment. We then explored if the spatial characteristics of development (e.g., housing density, clustering, proximity) corresponded with changes in prey composition and size. We anticipated that the density, configuration, and proximity of houses would all affect consumption of small prey species. We also examined if females and males had different diets and relationships to housing parameters. We anticipated that because females have higher housing density in their home ranges on average (Smith et al. 2015), they would kill in more developed areas and have higher composition of small prey in their diet than males. Finally, we assessed if diet patterns mirrored prey occupancy and detection rates along a housing density gradient.

Study Area

We conducted research in the Santa Cruz Mountains in the Central Coast region of California, USA. The Santa Cruz Mountains are bordered by the Bay Area

to the north, the Pacific Ocean to the west, Monterey Bay to the south, and a high-speed freeway to the east (Highway 101). Our 1,700-km² study area was composed of a mosaic of land-use types, including small towns, low-density residential development, resource extraction lands for logging and mining, and a diversity of public and private parks and preserves. One major 4-lane highway, Highway 17, and 1 2-lane highway, Highway 9, divided the study area north-to-south. The habitat largely comprised oak (*Quercus* spp.) woodland forest, redwood (*Sequoia* spp.) forest, mixed hardwood forest, chaparral, and grassland. The climate in this region is Mediterranean and is characterized by a summer dry season and winter wet season. The elevation ranges from 0 m to 1154 m, and topography is steep and mountainous. Pumas are the last large carnivore in the region, and black-tailed deer (*Odocoileus hemionus columbianus*) are the only remaining abundant ungulate (with the exception of a few pockets where non-native wild boar [*Sus scrofa*] are present). Other available prey species are largely meso- and small carnivores, pets, and livestock.

Methods

Puma Locations and Cluster Analysis

We captured and collared 32 adult (>2 yr old) pumas from 2008–2014 comprising 15 females and 17 males. We captured pumas with the use of trailing hound dogs, cage traps, or leg-hold snares. We used Telazol (Fort Dodge Laboratories, Fort Dodge, IA, USA) to anesthetize pumas. We followed animal care and use protocols authorized by the University of California, Santa Cruz, California,

USA (no. WILMC1011). We fitted each puma with a combined global positioning (GPS) radio-collar (Model GPS Plus 1or 2 D, Vectronics Aerospace, Berlin, Germany), programmed to take a GPS fix every 4 hours. We had 2 methods of obtaining location data: we remotely downloaded location data from active GPS collars with an ultra high frequency (UHF) terminal every 4 weeks, or we received locations transmitted via cell phone towers every 1–3 days. We attempted to remove and replace collars on pumas near the end of the collar's battery life to get continuous long-term data on collared pumas.

We developed a custom program integrated in the geographical information systems program ArcGIS (v.10; ESRI, Redlands, CA, USA) using the programming languages R (v.3.1.3; R Development Core Team 2013) and Python (v. 2.6; Python Software Foundation, Wilmington, DE, USA) to identify clusters of GPS locations that were potential kill sites (i.e., where a kill was consumed; Wilmers et al. 2013). We defined clusters as groups of ≥ 2 locations in which each location was within 100 m of the cluster centroid and 6 days of another GPS location of the same individual puma. We generated clusters immediately after remotely downloading GPS locations.

We investigated puma GPS clusters in the field for the presence of a kill from March 2009–July 2014. To avoid bias in visitation across habitat types and human use zones, we investigated clusters in reverse chronological order, regardless of accessibility or cluster size, with the exception that we visited clusters near other clusters in groups to optimize field time. We did not investigate some clusters

because of the inaccessibility of terrain or because we were not able to get permission from the property owner. We visited clusters within 30 days of the first location in the cluster. We investigated each cluster by navigating to the centroid of the cluster and searching the area by spiraling outward from the center for 30 minutes. If we found a prey item (or multiple prey items), we documented the species, age class, and sex of the prey when possible. We excluded prey weighing <1 kg from analyses because we lacked definitive evidence of puma predation.

Housing Descriptors

To calculate descriptors of housing impact at kill sites, we manually digitized every building in the Santa Cruz Mountains from high-resolution satellite imagery (source: ESRI World Imagery). We calculated proximity as the distance from a kill to the nearest house using the Near tool in ArcMap (v10.1, ESRI). We determined housing density at each kill at 2 scales to investigate the spatial extent of influence of housing on prey composition. Specifically, we constructed buffers around kill sites with radii of 150 m and 1 km, and calculated the number of houses/km² within each buffer using the Spatial Join tool in ArcMap. We chose the smaller buffer size to represent the local scale because the scale of human influence most likely to impact puma movements has been reported to be 150 m in this study area (Wilmers et al. 2013). We selected the 1-km buffer size to represent the regional scale to account for the estimated upper home range sizes of most small, synanthropic prey species (e.g., raccoons [*Procyon lotor*]; Beasley et al. 2007). We estimated the spatial clustering of

houses at each kill site by measuring the average distance to the nearest neighbor among houses within the buffer zones of 150 m and 1 km of a kill using the Generate Near Table tool in ArcMap. Lower values represent greater clustering.

We categorized kills into housing density levels to classify differential prey diversity and size by housing type. We binned the housing densities at both scales into 4 housing density levels as described by Theobald (2005): no housing, rural (>0.0 – 0.06 houses/ha), exurban (>0.06 – 1.24 houses/ha) and suburban (>1.24 – 9.88 houses/ha). No kills were present at urban densities (>9.88 houses/ha).

Prey Diversity and Small Prey Use

We calculated the proportion of diet contributed by each prey species with regard to both frequency of kills and edible biomass (Table 1). We assessed dietary diversity by calculating a prey diversity index using the Shannon-Wiener diversity index (Yip et al. 2013) for each housing density level at the 150-m and 1-km scales. We also calculated prey diversity for males and females and used Mann-Whitney U non-parametric tests to examine sex differences in housing metrics (i.e., proximity, density, clustering) and proportion of small prey consumed. We binned prey into large (>20 kg) and small (<20 kg) categories for subsequent analyses of housing covariates on prey size. We constructed a mixed effects binomial logistic regression model with individual puma as a random effect and prey size class as a binary response variable to determine which spatial housing characteristics at a kill site best predicted prey size. We used a random effect of puma to control for differences in

sample sizes among individuals for the scale representing the pumas' local environment (150-m scale) and the scale representing the regional area characteristics (1 km-scale). We excluded clusters associated with den sites (confirmed from field investigations) from this analysis. We normalized the housing covariates for the analysis so we would not bias coefficients of variables. For this portion of our analysis, we used only kill sites that had ≥ 1 house present in the scale of analysis (i.e., local or regional) to assess which spatial characteristics of development most influenced prey size given the presence of development. We constructed 7 models that represented every permutation of the 3 variables (i.e., housing density, proximity, clustering): 3 univariate models, 3 bivariate models, and a full model. We investigated correlations between each pair of the 3 descriptors, and found that no pair of descriptors was correlated at the 1-km scale ($r < 0.5$ for all pairs), but that housing density and proximity to a house were correlated at the 150-m scale ($r = 0.61$). Therefore, we excluded the 2 models containing both variables at the 150-m scale, leaving 5 candidate models. We compared Akaike's Information Criterion (AIC) values for the suite of models for each scale to identify which model best fit the data (Burnham and Anderson 2002).

We ran Mann-Whitney U non-parametric tests to compare prey size class in relation to the housing covariates in the best-fit model using all kill sites, including those where no housing was present. This analysis allowed us to quantify the magnitude of differences in housing covariates at kill sites of large and small prey at both scales examined.

Prey Species Occupancy and Detection

To gain insight on prey availability, we distributed 50 motion-sensor cameras on animal and human trails across a housing density gradient from no housing to suburban housing. We chose to use animal and human trails for camera placement because of the presence of extensive trail networks in our study area and the known use of trails for hunting by pumas in other regions (Harmsen et al. 2010). Camera placement on trails is appropriate for many of the primary prey species in our study area, including cats (*Felis catus*; Kays et al. 2015), deer, Virginia opossum (*Didelphis virginiana*), and raccoons (Erb et al. 2012). At each camera, we calculated housing density within 150-m and 1-km buffers and classified cameras into the same housing density levels used above (no housing, rural, exurban and suburban). We set cameras to take 3 photos at 1-second increments following a trigger with a 60-second break before the camera could be triggered again. We recorded every animal occurrence as 1 detection per set of 3 photos. For our target prey species, we then constructed a dataset comprising weekly detection histories from consolidated detections in weekly intervals from October 2011 through October 2012.

To determine if prey occupancy or detection was a function of housing density, we developed occupancy models for each prey species making up $\geq 2\%$ of puma diet using the weekly detection history dataset. Occupancy models estimate the probability of species site occupancy (Ψ) and detection (p) and can incorporate the effects of covariates on these probabilities. We qualitatively associate prey activity

with detection probability and prey presence with occupancy. We used 1-week detection intervals, where species were present or absent over each monitored weeklong period. This method allows us to model if each prey species was ever detected at a camera (ψ) and the probability of detecting each species at a camera (p), providing measures of presence and relative use (Royle and Nichols 2003, Royle et al. 2005). Because some species in our study area are rare and distributed heterogeneously whereas others are common but vary spatially in their abundance, occupancy modeling is the best approach to capture the variation in space use for a diversity of prey species across a housing density gradient.

Using the program Presence (v.5.9, Hines 2006), we tested 4 models: 1) occupancy and detection are constant across all sites (null model), 2) occupancy varies with housing density but detection is constant, 3) occupancy is constant but detection varies with housing density, and 4) both occupancy and detection vary with housing density. We used AIC to compare the 4 models to evaluate if housing density informed the probabilities of occurrence and detection of primary prey species.

Results

Kill Sites and Diet Composition

We visited a total of 1,476 clusters from 32 pumas, 439 of which had evidence of prey remains (Fig. 1). We visited on average 13.7 (± 2.3 SE) kills/puma, with a median of 10 kills. Small prey between 1 kg and 20 kg were visited by pumas for 6.2 ± 0.8 SE GPS locations on average, therefore we believe we reliably found a large

proportion of kills of this size. We found that 68% of kills had no housing within 150 m of the kill. However, within 1 km of a kill site, the majority of kills occurred at exurban housing densities (56%).

Black-tailed deer were the most common prey item, making up 79% of kills and 90% of edible prey biomass (Table 1). Other prey items included bobcat (*Lynx rufus*), coyote (*Canis latrans*), domestic cat, domestic chicken (*Gallus gallus domesticus*), domestic cow (*Bos taurus*), domestic goat (*Capra aegagrus hircus*), North American beaver (*Castor canadensis*), raccoon, striped skunk (*Mephitis mephitis*), turkey (*Meleagris gallopavo*), Virginia opossum, and wild boar (Table 1). Domestic animals made up 7% of kills, and other synanthropic species (raccoons, opossums, and skunks) comprised 10% of kills. Of alternative (non-deer) prey, the 4 other species making up $\geq 2\%$ of puma kills were raccoons (7%), domestic cats (4%), opossums (2%), and wild boar (2%). Of these species, domestic cat kill sites were present in the highest housing density areas on average at both housing density scales, followed by raccoons, opossums, deer and finally wild boar (Fig. 2). Of the primary prey species, domestic cats were killed closest to housing on average (97 ± 18 SE m), followed by opossums (169 ± 30 SE m), raccoons (382 ± 90 SE m), deer (454 ± 22 SE m) and wild boar (484 ± 73 SE m). The diversity of prey species killed and the proportion of small (<20 kg) prey at puma kill clusters increased with housing density at both examined scales (Table 2). Notably, diversity was lowest when no houses were present within 1 km of a kill site.

Spatial Patterns of Development and Use of Small Prey

Our best-fit models predicting prey size class for the local and regional scales both contained only the housing density covariate (Tables 3, 4), and all models containing the housing density covariate performed better than models without. Although 2 alternative models at the regional scale and 1 alternative model at the local scale fell within 2 Δ AIC, they each contained additional variables. This implies that although some models with additional housing variables were indistinguishable in terms of their fit of the data, these variables did not improve the fit of a density-only model.

Small prey were consumed at kill sites closer to a house ($W = 17,068$, $P \leq 0.001$), in more clustered housing ($W = 2,528$, $P = 0.002$ for local scale; $W = 13,864$, $P \leq 0.001$ for regional scale), and with higher housing densities ($W = 8,920$, $P \leq 0.001$ for local scale; $W = 8,334$, $P \leq 0.001$ for regional scale; Fig. 3). The average ($\pm$ SE) distance away from a house where a small kill was made was 290 ± 46 m, in contrast to 449 ± 21 m for large kills. At small kills, the average nearest neighbor distance for houses at the local scale was 44 ± 6 m, whereas it was 86 ± 10 m at kill sites of large prey. This pattern held at the regional scale, but the magnitude of the difference was less pronounced (72 ± 30 m for small prey, 84 ± 9 m for large prey). Average housing density at the local scale was 70 ± 13 houses/km² for small prey and 22 ± 3 houses/km² for large prey. Similarly, at the regional scale, average housing density was 75 ± 10 houses/km² for small prey and 35 ± 3 houses/km² for large prey.

Sex-Specific Responses to Housing and Prey

Males made kills at lower housing densities than females at the local ($W = 16,935$, $P \leq 0.001$) and regional ($W = 16,972$, $P = 0.003$) scales. Males also killed farther away from the nearest house on average ($W = 24,139$, $P = 0.004$), with a mean ($\pm$ SE) of 479 ± 35 m away in contrast to 400 ± 23 m for females. Clustering between houses did not differ among male and female kill sites at the local ($W = 2,111$, $P = 0.54$) or regional scales ($W = 14,567$, $P = 0.71$).

Despite differences in housing density at kill sites, males and females did not appear to differ in their use of small, alternative prey species. There was no significant difference in average use of small prey between sexes ($Z = 1.81$, $P = 0.07$), and diversity indices were similar ($H'_{\text{female}} = 0.885$, $H'_{\text{male}} = 0.905$).

Prey Species Occupancy and Detection

At the local scale, only occupancy of domestic cats was positively associated with housing density, whereas cat and raccoon occupancy was positively associated with housing density at the regional scale (Appendix A, available in Supporting Information online). However, the null model for each of the 3 above analyses was among the top models within $2 \Delta\text{AIC}$; therefore, it is possible that the housing parameter is uninformative (Arnold 2010). Deer occupancy was ubiquitous across the study area; deer were photographed at every camera station, but deer detection was positively associated with housing density at the local and regional scales. Wild boar occupancy and detection were negatively associated with housing density at the local

scale, whereas only boar occupancy was negatively associated with housing density at the regional scale. The null models for detection and occupancy of opossums performed best at both scales; however, the models including housing as a covariate to inform occupancy were within 2 Δ AIC of the null and cannot be ruled out as possible explanations of the data. Relationships between housing and occupancy of cats, raccoons, and wild boar (at the local and regional scale) indicated that the presence of these species were affected by development, whereas housing relationships to detection probabilities of deer and wild boar (at the local scale) indicated that although these species are present across housing density levels at these scales, they are likely to vary in frequency or activity in response to development.

Discussion

We found strong evidence for diet shifts in pumas associated with the density of nearby residential development. Pumas killed a higher diversity of prey and a higher proportion of small (<20 kg) prey in areas more greatly affected by development. Although we were regularly able to find small prey between 1 kg and 20 kg, we acknowledge possible undersampling of small prey due to the likelihood of fewer remains present at the kill site, and we anticipate that our estimates of small prey use are likely conservative. Patterns of higher diversity and small prey use in developed areas held at local and regional spatial scales examined for housing density, indicating that landscape-level changes affect puma prey composition similarly to immediate disturbances. In considering 1-km buffer zones around each

kill, the majority of kills occurred at an exurban housing density, although most kills had no housing present within a 150-m buffer zone. Pumas therefore are able to use a modified landscape for making kills but generally do so in lower housing density zones than the surrounding habitat.

Puma prey composition shifted primarily with regard to the number of houses present on the landscape at the local and regional scales. This result supports the notion that changes in prey habits are likely to be more greatly affected by the magnitude of development rather than the spatial features associated with development. However, housing clustering and proximity to housing did significantly differ by prey size, indicating that although the amount of housing development appeared to be the most important housing covariate, more clustered configuration of housing may also contribute to the hunting of smaller prey species. The Santa Cruz Mountains are predicted to experience continual development in the 21st century (U.S. Environmental Protection Agency 2010). If these projections are realized, pumas in this region will be increasingly exposed to habitat modifications, one of which is an altered prey community and disturbance landscape.

Unlike other western puma populations, pumas in the Santa Cruz Mountains have access to only 1 large, valuable prey item, the black-tailed deer. Deer are the only abundant ungulate that has persisted in the Santa Cruz Mountains (wild boar are not abundant and are patchily distributed), yet were rarely preyed upon when housing was at exurban or suburban densities within 150 m of the kill, despite having higher detection probabilities with increasing development. Our previous work shows that

risk avoidance behaviors increase at kill sites near residential areas and that pumas kill more often to compensate for the energetic costs of these behavioral adaptations (Smith et al. 2015). This result may explain why deer are not killed as regularly in the highest housing density areas and are replaced by small prey. Despite showing surprisingly weak evidence for positive associations with development, the proportion of small prey kills increased strongly with housing density. The discrepancy between species-specific patterns of occupancy and proportion of kills may be indicative of some selection by pumas for smaller prey in developed areas, possibly because they are more quickly consumed than deer and require less time investment in risky habitats. More work is needed to explore optimal decision making regarding prey choice in risky, human-dominated landscapes.

Although deer currently remain the primary prey species for pumas in the Santa Cruz Mountains, a development-mediated diet shift toward prey that are 5 to 10 times smaller than their primary prey likely affects puma movement because of reduced handling time. In addition, movement increases at kill sites near residential development because of behavioral avoidance of human disturbances (Smith et al. 2015). Previous work in our study area has found that pumas increase movement, with corresponding higher caloric demands, in more developed areas (Y. Wang, San Francisco Bay Bird Observatory, unpublished data). Changes in movement patterns related to prey habits and behavioral disturbances may interact to alter energetic costs in disturbed habitats. Future research should examine the relationship between prey densities, energetic value, handling time, and search time to understand the long-term

energetic effects of differential prey use on carnivore movement and energetics in developing landscapes.

Higher consumption of synanthropic species can also contribute to human-wildlife conflict. Domestic cats were the third most common prey item for pumas in our study area, representing a direct conflict between homeowners and pumas. However, the use of non-domestic human-associated species (e.g. raccoons) may also be a source of conflict if pumas hunt for these prey items near residential areas. Biocentric development planning can work to minimize this conflict by considering the impacts of different thresholds of development on puma hunting behavior and more effectively minimizing overlap between areas of human and puma use.

Disease transmission is another serious risk encountered by large carnivores preying upon synanthropic species. Although pumas are resistant to some diseases that afflict ungulates (Krumm et al. 2010), they are likely to be vulnerable to diseases carried by other carnivores. Pumas who regularly kill domestic cats may be at elevated risk of acquiring diseases that rely upon horizontal methods of transmission (e.g., direct contact between individuals), such as feline immunodeficiency virus (FIV; Bevens et al. 2012). Endangered Florida panthers (*P. c. coryi*), the only population of pumas living on the east coast, have already contracted FIV from domestic cats (Barr et al. 1989). Even between pumas and raccoons, despite their disparate lineages, there is evidence supporting regular cross-species transmissions of parvoviruses (Allison et al. 2013). For small, vulnerable populations of pumas

surrounded by urban habitats, low genetic diversity can exacerbate prevalence of disease (Ernest et al. 2003).

The most biologically significant changes in behavior are those that influence the long-term trajectory of an animal population by affecting the reproductive success of individuals. In pumas, females often make kills and bring their weaned but dependent kittens to the carcass to feed (Hornocker and Negri 2010). Kittens are then able to feed, while their mother leaves the kill area to search for another prey item. A transition to feeding on small prey would disrupt this pattern of moving kittens around to large food patches, possibly with negative energetic impacts for both kittens and their mother. Females tend to avoid human development when denning in our study area (Wilmers et al. 2013), which might be in part related to the suitability of a prey community to support the rearing of kittens. Further examination of the bioenergetic consequences of human-induced prey switching on kitten rearing is needed to understand the demographic ramifications of pervasive development.

Management Implications

Ultimately, we recommend that land use planners minimize development in puma habitat to promote the maintenance of behavior and species interactions. We observed diet shifts in even low levels of development, and these shifts were observable at the regional scale. Although our results suggest that puma hunting behaviors are altered with increasing development, high-density developments may actually serve to preserve species interactions if they offset extensive low-density

development and are paired with the establishment of ample protected areas and corridors in which pumas can continue exercising their evolved behaviors. Elimination of widespread low-density development will best preserve animal community dynamics by minimizing exposure to human disturbances and subsidies to wildlife.

Residents living on the urban fringe may perceive our results positively because pumas play an important role in preying on urban mesopredator pest species. However, if reduction of puma activity near residential development is a goal of local wildlife management, we encourage reduction of wildlife subsidies to puma prey species. In particular, containment of pets (particularly house cats) and garbage resources used by urban raccoon and opossum populations would reduce small prey available to pumas in developed areas. Detection rates of deer increased with housing density and may serve as an attractant for pumas. Increased use of deer fencing around lawns and gardens is likely to reduce deer activity and therefore available prey in residential areas. Actions to limit anthropogenic food subsidies to pumas and their prey may serve to reduce human-puma conflict in rural and exurban areas.

Table 3.1. Frequency and proportion of prey killed by puma in each of 4 housing density categories in the Santa Cruz Mountains, California, USA, 2009–2014 at the local (150-m buffer) and regional scale (1-km buffer) for all prey species over 1 kg. For prey size, S refers to small prey (1–20 kg) and L refers to large prey (>20 kg). Edible biomass estimates are included in the total column. Percentages in each housing column represent the proportion of the diet made up by the individual species within the given housing density. Species are listed in order of % of diet (frequency).

Species	Prey size (S, L)	Local scale				Regional scale				Total (% frequency / % edible biomass)
		No housing	Rural	Exurban	Suburban	No housing	Rural	Exurban	Suburban	
Black - tailed deer	L	253 (84.3%)	28 (84.8%)	51 (68.0%)	16 (51.6%)	46 (93.9%)	80 (83.3%)	195 (78.6%)	27 (58.7%)	348 (79.3% / 90.0% ^{ab})
Raccoon	S	14 (4.7%)	4 (12.1%)	8 (10.7%)	5 (16.1%)	3 (6.1%)	4 (4.2%)	18 (7.3%)	6 (13.0%)	31 (7.0% / 2.0% ^{cd})
Domestic cat	S	4 (1.3%)	0 (0%)	8 (10.7%)	6 (19.4%)	0 (0%)	1 (1.0%)	8 (3.2%)	9 (19.6%)	18 (4.1% / 0.9% ^{cd})
Virginia opossum	S	5 (1.7%)	0 (0%)	3 (4.0%)	2 (6.5%)	0 (0%)	0 (0%)	9 (3.6%)	1 (2.2%)	10 (2.3% / 0.2% ^{cd})

Wild boar	L	8 (2.7%)	0 (0%)	1 (1.3%)	0 (0%)	0 (0%)	3 (3.1%)	6 (2.4%)	0 (0%)	9 (2.1% / 1.9% ^{be})
Domestic goat	L	1 (0.3%)	0 (0%)	4 (5.3%)	2 (6.5%)	0 (0%)	1 (1.0%)	4 (1.6%)	2 (4.3%)	7 (1.6% / 1.6% ^{bf})
Domestic cow	L	4 (1.3%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	4 (4.2%)	0 (0%)	0 (0%)	4 (0.9% / 2.1% ^{bg})
Coyote	S	3 (1.0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	1 (1.0%)	1 (0.4%)	1 (2.2%)	3 (0.7% / 0.4% ^{cd})
Domestic pig	L	2 (0.7%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	2 (0.8%)	0 (0%)	2 (0.5% / 0.4% ^{be})
Striped skunk	S	2 (0.7%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	1 (1.0%)	1 (0.4%)	0 (0%)	2 (0.5% / 0.0% ^{cd})
North American beaver	S	1 (0.3%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	1 (0.4%)	0 (0%)	1 (0.2% / 0.2% ^{cd})
Bobcat	S	1 (0.3%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	1 (1.0%)	0 (0%)	0 (0%)	1 (0.2% / 0.1% ^{cd})
Wild turkey	L	1 (0.3%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	1 (0.4%)	0 (0%)	1 (0.2% / 0.1% ^{dh})
Domestic chicken	S	1 (0.3%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	1 (0.4%)	0 (0%)	1 (0.2% / 0.0% ^{di})
Gray fox	S	0 (0%)	1 (3.0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	1 (0.4%)	0 (0%)	1 (0.2% / 0.0% ^{cd})

a. Black-tailed deer mass (Rue 2004).

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- b. Ungulate proportion edible (Wilmer et al. 2003).
 - c. Mass of non-ungulate mammals: Jameson and Peeters 2004
 - d. Small prey proportion edible: Prange et al. 1979
 - e. Mass of pig and boar: Saunders and McLeod 1999
 - f. Mass of domestic goat: Gambaryan 1974
 - g. Mass of domestic cow: Beal et al. 1990
 - h. Mass of wild turkey: Sibley 2005
 - i. Mass of domestic chicken: Latshaw and Bishop 2001
-

Table 3.2. Species diversity (Shannon-Wiener H') of prey killed by pumas and percentage of kills that were small prey (1–20 kg) at 4 housing density levels in the Santa Cruz Mountains, California, USA, 2009–2014 for 2 scales of influence (local: 150-m buffer, regional: 1-km buffer) around confirmed puma kill sites.

Housing density class	H' diversity index		Small prey consumed (%)	
	Local	Regional	Local	Regional
No housing	0.775	0.230	10.7	6.2
Rural	0.501	0.763	15.2	8.3
Exurban	1.082	0.939	25.3	16.5
Suburban	1.307	1.200	41.9	37.0

Table 3.3. Results of mixed effects binomial logistic regression model predicting puma prey size class from 3 housing descriptors within 1 km of a kill site: housing density (density), average nearest neighbor distance (clustering), and distance to the nearest house (proximity) for kill sites in the Santa Cruz Mountains, California, USA, 2009–2014. Each housing density covariate has been normalized for comparison of coefficients, where positive coefficients indicate that larger values of the variable are associated with large prey. All models shown have a random intercept for individual puma and are listed in order of Akaike’s Information Criterion (AIC).

Model rank	AIC	Δ AIC	Covariates	Coefficient	SE
1	337.56	0.00	Density	−0.47	0.13
			Intercept	1.92	0.22
2	337.81	0.26	Density	−0.38	0.14
			Proximity	0.24	0.19
			Intercept	1.92	0.22
3	339.50	1.94	Density	−0.48	0.13
			Clustering	−0.04	0.15
			Intercept	1.91	0.21
4	339.57	2.01	Density	−0.39	0.14
			Clustering	−0.08	0.15
			Proximity	0.26	0.19
			Intercept	1.92	0.22
5	342.91	5.35	Proximity	0.44	0.17

			Intercept	1.90	0.22
6	344.84	7.28	Clustering	−0.04	0.17
			Proximity	0.45	0.18
			Intercept	1.90	0.22
7	350.30	12.7	Clustering	0.06	0.17
		4	Intercept	1.87	0.21

Table 3.4. Results of mixed effects binomial logistic regression model predicting puma prey size class from 3 housing descriptors within 150 m of a kill site: housing density (density), average nearest neighbor distance (clustering), and distance to the nearest house (proximity) for kill sites in the Santa Cruz Mountains, California, USA, 2009–2014. Each housing density covariate has been normalized for comparison of coefficients, where positive coefficients indicate that larger values of the variable are associated with large prey. All models shown have a random intercept for individual puma and are listed in order of Akaike’s Information Criterion (AIC).

Model rank	AIC	Δ AIC	Covariates	Coefficient	SE
1	146.91	0.00	Density	−0.64	0.23
			Intercept	1.96	0.52
2	147.28	0.37	Density	−0.49	0.25
			Clustering	0.47	0.44
			Intercept	1.93	0.51
3	148.80	1.89	Clustering	0.82	0.47
			Intercept	1.85	0.46
4	150.38	3.47	Clustering	0.72	0.48
			Proximity	0.17	0.26
			Intercept	1.85	0.47
5	151.97	5.06	Proximity	0.37	0.24
			Intercept	1.82	0.48

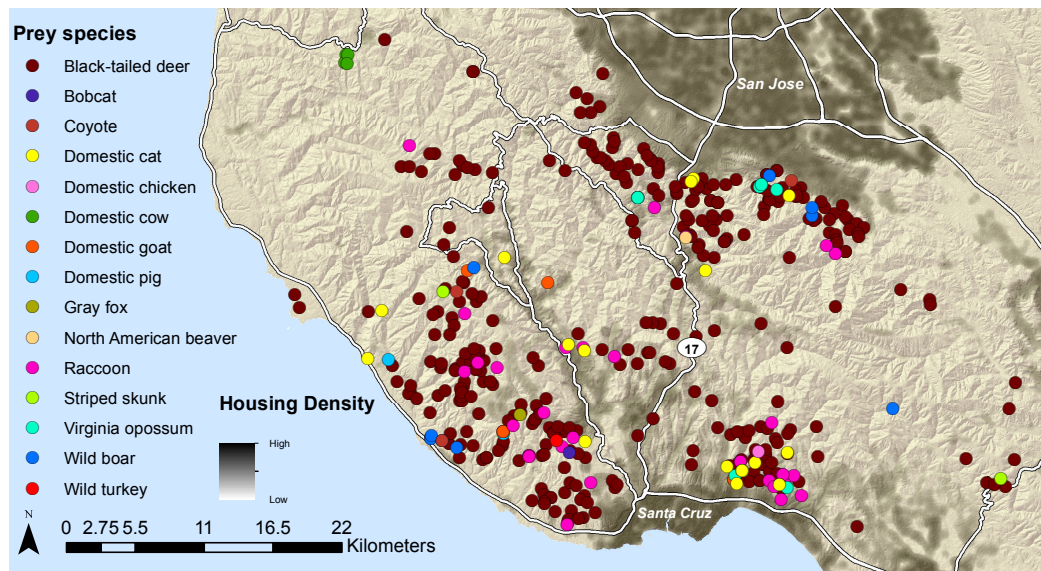


Figure 3.1. Study area in the Santa Cruz Mountains, California, USA with all confirmed kill sites of pumas color-coded by species, 2009–2014.

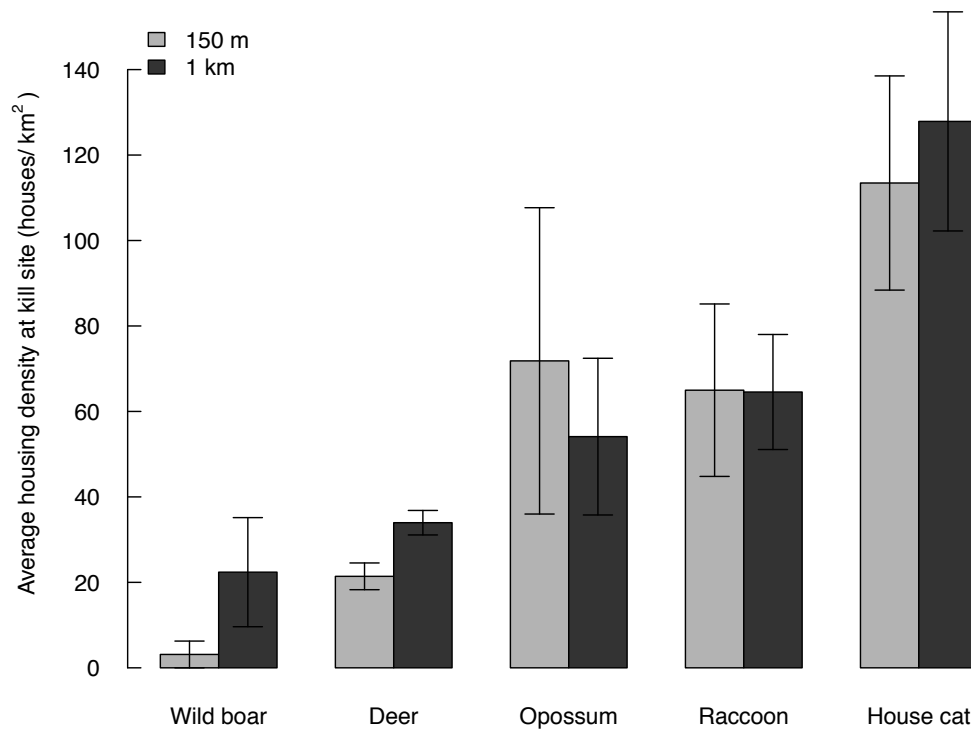


Figure 3.2. Average housing density ($\pm$ SE) of kill sites for species comprising $\geq 2\%$ of puma diet in the Santa Cruz Mountains, California, USA, 2009–2014. Housing density within 150 m (local scale) and 1 km (regional scale) of a kill site are shown.

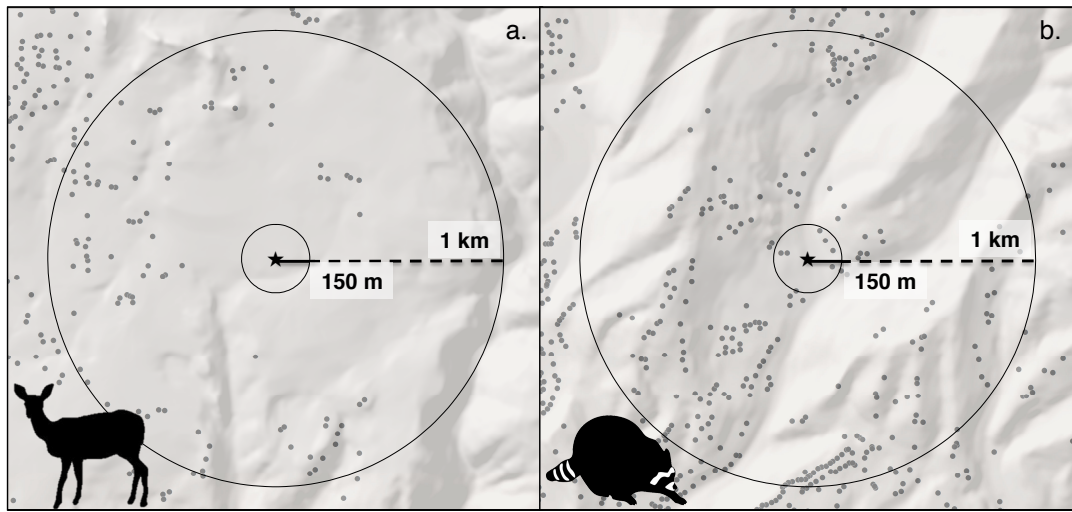


Figure 3.3. Representative examples of a) deer (large) and b) raccoon (small) kill sites (puma predation) in relation to housing in the Santa Cruz Mountains, California, USA, 2009–2014. Circles represent 150-m and 1-km buffers around kill sites, grey dots are houses and black stars are the kill sites. In comparison to small kills, large kills are characterized by little to no housing within 150 m, lower housing density within 1 km, less clustered housing, and greater distance to the nearest house.

Chapter 4

DNA metabarcoding reveals human-induced shifts in dietary niche partitioning in a carnivore guild

Abstract

Anthropogenic disturbances can constrain the realized niche space of wildlife by inducing avoidance behaviors. In carnivores, human activity has been linked to increased nocturnality, which could contribute to reduced partitioning of niche space by carnivores that consume similar resources. We investigated the influence of anthropogenic disturbance on dietary niche breadth and overlap among competing carnivores, and explored if altered resource partitioning could be explained by human-induced activity shifts toward nocturnality. To describe the diets of coyotes, bobcat, and gray foxes, we designed a citizen science program to collect carnivore scat samples and sequenced all predator and prey DNA in scats using a DNA metabarcoding approach. All pairs of carnivores increased dietary overlap with human use, whereby overlap between coyotes and gray foxes was 42% greater in high human use areas. Coyotes showed a trend toward consumption of more nocturnal prey where human disturbance was greater, whereas foxes appeared to reduce consumption of nocturnal prey. These results suggest that niche partitioning among carnivores is reduced by human activity, and that patterns in resource use may be related to human-induced shifts toward nocturnality by dominant and generalist carnivores. Our study highlights the importance of considering the indirect effects of

anthropogenic disturbances to understand altered species interactions in human-dominated habitats.

Introduction

As human activity amplifies in many regions across the globe, wildlife are increasingly exposed to novel cues and threats associated with anthropogenic development. For many species, responses to human disturbances are analogous to responses to predation risk (Frid and Dill 2002). Carnivores are particularly sensitive to risk from humans and respond by altering their space use, activity patterns, and feeding behavior (Wilmers et al. 2013, Barreto et al. 2014, Smith et al. 2015, Wang et al. 2015). It is this behavioral plasticity that often allows carnivores to persist in human-dominated systems by mitigating exposure to anthropogenic stressors and risks (Bateman and Fleming 2012, Oriol-Cotterill et al. 2015, Carter and Linnell 2016).

Although carnivores can directly benefit by behaviorally adapting to anthropogenic disturbance, human-induced changes in carnivore behavior might have unexpected direct and indirect effects on other species in the community. Thus human activity, by impacting carnivores, has the potential to alter the realized niche of other species (Hutchinson 1957). Alberti et al. (2003) argue that the realized niche of a population cannot be understood outside of the human context in many cases, particularly because anthropogenic disturbance hinders some species while benefitting others. This may be especially true for carnivores, which often partition

their use of space and time in order to access shared prey resources (Vanak et al. 2013). Although carnivores within a guild might share the same geographic ranges and habitat requirements, hierarchies among species force inferior competitors into altered niche space defined by fine scale selection of microhabitats or temporal activity patterns (Cozzi et al. 2012, Kamler et al. 2012, Remonti et al. 2012). In some instances, interspecific competition is the most impactful driver of temporal partitioning (Hayward and Slotow 2009), which allows for coexistence when carnivores exploit the same prey communities.

In our previous work, we documented a temporal shift among multiple carnivore species towards increased nocturnal and reduced diurnal activity in response to human disturbance (Wang et al. 2015). Reduced diurnal activity is likely to narrow dietary niche breadth by reducing access to diurnal prey species. Human impacts on niche partitioning should therefore contribute to altered competitive dynamics among carnivores by increasing temporal overlap while hunting. In this study, we sought to understand the relationship between human disturbance and resource partitioning in a carnivore community in the context of human-induced activity shifts. We hypothesized that carnivore dietary niche breadth would be narrower, and overlap between species would be greater, in open space preserves more heavily impacted by human use. We also hypothesized that these changes would be related to human-induced activity shifts toward increased nocturnal and reduced diurnal activity, resulting in temporally-driven changes in diet. We explore the evidence for these patterns and discuss implications for human-carnivore

coexistence and food web dynamics in human-dominated landscapes.

Methods

Study System

We conducted this study in the Santa Cruz Mountains on the central coast of California. The region has a Mediterranean climate with a wet season in the winter and dry season in the summer. Elevation ranges from sea level to 1155 m, and annual rainfall varies from 58–121 cm across the mountain range. The Santa Cruz Mountain region supports or contains many different land uses, including privately protected land, state and county parks, open space preserves, cities, exurban communities, and extractive industries. The extensive wildland-urban interface in the Santa Cruz Mountains is known to impact carnivore feeding behavior and utilization of prey species (Wilmers et al. 2013, Smith et al. 2015, 2016, Wang et al. 2015).

The northern region of the Santa Cruz Mountains abuts high-density suburban and urban development, yet much of its land is preserved as open space by the Midpeninsula Regional Open Space District. Many preserves are located directly adjacent to development, whereas others are buffered by protected areas. Preserves at the wildland-urban interface (hereafter referred to as “interface”) experience disturbance from houses as well as greater human foot traffic within the preserves due to their higher accessibility in comparison to more distant preserves surrounded by native habitat (hereafter referred to as “wildland”). Our work was conducted on three interface preserves (within 2 miles of an urban area) and four wildland preserves

(greater than 5 miles from an urban area; Fig. 1). Visitation data from 2007–2010 estimate that the three interface preserves studied experienced a total of 739,125 visitors/year, whereas the four wildland preserves saw 156,950 visitors/year (Midpeninsula Regional Open Space District 2011). All seven preserves in this study comprised oak, grassland, chaparral, and mixed evergreen habitat.

We chose coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and gray foxes (*Urocyon cinereoargenteus*) as our focal species due to their shared prey base, propensity to eat prey with distinct diel activity patterns (Neale and Sacks 2001), well-documented intraguild hierarchy (Chamberlain and Leopold 2005), and observed temporal responses to anthropogenic disturbances (Riley et al. 2003, Wang et al. 2015). In coastal California, coyotes and bobcats have become more nocturnal in areas of increased anthropogenic disturbance (Riley et al. 2003, Wang et al. 2015). In contrast, gray foxes, the subordinate of the three species, are highly nocturnal regardless of human activity but become slightly more active during morning hours when disturbed (Wang et al. 2015). The primary prey of these carnivores are closely tied to diel patterns; mice, voles, woodrats, and rabbits are more nocturnal, whereas tree squirrels, ground squirrels, and most songbirds are more diurnal. The flexibility in coyote and bobcat activity patterns and their generalist diets facilitate the exploitation of both diurnal and nocturnal prey species and the ability to switch prey given declines in preferred prey (Prugh 2005). Therefore, these species are well-suited to explore the influence of human disturbances on niche breadth and partitioning in a carnivore guild.

Scat Collection

We developed a citizen science program called Conservation Scats to collect scat samples and train community members in animal tracking. To minimize fecal DNA degradation (Murphy et al. 2007), we designed our sampling to ensure that we only collected scat samples less than seven days old to retain sufficient DNA product for analysis. Each scat collection period consisted of two field days: on the first day we removed all scats from our study trails; on the second day (seven days later) we collected all fresh coyote, bobcat, and gray fox scats from cleared trails. We collected all scats that were potentially from our target carnivore species, with the exception of those from domestic dogs, which could be identified by the composition and consistency of the scat. We conducted four scat collection periods, two in the summer of 2014, and two in the winter of 2015. We froze all collected samples at -20C for 3-13 months prior to DNA extraction.

Molecular Scat Analysis

We used a DNA metabarcoding diet analysis approach that allows for the identification of multiple species in complex mixed samples and does not require a priori knowledge of prey species (Pompanon et al. 2012). Traditional dietary analyses based on fecal dissection and microscopic examination of prey remains is often biased due to different digestibility of individual prey species and the identification skill of the observer (Pompanon et al. 2012), and many prey species, particularly of

small mammals and birds, are difficult to distinguish morphologically. In contrast, DNA metabarcoding allows for the identification of individual species from complex environmental DNA (eDNA) samples based on high-throughput sequencing of marker genes (Yoccoz 2012). DNA metabarcoding has recently been used to detail carnivore diets from fecal samples for single predator species (Shehzad et al. 2012, De Barba et al. 2014), but has yet to be used simultaneously on a guild of predators.

Scat processing

For molecular diet analysis from scats, DNA can be extracted from the prey remains that survive digestion (e.g. bones, fur) or from the scat matrix material (i.e. the part of the scat not made up of identifiable remains of bone, hair, or vegetation). Given that not all prey structures survive the digestive process equally, we chose to use the scat matrix material assuming that it is most representative of relative prey biomass.

Scats were removed from the freezer and thawed in sterile plastic containers lined with a nylon mesh paint strainer bag. Each container was filled with a sufficient quantity of 95% ethanol to cover the scat, and the scat was manually homogenized using a wooden tongue depressor. Once thoroughly broken apart, the paint strainer containing undigested structures was removed leaving behind ethanol preserved scat matrix in the container. DNA was extracted from the samples using the QIAamp Fast DNA Stool Mini Kit as per the manufacturer's instructions.

PCR amplification and sequencing

For this study, we focused on vertebrate prey species due to their association with diel activity patterns. We amplified a ~100bp region of the mitochondrial 12S gene using the pan-vertebrate primers identified in Riaz et al. (2011) that were designed using the program ecoPrimers in the Obitools package (De Barba et al. 2014, Boyer et al. 2016): F (5'- ACTGGGATTAGATACCCC -3') R (5'- TAGAACAGGCTCCTCTAG -3'). A two-stage labelling scheme was used to multiplex many individual scats on a single sequencing flow cell. For each scat, the initial PCR amplification was done with one of 16 labelled (10bp tag) forward primers. Amplicons from 16 uniquely labelled samples were then normalized, pooled and given a unique TruSeq Illumina adapter sequence via post-PCR ligation. Lastly, samples were pooled for 150bp SE sequencing on the Illumina MiSeq. To achieve our desired sequencing depth, scat amplicons were sequenced on two separate MiSeq runs.

Bioinformatics pipeline

Sequences were automatically sorted (MiSeq post processing) by amplicon pool using the indexed TruSeqTM adapter sequences. FASTQ sequence files for each library were imported into QIIME for demultiplexing and sequence assignment to species (Caporaso et al. 2010). For a sequence to be assigned to a sample it had to match the full forward and reverse primer sequences, and match the 10 bp primer tag for that sample (allowing for up to 2 mismatches in either primers or tag sequence).

We created a local reference library of all extant terrestrial vertebrates in the Santa Cruz Mountains using available 12s sequences in GenBank. For species for which there were no 12s gene sequences in GenBank, we instead used one congener or one confamilial sequence. In total, 66 species-specific sequences, 33 genus-specific sequences, and 3 family-specific sequences were used to represent potential diet species in our local database.

DNA sequences that were assigned to scat samples were clustered with USEARCH (similarity threshold = 0.99; minimum cluster size = 3; de novo chimera detection), and a representative sequence from each cluster was entered into a GenBank nucleotide BLAST search (Altschul et al. 1990, Edgar 2010). If the top matching species for any cluster was not included in the existing database (or the sequence differed indicating allelic variation), the top matching entry was put in the reference database. This procedure minimized the potential for incorrect species assignment or prey species exclusion.

For taxonomic assignment, a local BLAST search was done against our custom 12s reference database with each sequence assigned to a sample. A species was assigned to a sequence based on the best match in the database (threshold BLASTN e-value < 1e-20 and a minimum identity of 0.9), and the proportions of each species' sequences were quantified by sample after excluding predator sequences or any identified contaminants, including species representing fewer than 1% of the reads in each sample (Caporaso et al. 2010).

To confirm the quality of our species assignments, we entered a subset of

assigned sequences into a full GenBank BLASTN search. For each species with fewer than five occurrences across scat samples, we ran one sequence per sample. If the top species assignment did not match the assignment from our reference library, we eliminated the occurrence. For all other species, we ran a minimum of three sequences in a BLASTN search. If the BLASTN output for each of the three sequences matched the species assigned from the reference library with a maximum e-value of $1e-50$ (Hiiesalu et al. 2012), the remainder of assignments for that prey species were kept. For species with variability in assignment accuracy (i.e. some assignments matched the BLASTN results while others did not), we ran one sequence assigned as the species from each scat in which the species occurred and excluded incorrect matches from further analyses. For outputs in which multiple species had equal similarity matches, the lowest parsimonious taxonomic level was used.

Analytical Methods

We determined relative proportion of a prey species in the diet of each carnivore species using two methods: 1) frequency of occurrence (FOO) in scats; and 2) the proportion of DNA reads in each scat measured as relative read abundance (RRA; Kartzin et al. 2015). RRA theoretically better represents diet because it allows for dietary contributions to reflect biomass. However, RRA can be biased if the primer used does not match equally for all target prey species. Our primer region had 1-3 base pair mismatches in the majority of herpetofauna species, therefore we may have underestimated contribution of reptile and amphibian taxa (Pawluczyk et al.

2015, Piñol et al. 2015). In the case of uneven primer mismatches between species, FOO data may be less biased against contribution of particular prey species to carnivore diets. We calculated all diet measures using both RRA and FOO data to compare the qualitative differences between the two approaches. RRA was measured as the proportion of sequence reads in a sample divided by the total number of sequences in that sample (Kartzinel et al. 2015).

We measured niche breadth in wildland and interface preserves separately for gray foxes, bobcats, and coyotes using Hurlbert's standardized niche breadth (B_A), a measure of Levins' formula that can be interpreted on a [0,1] scale (Hurlbert 1978):

$$B_{Ajk} = \frac{(1/\sum p_{ijk}^2) - 1}{n_{jk} - 1}$$

where p_i is the relative proportion of each prey item i in the diet of carnivore j = [bobcat, coyote, gray fox] in human use type k = [wildland, interface] and n is the total number of prey species consumed by carnivore j in human use type k . B_{Ajk} ranges from 0 (highly specialized) to 1 (highly generalized). We used a subsampling approach to correct for differences in sample sizes, whereby we took the average of niche breadth measures calculated by subsampling 15 scats without replacement for 10,000 iterations for each carnivore by human use type.

We used Pianka's adaptation of the niche overlap (O_{jk}) metric to determine dietary overlap among all pairs of target carnivores in both human use types (Pianka 1973):

$$\hat{O}_{jmk} = \frac{\sum_i^n \hat{p}_{ijk} \hat{p}_{imk}}{\sqrt{\sum_i^n \hat{p}_{ijk}^2 \hat{p}_{imk}^2}}$$

where p_{ijk} is the proportion of prey species i in carnivore j in human use type k , p_{imk} is the proportion of prey species i in carnivore m in human use type k , and n is the total number of available prey species. A value of $O_{jmk} = 0$ represents no overlap, whereas a value of $O_{jmk} = 1$ represents complete overlap.

We ran a χ^2 test to assess differences in diet composition among carnivore species in each human use type. In order to visualize the nature of these differences, we also conducted a correspondence analysis (CA), which uses a contingency table of prey count data by carnivore to examine the statistical difference in partitioning of prey species by carnivores (Bendixen 1995). In the CA, we used only prey species making up at least 0.5% of a carnivore's diet to reduce noise caused by rare occurrences (McCune et al. 2002). We calculated the correlation coefficient of the CA for wildland and interface preserves, where a larger coefficient represents greater differentiation between the diets of carnivore species. Finally, to assess the role of human-induced activity shifts on carnivore diet, we compared the proportion of nocturnal prey consumed and the number of scats containing nocturnal prey in

interface and wildland preserves for each carnivore species using one-tailed two-proportion z-tests.

Results

We collected 302 carnivore scats, 284 of which could be identified to species, and detected 36 total prey species or taxonomic units (Table 1). Foxes ($\chi^2 = 53.96$, d.f. = 31, $P < 0.01$) and bobcats ($\chi^2 = 41.49$, d.f. = 23, $P = 0.01$) significantly altered their diet between wildland and interface preserves, whereas coyotes did not ($\chi^2 = 25.71$, d.f. = 24, $P = 0.37$). In interface preserves, bobcats consumed notably more dusky-footed woodrat and less California vole, deer mouse, Botta's pocket gopher, and gray squirrel (western or eastern). Coyotes consumed more woodrat, brush rabbit, and gray squirrel and less gopher, vole, and black-tailed deer in interface preserves. Gray fox diet in interface preserves was characterized by increased consumption of brush rabbit and decreased consumption of deer mouse and gopher, with high use of woodrat in both interface and wildland preserves. Although the three carnivore species consumed similar proportions of birds in total (range: 8.35% - 8.5%), foxes and bobcats consumed more birds in interface preserves, whereas coyotes consumed more birds in wildland preserves. All carnivores consumed more herpetofauna in interface preserves, but fox diet contained about three times more herpetofauna than bobcat or coyote diets. Niche breadth (B_A) was the only diet measure that varied qualitatively between the FOO and RRA approaches; in interface preserves, coyote

B_A was either higher (RRA) or about equal (FOO), bobcat B_A was lower (RRA) or higher (FOO), and fox B_A was approximately equal (RAA) or lower (FOO; Table 2).

Overlap between all pairs of carnivore species increased with human activity (Fig. 2). The largest increase in overlap was observed between coyotes and gray foxes, whereby overlap was 42% higher in interface preserves in comparison to wildland preserves. Bobcats and gray foxes had the most similar diets of any three pairs of carnivores with almost complete diet overlap in interface preserves, reaching an overlap value of 0.984 (Fig. 3). Overlap values using FOO data were qualitatively similar, but ubiquitously larger in magnitude. Although the diets of carnivore species were significantly different in both wildland and interface preserves ($\chi^2_{\text{wildland}} = 149.2$, $P_{\text{wildland}} < 0.001$; $\chi^2_{\text{interface}} = 127.6$, $P_{\text{interface}} < 0.001$), the CA indicated that differentiation between carnivore diets was higher in wildland ($R = 0.71$) than interface ($R = 0.65$) preserves (Fig. 3). CAs and χ^2 analyses conducted with FOO data show identical patterns, with slightly smaller correlation coefficients ($R_{\text{wildland}} = 0.54$, $R_{\text{interface}} = 0.47$) and χ^2 values ($\chi^2_{\text{wildland}} = 128.5$, $P_{\text{wildland}} < 0.001$; $\chi^2_{\text{interface}} = 97.1$, $P_{\text{interface}} < 0.001$).

A marginally significant increase in nocturnal prey consumption ($P = 0.05$) was observed in coyotes in interface preserves, where coyote diet comprised approximately 10% more nocturnal prey (Table 2). Proportion of coyote scats containing nocturnal prey increased from 82% in wildland preserves to 100% in interface preserves ($P = 0.02$). Grey foxes appeared to reduce their proportion of nocturnal prey consumed in interface preserves, although the difference in

proportions was only marginally significant ($P = 0.06$). Bobcats did not vary the proportion of nocturnal prey consumed by habitat type ($P = 0.40$), and neither fox nor bobcat scats in interface and wildland preserves differed in the number of scats containing nocturnal prey ($P = 0.28$ & $P = 0.57$, respectively; Table 2).

Discussion

We provide evidence that carnivores alter diet composition when in high human use habitats, and that human-induced diel activity patterns in carnivores are a possible contributor to diet shifts. We observed an increase in diet overlap among species within a carnivore guild with increased human activity. Coyotes and gray foxes displayed the most dramatic increase in dietary overlap when exposed to a greater degree of human activity, and gray foxes and bobcats were found to have nearly identical diets in preserves with high human activity. Although an increase in diet overlap cannot provide direct inference on the degree of exploitation competition without knowing the relative abundances of all available prey resources, it offers insight into constraints on fine-scale temporal and spatial niche partitioning. Carnivores with highly overlapping diets likely hunt in similar habitat types and times of day to access the same resources. Reduced partitioning could therefore result in increased antagonistic interspecific interactions among carnivores or spatial shifts resulting from interspecific avoidance (Remonti et al. 2012).

Our results suggest that increased overlap may be partially explained by shifts in coyote diet toward more nocturnal prey species, and that gray foxes might attempt

to mitigate increased coyote nocturnal hunting activity by hunting more diurnally-active prey. The proportion of coyote scats containing nocturnal prey increased from 82% in wildland preserves to 100% in interface preserves, supporting observed activity shifts for coyotes in our study area from a previous study where coyotes exhibited the greatest decrease in diurnal activity with increasing disturbance of our three study species (Wang et al. 2015). The increase in proportion of scats containing nocturnal prey reflects the extent of coyote encroachment on the niche space of highly nocturnal foxes. Although foxes may be able to adapt to some extent by consuming more diurnal prey items, their dependence on hunting at night is evidenced by their high proportion of scats containing nocturnal prey in both preserve classes. Coyote shifts toward increased nocturnal prey utilization could further constrain the realized niche of the less generalist gray fox.

Prey use appeared to also be tied to size and habitat preferences of the carnivores. Dusky-footed woodrat and brush rabbit were the most utilized diet items for the carnivore guild as a whole, but use of woodrat decreased with increasing carnivore species size. Larger prey species such as black-tailed jackrabbit, feral cat, Virginia opossum, and black-tailed deer were primarily consumed by coyotes, whereas the small and forest-associated deer mouse was consumed mostly by gray foxes. The pocket gopher and California ground squirrel, two grassland and diurnal species, were consumed in the highest proportions by coyotes. The partitioning of prey species by size and habitat association highlights the importance of habitat heterogeneity in supporting carnivore coexistence. Conservation of intact carnivore

guilds likely requires a holistic lens that focuses on the maintenance of diverse habitats, prey species, and access to prey in both day and night.

Feral cat was observed in the diet of all three carnivore species, but appeared to only be a prominent diet item for coyotes, making up 9% of coyote diet in interface preserves. Cats rarely showed up in scats in wildland preserves, indicating that they may not effectively establish far from residential areas. This result is consistent with diet analyses of the sympatric mountain lion population, which also consumes house cats in areas with higher housing densities (Smith et al. 2016). More work is needed to investigate the role of native large- and mesocarnivores in determining feral cat establishment and population densities.

In addition to human-induced shifts in temporal activity patterns, other factors might contribute to increased diet overlap among carnivores. We cannot discount that the patterns we observed could be influenced by differences in availability of prey species, which might vary depending on prey responses to human activity. Although logistical constraints for this study made acquiring density estimates for the large diversity of carnivore prey species infeasible, we attempted to minimize impacts of habitat by only sampling in preserves with similar habitat types. The potential for differential prey availability does not alter the interpretation of our results on carnivore diet and overlap in response to anthropogenic disturbance, but could influence inferences made regarding the mechanism for these changes. We suggest that the relationship between human impacts on prey abundances be a focus of future study. In addition, although we only analyzed use of vertebrate prey resources in this

study, canids hunting in preserves that abut residential areas could also experience some spillover of plant-based anthropogenic food not captured by our analysis. A combination of human-induced behavioral changes among carnivores, altered prey community composition, and influx of non-vertebrate anthropogenic subsidies might all contribute to shifts in carnivore diet composition and overlap.

Due to a reduction of top carnivores and increased human development, coyotes have expanded their range by 40% and are now the top predator in many ecosystems (Prugh et al. 2009). Coyotes can suppress the populations of subordinate mesocarnivores, including gray foxes (Fedriani et al. 2000, Chamberlain and Leopold 2005, Prugh et al. 2009). Our results support that coyotes are the most adaptable mesocarnivore in this system in their ability to expand (RRA) or maintain (FOO) their niche breadth in novel conditions, and are able to encroach on the dietary niche space of subordinate mesocarnivores. Further work should investigate the degree to which mesocarnivore declines in the presence of coyotes are accentuated or explained by enhanced exploitation competition due to human-imposed restrictions in dietary niches.

In this study, we were able to achieve diet measures for a carnivore guild from eDNA. Our genomic approach provides a simple method to obtain data on predator identity and prey composition from a single fecal sample, allowing the analysis of complex food webs from environmental samples. In addition, our novel citizen science sampling approach is a model for efficient scat collection, particularly in habitats near urban areas with trail networks used by carnivores. In only four

collection days, we collected 302 scats at approximately 2 scats per mile. Scat collection for species that utilize trails is well-suited for citizen science, as it requires minimal skill and can provide educational benefits to volunteers through training in animal tracking. Although scat-detection dogs are increasingly utilized for conservation research, they require extensive time and monetary investment (Long et al. 2007). In habitats with extensive trail networks and a substantial adjacent human population, using citizen science for scat collection can provide a cost-effective alternative that also increases public knowledge and investment in local research.

In our genomic approach, we detected some qualitative differences in inferences using FOO and RRA data. Although they were similar in their qualitative estimation of carnivore overlap and proportion of nocturnal prey consumed, FFO and RRA data produced substantially different estimations of niche breadth. For example, RRA data indicated that bobcat niche breadth contracted in interface preserves, whereas FOO data suggested the opposite result. This discrepancy could be explained by the characteristics of the data used; in interface preserves, bobcats might become more specialized from a biomass perspective, but still consume a greater diversity of species. Discrepancies in our analyses using both data types highlight the importance of considering the appropriate unit of analysis for any diet analysis using DNA metabarcoding techniques. It is also possible that species with base pair mismatches in the primer region were underestimated in the RRA data. Diet studies using genomic techniques should choose primer sets that minimize base pair mismatches whenever possible.

There are many additional potential indirect effects of human-induced change in food webs, including impacts on disease dynamics and the spread of toxins in the environment (Levi and Wilmers 2012). Adding to the extensive literature on trophic cascades resulting from human impacts on large carnivores (via mesocarnivores and large herbivores), our study begins to explore cascading community effects of human-induced shifts in mesocarnivore competitive dynamics and behavior, particularly in consumption of small mammals. Mesocarnivore abundance has been linked to disease prevalence and transmission due to mesocarnivores' role as small mammal predators (Levi et al. 2012). Small mammals are responsible for 80-90% of tick nymphs infected with Lyme disease in the Eastern US, making them the most important reservoirs of Lyme (Brisson et al. 2008), and western gray squirrels may be a uniquely important reservoirs in California (Salkeld et al. 2008, 2010). In addition, rodents are the primary pathway that brings anticoagulant rodenticides into natural areas, which bioaccumulate in wildlife and cause significant mortality in carnivores (Riley et al. 2007, Serieys et al. 2015). To determine the extent and significance of increasing human-wildlife interactions, human-induced changes in the relationship between small mammals and their primary mammalian predators should continue to be investigated.

Human activity is known to alter the composition of animal communities, but little attention is paid to indirect effects of animal behavioral adaptations to anthropogenic disturbances. Nearly all federally protected lands in the United States are open to recreation of some kind, and pressures on these lands are projected to

increase with high rates of housing development near protected areas (Radeloff et al. 2010). Recreation is often seen as essential to conservation by fostering biophilia and investment in public lands (Wilson 1986); however, even quiet and nonconsumptive recreational activities can reduce the use of protected areas by carnivores, indicating diminished suitability of the habitat for supporting wildlife (Reed and Merenlender 2008). Although land preservation is an essential first step to conserving ecosystems, human influences on the behavior of wildlife and how these cascade through food webs need to be understood if we are to maintain intact animal communities and relationships in the midst of global change.

Table 4.1. Prey species detected in coyote, bobcat, and gray fox scats in wildland and interface open space preserves in the Santa Cruz Mountains, California. Proportions are listed as the relative read abundance (RRA), with frequency of occurrence (FOO) counts in parentheses.

	Coyote			Bobcat			Gray Fox		
	Wildland	Interface		Wildland	Interface		Wildland	Interface	
Mammals									
<i>Chaetodipus californicus</i>	-	-	1.1 (4)	-	-	0.2 (4)	0.5 (3)		
<i>Didelphis virginiana</i>	-	2.6 (2)	<0.1 (1)	-	-	-	-		
<i>Felis catus</i>	1.0 (1)	8.9 (7)	0.8 (2)	0.1 (2)	-	-	0.2 (3)		
<i>Lepus californicus</i>	1.3 (7)	4.2 (12)	-	0.1 (1)	-	-	<0.1 (2)		
<i>Microtus californicus</i>	9.3 (5)	5.5 (7)	17.3 (42)	0.5 (5)	-	12.0 (26)	1.2 (20)		
<i>Neotoma fuscipes</i>	9.3 (11)	16.7 (24)	25.7 (43)	49.3 (25)	-	45.4 (41)	46.1 (67)		
<i>Odocoileus hemionus</i>	18.0 (10)	1.2 (3)	1.6 (6)	4.2 (6)	-	0.6 (4)	0.8 (3)		
<i>Peromyscus</i> spp.	1.0 (4)	0.7 (4)	5.9 (20)	2.6 (6)	-	16.5 (33)	8.6 (23)		

<i>Rattus</i> spp.	-	-	-	2.4 (3)	-	-
<i>Scapanus latimanus</i>	-	2 (<0.1)	0.9 (1)	<0.1 (1)	0.1 (1)	1.0 (4)
<i>Sciurus</i> spp.	0.2 (1)	4 (6.7)	8.2 (8)	1.5 (2)	0.4 (3)	2.3 (8)
<i>Spermophilus beecheyi</i>	0.5 (2)	6 (3.0)	0.2 (5)	0.1 (2)	-	0.1 (3)
<i>Sylvilagus</i> spp.	18.8 (12)	22 (21.7)	23.3 (32)	22.4 (15)	10.9 (17)	23.6 (42)
<i>Thomomys bottae</i>	30.6 (14)	20 (20.6)	7.5 (18)	5.2 (6)	3.7 (11)	3.1 (10)
Birds						
<i>Callipepla californica</i>	0.1 (1)	2.0 (1)	-	2.8 (1)	-	0.1 (2)
Cardinalidae	0.1 (1)	-	<0.1 (2)	-	1.2 (1)	-
<i>Cathartes aura</i>	2.8 (1)	-	-	-	-	-
Columbidae	-	1.8 (2)	-	-	-	1.9 (4)
<i>Gallus gallus</i>	-	0.5 (2)	-	0.5 (2)	0.1 (1)	2.2 (6)
Emberizidae	-	-	0.4 (2)	-	-	-
<i>Meleagris gallopavo</i>	5.3 (3)	0.8 (5)	3.7 (9)	5.7 (4)	1.4 (5)	2.4 (6)
<i>Mimus polyglottos</i>	-	-	-	-	0.6 (3)	0.2 (1)

Passeriformes (other)	0.9 (3)	0.7 (2)	3.3 (5)	0.1 (3)	1.5 (5)	0.1 (2)
<i>Pavo cristatus</i>	-	-	-	-	-	1.4 (1)
Pelicaniformes	<0.1 (1)	-	-	-	-	-
Picidae	-	-	-	-	0.1 (1)	-
Strigidae	-	-	-	-	0.3 (1)	-
Sylvioidea	-	-	-	<0.1 (1)	-	0.6 (1)
Troglodytidae	-	-	-	-	<0.1 (1)	-
Turdidae	0.5 (1)	1.0 (1)	<0.1 (1)	-	2.4 (4)	-
<i>Tyto alba</i>	-	<0.1 (1)	-	-	-	0.4 (2)
Amphibians						
<i>Anaxyrus boreas</i>	-	-	-	-	-	0.6 (1)
<i>Aneides flavipunctatus</i>	-	-	-	-	<0.1 (1)	-
<i>Batrachoseps attenuatus</i>	-	0.1 (1)	-	-	-	<0.1 (1)
<i>Pseudacris sierra</i>	-	-	-	-	<0.1 (1)	-

<i>Rana</i> spp.	0.4 (1)	1.2 (1)	<0.1 (1)	1.4 (3)	1.5 (4)	2.1 (6)
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Table 4.2. Summary statistics from coyote, bobcat, and gray fox diet analyses in wildland and interface open space preserves in the Santa Cruz Mountains, California. For measures of niche breadth and % nocturnal diet, we report estimates from both RRA data and FOO data (in parentheses).

	Coyote		Bobcat		Gray Fox	
	Wildland	Interface	Wildland	Interface	Wildland	Interface
No. of Scats	22	34	75	28	49	76
Prey Items/Scat	3.59	3.82	2.71	3.26	3.45	2.92
Species Richness	18	22	18	19	22	24
Niche Breadth	0.101	0.130	0.099	0.053	0.065	0.057
	(0.208)	(0.203)	(0.151)	(0.162)	(0.151)	(0.134)
% Nocturnal	71.2	81.0	81.5	82.7	90.0	84.6
	(67.1)	(77.5)	(80.2)	(71.6)	(80.3)	(78.7)
% Scats with Nocturnal Prey	81.8	100	94.7	100	100	96.1

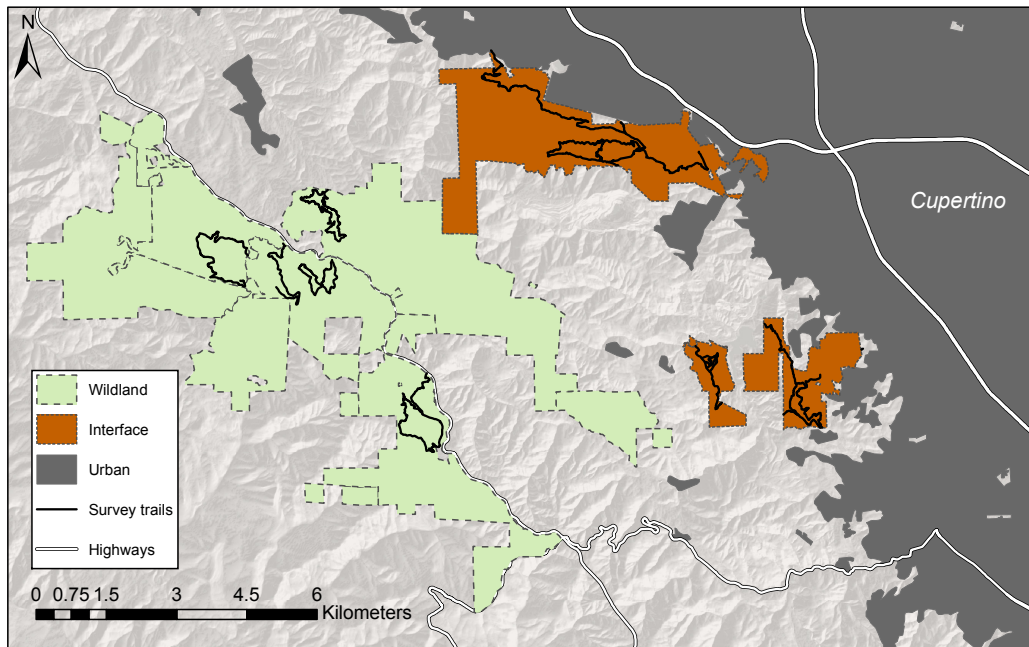


Figure 4.1. Midpeninsula Regional Open Space District preserve trails sampled for carnivore scats.

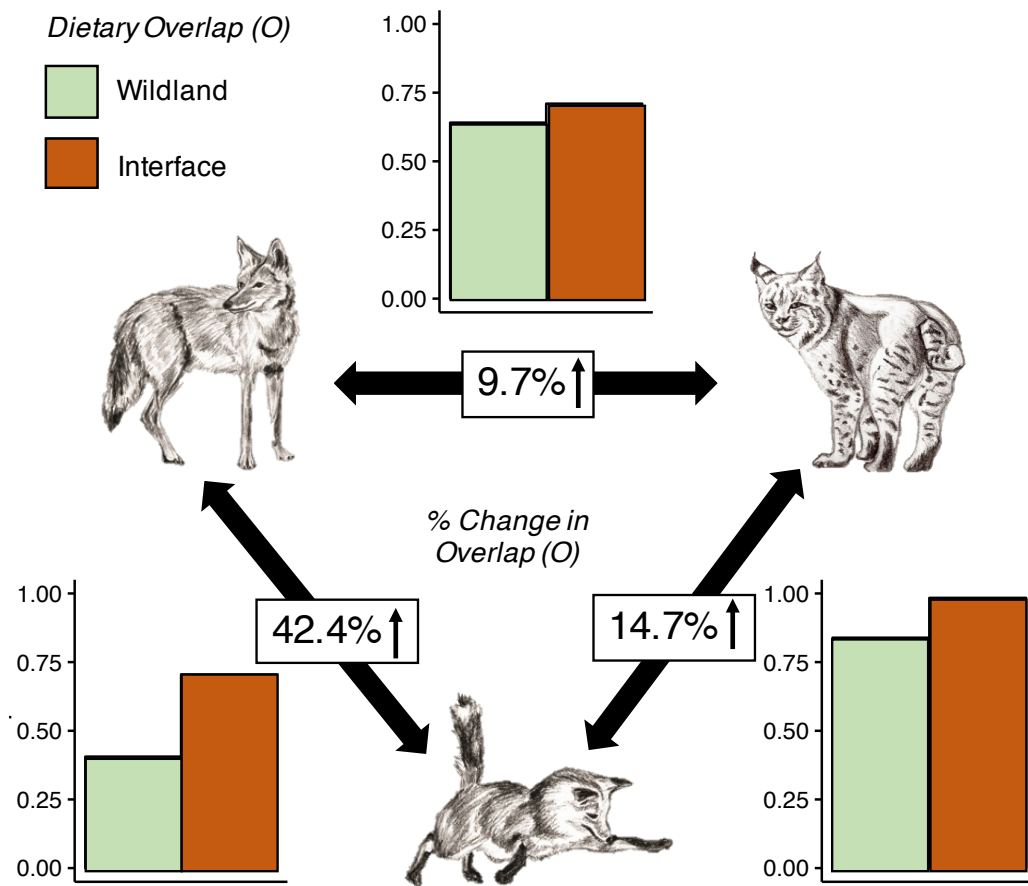


Figure 4.2. Dietary niche overlap (*O*; Pianka 1973) and percentage change in *O* among three carnivore species in wildland and interface open space preserves in the Santa Cruz Mountains.

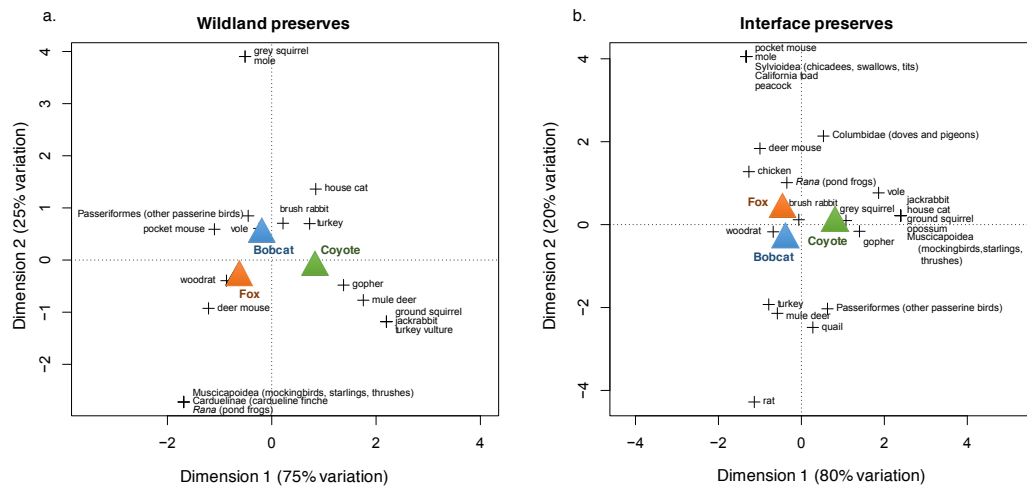


Figure 4.3. Correspondence analysis of carnivore diet associations in (a) wildland and (b) interface preserves. Shorter distances between carnivores represents increased similarity in their diets. Prey that appear close together are more similar in their proportional contribution to the diets of the carnivore species. Greater association between carnivores and their prey were observed in wildland preserves than in interface preserves. The correspondence analysis includes only prey constituting $\geq 0.5\%$ of the diet of a carnivore species.

Chapter 5

Preventing transformation of “soft barriers” to “hard barriers” to animal movement: an approach to promote permeability for large carnivores in a human-dominated landscape

Abstract

Anthropogenic development threatens connectivity for wildlife populations, yet regions with low-density or exurban development can still serve as a semi-permeable matrix for some species. In areas already impacted by low-density development, conservation planners must find creative approaches to maintain connectivity in light of development pressure that can transform “soft barriers” into “hard barriers” to movement, whereby functional permeability is drastically reduced. Here, we identify the threshold of housing density that functions as a “hard barrier” to a large carnivore, the puma. We apply this threshold to projected housing densities at parcels under a full buildout scenario in Santa Cruz County, and identify parcels at risk of increasing above the puma movement threshold. Finally, we prioritize these parcels for conservation using two measures of conservation value and two measures of risk of development. Our approach seeks to promote permeability at the population scale in regions at risk of becoming hard barriers to movement if allowable development occurs. We discuss implications for how conservation biologists can perceive and promote connectivity in landscapes already heavily impacted by anthropogenic development.

Introduction

Low-density residential development is the fastest-growing land use change in the United States and has already widely restructured biotic communities due to nonlinear changes in biodiversity and resilience (McKinney 2002, Hansen et al. 2005). Regions in the West have been disproportionately impacted by low-density residential growth in recent years, with rates two to three times the national average (Theobald 2003). Much of this low-density development abuts or intersects with wildlands, creating challenges for conservation. Of all development types in the West, residential development is the primary cause of expansion of the wildland-urban interface (Theobald and Romme 2007). California holds the largest number of housing units at the wildland-urban interface of any state (Radeloff et al. 2005) due to 65 years of sustained population growth and extensive immigration to pristine areas with low population sizes, such as the Central Coast (Fulton and Shigley 2005) or Sierra Nevada (Duane 1996, Duane 1999). Eighty-nine percent of land at the wildland-urban interface in the USA is privately owned, exacerbating challenges to wildlife management in these sensitive areas (Theobald and Romme 2007). The risks posed to wildlife in regions experiencing high growth rates of low-density development at the wildland-urban interface include increased human-caused mortality, habitat loss, conflict with non-native species, and habitat fragmentation (Hansen et al. 2005).

The clustering of development in a few target areas can minimize impacts of low-density residential development by disrupting less total land area (Dale et al. 2005, Hansen et al. 2005, Radeloff et al. 2005). However, if not planned and developed in ways that maintain ecological connectivity, prioritizing denser development can prevent movement of wildlife and reduce gene flow at the landscape scale (Hilty et al. 2006). Alternative approaches may be necessary for conservation planning in regions that are already heavily impacted by low-density development and are a mosaic of private and public lands. In some cases, undeveloped private landholdings can increase the permeability, or relative probability of animal movement, of low-density development that lies between public lands or protected areas. For many species, housing density below a threshold may act as only a “soft barrier” to animal movement, characterized by moderate resistance to movement with some functional permeability. These regions of low-density development may be vital to landscape connectivity if they serve as a permeable or semi-permeable “matrix”, which allows for some animal movement but does not maintain full movement potential. However, above this density threshold, housing may act as a “hard barrier”; although wildlife are capable of moving through housing at this density, they may do so only rarely because of behavioral avoidance strategies. Hence allowing areas with existing low-density development to increase in density can reduce their functional permeability until they are no longer viable areas for animal movement and become a hard barrier to such movement. Because housing development is more likely to occur where infrastructure already exists, existing low-housing-density areas are

particularly at risk of becoming hard barriers to animal movement and undeveloped private landholdings in these regions might pose nontraditional conservation opportunities.

Traditional connectivity planning at the landscape scale entails preserving large areas of open space with corridors of maximum permeability connecting them (Jongman 1995). Another approach, complementary to the corridor approach, is to restrict further development in developed areas with moderate permeability, so as to maintain a greater net potential for animal movement between protected areas (Fig. 1). Because disturbed landscapes can still serve as important movement pathways within the home range of an individual (Way et al. 2004, Wilmers et al. 2013), the strategic prevention of housing densification in low-density residential areas might be a good strategy for maintaining connectivity at the scale of a wildlife population. Here we develop a method for assessing the impact of exurban land conversion on the transformation of soft barriers into hard barriers to the movement of a large carnivore in the Santa Cruz Mountains of California.

Alternative Approaches to Assessing Connectivity

Least-cost path and resistance surface analyses have proved to be useful tools for identification of movement corridors for wildlife, particularly between populations, but they have drawbacks. Resistance surface approaches rely on expert opinion in the majority of studies and often impose arbitrary constraints on minimum corridor length and width (Sawyer et al. 2011, Zeller et al. 2012). Even when least-

cost paths or resistance surfaces are built on resource-selection functions from animal location data, movement decisions inferred from step- or path-selection functions are almost entirely absent from resistance surface analyses (Zeller et al. 2012). Step-selection functions and path-selection functions provide the most mechanistic approach to understand how animals make movement decision, and have potential to vastly improve connectivity analyses (Cushman and Lewis 2010, Zeller et al. 2012, 2016). Aside from the data used, one of the most important limitations of least-cost path approaches is that they assume that there is only one or few potential paths an animal will take. However, in habitats with extensive human disturbance, animals might experience instantaneous disturbances that influence their decision-making and movement processes due to fear responses (Smith et al. *in review*). In human-dominated landscapes, it might instead be preferable to maintain a large number of potential paths rather than pre-determining a small number of ideal paths. Finally, even when resistance surfaces incorporate measures of the human footprint (e.g. Baldwin et al. 2010), these variables are often treated as linear and continuous, despite evidence that animals do not respond linearly to disturbance (Hebblewhite and Merrill 2008). A combination approach that uses more mechanistic habitat selection models and a broader interpretation of sufficient environmental conditions might more appropriately characterize animal movement potential in semi-permeable landscapes.

Here, we use a step-selection function (SSF) to identify the threshold housing density signifying a hard barrier to puma movement. Instead of constructing a least

cost path or resistance surface, we instead assume that all land below a housing density threshold is valuable for puma movement and we prioritize parcel acquisition that maintains developed areas below this threshold. Our approach seeks to maintain puma movement potential throughout the landscape rather than identify high-quality corridors. To achieve this goal, we construct a local buildout analysis and apply the puma movement threshold to detect parcels that are likely to surpass the threshold at full buildout. We further prioritize parcel acquisition using parameters signifying parcel conservation value and threat of development pressure. Finally, we locate subregions with the greatest risk of development and conservation potential, and discuss context-specific considerations for conservation planning.

Methods

Study System

We conducted this study in Santa Cruz County, California. Santa Cruz County is one of three counties that make up the Santa Cruz Mountains, an isolated mountain range in the Central Coast region of California. In the next 50 years, Santa Cruz County is projected to grow by 18% and its neighboring counties, Santa Clara County and San Mateo County (which are the heart of Silicon Valley), will grow by 23% and 29% respectively (California State Department of Finance 2013). How continual growth affects current habitat in the Santa Cruz Mountains will likely be markedly different among counties based on their urban to rural ratio. Currently, San Mateo and Santa Clara counties are both less than 2% rural, whereas Santa Cruz County is 12%

rural (United States Census Bureau 2010). Part of this pattern may be attributed to the many open space parks and county parks that line the outskirts of the Bay Area on its southwest side, preventing extensive rural development. The general plan of Santa Cruz County also designates the majority of the county's unincorporated land for Rural Residential use, which has the potential to be converted to low-density residential development (Santa Cruz County 1994). Within the unincorporated areas of the Santa Cruz Mountains, Santa Cruz County has the highest projected development increase among the three counties projected from 2010-2100, and its growth rate is within the top 10% of counties nationwide (United States Environmental Protection Agency 2014). Therefore, it is Santa Cruz County that demands the most attention for comprehensive land planning to maintain landscape connectivity for wildlife in the Santa Cruz Mountains.

We chose the puma (*Puma concolor*) as our study species because of its large space requirements, long dispersal paths, and sensitivity to residential development (Sweaner et al. 2000, Wilmers et al. 2013, Smith et al. 2015). Because the puma's habitat generality regularly exposes it to human development in other regions in North America, including Los Angeles (Benson et al. 2016), the Front Range of Colorado (Lewis et al. 2015, Moss et al. 2015), and southern Florida (Land et al. 2008), our use of the puma as a study organism is pertinent to other areas coexisting with low-density residential expansion. The puma is the last extant large carnivore in the Santa Cruz Mountains.

Puma Selection of Movement Paths

To determine the housing density most likely to deter movement by pumas, we conducted a SSF using puma location data from GPS collars (methods regarding puma capture and tagging can be found in Wilmers et al. (2013)). We chose to focus on male pumas in this analysis because they are the primary disperser in this species, they have greater daily movement distances than females, and their home ranges are 3 times the size of the average female home range (Smith et al. 2015). We used a step interval of 4 hours and only included steps equal to or greater than 500 m because our goal was to capture large-scale movement decisions, while ensuring a fine enough scale to capture important details of the behavioral process (Thurfjell et al. 2014).

We fit a density curve to puma step lengths and turn angles using logspline density estimation (Kooperberg and Stone 1991). We drew randomly from these distributions of puma step features to generate five random steps from each puma location. We checked to ensure that step length and turn angle were not correlated ($r > 0.7$) at our scale of analysis. We then projected the random and real steps in a GIS (ArcMap 10.1), and eliminated simulated steps that overlapped the ocean. We extracted the number of houses within a 150-m buffer of each step and calculated housing density (houses/km²) using a housing layer manually digitized from high resolution satellite imagery because this was the scale at which pumas in our study area were found to respond negatively to residential development (Wilmers et al. 2013).

SSFs take an exponential form, but are commonly fit using conditional logistic regression (Fortin et al. 2005, Forester et al. 2009, Thurfjell et al. 2014). To estimate covariates for the SSF, we used the clogit command in the survival package in R (Therneau and Grambsch 2000, Therneau 2015), stratified by step starting location (i.e. the location from which each set of real and random paths originate) with housing density as the predictor variable. We used robust standard errors following Fortin et al. (2005), which account for inter-cluster correlation in assessing variation. To test for the presence of a threshold effect, we used piecewise regression to fit a two-segmented model that split housing density into two covariates with different slopes on either side of a breakpoint (Kohl et al. 2017). We used a grid search approach to determine the best location of the breakpoint by comparing the quasi-likelihood under independence criterion (QIC) values of candidate spline models, which are more conservative than AIC and allows for clusters of observations to have independent correlation structures (Pan 2001, Basille et al. 2015, Kohl et al. 2017). We compared the best segmented model to a model with a continuous response variable of housing density to test if the piecewise model better fit the data.

Importantly, we recognize that the presence of a breakpoint can imply very different relationships to housing, depending on if the curve shows accelerating or saturating avoidance. An accelerating avoidance curve would indicate that pumas do not strongly avoid housing until a certain density, and then increasingly avoid housing above the threshold value. A saturating avoidance curve would indicate that

pumas increasingly avoid housing density even at low levels (i.e. a soft barrier), but after a certain point relative probability of use is so low that the curve flattens out (i.e. a hard barrier). A breakpoint in either of these two curve shapes could be applied as a development density threshold, but the implications for pumas' relationship to development are very different. For an accelerating curve, development should not hinder puma movement until it reaches the threshold, when it would then decrease probability of use as housing increases. For a saturating curve, any development should be avoided, but development above the threshold is likely to become a hard barrier to movement, whereby development densities offer little movement potential.

Parcel Ranking and Prioritization

We constructed a buildout analysis of all potential new development allowed under the Santa Cruz County General Plan (1994). We used a database of parcels with the potential of incurring new development and subdivisions developed for the Conservation Blueprint for Santa Cruz County (Land Trust of Santa Cruz County 2011). This database was constructed by locating vacant underutilized parcels within and outside the urban services line (USL; Santa Cruz County 1994), a boundary that dictates infrastructure and services provided to residential units by the county. For properties within the USL, one housing unit was assigned for each potential parcel or new housing site. For rural properties outside the USL, new housing was limited by general plan restrictions on development with regard to slope, distance to water bodies, riparian woodland areas, fault zones, agriculture and mineral resource lands,

floodways, and FEMA Zone A (floodplain management). Further constraints on parcel size due to Least Disturbed Watershed coverage, Water Quality Constraints coverage, Water Supply Watershed coverage, and Groundwater Recharge Area coverage were applied to eliminate undevelopable parcels. Parcels not excluded as undevelopable were assigned new residential units based on vacancy status (i.e. if the land is undeveloped) and potential lot splits according to allowable densities specified by land-use category designations in the General Plan (Santa Cruz County 1994).

To assess current housing density, we digitized all buildings in Santa Cruz County from high resolution satellite imagery and derived housing density within a 150-m buffer of the parcel boundaries. We used a 150-m buffer to stay consistent with our scale of analysis from the SSF analysis. We added potential new units in developable parcels according to the buildout analysis and amended them to the digitized buildings dataset to recalculate housing density at full buildout. We identified parcels whose maximum housing density was both (1) below the puma movement threshold prior to buildout and (2) above the threshold post-buildout. This subset of parcels (hereafter, “threshold parcels”) was used in the subsequent rank analysis for conservation prioritization explained in the next paragraph. Threshold parcels are therefore those that, if developed in accordance with the Santa Cruz General Plan, could impede puma movement after such development. All other parcels are either already impeding such movement or would not impede puma movement even if they are developed to densities allowed under the General Plan.

We then ranked threshold parcels using measures of conservation value, conservation potential, current risk, and future risk (Table 1). The first measure is the area of the parcel itself (*conservation value*), where larger parcels are considered more valuable for conservation and landscape connectivity. The second measure is the cumulative area of the parcel and all adjacent developable parcels (*conservation potential*), where greater area of adjacent undeveloped parcels represents greater potential for conservation. The third measure is the current housing density (*current risk*), where development of higher housing density parcels is considered to have greater risk of closing off puma movement pathways with future development. Projected housing densities in 2050 based on demographic patterns from the Spatially Explicit Regional Growth Model (SERGoM; Theobald 2005) are considered *future risk*, where parcels with higher projected housing density are assumed to be at greater risk of development. SERGoM distributes housing units on available land and are informed by road density, distance to an urban center, previous growth patterns, current population size, and population growth estimates based on 1990-2000 census block data. We used the baseline scenario for SERGoM projections.

We then created a single conservation rank based on the four measures of risk and value associated with each parcel. We split parcel area, adjacent parcel area, and current housing density into quartiles that we assigned scores from 1 to 4. To assign scores to the SERGoM housing density projections, we used housing density level: 1 for no housing, 2 for rural housing density, 3 for exurban housing density, and 4 for

suburban housing density¹². We summed the scores from each of the four measures to create a single conservation rank for each parcel with a potential range of 4 to 16, where 16 is the highest priority. Finally, we identified seven subregions in the county and calculated summary data on each of the four conservation/risk ranks, the cumulative conservation rank, current and future housing density, the distribution of parcels relative to the puma movement threshold, and the percent increase in housing density at buildout. Subregion boundaries were delineated subjectively using local knowledge of areas of development and conservation significance.

Results

We used 11,765 total steps from 28 male pumas in our puma step-selection function. On average, used steps had a housing density of 19.68 ± 0.51 SE houses/km² and available steps had a housing density of 27.89 ± 0.31 SE houses/km². The linear model with a housing density covariate (QIC = 41479.68, Δ QIC = 178.76) did not fit the data as well as the best linear spline model (QIC = 41300.92, Δ QIC = 0), supporting the presence of a response threshold. The best-fit linear spline model had a knot at housing density of 41 houses/km² (1 house per 6 acres). The shape of the relationship between puma probability of use and housing density indicated saturating avoidance, whereby pumas showed a decline in probability of use until the housing density threshold, followed by consistently low probability of use above the

¹ Rural: 0.0001 – 0.0620 houses/hectare. Exurban: 0.0621 – 1.2360 houses/hectare. Suburban: 1.2361 – 9.8840 houses/hectare.

² No threshold parcels were projected to be urban in 2050.

threshold (Fig. 2). This relationship suggests that low levels of housing density act as a soft barrier to puma movement, while relative probability of use saturates at the breakpoint to create a hard barrier to movement.

Of the 96,828 parcels in Santa Cruz County, 11,175 were determined to have the potential for further development. Developable parcels currently have 552.79 ± 5.77 SE houses/km² but are projected to increase their average housing density to 736.16 ± 7.31 SE houses/km² at buildout (Fig. 3). Developable parcels outside the USL had considerably lower current housing densities (131.38 ± 2.44 SE houses/km²) and buildout housing densities (187.14 ± 2.97 SE houses/km²). Most developable parcels (78%) and developable parcels outside the USL (60%) were already above the puma movement threshold at current housing density levels, yet after buildout the proportion increased to 85% of all developable parcels and 72% of developable parcels outside the USL. Of developable parcels, 753 were identified as threshold parcels, or parcels at risk of increasing from below to above the puma movement threshold of 41 houses/km², therefore their conservation could assist in maintaining permeability (Fig. 4). Before buildout, threshold parcels had an average maximum of 22.73 ± 0.48 SE houses/km², whereas the average maximum housing density in a parcel after buildout was 92.26 ± 3.18 SE houses/km². Of threshold parcels, only 43 were within the USL (35 of which were part of a single complex in Santa Cruz owned by the University of California), and 1 was within the RSL (rural services line). Therefore, nearly all parcels at risk of increasing to above the puma movement threshold fall outside of both the USL and the RSL.

Of the eight subregions, Happy Valley had the highest average conservation rank, followed by the Lower Hwy 9 and Upper Hwy 9 subregions (Fig. 5, Table 2). The Happy Valley subregion contained the highest current housing density in threshold parcels, yet had the lowest buildout housing density in threshold parcels (Table 3). Only 15.6% of developable parcels in the Happy Valley subregion were threshold parcels, largely because 66.4% are already above the threshold at current densities. The top ranked subregions had relatively high scores in all categories with the exception of the cumulative adjacent parcel area. The three regions with the highest current housing density, Happy Valley, Lower Hwy 9, and Corralitos, had the lowest proportions of threshold parcels and were among the four subregions with the highest proportions of parcel already above the puma movement threshold. Interestingly, these three subregions also had among the four largest average parcels in the threshold subset but the smallest cumulative developable adjacent parcel areas. The only subregion in which over 50% of developable parcels remain below the puma movement threshold at buildout was Loma Prieta. Over 50% of developable parcels are already above the puma threshold at current housing density levels in the subregions of Lower Hwy 9, Corralitos, Happy Valley, and Loch Lomond. The Loch Lomond subregion is at risk of the greatest percentage housing increase at buildout by far, but its low current housing density and small average parcel size designated it the subregion with the lowest average conservation rank.

Discussion

Our study uses a novel approach to identify areas for conservation that currently maintain marginal but permeable habitats for puma movement. In our application of a SSF to identify parcels of concern in our buildout analysis, we were able to: 1) utilize animal behavior to inform conservation priorities; and 2) provide a simple rule-based outcome that can be easily interpreted easily by planners and other land use decision-makers. Our threshold-based approach can help prevent further functional fragmentation of landscapes through the development of hard barriers in landscapes where ideal conditions of larger, fully-permeable movement corridors are not possible to maintain for individual species in the long term. Pumas in our study area showed a saturating avoidance to housing density, indicating that any level of development deters puma movement. However, increasing above the puma movement threshold causes housing development to transform from a to a hard barrier to movement. More conservative planning for connectivity may want to use a lower level of acceptable housing density that retains a higher relative probability of use.

The small size and isolation of the Santa Cruz Mountains makes connecting core protected areas crucial to the persistence of the local puma population (Thorne et al. 2006). This will likely require maintaining connectivity through areas impacted by low-density residential development, which already spans much of the mountain range. Santa Cruz County has enacted measures to curtail development in rural areas, including restricting services to properties outside the URL and RRL (Santa Cruz County 1994). However, the majority of developable parcels outside of the URL and

RRL are already above the puma movement threshold. These developed parcels represent a hard barrier to puma movement that has a range of conservation consequences. County development restrictions could benefit from being more informed by biological data on species responses to development on a gradient of densities.

We identified seven subregions to both understand the diversity of rural growth patterns in the Santa Cruz Mountains and to highlight regions that have the greatest potential to be managed to promote puma movement. The Happy Valley subregion had the highest conservation score of any of the subregions. Maintaining permeability in the Happy Valley subregion is necessary for connectivity across the southern portion of the Santa Cruz Mountains, yet it has the highest current housing density in threshold parcels of any subregion. Preventing further degradation of habitat permeability in this subregion therefore has very high value, but it also faces the challenge of high development pressure from the nearby city of Santa Cruz.

Lower Hwy 9 and Upper Hwy 9 had the second and third highest conservation scores of the seven subregions. Highway 9 runs the entire length of the Santa Cruz Mountains from north to south, and is already home to a number of towns including Felton (population: 4057), Ben Lomond (population 6234), and Boulder Creek (population 4923; United States Census Bureau 2010). Highway 9 already serves as a barrier to pumas, as the borders of resident puma home ranges often run along it rather than intersect it (Smith et al. 2015). Efforts to maintain landscape connectivity may therefore focus on these subregions, which are both at risk of high population

pressure (Table 2). Lower Highway 9 has the highest proportion of developable parcels already over the puma movement threshold, so preserving the remaining parcels and while also initiating restoration efforts might be important for improving permeability for pumas. Further efforts to establish wildlife corridors could also assist in preserving the connectivity of this region.

Another area of interest is the Laurel Curve subregion, in which a wildlife underpass is in the development phases that will allow pumas to travel safely under the 4-lane, high-speed Highway 17 (Land Trust of Santa Cruz County 2015). Maintaining connectivity around the underpass is crucial to its success as a wildlife crossing. The Laurel Curve subregion fell in the middle of the pack for most risk and conservation value metrics, including parcel size and current and projected housing densities. Over 50% of developable parcels have the potential to be maintained under the puma movement threshold, so future parcel acquisitions for conservation should focus on these parcels and their spatial relationship to potential movement pathways.

Conservation goals vary across agencies, nonprofits, and local planning departments. The success of any landscape conservation planning initiative relies heavily on the political and economic support for the goals, values, costs, and projected outcomes of a given plan (Duane 2007). Our analysis therefore cannot determine alone which regions should undergo revisions to planning guidelines or which developments should be allowed on which parcels. Instead, we provide information on different threats to and value of undeveloped parcels that could be preserved to maintain landscape permeability for pumas. The data we provide can

then be used by agencies, nonprofits, and planners to prioritize individual parcel acquisition for small local projects, determine landscape-level priorities across the county, or to alter planning guidelines. As noted above, our analysis suggests that any housing development can deter puma movement, therefore nonprofits and agencies may want to use a more conservative housing density threshold than the one we report here.

A number of active local land trusts have purchased properties in the Santa Cruz Mountains for conservation, including the San Vicente Redwoods property (34 km²) protected in 2011 (Diehl 2013). Land trusts and open space districts can fill the gaps left open by county land use regulations to preserve landscape connectivity (Rissman et al. 2007). Although many of the parcels that our analysis prioritizes for conservation are not particularly large, they can be essential components of connectivity in a fragmented landscape. Due to the very high cost of land and property in Santa Cruz County, which has the 6th highest median house price in the country (United States Census Bureau 2010), our approach facilitates cost-effective conservation planning by identifying parcels with high conservation value for connectivity in a puma population. However, we acknowledge that land trusts might prefer to focus on larger regions of open space, and more work validating the utility of our method is needed to make it attractive to conservation planners.

Challenges to conservation in habitats with low-density development are primarily intrinsic to their spatial arrangement on the landscape. Zoning regulations for conservation purposes have mostly been used to decrease housing density, yet

these measures have been criticized as resulting in greater environmental degradation by causing more extensive land development (“sprawl”) and increased vehicle miles travelled (Hansen et al. 2005, Robinson et al. 2005, Merenlender 2007). We suggest that, although the best way to prevent impacts of low-density development is to prevent it (Dale et al. 2005), efforts to curb increasing housing density can still provide conservation value. Solely promoting denser development plans carries with it its own ecological dangers. Our approach can complement efforts targeted at maintaining core habitats and high quality movement corridors by identifying where further densification is likely to create hard barriers to animal movement.

The limitation of our approach is that it prioritizes movement, without taking into account the other necessary measures needed to maintain healthy populations of pumas, such as protecting denning habitat (Wilmers et al. 2013). We emphasize that this analysis solely focuses on maintaining landscape connectivity within a population for the purposes of movement and dispersal. Connectivity is only one important component of population viability, and other information on demographic processes are needed to make holistic conservation plans for wide-ranging species such as the puma.

We emphasize that we do not promote the further expansion of exurban sprawl or the development of low-density housing as an alternative to clustered development. Low-density and exurban developments can cause ecological breakdowns, and often do not serve as habitats in which wildlife can live (Odell and Knight 2001, Hansen et al. 2005, Merenlender et al. 2009). We present here a method

to prevent further fragmentation of landscapes that occurs as housing density increases and soft barriers are created. Of course, *a priori* designs built on principles of smart growth and conservation planning are preferred in areas not yet developed or fragmented (Daniels and Lapping 2005, Underwood et al. 2011). Our approach acknowledges that many landscapes are already impacted by anthropogenic development, and that the remaining conservation potential of these areas should be maintained whenever possible.

Habitat loss, modification, and conversion are the most significant contributors to species loss and declines worldwide (Dirzo and Raven 2003). Although low-density development can reduce the functionality of wildlife habitat, it can also provide movement potential as a semi-permeable matrix. The risk low-density housing poses to connectivity is that it is more likely to be developed than areas with no existing development due to infrastructure access (e.g. roads and electricity). Increasing development densities in these areas beyond threshold densities therefore risks establishing hard barriers to animal movement. Future connectivity work should therefore continue to expand on the way we perceive landscape connectivity and the context in which lands are considered for conservation.

Table 5.1. Scoring rules for measures contributing to cumulative conservation rank.

Score	Threshold parcel size (km ²)	Cumulative size of adjacent developable parcels (km ²)	Current housing density in threshold parcels (houses/km ²)	SERGoM projected housing density class
4	0.023 – 0.958	2.508 – 23.650	34.44 – 40.95	Suburban
3	0.010 – 0.023	0.191 – 2.51	25.78 – 34.44	Exurban
2	0.002 – 0.010	0.009 – 0.191	11.85 – 25.78	Rural
1	0.000 – 0.002	0.000 – 0.009	0.00 – 11.85	No Housing

Table 5.2. Average values in threshold parcels for each measure used in deriving cumulative conservation rank and average conservation rank by subregion.

Santa Cruz	Average	Average cumulative size	Average current housing	Average SERGoM	Average
County	threshold parcel	of adjacent developable	density in threshold	projected housing	conservation rank
Subregion	size (km ²)	parcels (km ²)	parcels (houses/km ²)	density class	
Happy Valley	0.038	0.48	32.9	Exurban (3.2)	12.05
Lower Hwy 9	0.036	0.7	31.4	Exurban (3.4)	11.93
Upper Hwy 9	0.041	5.53	22.2	Exurban (3.0)	11.76
Corralitos	0.037	0.61	29.9	Exurban (3.0)	11.71
Loma Prieta	0.017	21.35	19.2	Rural (2.8)	11.25
Laurel Curve	0.026	1.02	26.8	Exurban (3.0)	11.08
Loch Lomond	0.013	2.54	15.4	Exurban (3.3)	8.71

Table 5.3. Housing characteristics by subregion, including proportion of parcels that remain under, remain over, and increase over the puma movement threshold, and housing density at current levels and at full buildout.

Santa Cruz County subregions	Developable parcels				Housing density	
	Total	Proportion that increase over threshold	Proportion that remain under threshold at buildout	Proportion that remain over threshold at buildout	Current average in threshold parcels (houses/km ²)	Buildout average in threshold parcels (houses/km ²) Percent increase at buildout (%)
Happy Valley	333	15.6	18.0	66.4	32.9	52.1 159
Lower Hwy 9	695	3.7	8.1	88.2	31.4	70.3 224
Upper Hwy 9	491	15.1	42.6	42.4	22.2	52.8 237
Corralitos	352	9.9	18.5	71.6	29.9	54.5 182
Loma Prieta	254	28.3	64.2	7.5	19.2	65.7 343
Laurel Curve	432	16.7	34.7	48.6	26.8	54.9 205
Loch Lomond	823	22.6	10.0	67.4	15.4	133.0 865

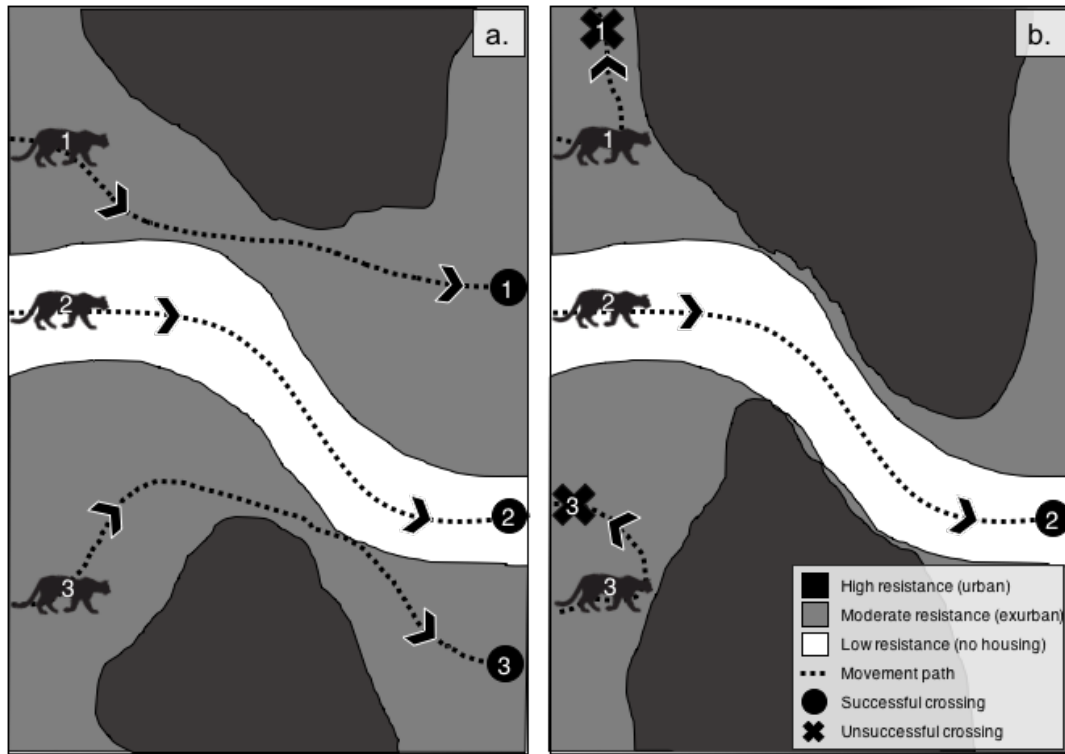


Figure 5.1. Simplified conceptualization of puma movement paths in a landscape with high- and low-density development. Connectivity measures that only consider corridors identified from least-cost path approaches may miss other opportunities to promote connectivity, such as preventing housing density increases in low-density areas with moderate resistance to movement. Panel (a) shows a scenario where permeable exurban housing (moderate resistance) is preserved on the landscape, and panel (b) shows the extent of lost connectivity if exurban areas are not valued as habitat and are allowed to densify into urban areas.

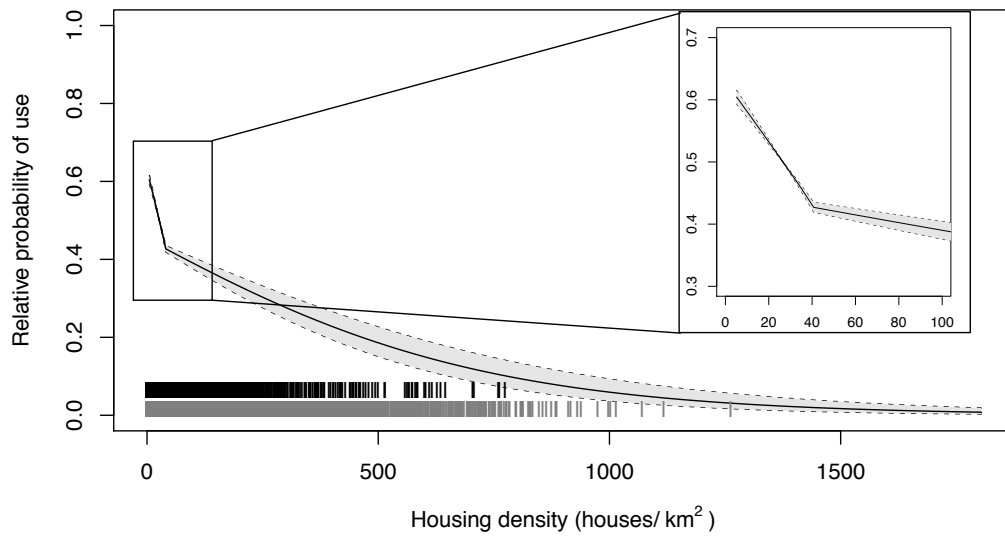


Figure 5.2. Puma relative probability of use of movement paths in relation to housing density. Puma probability of use declines steeply with increasing housing density until approximately 41 houses/km², then remains at low probability of use beyond that threshold. The inset highlights the change in relative probability of use at the threshold location. Black vertical lines along the x-axis represent housing densities of puma paths used in the analysis, with a maximum of 775. Grey vertical lines represent housing densities of simulated paths.

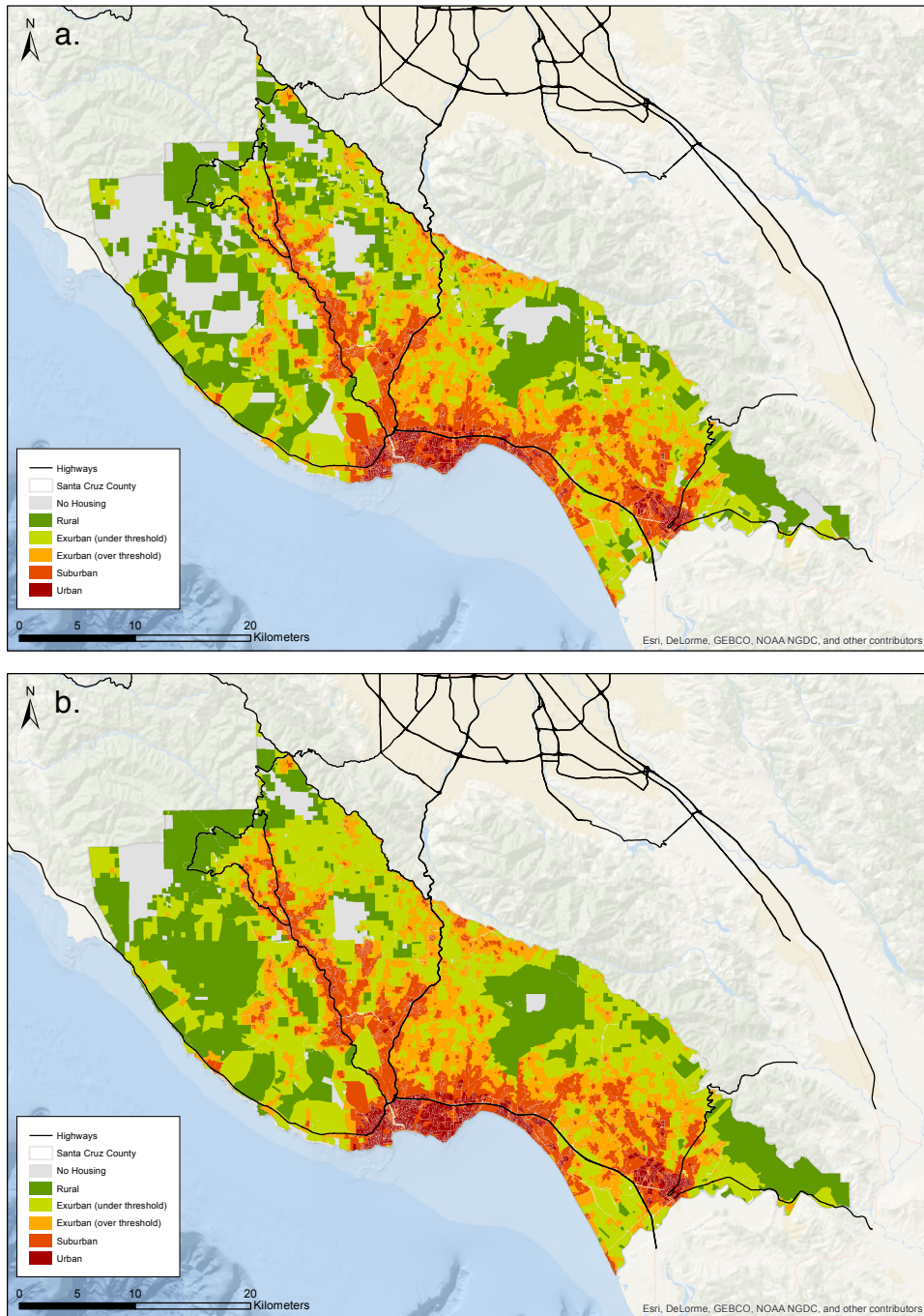


Figure 5.3. Housing density class by parcel for (a) current housing and (b) housing at buildout.

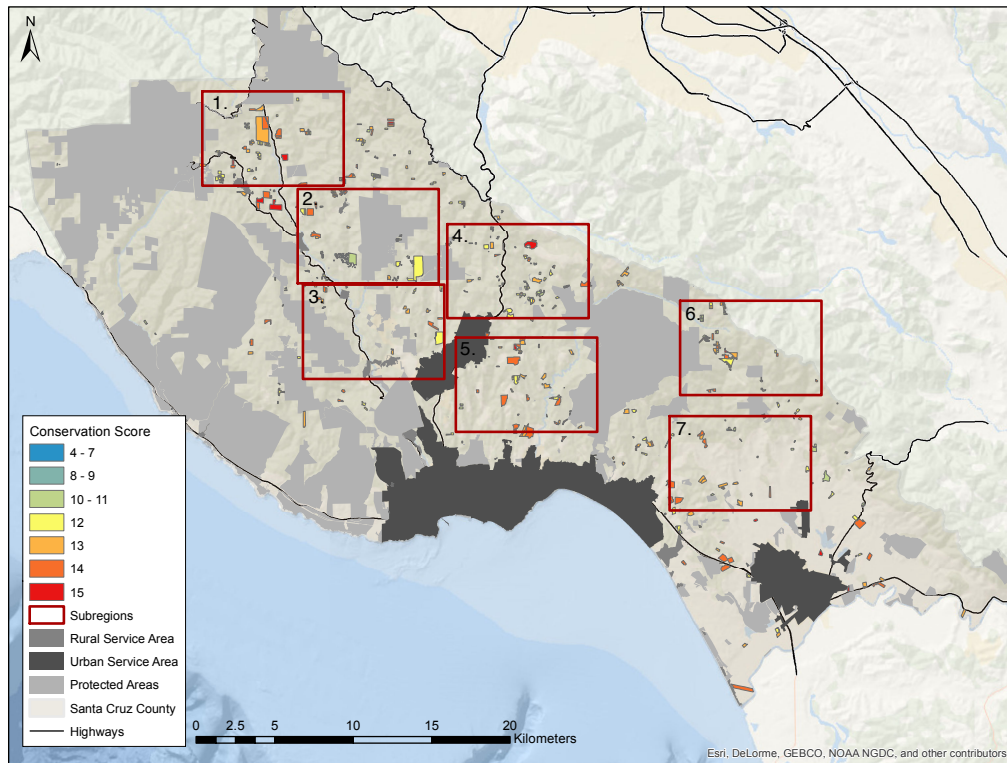


Figure 5.4. Threshold parcels, or parcels at risk of increasing from below the puma movement threshold housing density to above it at buildout, by prioritization rank (range 4-15). Subregions are outlined in red: 1) Upper Hwy 9; 2) Loch Lomond; 3) Lower Hwy 9; 4) Laurel Curve; 5) Happy Valley; 6) Loma Prieta; and 7) Corralitos.

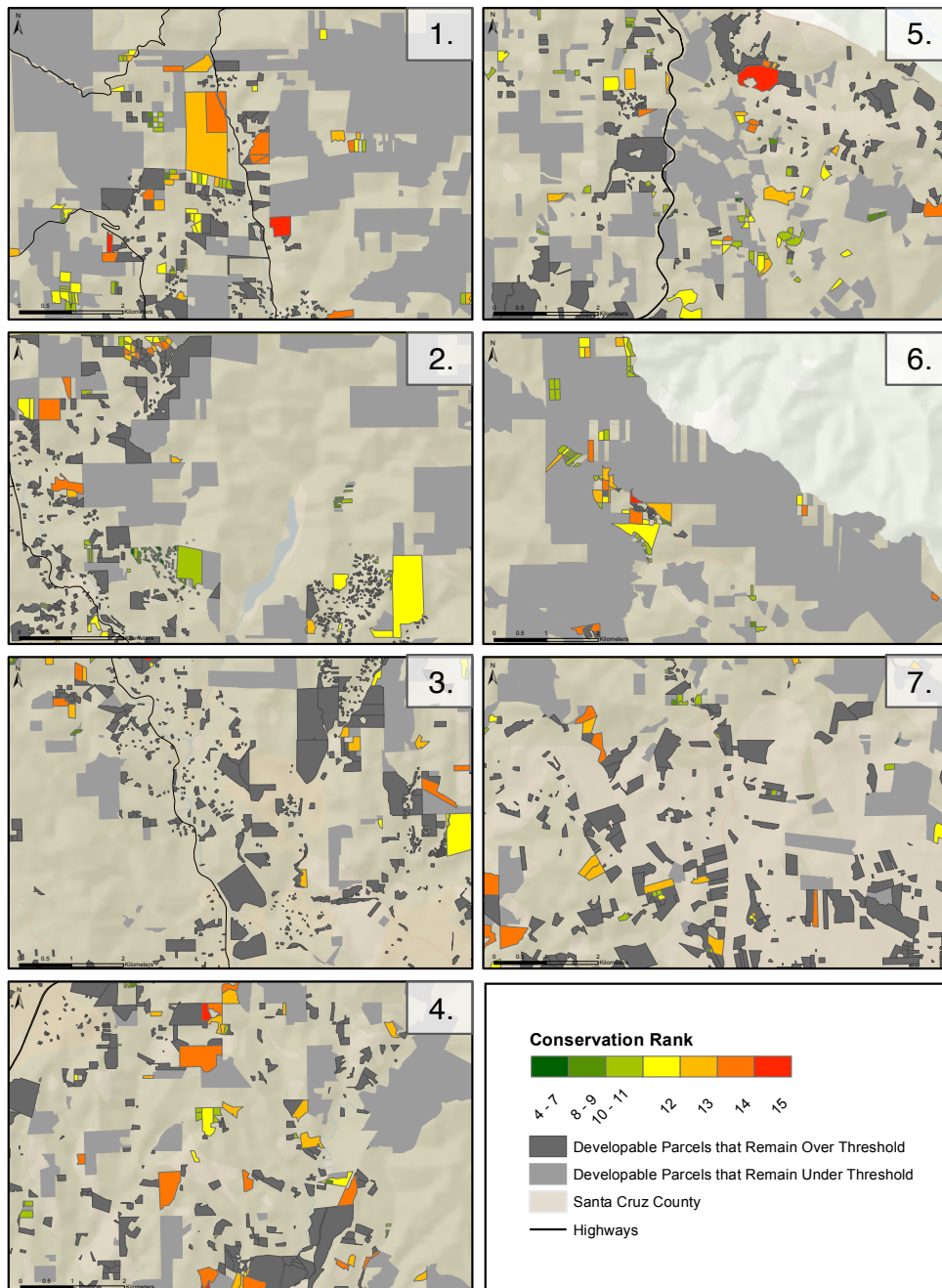


Figure 5.5. Threshold parcels by conservation rank in the subregions of 1) Upper Hwy 9; 2) Loch Lomond; 3) Lower Hwy 9; 4) Laurel Curve; 5) Happy Valley; 6) Loma Prieta; and 7) Corralitos. Higher ranked parcels are more essential to maintain permeability for puma movement.

CONCLUSION

Although large carnivore populations have been extirpated from many landscapes around the globe, we now face the potential for a restoration renaissance. Carnivores are recolonizing previously occupied habitats, both passively through landscape connectivity and actively through reintroductions (Fritts et al. 1997, LaRue et al. 2012). However, there are new challenges facing carnivores, as development has continued to alter, fragment, and replace historical carnivore habitat. Outside of natural parks and wilderness areas, many large carnivores will confront risks of hunting, carnivore-livestock conflict, and vehicle collisions.

Pumas have been slowly moving east from the Rocky Mountain West, already reestablishing a population in Nebraska. Dispersing pumas have been confirmed in Tennessee, Missouri, Kentucky, and even Connecticut (LaRue et al. 2012, Cougar Network 2017). Wolves are starting to repopulate northern California, which in 2014 saw its first resident wolf pack in nearly a century (House 2015). All of these landscapes are increasingly human-dominated, and co-adaptation by both humans and carnivores will prove to be essential for coexistence (Oriol-Cotterill et al. 2015, Carter and Linnell 2016).

Many of the justifications for allowing or promoting carnivore restoration are anthropocentric in nature. Carnivores prevent herbivores from being overpopulated, and can save countless lives and dollars wasted on vehicle-deer collisions (Gilbert et al. 2016). Carnivores bring tourism dollars to parks and mountain towns (Duffield et al. 2008). Carnivores suppress populations of invasive mesopredators, which have

evaded control by management agencies (Ripple et al. 2013). The ability for carnivores to provide these anthropocentric values relies on both their adaptability to the human environment and the maintenance of their regulatory role in the animal community. These goals inherently depend on specific behavioral responses to anthropogenic disturbances, whereby carnivores are not too afraid to be present, but afraid enough not to cause conflict. This narrow line carnivores must walk may be possible for some species and not for others. Much more research is needed to determine how carnivore behavioral responses to humans impacts their individual fitness, population dynamics, and community interactions.

My dissertation provides a somewhat optimistic picture for pumas and mesocarnivores in the Santa Cruz Mountains. Although these species alter their behavior and species interactions in response to anthropogenic disturbance, we have not seen obvious demographic or ecosystem consequences of these behaviors. Unfortunately, the research presented here represents only a snapshot in time, and tracking the long-term ramifications of observed behavioral change in carnivores is necessary to understand novel ecological dynamics. As the restoration of carnivores continues to occur synchronously with continuous land conversion in North America, further investigation of human-induced behavior-mediated trophic cascades will dictate the success of conservation in human-dominated landscapes.

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