UC Santa Cruz
UC Santa Cruz Electronic Theses and Dissertations

Title

The Intersection of Carnivores and Humans: Addressing current challenges in carnivore ecology, conservation, and management

Permalink

https://escholarship.org/uc/item/14p279h4

Author

Yovovich, Veronica

Publication Date

2016

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA

SANTA CRUZ

THE INTERSECTION OF CARNIVORES AND HUMANS: ADDRESSING CURRENT CHALLENGES IN CARNIVORE ECOLOGY, CONSERVATION, AND MANAGEMENT

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

DOCTOR OF PHILOSOPHY

in

ENVIRONMENTAL STUDIES

by

Veronica Yovovich

June 2016

The Dissertation of Veronica Yovovich is
approved:

_____
Professor Christopher C. Wilmers, Chair

_____
Professor Brent M. Haddad

_____
Professor Meredith Thomsen

_____
Tyrus Miller
Vice Provost and Dean of Graduate Studies

TABLE OF CONTENTS

LIST OF FIGURES

THE INTERSECTION OF CARNIVORES AND HUMANS: ADDRESSING CURRENT
CHALLENGES IN CARNIVORE ECOLOGY, CONSERVATION, AND MANAGEMENT

Veronica Yovovich

ABSTRACT

Conflict between humans and carnivores, be it competition for space, food
(wild prey or livestock), or other resources, has led to carnivore declines across the
globe. Conservation goals can no longer be accomplished solely by setting aside
protected areas. An expanding human population is increasingly forcing us to create
new viable strategies to coexist with wildlife across rapidly changing landscapes.
Managing the needs of our growing human population while also maintaining the
resources necessary for large carnivore survival will become increasingly important.
This will require building new understandings of coupled human-carnivore systems,
and developing innovative tools for conflict mitigation. Preventing conflict is critical
for minimizing negative impacts to people and predators alike, and an important first
step is understanding the interactions between the two.

My research uses a variety of tools to explore the influence of anthropogenic
activities on various components of puma (*Puma concolor*) behavior and ecology in
the Santa Cruz Mountains of California. In my first chapter, I describe the spatial
interaction between anthropogenic activities and habitat for sensitive puma
reproductive behaviors. I found that future development will shrink suitable habitat
and increase patchiness, making it increasingly difficult for pumas to locate and
access suitable nursery and communication areas. My second chapter addresses the

spatial interactions between humans, top carnivores, herbivores, and woody plants. This research links a human-initiated trophic cascade to changes in individual plant architecture, changes which have the potential to create a positive feedback loop further amplifying the influence of these altered relationships. My final chapter evaluates the agreement between GPS- and stable isotope-based methods for estimating carnivore diets and integrates puma energetics to predict prey consumption. I found that stable isotope analyses and GPS cluster methods showed similar prey item use on the population-level, but differed significantly on an individual-level.

INTRODUCTION

"If wildness can stop being (just) out there and start being (also) in here, if it can start being as humane as it is natural, then perhaps we can get on with the unending task of struggling to live rightly in the world—not just in the garden, not just in the wilderness, but in the home that encompasses them both."

William Cronon, The Trouble with
Wilderness; or, Getting Back to the
Wrong Nature

Our modern conception of nature "over there" and human places "over here" creates an artificial boundary between where we dwell and wild spaces worth protecting. As our human population continues to grow, and our development expands, a greater portion of "nature" will need to exist within our human domain. My research takes a two-pronged approach to reconciling the "wild" in our everyday experience in order to resolve environmental problems. Building ecological knowledge helps us identify and prioritize key relationships, habitats, or processes necessary to enhance and support *ecological* carrying capacity. When we understand the essential requirements for human and non-human players, we can more specifically identify (and better address) the sources of conflict between the two. Identifying and building on these opportunities to meet the needs of the one without undermining the survival of the other increases *social* carrying capacity. By incorporating human and non-human dimensions in conservation research, we can borrow methods from both natural and social sciences to make conservation practices relevant, and increase conservation efficacy and efficiency.

1

Conflict between humans and large carnivores primarily arises when the two complete for habitat or clash over resource consumption (livestock depredation, contention over wild game, etc.), often resulting in preventative carnivore persecution or in retaliatory killing. As previously threatened carnivore populations recover in the U.S., and human populations increase, we can expect to see a rise in human-carnivore conflicts in the coming years (Treves et al. 2002, Treves and Karanth 2003, Breck et al. 2012). Some conflicts are a result of very real threats to personal livelihoods; however, some of the unease with carnivores stems from misattributed blame or deep-seated fear (Chavez 2002, Linnell et al. 2003). New research is focusing on developing new tools and approaches to help mitigate economic threats and assuage socially-based fears (Linnell et al. 2003, Dickman 2010, Baruch-Mordo et al. 2013, Miller 2015).

The three chapters of my dissertation primarily focus on carnivore-human interaction through the lens of puma (*Puma concolor*) ecology and behavior in the context of anthropogenic influences in the Santa Cruz Mountains of California. My first chapter describes the spatial interaction between anthropogenic development and habitat for sensitive puma reproductive behaviors. In this chapter, I developed a modeling framework that allowed me to predict nursery and communication site availability in response to projected human development. These results suggest that future development will shrink suitable habitat and increase patchiness, making it harder for pumas to find and access suitable areas for nurseries and communication. My results indicate that future development could have significant implications for

long-term puma population viability. These findings could be used to inform strategic conservation planning for human-wildlife coexistence. Further, these human-carnivore interactions are widely applicable to globally declining apex carnivores, such as snow leopards, Ethiopian wolves, and clouded leopards, making these results and tools broadly relevant.

My second chapter describes spatial interactions between humans, top carnivores, herbivores, and woody plants. Other research has addressed human influences on species interactions or predator effects on plant communities. This research is the first to link a human-initiated trophic cascade to changes in individual plant architecture, changes which have the potential to create a positive feedback loop further increasing these modifications. In addition, I was able to capitalize on the unique situation in the Santa Cruz Mountains, in that the apex predator was never extirpated and is currently at a relatively stable population size. This means I could investigate trophic dynamics in a natural context, rather than evaluating the effects of a recent gain or loss of a predator species. Finally, pumas and deer are widely distributed throughout the western hemisphere, so the interactions documented in this research have the potential to be widespread throughout the species' joint ranges.

Chapter three evaluates the agreement between two diet estimation tools, stable isotope analyses and GPS cluster investigations, for measuring puma prey composition. Identifying feeding locations based on spatially and temporally clustered GPS data is a leading method for estimating carnivore prey composition, but this approach is highly demanding in terms of labor and resources. Stable isotope

analyses are a far less expensive, non-invasive tool that allows researchers to estimate the relative contributions of different prey items in carnivore diets. This method is growing in popularity, but it had not yet been compared to widely used GPS cluster investigations. I found that stable isotope analyses and GPS cluster methods showed similar prey item use on the population-level, but differed significantly on an individual-level. This is the first study to field calibrate stable isotope analyses with a closely-monitored wild carnivore population. Many threatened carnivore species have been eradicated in all but the most remote and rugged corners of their previous distributions, making it difficult for researchers to access and monitor remnant populations. Calibrating alternative methods could open new possibilities for studying and conserving threatened carnivore species.

The ultimate goal of my research is to develop the social and ecological information to help protect human livelihoods and security while decreasing carnivore vulnerability. With a better understanding of the social structures and ecological mechanisms that leave ecosystems susceptible to degradation, we can breed tolerance for our nature, for the nature of non-human beings, and the ways we interface into a global, mutually beneficial, community—over here and over there.

CHAPTER 1

**Predicting carnivore behavioral responses to future human development: a
framework to enhance strategic conservation planning**

ABSTRACT

Habitat transformation is a major driver of species distribution and survival,
yet we have few tools to predict how changing patterns of anthropogenic
development are likely to impact wildlife behavior, an important precursor to
survival. We developed a modeling framework that allows us to understand the
spatial relationship between carnivore habitat selection and anthropogenic
development, and uses animal behavior to predict future impacts of human
development on wildlife. First, we identified habitat requirements for key
reproductive behaviors: nursery and communication site selection. We found that
female pumas have a relatively small nursery home range (9 km^2 ±1.72 SE) made up
of predominantly low density development (< 1 housing unit per 40 acres), and that
areas within 600m of communication sites were nearly entirely (97% ±0.35 SE) low
density development as well. Second, we modeled projected human development for
the year 2065, and compared this to current land use. We found that increases in
human development by 2065 will decrease available habitat for both behaviors,
eliminating 20% of current puma nursery habitat and nearly 50% of communication
site habitat. Further, development will make suitable habitat patchier, making it
harder for pumas to find and access suitable areas for nurseries and communication.

These findings indicate that future development could have large implications for long-term population viability, and could be used to inform strategic conservation planning for human-wildlife coexistence.

Early conservation efforts focused on setting aside large areas of land in order to preserve intact ecosystems. As human populations have expanded in size and spatial extent, the goals of conservation biology have shifted however, and can no longer be accomplished by establishing protected areas alone (Cronon 1996, Vitousek et al. 1997). Instead, expanding human development makes it increasingly important to create new viable conservation strategies to promote coexistence with wildlife across rapidly changing landscapes (Pressey et al. 2007).

Since the 1950s, American families have been leaving cities for rural living (Rudzitis 1999). These newly occupied areas, known as exurban development or "urban sprawl", are defined by low to medium housing density with a per-unit footprint 10 times the size of equivalent urban areas (Theobald 2005). Exurban development currently occupies 25% of the lower 48 states, and is growing more quickly than any other land use category (Theobald 2005). This number is projected to increase by over 75% in the next 25 years, with the highest rates of growth in coastal areas (Alig et al. 2004).

Understanding the functional responses of wildlife to exurban development, as an amorphous transition zone between rural and urban land use, is an emerging conservation concern. Ecologists recognize that anthropogenic development affects species abundance and distribution (Gehrt 2010); but we have yet to fully determine the indirect behavioral effects of habitat modification. One way in which animals adapt to human disturbance is through shifting their temporal and spatial activities

(Hebblewhite et al. 2005).   For example, wolves in Banff National Park became more nocturnal in sites near human disturbance (Hebblewhite et al. 2005). The differences in how species respond to disturbance may disrupt community structure and alter the landscape for predator-prey relationships (Hebblewhite et al. 2005) and community dynamics (Wang et al. 2015). There could be latent indirect impacts of development that potentially decouple behavioral ecology from ecosystem processes – the consequences of which may not be apparent until after restoration is no longer possible (Scheffer et al. 2001, Hinam and Clair 2008, Hovel and Regan 2008).

Expansive home ranges, large body size, high energetic demands, and preemptive or retaliatory killing make carnivores particularly vulnerable to habitat modification (Cardillo et al. 2004, Ripple et al. 2014). Even low levels of human disturbance can be detrimental to already declining carnivore populations (Crooks 2002, Ripple et al. 2014). Maintaining a full range of behaviors is as important as conserving genetic diversity (Caro and Sherman 2012), and becomes more important as development rapidly shifts habitat conditions and stretches behavioral plasticity to its limits (Sih et al. 2004, Caro and Sherman 2012). For carnivores, prey loss (Noss et al. 1996) and potential for conflict with humans further compound the influences of habitat disturbance (Woodroffe 2000). Low population densities, cryptic behavior, and wariness of humans make the effects of habitat modification difficult to study in large carnivores (Sargeant et al. 1998).

Pumas are not a wilderness-obligate species, however some of their behaviors are sensitive to human development (Beier et al. 1995, Riley et al. 2014, Wilmers et

al. 2013). Resource demands differ between male and female pumas (Wang 2014), as do their responses to human development (Wilmers et al. 2013). Although movement and hunting behaviors are relatively insensitive to habitat modification, key reproductive behaviors are highly influenced by habitat conditions and modification (Wilmers et al. 2013). Here, we explore how nursery site selection, home range size, and communication site selection are affected by human development. These behaviors are important for puma life history and have previously been found to be particularly sensitive to human disturbance (Wilmers et al. 2013).

Pumas choose suitable nursery sites for their ability to provide kittens with protection from predators and potentially dangerous conspecifics (Logan and Sweanor 2001). Female pumas use existing structures such as rock piles, dense vegetation, or fallen logs to conceal their kittens (Logan and Sweanor 2001). They localize at these sites after giving birth until their kittens are mobile. Puma mortality is highest in nursling kittens (Logan and Sweanor 2001), and mothers will move kittens to keep them safe. During this time, the mother acts as a central place forager, venturing away from the nursery site to feed and returning to nurse her kittens (Logan and Sweanor 2001). All the necessary resources to support growing kittens must be readily available within the surrounding area, and attempting to utilize suboptimal habitat could increase kitten mortality and shorten inter-birth interval, with energetically expensive consequences to puma mothers.

Community scrape sites are areas used for conspecific communication via scent marking and are important for mating and defining territories (Logan and

Sweanor 2001, Allen et al. 2015). Males create scrapes by using their hind feet to dig

two grooves with a mound of soil and duff at one end, and will sometimes urinate or

defecate on the mound (Allen et al. 2014). Male pumas communicate their presence

to one another using scrapes (Logan and Sweanor 2001, Allen et al. 2015), and

advertise to females for breeding opportunities (Allen et al. 2015). Scrapes are often

placed at prominent landscape locations, such as trail junctions, saddles, or under

large trees. Community scrapes are most frequently visited by males, however

females use these sites as well (Allen et al. 2015, Allen et al. 2014). When a female

is ready to breed, she will linger at these locations and sometimes caterwaul to

increase her chances of encountering a receptive mate (Logan and Sweanor 2001,

Allen et al. 2015).

Here, we created a modeling framework for understanding puma behavior in

the context of human development. The Santa Cruz Mountains of California, ranging

from urban Silicon Valley to large areas of preserved open space, provides a

backdrop for quantifying how varying levels of development affect puma behavior.

We studied puma habitat selection for sensitive reproductive behaviors across a

gradient of anthropogenic influence, and modeled how future human development

will change the landscape for these behaviors. Human development is projected to

substantially increase across puma habitat over the next half century (Alig et al. 2004)

(Figure 1.1), with most changes converting rural land to exurban development. Since

puma reproductive behaviors are particularly sensitive to human activities, this

transformation of sparsely developed open and rural landscapes to exurban development could impact puma reproductive ecology.

MATERIALS AND METHODS

Study Area

We conducted our study in the Santa Cruz Mountains of California, south of San Francisco. The climate is Mediterranean with hot, dry summers, and cool, wet winters, with most of the annual precipitation occurring as rain between November and April. Our 1,600 km^2 study area ranges from sea level to approximately 1,155 meters in elevation, with two distinct climactic zones: coastal climate on the west side, and inland to the east. Habitat types in the study area have been described in greater detail elsewhere (Wilmers et al. 2013). The study area encompasses a spectrum of human development and protected lands, creating a mosaic of land use where human density ranges from 0 to 40 housing units per acre. There are large areas of preserved habitat managed by state, county, and city parks as well as private entities. In between are areas of human influence ranging from rural to urban development, as well as many trails, fire roads, residential roads, and highways.

Field Methods

We captured 45 free-ranging pumas from 2008-2014 with cage traps, leg hold snares, or trailing hounds as described in Wilmers et al. (2013). Puma capturing, handling, and sampling protocols were approved by the Animal Care and Use

Committee at the University of California, Santa Cruz (protocol #Wilmc1101), and the California Department of Fish and Wildlife. Individuals were tranquilized using Telezol (Fort Dodge Laboratories, Fort Dodge, IA, USA) and fitted with a GPS/VHF tracking collar (GPS PLUS, Vectronics Aerospace, Berlin, Germany). Collars were programmed to acquire a GPS location every 4 hours, and the GPS data were remotely downloaded monthly via UHF, or transmitted via cell phone towers every 1-3 days depending on collar program configuration and cell phone coverage.

We used female GPS collar data to locate potential nursery sites. We searched for clusters of spatially aggregated GPS locations that persisted for >1 week, and were characterized by repeated excursions to and from the site. In the instance of GPS failure, we used the collar's VHF signal to repeatedly triangulate the position of her nursery over the course of several days. We field-investigated potential nursery GPS clusters between 3 and 6 weeks of when the female first localized to confirm the site as a nursery. When we found kittens or kitten sign, we recorded the nursery coordinates using a handheld GPS unit, and subsequently monitored the nursery outcome.

We defined community scrapes as frequently used scent marking areas containing ≥3 scrapes within 9 m^2 of one another (Allen et al. 2014). We located community scrapes by one of two methods. We used a custom algorithm for male puma GPS collar data (Wilmers et al. 2013) to locate sites within 300 m of previous locations in which males had visited, with visits separated by >7 days to eliminate feeding sites. Then we field-checked locations identified by the algorithm for

scrapes. We also located scrape sites opportunistically during our daily field

activities. When we found a community scrape, we recorded the coordinates with

handheld GPS units.

Habitat Variables

We employed several categories of landscape features in our spatial analyses

(Appendix 1). We used a digitized housing layer (described by Wilmers et al. 2013)

to classify the landscape into housing density categories as defined by EPA ICLUS

model (Bierwagen et al. 2009) (Table 1.1). We calculated distances to each

landscape feature included in the analyses (rivers, roads, etc.) in ArcGIS and

converted to raster format. Aspect was transformed from a circular variable to a

linear variable using sine and cosine transformations before analyses. We categorized

vegetation communities as grassland, forest, or shrub (US Geological Survey, Gap

Analysis Program (GAP) May 2011. National Land Cover, Version 2). Land

designated as agriculture was almost entirely rangeland, so those areas were collapsed

into the grassland category. We normalized all continuous variables, x_i, to center

each of the variables around 0 with a variance of 1 (Zuur 2007) using the formula:

$$x_i^{new} = (x_i - x_{mean})/x_{sd}$$

ICLUS Model

We employed a spatially explicit regional growth model (SERGoM) developed

by the Integrated Climate and Land Use Scenarios (ICLUS) (Bierwagen et al. 2009)

to project future development in our study area. SERGoM uses several categories of

input to create projections: 2000 Census data, land ownership data to create an undeveloped and undevelopable land dataset, road density, groundwater well density, county population projections, and commercial/industrial land use (Bierwagen et al. 2009). This model is described in greater detail in Theobald (2005).

One particular advantage to SERGoM is the attention paid to exurban/low-density development. These areas are particularly relevant to our study area for two reasons. First, exurban development is the housing density category projected to see the most change in the next fifty years in the Santa Cruz Mountains (Figure 1.1). Second, exurban development is an intermediate-intensity of housing, which we hypothesize may be the tipping point between suitable habitat and human-dominated landscapes which area unsuitable for sensitive puma behaviors.

For our analyses, we used the "base case" development projection as a conservative prediction of human development in Santa Cruz Mountain 50 years into the future to the year 2065. This projection assumes a "business-as-usual" development pattern and the midline U.S. Census Bureau projection for population growth. For a detailed description of model assumptions see Bierwagen et al. (2009). The resulting SERGoM model output was a 100m resolution raster of housing development categories, which we then input into ArcGIS for analyses.

Statistical Methods

We processed all spatial data in Geographical Information Systems program ArcGIS (v.10.1; ESRI, 2012) and R (v.2.1.3.1; R Development Core Team, 2010), and used R for our statistical analyses.

i. Home range size and housing density

We used a 95% adaptive local convex hull (LoCoH) construction method to estimate an annual home range for each puma (Getz et al. 2007). Subadult pumas are seldom involved in reproductive behaviors, so we restricted our analyses to mature resident pumas. We eliminated data for pumas collared for fewer than 12 continuous months from analyses. In order to avoid overestimating home range size due to shifts in territories, we used the first year of collar data for individuals with data spanning longer than 1 year (n=24). We calculated the percent composition of each housing density category within each individual's home range. Each of the two puma behaviors: 1) nursery site selection and 2) communication site selection, were indiscriminant to open versus rural housing density categories. Pumas did not exhibit any selective behavior to human development below the threshold of rural housing density. We therefore combined open and rural density categories into a "lightly modified" development category to capture the true relationship between puma behavior and human development for analyses. We then used a linear regression to quantify the relationship between the percent of human-dominated area contained within a home range and home range size by sex. The percent of the puma's home

range that was developed habitat was the independent variable and the size of their home range was the dependent variable.

ii. Modeling Current Suitability: Potential 2014 Nursery and Scrape Sites

We employed a use-availability resource selection function (RSF) to investigate the impact of habitat variables on nursery site and scrape site selection (Manly et al. 2002). RSF models allowed us to quantify utilization of various habitat features and create a relative index of use across a landscape (Manly et al. 2002).

In each case, we defined used points as GPS locations in which the behavior took place, and available points as random points, generated at a ratio of 1:5 (used:available) (Johnson et al. 1992). For the nursery analysis, we selected available points from within each female's home range, and generated available points in proportion to the number of nursery sites for each individual female. For the scrape analysis, we generated available points from a merged LoCoH for all males. Since we cannot attribute individual male pumas to each community scrape, random available sites were bounded by the spatial extent of the activities of all resident males.

Then we extracted landscape attributes (slope, development category, etc.) at each point and compared used versus available points using a logistic regression model. For nurseries, we created a series of univariate regressions, one model for each of the habitat variables, to determine significant factors contributing to site selection while avoiding over-parameterizing our model.

In order to model scrape site selection, we adapted the model from Wilmers et al. (2013), an RSF model with development as a categorical variable, and slope as a continuous variable. We could not adequately predict distance to the nearest road with the SERGoM model because the model output does not explicitly map road locations. However, the distance to roads had a marginal influence on site suitability (Wilmers et al. 2013), and the SERGoM does implicitly incorporate road density into their model output. This allowed our model to account for the influence of roads by including their effects as a component of development.

We also looked beyond the point-level influence of site selection, and measured how the area surrounding each site influenced the selection of nurseries and community scrapes. Wilmers et al. (2013) determined that female pumas have a 600 m radius of sensitivity when selecting nursery sites, and that males are similarly sensitive when creating community scrape sites. We placed a 600 m radius circle around each scrape or nursery site to define the area influencing site selection. Then we performed analyses to compare the landscape encompassing used and available points using a compositional analysis (described in Aebischer et al. 1993), as well as a t-test. The analysis utilized MANOVA/MANCOVA-type linear model to compare the level of human development in used versus available areas. We analyzed these relationships at three spatial resolutions. We compared anthropogenic development immediately surrounding nursery sites to 1) comparably-sized random sites selected within each female's home range, 2) each female's overall home range, and 3) the study area. Since we cannot attribute scrapes to individual males, we were unable to

17

perform the two first analyses, but we did conduct the third analysis for scrape sites as well.

Our second level analyses of nursery sites incorporated kitten-rearing behavior in site selection. In these analyses, we used the area a female utilized while she was bound to the nursery to determine the broader habitat influence. Male pumas and females without young kittens move continuously throughout their home ranges, acquiring the necessary resources to survive along the way. However, in order to protect and raise young (i.e., <3 months), vulnerable kittens, a female must act as a central place forager, returning to the nursery site in order to feed dependent young. We modeled this behavior by creating nursery LoCoHs, or nursery home range, with GPS points collected while the female was behaving as a central place forager maintaining growing kittens (Figure 1.2) (Getz et al. 2007). Similar to the home range estimates, we used a 95% a-LoCoH construction method. We used the rule of covering spurious holes, but not all of the holes were covered due to the limited number of nursery LoCoH data points available. These 'used' areas LoCoHs were constructed from the female's GPS points recorded when kittens were born until they were 8 weeks old. This is the period during which the mother keeps her kittens at a nursery site and behaves like a central place forager. We created comparable 'available' areas by generating variable buffers around random points. The 'available' areas were selected randomly from a vector of nursery LoCoH areas. We then compared anthropogenic development in: 1) used nursery LoCoHs compared to

available LoCoHs, and 2) used nursery LoCoHs compared to the broader habitat as defined by the area covered by all of the female MCPs merged together.

We performed a compositional analysis, which considered selection at two levels: 1) selection of habitat use within the home range, and 2) selection of habitat use within the study area. We determined whether pumas were selecting for or against each category based on the positive or negative relationship. We assumed that the current habitat conditions were the requirements for suitable habitat. Therefore, we could use the mean amount of each kind of development present at each nursery site to model suitable habitat across the study area. For development categories that were being selected against, we used the mean value, plus the standard error, as the maximum threshold for nursery site suitability in our predictive model. For categories that were being selected for, we set the average value, minus the standard error, as the minimum threshold for modeling nursery site selection. We used these mean values, plus or minus the standard error, to model current habitat suitability across the study area, as well as project how suability will be influenced by development.

Modeling the Future (2065) Landscape

We mapped projected future housing density for the Santa Cruz Mountains for the year 2065 using the SERGoM GIS tool (Bierwagen et al. 2009). Using the tolerance/attraction thresholds generated from the compositional analysis (Table 1.2), we created a moving window analysis to create a binary (suitable/unsuitable) raster

for potential nursery sites and a binary layer for potential scrape sites. In order to measure the distribution of suitable patches, we made a simulated puma home range grid with cell sizes the average size of a puma home range. We eliminated grid cells in urban areas as these areas would be unsuitable habitat for a puma.

Females need nursery patches large enough to encompass sufficient resources to sustain them while they support their immobile young. We generated nursery LoCoHs, and used the mean size of successful nursery patches as a minimum sufficient area required to raise kittens to an age beyond the use of the first nursery site. In our analyses, we used binomial or quasibinomial regression (Crawley 2012) to determine how projected development will influence the properties and distribution of suitable patches and sufficiently large patches.

When selecting scrape sites, males are sensitive to development as well as slope (Wilmers et al. 2013). Therefore, we incorporated slope into our modeled suitability using the estimated parameter coefficient. The ability of the model to discriminate between scrape sites and non-scrape sites was 'acceptable' as determined by an area of 0.79 under the receiver operator curve (Hosmer and Lemeshow 2004).

RESULTS

We used GPS data from 15 female and 10 male pumas, which were monitored for a mean of 636 (±102 SE) days and 428 (±52 SE) days respectively. We documented 23 nursery sites for 12 female pumas. We also located and documented 299 community scrapes.

Female pumas had a mean home range size of 62 (±8 SE) km^2, significantly smaller than males (t-test: t_{22}=-3.56, $p<0.01$), which had a mean of 172 (±20 SE) km^2. Overall, the size of home ranges was not significantly correlated with the percent of developed landscape found within it. When we analyzed males and females separately, however, we found that female home range sizes were sensitive to human development with a significant positive relationship (linear regression: t_{10}=-2.207, p=0.03, r^2=0.28), while male home ranges did not have a significant relationship (linear regression: t_8=-0.277, p=0.80) (Figure 1.3). For every one percent of habitat converted to rural development, female puma home ranges increased by 1.68 km^2.

2014: Current Nursery and Scrape Site Selection

The mean area a female utilized while supporting her kittens and acting as a central place forager was 9 km^2 (±1.72 SE) (Figure 1.2). Of our documented nursery sites 100% (n=23) were located in the very low human development habitat category. In addition, development was the only predictor variable for nursery site selection that was significant (RSF: $p<0.01$ Appendix 2). In 2014, 77.38% of our study area was categorized as very lightly developed, 6.43% was exurban, 11.07% suburban, and 5.12% urban (Table 1.3).

Our analyses show that female pumas select for the lowest development areas over any other housing density category on every spatial scale. Our smallest spatial scale, areas within a 600m radius of a nursery site, were higher in lightly modified development than random sites (CA: mean$_{nursery}$=91% ±6 SE, mean$_{available}$=73% ±6

SE, $p<0.01$). At our medium spatial scale, the LoCoH areas utilized while the female was centralized at her nursery site, were also higher in lightly modified development (CA: $mean_{nursery\ LoCoH}$ =88% ±3 SE, $mean_{study\ area}$ =76% ±0 SE, $p<0.01$). Regardless of the scale, suburban or urban development made up a very small portion of the area used while supporting young kittens ($mean_{600m\ nursery\ area}$ =0.0002% ±0.0001 SE, $mean_{LoCoH}$ =0.0016% ±0.0012 SE).

All of the community scrape sites were located in lightly modified habitat (n=299). When looking at the conditions at the scrape site itself, our RSF results suggest that males significantly selected for undeveloped habitat (RSF: $\beta_{lightly\ modified\ habitat}$=5.19) and against urban habitat (RSF: β_{urban}=-11.47, Table 1.4). They also preferred relatively flat areas (RSF: β_{slope}=0.02 ±0.086 SE, Table 1.4). Similar to site-level conditions, the areas within a 600m radius of the scrape sites were predominantly open habitat as well. Used areas were significantly higher in very lightly modified habitat than areas around random points (CA: $mean_{used}$=97% ±0.35 SE, $mean_{random}$=88% ±1.00 SE, t_{299}=-8.07, $p<0.01$, Table 1.5).

2065: Future Landscape for Suitable Nursery and Scrape Sites

For both scrapes and nursery sites, our predictions for human development over the next half century would reduce availability of suitable sites (Figure 1.4). In 2065, 32.61% of our study area was categorized as very lightly developed, 49.23% was exurban, 12.63% was suburban, and 5.52% was urban. As a result, increased human development is projected to reduce potential nursery habitat by 20%.

Increasing habitat fragmentation is also projected to leave some females without suitable nursery habitat within their home range, dropping from 100% of modeled female home ranges having sufficient nursery patches in 2014, to 77% in 2065. In addition, future suitable habitat patches are projected to become farther apart as well, with the average distance between sufficiently large nursery patches in 2065 projected to be triple the distance from 2014 (compositional analysis: $mean_{2014}=787$ ±117 SE, $mean_{2065}=2749$ ±260 SE, $p<0.01$).

A similar pattern was true for potential scrape sites. In 2014, 30% of the study area was considered suitable for scrape sites, but our projections for 2065 shrank potential scrape site area by nearly a half to 18%. Again, as the remaining potential habitat was reduced, it also became patchier.

DISCUSSION

We explored the relationship between anthropogenic development and puma reproductive behavior, specifically how current and projected human development influence the landscape for scrape and nursery selection behaviors. Our research addressed the scale of habitat selection, the spatial requirements of females while they are geographically bound to their nursery, and developed a framework for predicting future impacts of human development on wildlife. The two puma behaviors we focused on are important reproductive behaviors and are particularly vulnerable to exurban encroachment. Our findings suggest that future development patterns will strongly influence habitat availability resulting in potential fitness costs (Hinam and

Clair 2008, Gehrt 2010). Studies using strategic conservation planning in other places or with other species can use similar methods to ensure protection of essential habitat.

The first aim of this study was to describe nursery site selection and scrape site selection habitat requirements for pumas. When choosing nursery sites, female pumas selected against human development on every scale. All of the documented nursery sites were located in undeveloped habitat (< 1 housing unit per 100 acres). Expanding the spatial scale to include the area within 600 m of each nursery, and then to the nursery home range, females tolerated small increases in the amount of development at each increased spatial scale. However, on every level, females had a strong preference for undeveloped habitat. Undisturbed habitat likely increases kitten survival. Habitat near humans may have elevated populations of synanthropic carnivores, such as coyotes or domestic dogs, that could kill vulnerable kittens (Gehrt et al. 2011), while humans themselves may also be perceived as a threat to growing kittens. This is important because when a female is disturbed, she will often move her kittens to a new nursery (Logan and Sweanor 2001). Lower levels of disturbance may therefore decrease the number of times a female needs to change nursery sites, leaving her more time for hunting and caring for kittens.

This is the first study to address the spatial requirements for female pumas during the brief period during which they behave as central place foragers, a neglected area of research. When kittens are young (<8 weeks old), the mother is geographically bound to the nursery, as she must continually return to feed the kittens. We found that the average area utilized during this time window was just

24

15% of an average annual female home range, but from a population scale nursery sites may be the most important area of a female's home range. In addition to requiring protective cover for the kittens, the surrounding area must also contain sufficient resources (prey, water, etc.) for the mother to support her growing young. In 2014 there were sufficiently large suitable nursery patches in every potential female puma home range. However, expanded exurban development will eliminate sufficiently large patches in nearly a quarter of potential female home ranges, potentially limiting puma reproductive success.

Similar to nursery site qualifications, males selected for lightly modified habitat at the site- and area-level when creating community scrapes. They also preferred relatively flat areas, usually in the form of ridgelines and canyon rims. In the steep Santa Cruz Mountains, factoring in an aversion to precipitous slopes greatly narrows the habitat available for scraping. Pumas may select scrape sites that maximize their opportunities for communication between conspecifics (sensu Allen et al. 2014) while minimizing disturbance from human disturbance. The cues left at community scrapes are both chemical and physical (Allen et al. 2014), and as such are likely vulnerable to human disruption. Males may prefer remote locations because hikers, bikers, pet dogs, and other recreationalists inadvertently disturb scrape sites, making community scrape sites dependent on areas with little human impact. Flat ridgelines and canyon rims likely provide excellent movement corridors for wildlife (Lindenmayer and Nix 1993), while the remoteness and lack of development guards against disturbance.

The second aim of this study was to model the difference between current and future landscape for potential nursery and scrape sites. Between 2014 and 2065, nearly half of lightly modified habitat is predicted to be converted into exurban and suburban development. Predicted land conversion would reduce available nursery habitat by 20% and potential scrape habitat by nearly a half. In addition to habitat loss itself, the projections suggest that the remaining habitat will be patchier as well. In 2065, 23% of females will only have access to suboptimal habitat in which to rear their young.

Habitat loss and increasing habitat patchiness in 2065 could confer large energetic penalties to female pumas and reduce fecundity. Nursling kittens experience a higher mortality rate than any other age group (Logan and Sweanor 2001). Nursing females are also unable to traverse long distances in search of prey because they need to make kills quickly to feed themselves, and then quickly return to their kittens. Attempting to raise kittens in heavily modified habitat would likely increase nursery failure rates and shorten the inter-birth interval; and pregnancy, lactation, and kitten rearing are energetically expensive (Oftendal and Girrleman 1989). A shorter inter-birth interval would lead to a more frequent cycle of growing kittens, nursing them, and losing them, which would be energetically demanding.

The amount of anthropogenic development and female home range size were positively correlated, further suggesting that human-dominated habitat was lower in resources than wild habitat and required females to make use of larger areas to make up for poor quality habitat, as seen in other carnivore species (Gehrt 2010). As

exurban development increases, females will need larger home ranges, potentially

decreasing the population size our study area can support (Figure 1.3).

Inadequate access to scrape habitat could generate fitness costs on multiple

fronts. Scrape sites provide an indirect, non-combative opportunity for resident males

to communicate their presence to other males. Resident male pumas patrol their

territories to refresh these sites every 2 to 3 weeks (Allen et al. 2015). The

communicating males likely use scent cues from the scrape to establish dominance

and define boundaries (Allen et al. 2015), allowing competing males to avoid

physically confronting one another (Logan and Sweanor 2001). With limited access

to suitable scrape sites, we could see a breakdown of territorial boundaries and

effective communication, increasing male-male conflict. Intraspecific strife can be an

important population driver (Rankin 2007), especially as isolation from other puma

populations increases (Riley et al. 2014). The impacts could range from low cost

outcomes, such as inefficient use of time or energy, to much graver ends including

bodily harm or death.

Community scrapes also serve as a way for males to advertise themselves to

potential mates (Allen et al. 2014), and provide a location for females to

communicate their receptivity to breeding (Allen et al. 2015). Without these sites,

males and females could have a more difficult time finding mates, resulting in

decreased reproductive success across the population (e.g., Slabbekoorn and

Ripmeester 2008). Breeding success is correlated with territory maintenance, as

kittens are generally sired by a territory-holding male (Logan and Sweanor 2001,

Allen et al. 2015). Thus, the ability to hold a territory can have significant implications for reproductive success of a particular male (Logan and Sweanor 2001). Access to adequate communication sites will likely be of great importance to future puma populations.

Historically, pumas held a wide distribution and occupied nearly every habitat from the desert to tropical rain forests (Logan and Sweanor 2001), all of which suggests a high degree of adaptability. Our analyses did not take behavioral plasticity to an increasingly human-dominated landscape into account. With diminished access to ideal sites, it could be that pumas will substitute poorer quality sites to make up the difference. Pumas have demonstrated the ability to adapt and persist in areas lightly influenced by humans (Riley et al. 2014). However, our study area is situated in an area already highly impacted by people, which could mean that they are already living on the lower end of their acceptable spectrum. If they are currently subsisting in suboptimal habitat, further flexibility may not be possible. In addition, increased development will likely have additional negative implications for prey (Ripple et al. 2015), dispersal permeability and gene flow (Riley et al. 2014), as well as overall habitat loss (Vitousek et al. 1997).

The results presented here provide insight into how anthropogenic habitat changes influence two key reproductive behaviors, and extend those findings to investigate how the future of development will change habitat suitability for those behaviors. By explicitly modeling the spatial components of reproductive behaviors, we are able to predict how animals are likely to respond to increased development

and fragmentation. Spatially explicit modeling of how development impacts important wildlife behaviors will help inform strategic conservation planning, and will expand our understanding of how development affects population-level processes. These data highlight the need for regional planning to pay special attention to exurban development. Ninety six percent of the land use change is predicted in the next 50 years will transform suitable habitat to unsuitable exurban development (Table 1.3, Figure 1.1). Redirecting some of this development into suburban or urban areas would allow space for both humans and pumas to persist. The pervasiveness of habitat loss and transformation make it all the more important to carefully develop around remaining habitat. Gaining a better understanding of how habitat modification influences wildlife can also help garner public support for sound conservation practices, and guide future development plans to ensure that wild populations can thrive alongside human development.

History, and the UC Santa Cruz Environmental Studies Department for their generous

funding.

Table 1.1. A summary of the definitions we used for each housing density category, which are the same criteria as the Environmental Protection Agency.

Model category	Development category	Acres per housing unit	Hectares per housing unit
01*	Lightly Modified	>40	>16.18
0	Open	>100	>40.5
1	Rural	40-100	16.18-40.5
2	Exurban	2-40	0.8-16.18
3	Suburban	0.25-1	0.10-0.40
4	Urban	<0.25	<0.10

*We combined the values of Open and Rural categories into one "Lightly Modified" category

Table 1.2. Suitability thresholds, the relative housing densities used to model nursery and scrape site suitability in the moving window analysis. In order for an area to be deemed suitable for nursery sites, the area must have 91% or greater open/rural development, while for scrape sites it must have 98% or greater open/rural habitat. For all other development categories, these thresholds depict the upper limit for suitable habitat. For example, suitable nursery areas could not contain greater than 7% exurban development, while the scrape maximum was 2%.

Development Category	Nursery Area	Scrape Area
Open & Rural	≥ 91	≥ 98
Exurban	≤ 7	≤ 2
Suburban	≤ 8	≤ 2
Urban	< 1	< 1

Table 1.3: The degree of human development in our study area is predicted to change substantially between 2014 and 2065. We provide the percent of each category for our study area in 2014 and 2065, along with the difference. The ICLUS model predicts that 44.76% of current lightly modified land will be converted to either exurban development or suburban development, representing a substantial shift from land useable to unusable for puma nursery and communication sites.

	Percent		
Development	**2014**	**2065**	*Difference*
Lightly Modified	77.38	32.61	-44.76
Exurban	6.43	49.23	*42.80*
Suburban	11.07	12.63	*1.56*
Urban	5.12	5.52	*0.40*

Table 1.4. Best fit resource selection function model for scrape site selection (n=299). Males strongly selected against very high-density development and selected for undeveloped to lightly modified habitat.

Habitat Variable	Coefficient	Std. error
Slope	0.02	0.086
Development Category		
Lightly Modified	5.19	1.011
Low Density	4.27	1.025
Medium Density	4.22	1.123
High Density	3.35	1.014
Very High Density	-11.47	381.820

Table 1.5. Results of our t-tests comparing development in scrape sites versus the surrounding area. Here we compare the mean percent composition of each development category found within a 600 m radius of scrapes and random sites. Similar to the point-level comparisons using an RSF, males select for very lightly modified, or open, habitats.

| Habitat Variable | Mean | | p | t | df |
	Used	Random			
Lightly Modified	97.59	88.35	<0.01	-8.07	596
Exurban	1.8	6.82	<0.01	-8.16	596
Suburban	0.62	4.64	<0.01	-6.28	596
Urban	0.01	0.15	0.5	-1.77	596
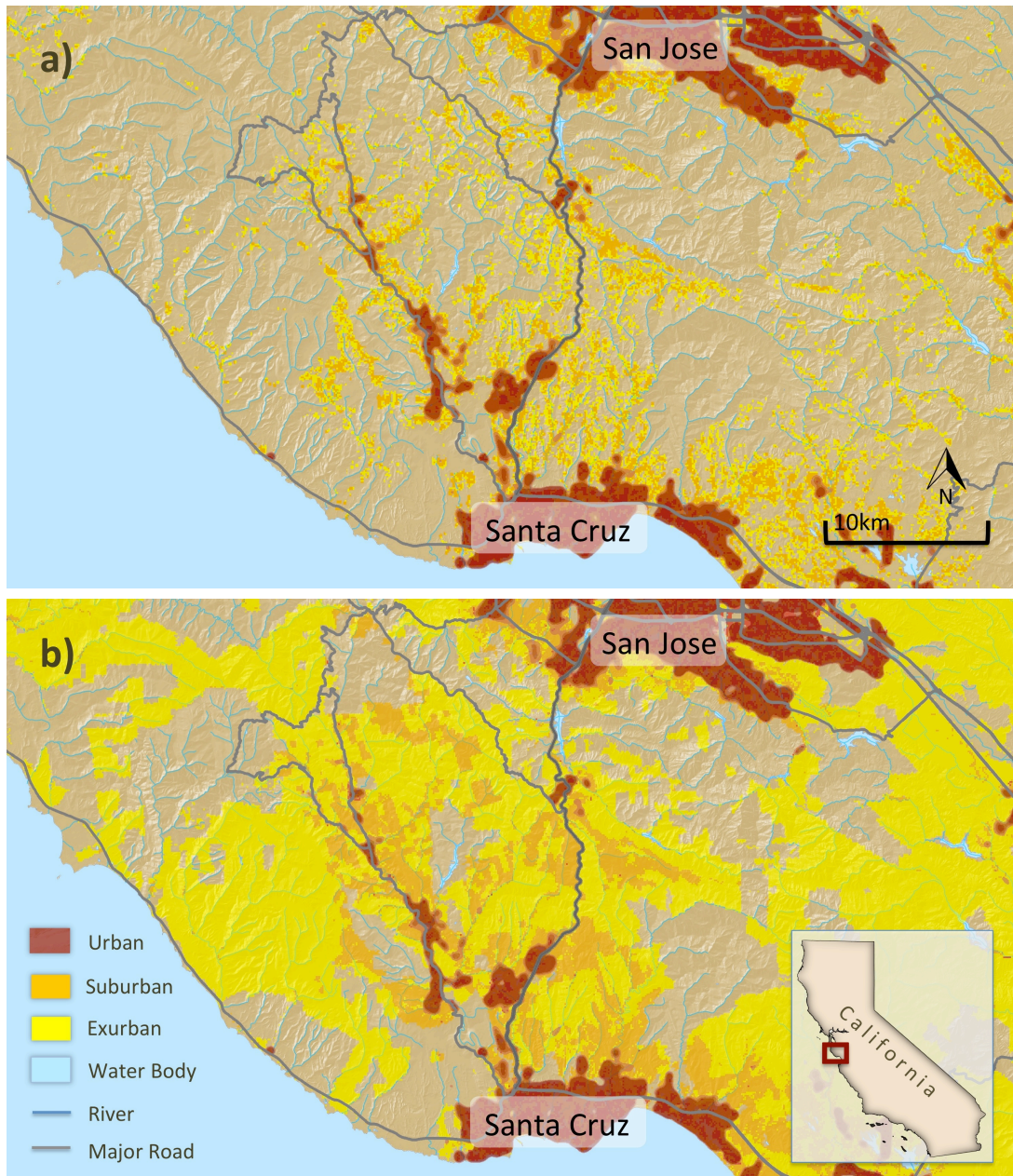
Figure 1.1. Over the next 50 years, development will greatly increase in the Santa Cruz Mountains. The fastest growing projected land use change between 2014 (a) and 2065 (b) will be habitat shifting from open or rural development to exurban development.
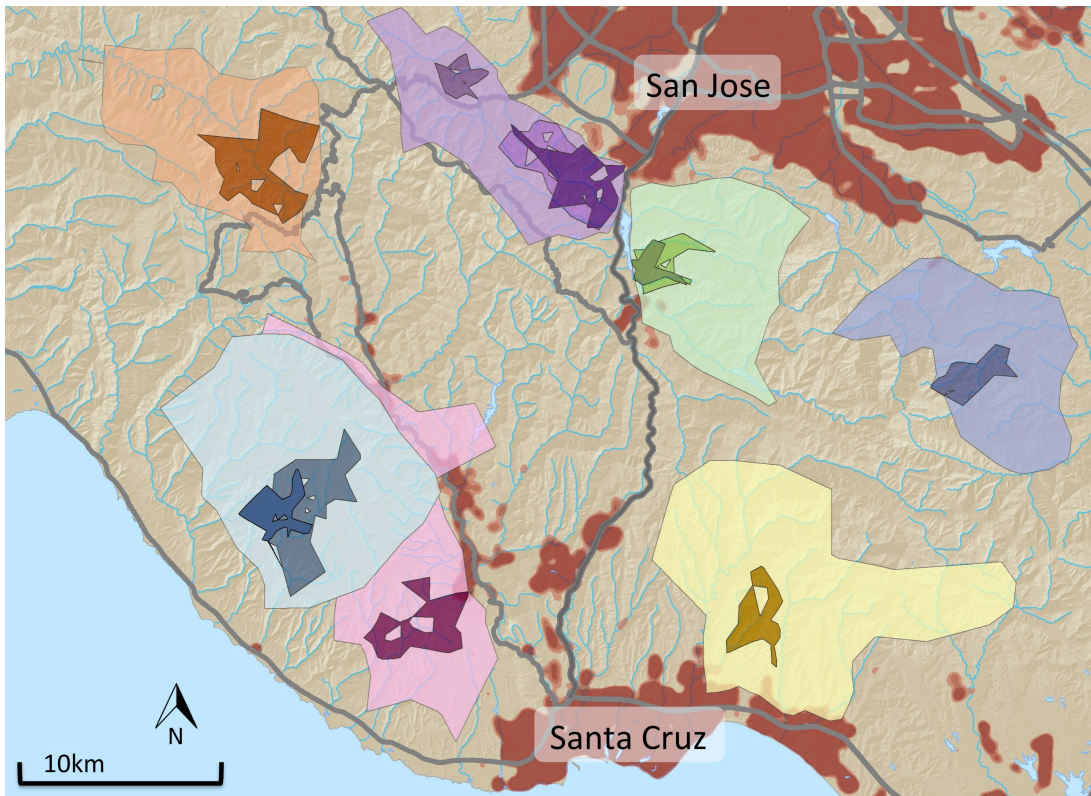
Figure 1.2. An illustration of the contrast between home range and nursery areas. Each pastel translucent area is an individual female home range (measured using a LoCoH). Each smaller dark, opaque colored area is the home range the correspondingly-colored female utilized while maintaining a nursery. The average size of a female's home range was 64km^2 and the average area female utilized while bounded to a nursery site (also measured using a LoCoH) was 9km^2.
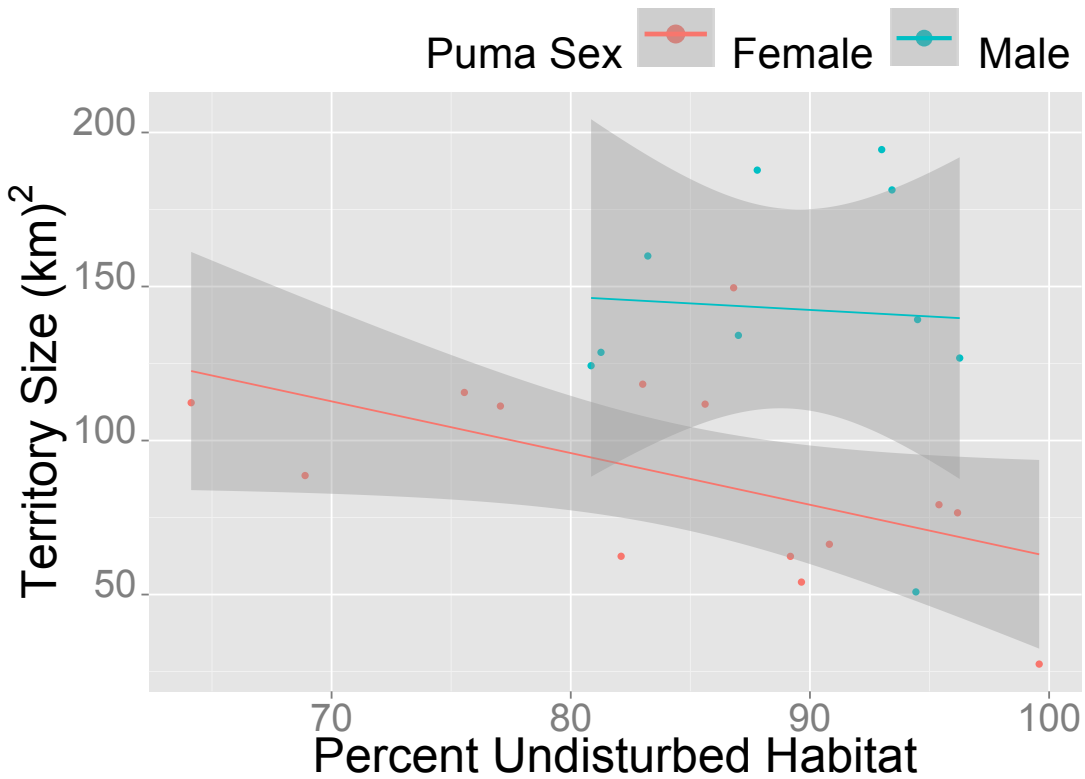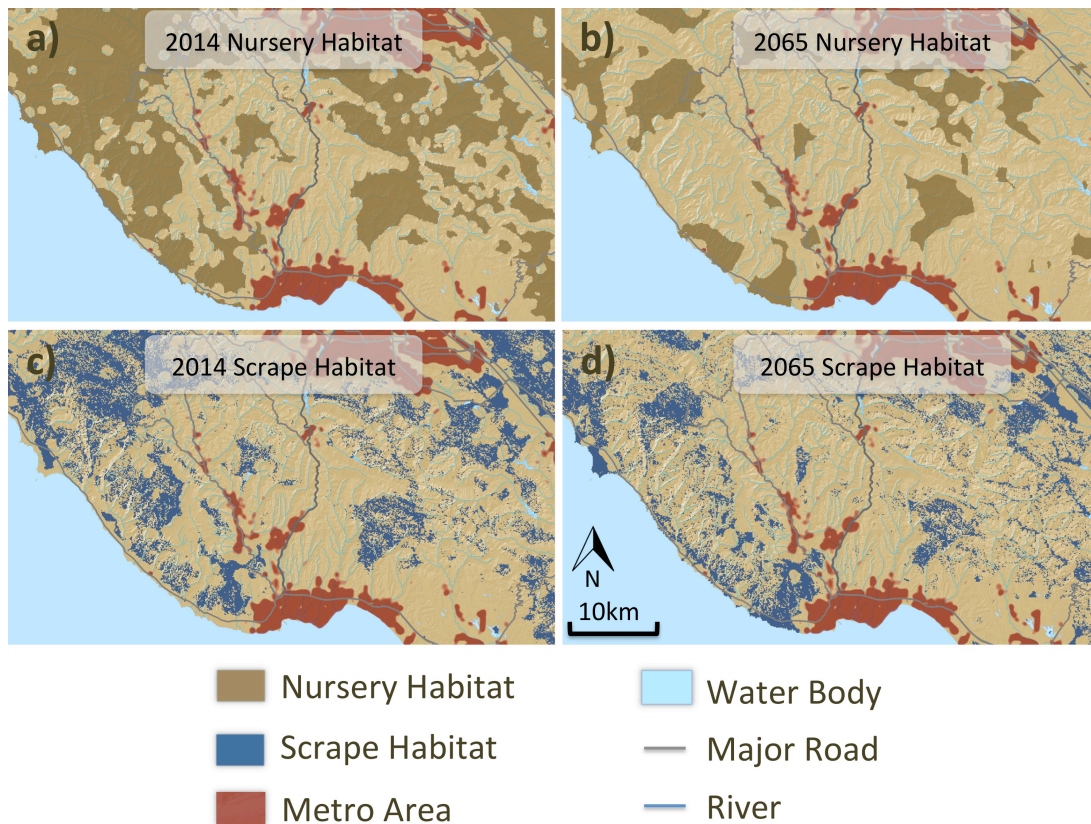
Figure 1.4. The spatial extent of suitable nursery and communication site habitat will shrink over the next 50 years. In 2014 available nursery habitat (in brown) covers 74% of the study area (a). In 2065, this habitat is projected to decrease to 54% of the study area (b). In 2014 available scrape habitat (in blue) makes up 30% of the study area (c). In 2065, this habitat is projected to decrease to 18% of the study area (d).

CHAPTER 2

Cascading fear: plant architecture reflects human-carnivore-herbivore relationships

ABSTRACT

Fear of predation elicits strong behavioral responses from prey, with impacts that trigger cascades through food chains. The ecology of fear responses to natural predators is becoming better understood, but little is known about how humans - the world's most ubiquitous super-predator - influence subsequent trophic levels, through changes in carnivore habitat use and behavior. We combined GPS puma tracking data and field experiments to demonstrate a trophic cascade precipitated by anthropogenic development. Starting with the top of the chain, we examined the spatial patterns in puma feeding sites, and found that pumas select hunting areas away from human disturbance. Puma aversion to disturbed areas created predator refugia for deer. We determined that deer take advantage of this aversion by increasing their activity near human development. Our data revealed greater browse pressure in sites near humans, and that browsed woody plants develop a greater number of branches that are within reach of browsing deer. The impact on plant architecture is likely to create a feedback in which increased browse pressure cultivates more abundant deer forage in areas avoided by pumas. Our study is the first to link a human-initiated trophic cascade to changes in plant physical structure. We expect that higher browse pressure in low predation risk sites near humans may cause a shift in plant species composition over time. However, our study area is a landscape in which puma

40

recovery and human development is fairly recent on the timescale of tree life

histories. Therefore, the full extent of the relationship is likely not yet expressed in a

way that we can detect.

Behavior-mediated trophic cascades have been widely documented across multiple habitat types and species communities (Schoener 1993, Schmitz et al. 2000). Anthropogenic habitat modification has also become a nearly globally understood presence as well. While the magnitude of human-caused trophic cascades is hotly-debated, we do know that human activities can influence carnivore behavior (Hebblewhite et al. 2005, Wilmers et al. 2013). However little is known about how anthropogenic activities cascade through the ecosystem and affect each subsequent trophic level.

Direct habitat loss from human transformation of wild lands plays a key role in in species decline (Gibbons et al. 2000). However, recent research has shed new light on how human activities extend beyond the urban-wildland interface, impacting carnivore behavior (Wilmers et al. 2013), influencing community dynamics (Hebblewhite et al. 2005, Wang et al. 2015), contributing to species decline (Gibbons et al. 2000), and altering ecosystem function (McKinney 2002) .

In a tri-trophic cascade, predators limit prey density and/or change prey behavior, indirectly benefiting local primary producers (Paine 1969, Estes and Palmisano 1974, Power 1990, Hebblewhite et al. 2005). Human activities can add an additional "super predator" trophic level, directly or indirectly influencing carnivore abundance, and thereby altering predator-prey interactions (Hebblewhite et al. 2005). Humans have both consumptive and non-consumptive effects on predators, lowering predator density or altering their habitat use. In turn, prey respond either behaviorally

or numerically to shifts in predation risk, changing where and to what degree they forage. In some cases prey use human activities as a shield against predation (Martin and Szuter 1999, Berger 2007). Heavy grazing or browsing, in preferred safe prey habitat, can significantly impact plant abundance and shift species composition towards less palatable vegetation (Augustine and McNaughton 1998), or change plant architecture (Ford et al. 2014). In this way, adding a "super-predator" to the system can have impacts extending throughout the community, ultimately restructuring physical ecosystem properties (Beschta and Ripple 2012).

Activities associated with human development have varying and, in some cases, opposing influences on trophic dynamics. Development can limit carnivore populations via direct mortality or indirect behavioral avoidance. At the same time, development can enrich browse quality by providing indirect bottom-up subsidies to prey via nutrient deposition. Exhaust from automobiles and fertilized runoff can release biologically reactive nitrogen into the air and water, increasing primary productivity and enhancing nutrient content in herbivore forage (Vallano and Sparks 2008). Furthermore, human development in forested habitats often involves land clearing, increasing the amount of edge-impacted forest. Greater availability of edge habitats can have numerical and behavioral impacts on the populations of edge-adapted species (Fahrig 2003).

Changes in anti-predator herbivore strategies -- spatial or behavioral -- are likely to influence primary producers. Herbivore removal of plant tissue can reduce photosynthetic output, retard growth, delay the onset of reproductive maturity, and

increase plant stress and mortality (McGinley and Whitham 1985, Bergelson and

Crawley 1992); in some cases,   herbivores exert a controlling effect on plant

community composition (Augustine and McNaughton 1998). More subtly, browsing

frequently alters plant architecture, resulting in an overall shorter, bushier growth

form (Bell et al. 2012) which can benefit herbivores. As branches are repeatedly

pruned, a plant grows wider rather than taller, keeping branches low and within reach

for subsequent browsing (De Jager and Pastor 2010). Furthermore, removing apical

meristems promotes lateral bud development, increasing the number of branches and

leaves produced by an individual plant within browse height (De Jager and Pastor

2010). Ultimately, this feedback means that browsing allows herbivores effectively

cultivate more forage for themselves.

Here, we studied the dynamics of pumas (*Puma concolor*), black-tailed deer

(*Odcoileus hemionus columbianus*), and woody plant species in the context of human

development. We addressed four interlocking hypotheses to elucidate the nature of

the interactions among these species: 1) human activity drives puma feeding site

selection, 2) predation risk influences deer habitat selection and behavior, 3) deer

prefer to browse in low risk areas, and 4) preferential use of low risk areas will

influence woody plant architecture (Figure 2.1). We studied these dynamics in the

Santa Cruz Mountains. However, pumas, deer, and woody plants are each widely

distributed across the Americas, making the results of this study highly applicable to a

broad geographic area. As the human population grows, it further increases the

likelihood and spatial extent of these interactions.

MATERIALS AND METHODS

Study Area

We conducted our study in the Santa Cruz Mountains in California, southwest of Silicon Valley. The climate is Mediterranean with warm, dry summers, and cool, wet winters. Most of the annual precipitation occurs in the form of rain falling between November and April. Our 1,600km^2 study area ranges from sea level to approximately 1,155m in elevation, with two distinct climactic zones: coastal climate on the west side, and inland to the east. The coastal side is cooler and wetter, with an average of 77cm annual precipitation, an average summer high temperature of 20°C, and an average low is 7.5°C. Vegetation is dominated by mixed evergreen forest, with redwood (*Sequoia sempervirens*), tanoak (*Lithocarpus densiflorus*), coast live oak (*Quercus agrifolia*), and Douglas fir (*Pseudotsuga menziesii*), interspersed with chaparral and open grassland. In areas adjacent to the ocean, there are remnant coastal prairies and coastal scrub. On the inland side of the study area, the average precipitation is 46cm, the average summer high is 33°C, and the average low is 1°C. Vegetation is dominated by chaparral on the south-and west-facing slopes, with mixed oak (*Quercus spp.*), bay laurel (*Umbellularia californica*), and tanoak on the north-facing slopes, and patches knobcone pine (*Pinus attenuata*) at higher elevations. In both climactic zones, vegetation community is highly diverse and heterogeneous, depending upon the distance to the ocean, elevation, slope, and aspect. In the dry season, herbaceous plants die back and mostly woody species remain. The

study area encompasses a spectrum of human development and protected lands, creating a mosaic of land use. There are large blocks of preserved habitat managed by state, county, and city parks as well as private entities. Interspersed are human-dominated areas that range from rural to urban development with housing density ranging from 0 to 40 units per acre, as well as many trails, fire roads, residential roads, and highways.

Animal Captures and Monitoring

We captured free-ranging pumas from 2008-2014 with cage traps, leg hold snares, or trailing hounds as described in Wilmers et al. (2013). Individuals were tranquilized using Telezol and outfitted with a GPS/VHF tracking collar (Vectronics Aerospace GPS PLUS model, Mesa, Arizona, USA). Collars were programmed to acquire a GPS fix every 4 hours. Data were remotely downloaded monthly via UHF, or transmitted via cell phone towers every 1–3 days depending on collar program configuration and local cell phone coverage. The puma capturing, handling, and monitoring protocols for this research were approved by the Animal Care and Use Committee at the University of California, Santa Cruz (protocol #Wilmc1101), and approved by the California Department of Fish and Wildlife.

Statistical Analyses

We used program R version 3.0.0 (R Core Team 2013) for our statistical analyses. Before performing each statistical analysis, we tested each continuous

variable data set for normality with Shapiro–Wilk's normality test and tested for homoscedasticity of variance with Levene's test. Non-normal data were transformed as noted below.

Top Trophic Level: Human influence on puma hunting behavior

We analyzed the spatial relationship between puma feeding sites and human development to model how habitat variables influence feeding site selection and, by extension, deer predation risk. We created a resource selection function (RSF) (Manly et al. 2002) and compared habitat features of "used" and "available" points.

First, we identified "used" points (puma feeding sites) using puma GPS collar data. We adapted an algorithm developed by Knopff et al. (2009) to identify spatially aggregated GPS locations as potential puma feeding sites for large prey items. We verified these locations with field site visits (for full feeding site identification and cluster investigation methods, see Wilmers et al. 2013). Pumas with only one verified feeding site were eliminated from the analysis, as were juveniles and kittens. We investigated 777 sites identified as potential puma feeding locations from 25 pumas (15 females and 10 males), and identified prey remains at 265 GPS clusters. Next, we drew random, "available," comparison points from within each puma's home range. We created a 95% minimum convex polygon (MCP) from each puma's GPS collar data. Then, we generated random points from each MCP at a rate of 5 available random points for each used feeding site location (e.g. Johnson and Gillingham 2005).

We quantified habitat data by extracting underlying GIS layer information for the used and available points in ArcGIS. We created a distance to feature raster layer for each anthropogenic features (roads and structures), and landscape features (rivers and lakes). Each raster layer had a resolution of 30m. We categorized roads into two groups depending on their speed limits; arterial roads with speed limits of 35mph or greater, and neighborhood or fire roads with speed limits below 35mph. We created a housing density map by combining county-level spatial housing data with digital aerial photos of the study area. We superimposed the two layers and hand-selected visible structures absent from the housing data. We then created a housing density raster layer by applying a kernel with a scale parameter to the location of each structure and summing the resulting densities. In order to evaluate how best to model puma behavioral responses to housing density, we used a variety of scaling parameter values and chose the most appropriate value based on model results.

We used four scales of vegetation cover type to determine which resolution was most appropriate for our analysis (US Geological Survey, Gap Analysis Program (GAP). May 2011. National Land Cover, Version 2). The scales range from a resolution of 26 vegetation community types, to a binary vegetation layer in which '0' is open habitat and '1' is habitat where the year-round dominant vegetation is sufficient cover to conceal a stalking puma. We defined vegetation sufficient to conceal a puma as shrubby plants or trees growing to puma shoulder height (52 cm) or above.

Predation Risk Model

We created a resource selection function (RSF) to predict habitat risk across the landscape (Manly et al. 2002). Resource selection functions allow us to model the proportional probability of use of a resource by comparing used versus available resource units (Boyce et al. 2002). These types of models are able to incorporate categorical and continuous covariates, nonlinear relationships, and autocorrelation, and have emerged as an appropriate tool for modeling landscape predation risk (Hebblewhite and Merrill 2008). Feeding site locations served as the used points in our RSF model. Each of the *i* model variables, *x*, was normalized as follows,

$$x_i^{\text{norm}} = (x_i - x^{\text{mean}})/std$$

We modeled the relative probability of resource use with a generalized linear mixed effects model with a binomial link (LMER package in R version 2.15.0). Used/available was our binomial dependent variable, and habitat variables were fixed effects. In order to account or variation in individual preferences, we included individual puma identity as a random effect. We selected the best model by comparing ΔAIC values for full and reduced models.

We included anthropogenic feature, vegetation, and topographic feature covariates as predictor variables in our model. In order to determine which housing density kernel was appropriate for analysis, we varied the housing density scaling parameter from 10m to 200m in 10m increments and 200m to 600m in 100m increments and compared competing models using ΔAIC. We used the same process to determine the appropriate vegetation classification scheme. In order to determine

which resolution was the most appropriate resolution for analysis, we compared the ΔAIC for each full model, as well as each full model plus one vegetation classification level.

Next, we used the predation risk model to determine which areas were less likely to be used as puma feeding sites, or low predation risk areas. The model output is a relative predation risk probability, which we bounded between 0 and 1. We considered a relative probability of 25 percent or below to be low risk and a relative risk of 75 percent or above to be high risk. Human development was the single strongest factor influencing predation risk for deer. As such, we held other variables constant and varied housing density to determine high risk and low risk sites. We measured the average distance between high and low risk areas to the nearest edge of human development. The average distance between human development and predicted low risk areas was 70m, and the average distance between human development and high risk areas 340m (Figure 2.2).

Middle Trophic Level: Puma influence on deer behavior

We conducted a randomized block design study to test the impact of housing density and predation risk on deer behavior. We established 15 pairs (1 low risk and 1 high risk) of forested plots across the study area; each pair of plots is referred to here as a site. Low-risk plots were located between 70 and 100 m from the nearest human development, while high-risk plots were 340-400m away from development. This arrangement provided one experimental factor (risk) with 15 replicates for each of the two levels. We selected plots within closed-canopy forest and matched vegetation type within pairs (e.g. paired redwood low-risk plots with redwood high risk plots, paired mixed deciduous stands, etc.) to minimize site-level habitat

differences. We then verified our design by comparing the plots with statistical tests. We used paired t-tests to compare slope, aspect, elevation, distance to edge habitat, and the distance to the nearest river as determined from GIS layers (Bates 2015). All plots were located within forested areas, and edge habitat was defined as boundaries between changes in habitat (e.g. forest to grassland or forest to shrubland). We took digital hemispherical canopy photos using a fish-eye lens facing north, mounted at a height of 1m above the ground and calculated the percent canopy closure using Gap Light Analyzer v.2 (Frazer et al. 1999). We used a paired t-test to validate whether plots within sites were similar in canopy cover.

To evaluate the potential influence of anthropogenic alteration of N availability and potential corresponding changes in browsing rates in high versus low risk sites, we measured foliar nitrogen. During the last week of April and the first week of May 2013, we collected tanoak leaf samples from all plots. Tanoak was selected for analysis because it was the most heavily utilized browse species and found in all sites. Ten leaf samples were collected from each plot. Plants were chosen randomly along the browse survey transect, and samples were taken from the current year's growth on branches originating from a height of 20 to 50cm. Collected leaves were stored in coin envelopes and dried at 65°C for 48 hours.

We clipped off a 0.10g sample from each leaf and pooled samples by plot. The pooled sample was homogenized in a ball-mill grinder for seven minutes to create a fine powder. Three milligrams of each pooled sample were loaded into tin capsules, and stored until the time of analysis. Leaf nitrogen and carbon

concentrations were measured by Dumas combustion using a Carlo Erba 1108 elemental analyzer. All analyses were conducted at the University of California, Santa Cruz Stable Isotope Laboratory. We transformed percent N with a reciprocal transformation and used paired t-tests to compare N content of leaves from high- versus low-risk plots.

We deployed a digital motion-detecting camera (Bushnell Trophy Cam HD; Bushnell Corp., Overland Park, KS, USA) on a game trail in each plot from the winter of 2012 through winter of 2013 in order to collect data on deer use. Cameras were mounted on a tree at a height of 0.5 to 1m, and programed to take three photos when triggered, with a one-minute lag period between trigger bouts. Deer cannot be uniquely identified with accuracy, so we calculated a relative index of deer activity for each plot (number of deer photos recorded / number of days the camera was deployed at that plot). We compared deer activity in high risk versus low risk plots using a paired t-test. Deer activity data were non-normal, so we experimentally tested a series of transformations and $x^{0.2}$ normalized the data the best.

In the winter of 2013, we conducted a second round of camera trapping to collect data on deer vigilance. Cameras were set to record video for 1 minute at a time with a 1 second lag time between recording bouts, and were deployed with 1 liter of certified weed free alfalfa pellets. The pellets served as a standard forage in order to capture deer feeding behavior while controlling for differences in forage quality. Deer monitoring activities were approved by the Animal Care and Use Committee at the University of California, Santa Cruz (protocol Wilmc1308), and

approved by the California Department of Fish and Wildlife. Focal observations were scored for each deer video (Table 2.1). We measured the percent time deer spent vigilant, feeding, or moving. We compared the amount of time spent exhibiting vigilance behavior in high risk and low risk plots using a paired t-test.

Lower Trophic Level: Deer influence on plants (Herbivory and N)

In the fall of 2013, we surveyed woody plant species and browse pressure in each of the paired plots used in the camera trapping study. In the Mediterranean climate of the Santa Cruz Mountains, the majority of plant growth occurs during the wet winters (Gogan and Barrett 1995). We conducted a browse survey in the fall, after peak summer woody plant utilization, and before the start of the next year's growth period. In addition to being a critical summer food source, woody species persist year-round and hold the marks of current, as well as previous, herbivory. This standing record can serve as an important metric for assessing deer perceptions of predation risk across space and time (Beschta and Ripple 2013).

We used a line-intersect method, as described by Cummings and Smith 2000 to measure woody plant species composition, abundance, browse availability, and browse use. All woody vegetation within a 1m band on either side of a 25m transect tape and a height below 2m was counted and measured. Data were collected on broadleaf species for all branches and parts of branches 2m and below, as 2m is the maximum height deer can reach (Gill 1992). We only surveyed browsing on the unbranched growth of the current year. For each woody plant within browse height

encountered along the transect, the following data were collected: species, number of bites available, the number of bites taken, and rank of evidence of previous browse on branches older than this year's growth (0= none, 1= one or more browsed branches). Bites were defined as a group of leaves likely to be taken as a single bite based on size and position on the branch, or as bitten stem ends/groups of bitten stem ends of similar size and orientation. Deer herbivory can be distinguished from rodent herbivory based on the physical properties of the bite marks (Swift 2014).

We examined similarity in the species composition of woody plants within browse height within sites using nonmetric multi-dimensional scaling (NMDS) of Bray-Curtis similarity estimates. We visually assessed potential spatial grouping of points in the similarity plots (Legendre and Legendre 1998). We also compared the density of browsable plants in low risk and high risk sites using a paired t-test.

We compared herbivory pressure in low- versus high-risk plots in several ways. First, we calculated percent consumption by dividing the number of bites taken by the number of bites available (taken plus remaining) for each plot. We also calculated a relative index of browse pressure per deer unit by dividing the number of bites taken by the number of deer photographed per day. We compared each measure of browse intensity using paired t-tests. We transformed the percent of plants with evidence of previous browsing with a square root transformation and then compared high- and low-risk plots with a paired t-test.

We also tested whether deer were selecting browse species at random using an electivity index:

$$E_i = ln\left[\frac{r_i(1 - p_i)}{p_i(1 - r_i)}\right]$$

where r_i, is the proportion of bites taken from species i and p_i is the proportion of bites of species i available. Electivity index values greater than zero indicate a preference for that species, and values less than zero suggest avoidance. We calculated X^2 values to evaluate the statistical significance of E_i based on one degree of freedom (Jenkins 1979):

$$X^2 = \frac{E_1^2}{\left(\frac{1}{x_i} + \frac{1}{m - x_i}\right) + \left(\frac{1}{y_i} + \frac{1}{n - y_i}\right)}$$

where x_i is the number of bites taken of species i, y_i is the number of bites of species i available, m is the total sum of bites taken across all species, and n is the total number of bites available across all species.

RESULTS

Deer abundance and anti-predator behavior

We found no significant differences in slope, aspect, elevation, canopy cover, or distance to forest edge between high- and low-risk plots (Table 2.2). We also found no significant difference between leaf nitrogen in low-risk (1.24 ±0.07se) versus high-risk plots (1.26 ±0.10se) (Table 2.3).

We recorded a total of 52,260 camera trap photos collected from 30 trapping stations, each deployed for an average of 400 days (±17 se). In addition, we captured 1930 minutes of deer videos from 28 cameras. Seven out of 28 cameras failed to

collect adequate numbers of feeding bouts for behavioral analysis. Deer spent on average 25.8% (±2.4se) of their time displaying vigilant behaviors in low-risk sites and 24.1% (±2.5se) of their time displaying vigilant behaviors in high-risk sites and this difference was not significant (Table 2.3). There were nearly three times as many deer visits per camera day in low risk plots (2.94 ±1.00se) than in high risk plots (1.13 ±0.30se) (Figure 2.3).

Plants and browse pressure

There was no spatial segregation within the Bray-Curtis similarity plots, indicating that high- and low-risk plots within sites had indistinguishable species composition. We also found no significant difference in the density of individual browseable plants in low risk (0.48 plants/m^2 ±0.06se) versus high-risk (0.48 plants/m^2 ±0.07se) plots (Table 2.3). However, there were nearly 20% more total bites available in low risk plots (6.90 ±0.43se) than in high-risk plots (5.79±0.35se) (Table 2.3). Furthermore, in low risk plots, deer utilized available forage at a rate five times higher than in high risk plots (mean$_{low risk}$= 35.82% ±1.98se, mean$_{high risk}$= 7.94% ±1.07se) (Table 2.3). There was no significant difference between high- and low-risk sites with respect to bites taken per deer unit (Table 2.3). In addition, the percent of plants showing evidence of browse from previous years was higher in low-risk plots (94.29% ±1.26se) than it was in high-risk plots (87.79% ±3.46se) with a large effect size (ϕ=0.6, Table 2.3).

56

Deer significantly selected against tanoak, which constituted 42.3 percent of all bites taken and 73.6 percent of bites available, against huckleberry, which constituted 0.4 percent of stems browsed and 65.6 percent of stems available, and against hazelnut, which was 2.7 percent of stems available. Deer selected for coast live oak (*Quercus agrifolia*), which comprised 47.8 percent of all bites taken but only 25 percent of bites available.

DISCUSSION

Our data are consistent with a human-initiated trophic cascade. In high predation risk plots farther from human disturbance, we see a sequence in which a top predator, the puma, exerts pressure on subsequent trophic levels with alternating relationships of inhibition and release (Figure 2.1). In low predation risk plots close to human structures, we see the non-consumptive impacts of a super-predator (humans) on puma feeding site selection, with corresponding alternating influences on pumas, deer, and plants. Woody plants below a height of 2m were released from herbivory in high risk areas, and more heavily browsed in human-dominated areas. The end result is that woody plants growing near human development grew bushier than their counterparts in habitats identical in aspects other than predation risk. This pattern creates an advantageous feedback for deer: by promoting dormant bud development, deer create more browseable branch ends, effectively pruning plants to create more forage in preferred, low risk habitat (De Jager and Pastor 2010) (Figure 2.1).

Sub-lethal herbivory induces changes in plant architecture that can change community-level feedbacks. Changes in plant structure can influence competitive interactions between insect species, plant-pollinator interactions, relationships between plants and fungal pathogens or microorganisms (Ohgusi 2005), and nutrient turnover (McNaughton et al. 1997). Increasing structural complexity in plants increases the number of microhabitats, supporting a greater number of species (Bell et al. 2012, Ripple and Beschta 2012).

Although we did not detect any differences in the browse layer composition of high- vs. low-risk plots, this may reflect the lagged effect of increased browsing as human development has expanded in the Santa Cruz Mountains. Tolerant trees and shrubs can survive for long periods in a suppressed, heavily-browsed state (Augustine and McNaughton 1998), delaying the emergence of herbivore-induced changes in forest composition. Our electivity analyses indicate that deer preferentially select coast live oak, a species that is deer-limited in some systems (Tyler et al. 2006, Tyler et al. 2008), while under-consuming the much more abundant tanoak. If deer browsing significantly affects young tree survival, selective browsing could alter woody plant composition over the longer term.

The changes in plant architecture we detected were brought about by herbivore anti-predator behavior. Two common anti-predator strategies employed by prey include modifying habitat selection and changing foraging behavior (Lima and Dill 1990). Other studies have documented prey animals capitalizing on the protection against predation garnered by situating themselves in close proximity to

human activity (Martin and Szuter 1999, Hebblewhite et al. 2005, Berger 2007). For example, Hebbewhite et al. (2005) found that wolves in Banff National Park avoided areas with greater human activity. As a result, elk spent more time near human structures. Similarly, pumas in our study area avoided areas occupied by humans. As a result, deer increased their visitation to plots closer to human structures, increased their browsing rate while they were there, and consumed a greater percentage of the available forage in low risk areas. We did not see the pattern we predicted with vigilance, but that is likely the result of low sample size.

In contrast to other studies, the patterns in deer habitat use we saw were likely demonstrative of fine-scale behavioral modification within an individual. Non-migratory mule deer, like those found in the Santa Cruz Mountains, have steady home ranges of roughly 1.3 km^2 for females and 2 km^2 for males (Taber and Dasmann 1957), which means that the low risk and high risk plots in our study could be within the home range of a single individual. Rather than observing population-level differences in habitat use, our study highlights individual selection for particular areas within their home ranges.

In order to ensure that the relationships we describe were derived from human-induced changes in predation risk, we explored potential alternative explanations for the observed increases in deer activity near human development (Augustine and Naughton 1998). Deer are an edge-adapted species and could have been selecting for preferred edge habitat with a more well-developed understory, rather than protection from predation. We measured distance of the plot to the closest

habitat edge, canopy closure and the number of plants within browse height within each plot, and found no significant difference between low risk and high risk plots in any of these metrics.

A second alternative explanation to higher browse pressure in plots close to human development is that deer were responding to increased anthropogenic resources, such as irrigated landscapes, gardens, or other human-derived subsidies in adjacent developed areas (Fenn et al. 2003). Deer were not individually identifiable, so we were unable to discern between increased browsing activity of resident deer versus collateral browse from increased numbers of deer passing through on their way to a human-provided attractant. However, our comparison found no significant correlation between risk level and the number of bites taken per deer unit, suggesting that deer spent more time in low risk areas, and fed there at the same rate as they would feed elsewhere, resulting in heavier browse pressure in safe areas.

A third alternative explanation is that deer were attracted to plots closer to human-dominated areas by differences in resource availability. Fertilizer and pollution from human-altered landscapes can increase plant growth rates (Fenn et al. 2003) or enhance tissue chemical composition (Vallano and Sparks 2008), by extension, increasing foraging reward in plots near development. However, when we measured leaf nitrogen, we found no significant differences between high- and low risk plots. In total, our exploration of alternative hypotheses leads us to the conclusion that increased browse pressure in low risk plots reflects increased

protection against predators rather than differences in proximity to preferred edge habitat, woody plant availability, or the nutritional content of plant tissues.

Extending these results beyond our local study area, these trophodynamics are likely playing out over a large spatial extent. Pumas can be found across the Americas, from the southern tip of South America to the sub-Arctic. Cervids are even more widely distributed, as are the woody plants they consume. Low-density exurban development is projected to increase by over 75% in the next 25 years (Alig et al. 2004), and so will the urban-wildland interface where anthropogenic activities abut wild habitats. The dynamics described here are likely to accompany human development, altering trophic relationships and species interactions across a broad area.

One feature that sets this study apart from others is that this system experienced changes in predator functional response rather than numerical. It is far more common to study these dynamics in a system in which a human-induced mortality event changed predator density, rather than altering local predator abundance via behavioral avoidance (Estes and Palmisano 1974, Power 1990, Terborgh and Estes 2010, Ripple and Beschta 2012, Beschta and Ripple 2013).

Our results support the findings from Wilmers et al. (2013) that pumas select feeding sites in a manner to avoid human development. We then extend the results of Wilmers et al. (2013), demonstrating how puma-human dynamics influence lower trophic levels. Human activities can lead to many indirect and unintended consequences. Though the impacts may be subtle at first, compounding these

influences over space and time could cause substantial and difficult to remedy ecosystem-level shifts. There are rich literatures about the effects of human development on surrounding ecosystems, as well as on trophic cascades. However, this is the first study to trace a human-initiated trophic cascade through an ecosystem and link it to changes in plant architecture. In order to quantify the influence that altering plant structure has on the surrounding ecosystem, future research is needed to investigate how observed differences contribute to changes in individual plant life history, as well as local bird, invertebrate, or non-woody plant species composition.

A)

B)

Illustration by Corlis Schneider

Figure 2.1: Pumas avoid hunting near human development, making habitat close to humans more attractive to deer. In response, deer use development as a shield against predation and increase their activity in those areas. They spend more time browsing in those sites, which removes new growth and promotes lateral bud development. The heavier browse pressure increases structural complexity in woody plants near

human development. All together, the human-induced cascade makes bushes bushier (panel A), than in areas farther from humans where pumas are more active, deer decrease their foraging activity, and woody plants grow fewer branch ends (panel B).
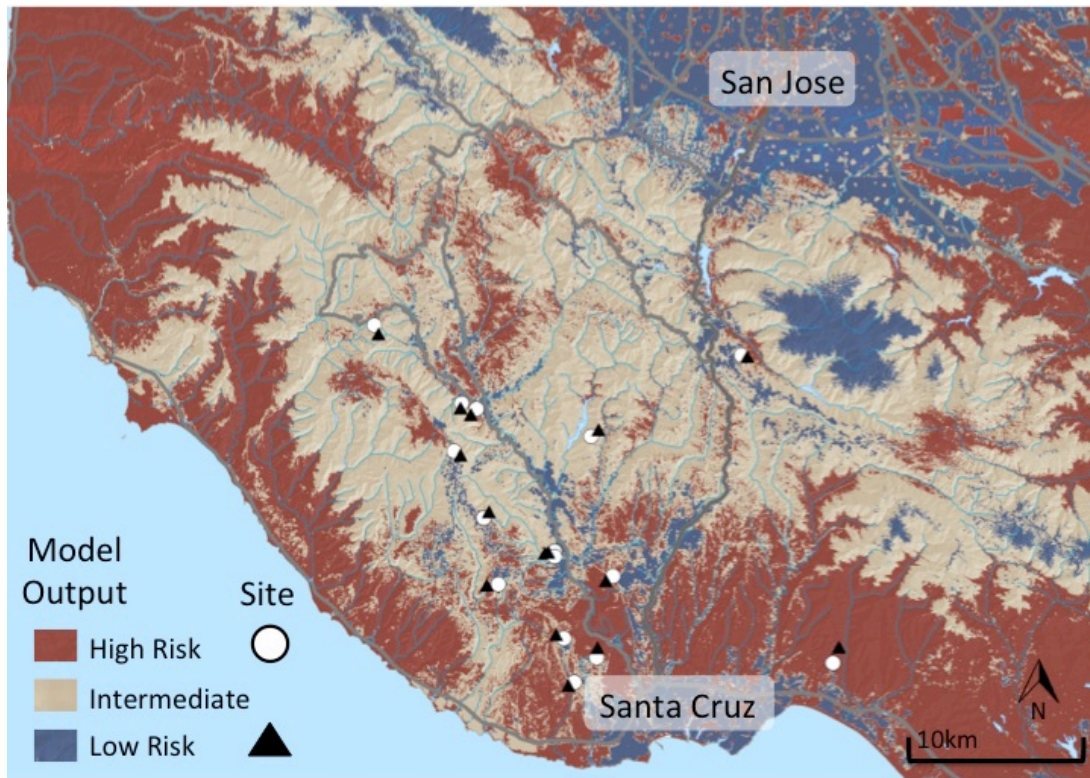
Figure 2.2: Predation risk map in which blue shows modeled low predation risk areas and the red shows high predation risk areas. Paired plots were placed with one plot in a high risk area (black triangle) and one in a low risk area (white circles). All sites were placed in closed canopy forest and we controlled for differences in slope, aspect, canopy closure, and forest composition within pairs.

a) b) c)

Risk Level
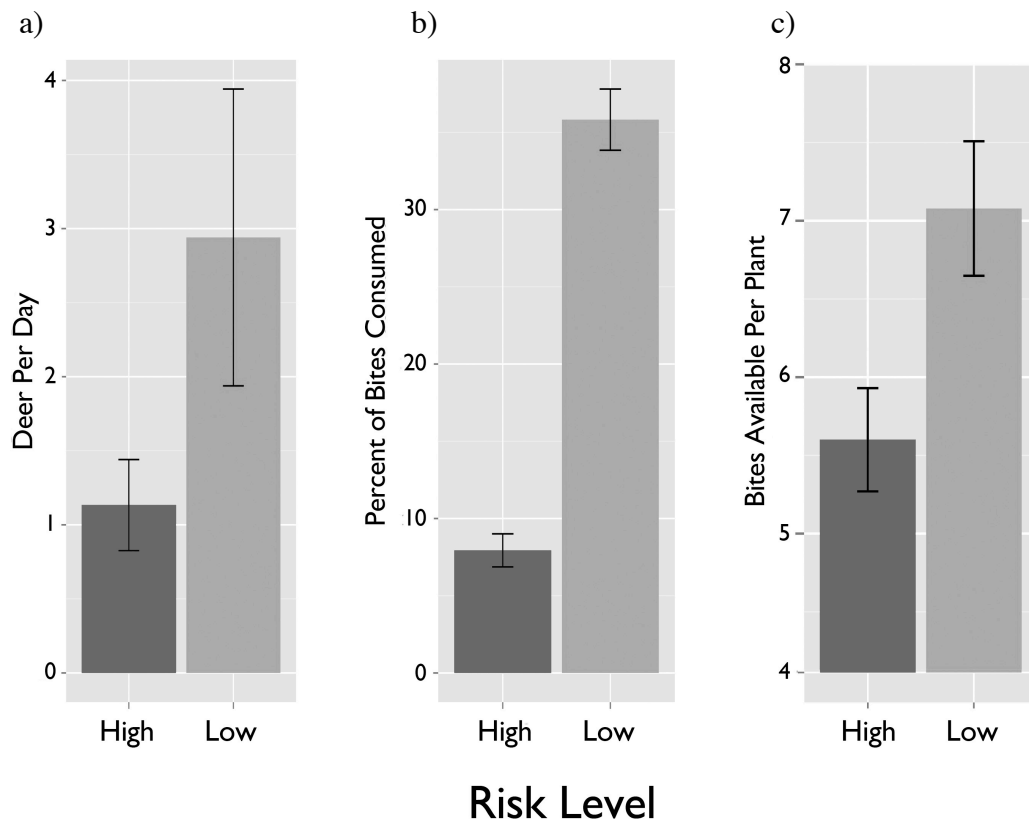
Figure 2.3: Comparisons of the number of deer photographed per day, the percent of available bites consumed by deer, and the bites available per plant in high- vs. low-risk plots. Bars represent mean values and error bars represent standard error around the mean. All comparisons were significant in paired t-tests ($p<0.05$).

Table 2.1: Descriptions of each deer behavior measured during video focal observations following Benhaiem et al. (2008).

Behavior	Definition
Vigilant	Head raised above shoulders while scanning the vicinity
Vigilant - Chewing	Vigilant while chewing
Vigilant - Other	Unable to discern type of vigilance
Feeding	Head down while gathering food
Scanning	Head below shoulder level without gathering food
Moving	Walking, trotting, or running
Moving - Chewing	Walking around with head up while chewing
Bedded	Bedded down
Other	Other

Table 2.2: Physical properties comparisons made between high and low risk plots. We compared plot characteristics using a paired t-test with the site as the pair. None of the habitat variables we measured differed significantly between high and low risk plots. (DF for each comparison was 13).

Physical Property	$|t|$	P
Slope	0.61	0.55
Elevation	1.37	0.19
Distance to Habitat Edge	1.69	0.11
Aspect - North	0.11	0.91
Aspect - East	0.30	0.77
Distance to River	0.19	0.85
Canopy Closure	0.53	0.60

Table 2.3: Comparisons made between pairs of high-risk plots far from human development and low-risk plots near human development. All analyses were paired t-tests with df=13. Asterisks denote significant p-values.

Comparison	$|t|$	P	
Leaf Nitrogen	0.20	0.84	
Browsable Plant Density	0.27	0.79	
Bites Available	2.18	0.03	*
Previous Browse	2.38	0.03	*
Percent Browse Utilized	4.74	<0.01	*
Bites Taken per Deer Unit	0.89	0.33	
Deer Visit per Day	2.19	0.04	*
Time Spent Vigilant	0.39	0.71	

Table 2.4: Browse availability, consumption, and electivity index for woody species within browse height in the plots. A positive electivity index indicates a preference for a given species and a negative electivity index suggests avoidance of that species.

Species	Bites available	% Bites taken	% Of all bites browsed	Electivity	
Tanoak	2496	19.0	49.4	-0.92	*
Coast Live Oak	952	47.8	47.4	1.45	*
Woodrose	54	14.8	0.8	-0.67	
Bay Laurel	9	55.6	0.5	1.31	
Hazelnut	105	7.6	0.8	-1.43	*
Huckleberry	166	2.4	0.4	-2.67	*
Blackberry	22	22.7	0.5	-0.14	

* Indicates whether the preference or avoidance was significant for a given species ($p < 0.05$)

Comparing and integrating GPS- and stable isotope-based methods for estimating carnivore diets

ABSTRACT

Quantifying large predator kill rates and prey selection is a central focus in community ecology, but these data are often difficult, time-consuming, invasive, and expensive to collect. Stable isotope analyses allow researchers to non-invasively estimate the relative contributions of different prey items to carnivore diets, but these methods have not yet been compared to more conventionally used GPS cluster investigations, or evaluated for their potential to estimate predator kill rates. We reconstructed puma (*Puma concolor*) diets using stable isotopes of N and C from hair samples collected from 68 individuals, and compared these with prey composition by the same individuals estimated from 631 feeding sites located using GPS collars. Large ungulates comprised a minimum of 92 percent of prey biomass regardless of estimation method. The remaining biomass was comprised of raccoon, opossum, and house cat, in decreasing order of importance. We then combined prey biomass estimates with energetic models to calculate the minimum number of prey required to sustain a puma. According to the stable isotope estimates, females kill on average 32.6 deer equivalents (deer or pig), 1.9 raccoons, 10.7 opossums, and 1.8 house cats in order to meet their energetic demands, while males kill on average 34.0 deer equivalents, 3.4 raccoons, 20.0 opossums, and 2.9 house cats. Stable isotope analyses and GPS cluster methods showed statistically similar prey item use at the population

level, but differed significantly at the individual level. At both the population- and individual-level, stable isotope methods predicted a greater representation of small prey items than did GPS methods, but this difference was significant at the individual-level. Predicted kill rates of deer were similar to our previous estimate of kill rates using GPS methods by male pumas but were less than what we had predicted for females, possibly due to the fact that females kill for both themselves and their cubs. Further honing dietary estimation tools builds opportunities for improving future conservation efforts.

Large carnivores play a key role in shaping community dynamics. They exert top-down pressure, regulating prey density and composition, with rippling influences on broader community structure (Estes & Palimisano 1974, Peckarsky et al. 2008, Estes et al. 2011). Evaluating their ecological influence by documenting prey selection and kill rate has been a major focus of carnivore research (Anderson & Lindzey 2003, Vucetich et al. 2011, Elbroch et al. 2014, etc.). Understanding kill rate and prey selection has allowed researchers to gain insight into a multitude of community-level interactions such as scavenger facilitation (Wilmers and Post 2006), apparent competition (DeCesare et al. 2010), and trophic downgrading (Estes et al. 2011). Interactions between carnivores and their prey have strong economic and social consequences in addition to ecological importance (Treves & Karanth 2003, Ripple et al. 2014). Consequently, collecting accurate data on prey composition and kill rates are essential to promoting appropriate conservation measures and management (Beschta & Ripple 2012).

Large home ranges and cryptic behavior make directly observing wild carnivore kill rates difficult. As such, there have been many indirect methods employed for describing carnivore diet, each with its own strengths and weaknesses. Global positioning system (GPS) tracking technology is the prevailing tool for quantifying carnivore diets. Technological advances in GPS tracking devices deployed on carnivores have revolutionized researchers' ability to find feeding locations and study diet composition and, by extension, community interactions (Knopff et al. 2009, see

review Wilmers et al. 2015). This technique uses tracking collar data (telemetry or GPS) to locate prey remains at kill sites. Animals are limited by the amount of food they can consume in one feeding bout, so when a carnivore has successfully killed a large animal, they tend to remain near the site as they consume their prey over the course of hours or days. Researchers use spatially and temporally aggregated GPS locations, or GPS clusters, generated by this lingering behavior as an indication that the location may be a kill site, and may visit these locations to identify prey remains.

GPS cluster investigations are being utilized as a reliable means for analyzing carnivore diet composition (Knopff et al. 2009, Hebblewhite et al. 2005, Wilmers et al. 2013, etc.), however, they have a few key shortcomings. First, this method relies on protracted prey handling time. Prey items that are consumed quickly may fail to produce a detectable GPS cluster, biasing GPS data against small prey items (Zimmermann et al. 2007, Bacon et al. 2011). In highly social animals such as wolves, even large prey items may be consumed too quickly for GPS cluster detection (Anderson and Lindzey 2003). Increasing the frequency of GPS acquisition schedule can sometimes resolve this issue but can also lead to more false positives. Additionally, capturing animals to apply GPS tags is costly and can become increasingly difficult as animals become savvy to capture methods. Finally, carnivores living in multi-prey systems may display a variety of feeding behaviors, and algorithm variables that adequately characterize one prey species may prove inaccurate for others (Sand et al. 2006).

Non-invasive stable isotope techniques could provide a reliable alternative to GPS cluster investigations for determining large predator kill rates and prey selection. Stable isotopes can be an effective and cost-efficient tool for understanding foraging ecology, trophic positioning, habitat use, and movements of species (Ben-David & Flaherty 2012). However, this method has yet to be compared to widely-used GPS cluster methods. It relies on the mechanisms by which stable isotopes of carbon (C) and nitrogen (N) are transferred through food webs in a predictable pattern as a result of biochemical processes (McConnaughey and McRoy 1979). For example, the ratio of $^{15}N/^{14}N$ typically increases with trophic level, primarily as a result of metabolic processes that discriminate against the light isotope. In contrast, $^{13}C/^{12}C$ ratios are affected by photosynthetic pathways and nutrient utilization, and are typically used as an indicator of the foraging habitat (Ben-David & Flaherty 2012). Together, stable isotope values found in hair, blood, or tissue can be used to infer foraging activities during the time of tissue growth (Ben-David & Flaherty 2012).

Isotope data can be used as simple tool for measuring foraging behavior, and stable isotope mixing models can be employed to estimate the contribution of specific prey sources to consumer diets (McConnaughey and McRoy 1979). Bayesian mixing models estimate the proportional contribution of assimilated prey to a consumer's diet using data on the isotope values in prey and predator tissues, the offset between these tissues as a result of assimilation and other metabolic processes (trophic discrimination factors (TDF)), and their associated uncertainties (Parnell et al. 2010).

75

In order to ensure accurate results, careful attention must be paid to a few key model aspects. Isotopic mixing models can be sensitive to input parameters, and have poor discriminatory power when the isotope values of prey overlap, making appropriate TDF selection very important (Phillips et el. 2005). Validating mixing models typically relies on captive studies where animals are fed a known diet; however, for large carnivores, the diet of captive animals is often less varied and has minimal overlap with the diet of wild animals. In addition, published TDFs are only available for a small subset of carnivores, and calculated values are strongly affected by a variety of factors, including taxonomy, protein content and quality, lipid content, and the isotope values of prey (Phillips et al. 2005). These factors create a need for studies validating diet estimates using isotopes in wild, free-roaming carnivores.

In this study, we compare the results of two methods of carnivore diet estimation: GPS cluster investigations and stable isotope analyses. Our first objective was to evaluate the relative agreement between the two methods for both population- and individual-level diet estimates. We then combined these data with energetic models to estimate annual prey consumption rates for pumas. Males and females have different biological requirements that influence their energetic demands so we estimated male and female kill rates separately (Laundré 2005, Smith et al. 2015). We quantified the relative contributions of the five most frequent prey items in puma diets using GPS cluster investigations and compared those data to isotopic reconstructions from puma and prey hair samples. Pumas are a generalist carnivore with a diet that primarily relies on large ungulates, however diet composition may

vary with prey availability, habitat type, sex, life stage, and proximity to human development (Moss et al. 2015).

MATERIALS AND METHODS

Study Area

We conducted our study in the Santa Cruz Mountains in California. The 1,600 km^2 study area ranged from sea level to approximately 1,155 m in elevation and included two distinct climactic zones: a wet coastal climate on the west side of the Santa Cruz Mountains and dry inland side to the east of the Santa Cruz Mountains. The study area encompasses a spectrum of human development and protected lands, with large blocks of preserved habitat that range from rural to urban development (Figure 1). Habitat types in the study area have been described in greater detail elsewhere (Wilmers et al. 2013).

Puma capture and sampling

We captured free-ranging pumas of all age and sex classes from 2008-2015 with cage traps, or trailing hounds based on established protocols (Wilmers et al. 2013). Individuals were tranquilized using Telezol (Fort Dodge Laboratories, Fort Dodge, IA, USA), aged, sexed, sampled, and outfitted with a GPS/VHF tracking

collar. Puma age was determined using dental characteristics described by Ashman et al. (1983). Body fur samples were collected at the time of capture and stored in coin envelopes in a freezer until they were processed. Additional samples were collected during recaptures and treated as independent samples if the subsequent captures were >6 months from the previous capture event. Tracking collars (GPS PLUS, Vectronics Aerospace, Berlin, Germany) were programmed to acquire a GPS fix every 4 hours, and GPS data were remotely downloaded monthly via UHF or transmitted via cell phone towers every 1–3 days depending on collar program configuration and cell phone coverage.

Diet - GPS Clusters

We adapted an algorithm developed by Knopff et al. (2009) to identify potential puma feeding sites using GPS collar data. The algorithm identifies temporally- and spatially-clustered GPS locations, defined as two points occurring within 100 m and six days of one another. When two points met these criteria, the algorithm calculated the geometric center, searched for additional points within 100 m and six days, and recalculated the geometric center as additional candidate points were identified. This process was repeated until all appropriate points were included within the cluster. We field-investigated potential feeding sites by searching the area for a minimum of thirty minutes, starting at the geometric center and spiraling outwards until we reached the maximum distance between the center and the farthest

78

point associated with that cluster. We identified the species of prey remains based on

hair and bones found at the site, and used a hand-held GPS unit to record the

coordinates of the exact location.

This method allowed us to count the number and type of prey consumed by

each individual. Stable isotope analyses, on the other hand, estimate the relative

contribution of each prey type as a function of biomass. In order to draw appropriate

comparisons between the two methods, we converted the relative contributions of

prey remains located at feeding sites into biomass using the mean mass for each

species described in the literature (Table 1).

Diet - Stable isotope mixing models

Prey hair samples were collected between 2009 and 2015 from the five most

common prey items identified from GPS cluster analyses: black-tailed deer

(*Odcoileus hemionus columbianus*), wild pigs (*Sus scrofa*), raccoon (*Procyon lotor*),

opossum (*Didelphis virginiana*), and house cats (*Felis catus*) (Smith et al. *in press*).

Puma and prey hair were rinsed in petroleum ether to remove surface debris,

homogenized using surgical scissors, and weighed into tin capsules. The carbon (C)

and nitrogen (N) composition of samples were measured using a Carlo Erba

elemental analyzer coupled to a ThermoFinnigan DELTAplus XP mass spectrometer

at the University of California, Santa Cruz Stable Isotope Laboratory. Results are

presented in δ notation and calculated as $\delta^{13}C$ or $\delta^{15}N = [R_{sample} / R_{standard}) - 1] \times 1000$

where R = $^{15}N/^{14}N$ or $^{13}C/^{12}C$ in the sample or standard. The standard for C was Vienna-Pee Belemnite Limestone, and atmospheric N_2 (air) for N. Precision of an internal laboratory standard was less than 0.2‰ for $\delta^{13}C$ and $\delta^{15}N$.

We used a Bayesian-based stable isotope mixing model to quantify puma diet composition (R package SIAR), an isotopic source partitioning model in R programming language (Parnell et al. 2010). Each prey species was statistically distinguishable from each other species in $\delta^{13}C$ and/or $\delta^{15}N$ values (one-way ANOVA followed by Tukey's post-hoc tests, $p \leq 0.05$), thus we included each species as a distinct prey source. Prey isotope values were representative of tissue not assimilated by pumas during consumption (hair), and hair is typically enriched in ^{13}C compared with tissues that would be assimilated (e.g., muscle). To correct for this, a value of - 1.5 ‰ was added to the mean $\delta^{13}C$ values of each prey source (Newsome et el. 2015). We used TDFs of 5.5 ± 0.5 ‰ for $\delta^{13}C$ and 4.1 ± 0.1 ‰ for $\delta^{15}N$ to represent the isotope difference (and variability in that difference) between the estimated prey muscle values and puma hair that occur as a result of metabolism and assimilation into predator tissues (Parng et al. 2014). These TDFs were calculated from captive bobcats fed a diet whole animals and animal parts, which closely approximates a diet of wild felids (Nardoto et al. 2006). Results from the mixing model represent puma diet during the period of hair growth. Pumas have two molts each year, a winter coat grown in November and a summer coat grown in May (The Fund for Animals Wildlife Center, pers. comm).

First, we assessed the agreement between methods for measuring individual puma diet composition. We generated stable isotope diet composition estimates for puma individuals sampled more than once by averaging across the multiple samples. We generated GPS cluster estimates for individuals by averaging GPS data subsampled from similar time periods as represented by hair. We used a two-sample z-test for proportions to compare the relative prey contributions estimated by GPS cluster investigations and stable isotopic analyses of hair samples (Fleiss et al. 2013). In addition, we created a mixed effects model to explore whether there were patterns in small mammal use. Season, percent undisturbed habitat in each home range, and sex were fixed effects variables, puma identity was the random effect, and C13, N15, or C13*N15 were the dependent variables. Prey availability changes with the season as deer fawns become available in the spring and provide a pulse of vulnerable prey. The percent of undisturbed habitat found within each animal's home range served as a measurement of anthropogenic influence. Human activities attract or subsidize synanthropic species, such as opossums, raccoons, and house cats, that could increase local puma consumption of these species.

Then, we compared diet estimation methods at the population level. We compared mean prey composition between GPS cluster methods and stable isotope methods using a two-sample z-test for proportions. Since males and females have different foraging strategies, we compared the two methods within each sex. We found no difference between isotope median and mean prey dietary estimates for any species, so we report prey contributions as means rather than medians. We had a

significant cutoff of p<0.05. All statistical analyses were performed with the program

R version 3.0.0 (R Core Team 2013).

Kill Rate and Bioenergetic Modeling

In order to estimate kill rate, we calculated puma energy requirements, along

with prey energy content, and estimated the number of prey required to meet puma

energetic demands. We examined individual variation in small prey use and how the

two diet estimation methods captured this variation. Field metabolic rates were

generated by Wang et al. (2016). Females averaged 20,334 kJ/day and males

averaged 21,527 kJ/day. The resulting energy requirements do not account for the

costs associated with reproduction; hence these values are representative of non-

reproductive adult pumas. The total available energy per prey species was estimated

using the equation,

$$P_i = \left(M_i - M_{sk_i}\right) E_i$$

where M_i is the mass, M_{sk} the skeletal mass, and E_i is the per kg energy content of

flesh of prey i.

Estimates of skeletal mass were calculated using the scaling equation in Prange

(1979).

Mass estimates and energetic content of flesh of each prey item were obtained from previous studies (Table 1).

RESULTS

Puma capture and GPS cluster prey estimation

Between 2008 and 2015, we collared 56 pumas, investigated 1665 potential feeding sites, and identified 631 locations at which prey remains were present. We restricted our analyses to adults and independent subadults, including 18 females and 18 males with 582 identified prey remains. When measured using GPS cluster data, deer comprised the vast majority of biomass consumed (95.18% ±0.99se) and opossum contributed the least (0.15% ±0.11se) (Figure 2/Table 2). The pattern was the same when we looked at males and females separately as well, however it is worth noting that we only recorded one instance of a male creating a GPS cluster after killing and eating an opossum (36M). There was no prey category in which male and female consumption was significantly different (two-sample z-test for proportion p-values comparing male and female diets for each species: $p_{large\ prey}$=0.42, $p_{raccoon}$=0.34, $p_{opossum}$=0.26 p_{cat}=0.39).

Isotopes

We examined 68 puma hair samples, 35 collected from males and 33 collected from females. Seventeen of these samples came from pumas that were recaptured

over the course of the study (12 were captured twice and 5 were captured 3 times). Female δC13 values ranged from -24.3‰ to -17.7‰, and δN15 values ranged from 5.2‰ to 9.1‰. Male δC13 values ranged from -23.2‰ to -19.2‰, and δN15 values ranged from 6.2‰ to 9.9‰ (Figure 3). Our mixed effects model found no significant influence from season or the percent of undisturbed habitat found within each home range on δC13, δN15 or δC15*δN15. Puma sex had a significant but small influence on N15 (p=0.037, β=0.54); female pumas had marginally lower δN15 values, suggesting their diet consists of a greater proportion of large mammals and males consume a higher proportion of small mammals.

We analyzed 53 prey hair samples from 24 deer, 14 raccoons, 6 pigs, 5 opossum, and 5 house cats (Table 3, Figure 3). Prey hair δC13 values ranged from -25.47‰ to -15.02‰, and δN15 values ranged from 2.89‰ to 7.66‰. Deer had the lowest mean (±SD) δC13 value (-25.47 ±1.16‰) and lowest mean δN15 value (2.89 ±1.49‰). House cats had the highest mean (±SD) δC13 (-15.60 ±0.86‰), and opossum had the highest mean δN15 value (7.66 ±1.22‰). While mean pig isotope values (δC13 -21.50 ±1.25‰, δN15 4.86 ±1.54‰) were statistically different from deer, the two prey groups were similar enough that the model struggled to differentiate prey contributions from either species. To increase our model reliability, pig and deer were combined into a large prey group. Pigs are large prey items that are likely easy to find using GPS clusters, and the cluster data show that pigs make a relatively small contribution to puma diet (2.17% ±5.00), therefore combining these two prey groups should not significantly influence our results.

The Bayesian mixing model results estimate that females consumed a mean

($\pm$SD) of 95.14 $\pm$3.96% large mammals, 2.53 $\pm$2.08% opossum, 1.37 $\pm$1.20% raccoon,

and 0.96 $\pm$0.84% house cat. Males consumed a mean ($\pm$SD) of 91.96 $\pm$6.42% large

mammals, 4.37 $\pm$3.29% opossum, 2.23 $\pm$1.92% raccoon, and 1.45 $\pm$1.24% house cat

(Table 2).

Diet Estimation Method Comparison

At the population level, we found no significant differences between mean

($\pm$SD) puma diet composition estimated with GPS cluster methods versus diet

estimated with stable isotope analyses for large prey items (mean$_{GPS}$=97.35 $\pm$5.93,

mean$_{isotope}$=94.93 $\pm$4.42), raccoons (mean$_{GPS}$=1.88 $\pm$2.1, mean$_{isotope}$=1.23 $\pm$1.08), and

house cats (mean$_{GPS}$=0.62 $\pm$1.02, mean$_{isotope}$=0.80 $\pm$0.69, Table 2). Opossum use

differed significantly ($p<0.05$), with lower use measured by GPS cluster methods

(mean$_{GPS}$=0.15 $\pm$0.65, mean$_{isotope}$=3.03 $\pm$2.23, Table 2). Both methods suggested that

the majority of biomass consumed was derived from large prey items. The relative

order of prey use differed slightly between the two GPS clusters and stable isotope

analyses, however this difference was not significant. GPS cluster diet estimates

ranked prey consumption as large prey >> raccoon > cat > opossum in order of

decreasing importance, while stable isotope diet estimates ranked prey use as large

prey >> opossum > raccoon > cat in order of decreasing importance. When we

compare diet estimation methods within males or females, the only prey category in

which diets significantly differed between methods was opossum use ($p<0.05$). Both

male and female isotope diet estimates indicated greater opossum use than did GPS cluster investigation estimates (Table 2).

In contrast, when we compared individual diet estimations, we did find significant differences between methods (Figures 4 and 5). As we hypothesized, large mammals had greater representation in GPS clusters, while stable isotope methods estimated higher small mammal use. Large prey comprised to 87.3 to 100 percent of puma diets when measured with GPS clusters, while stable isotope analyses estimated large mammal use between 68.0 to 88.0 percent. Within the small prey items opossum showed the greatest difference between methods. GPS cluster methods estimated opossum use to be between 0 and 0.6 percent, whereas stable isotope methods estimated use between 4.8 and 16.2 percent. These results should be regarded with some caution, however, as our sample sizes were quite small. We had a maximum of three hair samples and four GPS sampling periods per individual puma and high variance in prey utilization between samples, leading to low statistical power. These estimates would be more reliable with larger GPS and isotope sample size.

Kill Rate

Female FMR was 8.3×10^6 kJ/year, and male FMR was 9.0×10^6 kJ/year. An individual deer provided the greatest amount of energy per prey item (7.5×10^6 kJ/deer), and a single cat provided the least (6.3×10^4 kJ). Following the diet composition from our isotope mixing model, female pumas would need to consume

32.6 deer equivalents (deer or pigs), 1.9 raccoons, 10.7 opossums, and 1.8 house cats to meet their annual energetic demands. Males would need to consume 34.0 deer or pigs, 3.4 raccoons, 20.0 opossums, and 2.9 house cats each year.

DISCUSSION

We found significant differences between methods when estimating individual diets (Figure 4). We detected higher rates of small prey use with stable isotope estimates than with GPS clusters. Individual stable isotope estimates had an average of 18 percent lower large prey use, 11 percent higher opossum, 4 percent higher raccoon, and 3 percent greater house cat consumption (Figure 5). For example, using stable isotope data, female number 24 had among the highest recorded small prey use among all individuals (over 30 percent in one hair sample), yet we failed to locate any of her small prey kills during our GPS cluster investigations. Similarly, we only detected one opossum kill made by any male in the study (36M), yet isotope data suggest that opossums comprise an average of 8% of male biomass intake. A priori, we know that GPS cluster investigations are likely better suited for detecting large-bodied prey. It follows that, as the smallest prey we measured, opossums would be the most difficult to detect and the most underestimated small prey source.

At a population level, on the other hand, there was no significant difference between diet composition estimates calculated with GPS cluster investigations versus stable isotope methods. This was true whether we compared the population as a whole or by sex. Large-bodied ungulates were the dominant prey type for males and

females, regardless of estimation method. Comparisons of male vs. female diets revealed that female diets consisted of a significantly higher proportion of large prey items than male diets ($p<0.05$, Table 2), a pattern consistent with previous studies (Anderson & Lindzey 2003, Moss et al. 2015). Female pumas are often providing for cubs in addition to feeding themselves, requiring that females acquire a greater quantity of food than they would consume otherwise (Laundré 2005). Large prey items provide a greater quantity of biomass, and may be less likely to be lost to scavengers, providing a better energetic return than small prey items. In contrast, male pumas are territorial, and must patrol their home range for intruders and refresh communication sites. These behaviors may cause males to abandon kills earlier than females (Smith et al. 2015), which may make it more advantageous for them to target small prey that require a shorter handling and processing time.

The similarities in population-level estimates and differences in individual-level estimates could indicate that GPS cluster analyses may be more appropriate for studies addressing population-level questions or trying to quantify kill rates on large prey, while stable isotope analyses may be more appropriate for studies targeting sub-population level diet estimation, or in populations where small prey comprise a greater percent of diet. Alternatively, the difference in agreement between methods could have been a function of data quality. The GPS cluster estimates integrated a large amount of data over space and time at the population level, an advantage our sized individual comparisons did not have. Furthermore, small prey estimates all had proportionally high variance, making detecting population-level differences difficult.

We extended our population-level results by calculating the necessary number of prey pumas needed to kill and consume to meet their energetic demands. We combined our diet composition estimates with an energetics model to predict the quantity of each species required to sustain a puma. Our kill rates were well within ranged determined by previous studies performed in the same region (Smith et al. *in press*).

During our GPS cluster investigations we located an average of 2 small mammal kills per year for males and 2 small prey kills for females. Our energetic-based kill rate estimates suggest that females kill an average of 14 small prey items each year. This would mean that our field investigations failed to locate an average of 12 small prey kills each year for females. This number of kills represents 26.5 percent of annual kills made; however it makes up only a small portion of calories. Our energetic model predicts that males kill 26 small mammals each year, suggesting that we failed to field locate an average of 24 small mammal kills per male per year. These undetected small prey represent 40.2% of annual prey items killed. Though the estimated percent biomass per prey did not significantly differ between methods on the population scale, these data provide further support that isotopes are indeed more sensitive to estimating small prey item consumption.

One factor hindering GPS cluster investigations is that small prey items may be more difficult to find once the kill is no longer fresh. Small prey bones are thinner and easier to chew, enabling pumas to consume a greater portion of each carcass (Ackerman et al. 1986, Wilmers et al. 2003). Smaller kills often leave only clumps of

hair and other trace remains for kill site verification and species identification. In addition, scavengers may scatter what scant parts remain. Large prey remains are almost certainly easier to detect than small prey carcasses, especially after a protracted time between kill date and detection date, potentially over representing large prey items in GPS cluster diet estimates.

Fine-scale data on specific individuals or demographic groups may be very important for targeted conservation efforts. For example, loggerhead turtle populations were in decline and conservation efforts misdirected until models sensitive to distinct demographic groups identified the sub-population in need of protection (Crouse et al. 1987). Similar patterns may emerge when delving deeper into within-population diet data. Large-bodied ungulates comprise the majority of large terrestrial carnivore diets (Gittleman 2013), however, anthropogenic activities may reduce preferred prey, causing carnivores to shift to smaller-bodied prey that have a higher relative abundance (Springer et al. 2003, Ripple 2015). Small prey items, such as opossums, raccoons, and house cats occur more frequently near human development (Ordeñana et al. 2010), and are therefore more likely to be used by pumas whose home ranges encompass areas influenced by humans (Moss et al. 2015, Smith et al. *in press*). Small prey items may be difficult to detect via GPS data alone, making stable isotope analyses an increasingly important tool for studying pumas in fragmented systems.

Clearly understanding prey use can sometimes reveal surprising ecological roles. For example, researchers studying puma scats in La Pampa Provence,

Argentina found that eared doves (*Zenaida auriculata*) comprised 54% of prey items consumed (Sarasola et al. 2016). These doves weigh roughly 113 grams and likely require a handling time insufficient to generate an identifiable GPS cluster. Using stable isotope analyses methods, on the other hand, would likely detect this important dietary component. In this system, GPS cluster methods would likely miss the important contribution doves make to puma diet, and the corresponding ecological role pumas play as a plant seed disperser (Sarasola et al. 2016).

Stable isotope analyses provide an independent technique for evaluating GPS cluster methods. Other methods, such as scat analyses (Perilli et al. 2106), gastric lavage (Votier et al. 2003), or fatty acid analysis (Iverson et al. 2004), are highly invasive and/or have biases of their own. Until GPS devices paired with accelerometers are further developed and calibrated, stable isotope analyses is likely the best method we have for detecting small prey use. Additionally, non-invasive sampling is an increasingly powerful tool for conservation, especially in locations where trapping or other field activities are difficult. Many carnivore species have been eradicated in all but the most remote and rugged terrain. Where remaining habitat which lacks infrastructure and funding for intensive capturing and monitoring, wildlife managers may lack sufficient data to appropriately direct conservation activities (IUCN 2012). Employing hair snares or other non-invasive techniques could provide essential data where trapping is not feasible. Finer honing of these tools by pairing GPS cluster investigations with isotope analyses allows us to compare results across techniques to explore population-level dynamics. In addition,

we show that stable isotope analyses can be a finer-scale tool for measuring kill rates and prey use by individuals. Stable isotope analyses provide insights into diet and community ecology that are either impossible or impractical with traditional methods (Darimont et al. 2007).

Figure 3.1: Map of study area in the Santa Cruz Mountains in California. The red areas are urban areas, while green are state parks. The grey lines show arterial roads that crisscross the study area. The main North-South road is Highway 17, a heavily trafficked road that is the main connection between Santa Cruz and Silicone valley and is a substantial source of puma mortality.
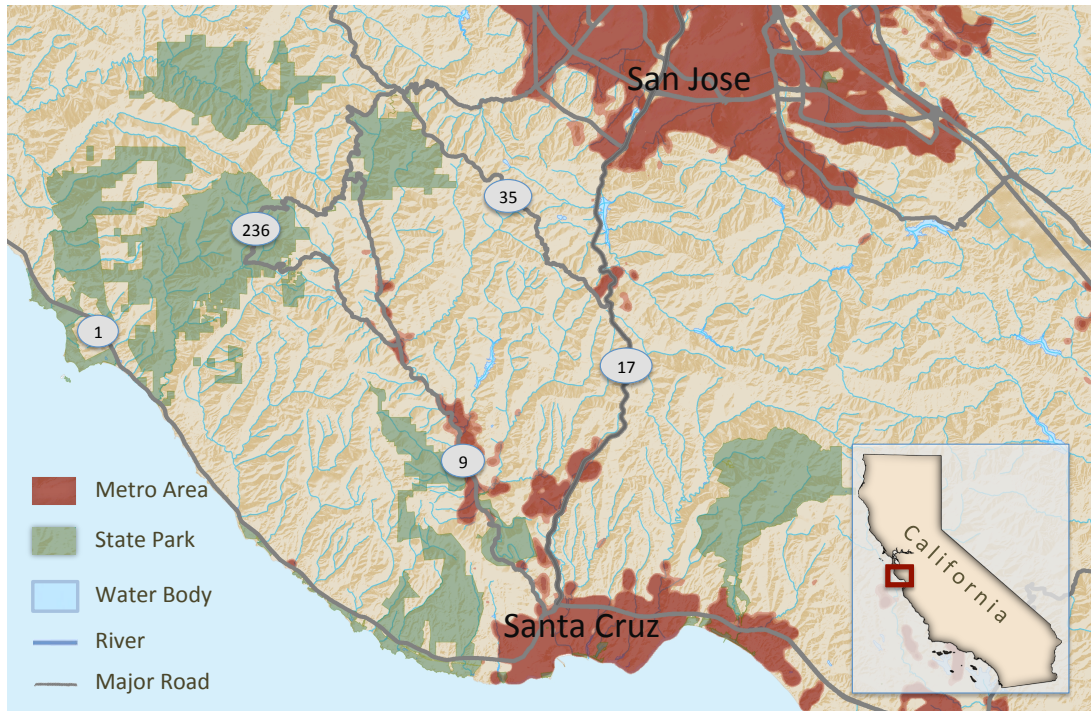
Figure 3.2: Comparison of puma population diet composition using GPS cluster investigations (in orange) and stable isotope analyses (in green). The bars represent the mean proportion of diet composition for each of the most common puma prey items (with deer and pigs in a combined large prey group). Error bars depict standard deviation. Though prey use measured by each method differs slightly, there was no statistical difference between methods on a population level.
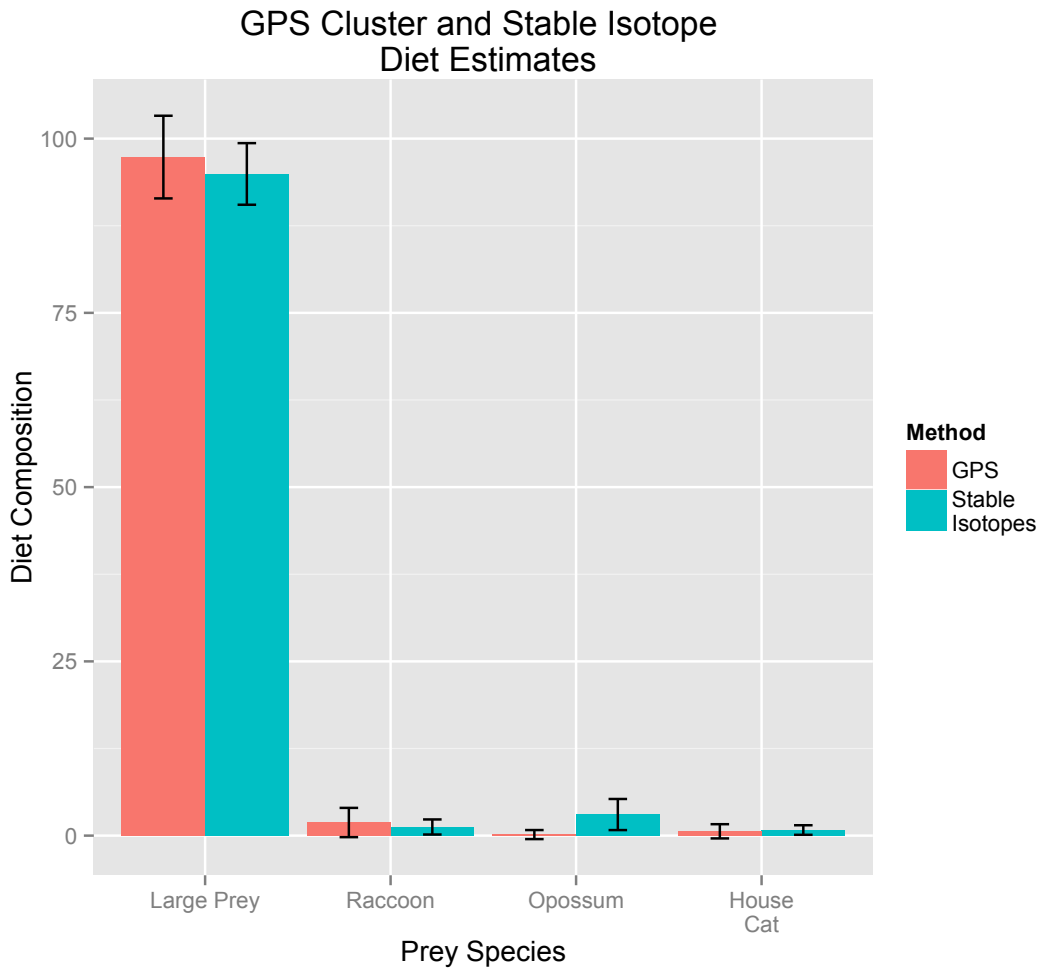
Figure 3.3: Puma and prey hair samples plotted in isotopic space. The error bars for prey items represent standard error. Hair isotope values of potential prey have been corrected for trophic discrimination. Most of the biomass that pumas eat is derived from deer, but pumas living in marginal habitat consume smaller prey items as well.
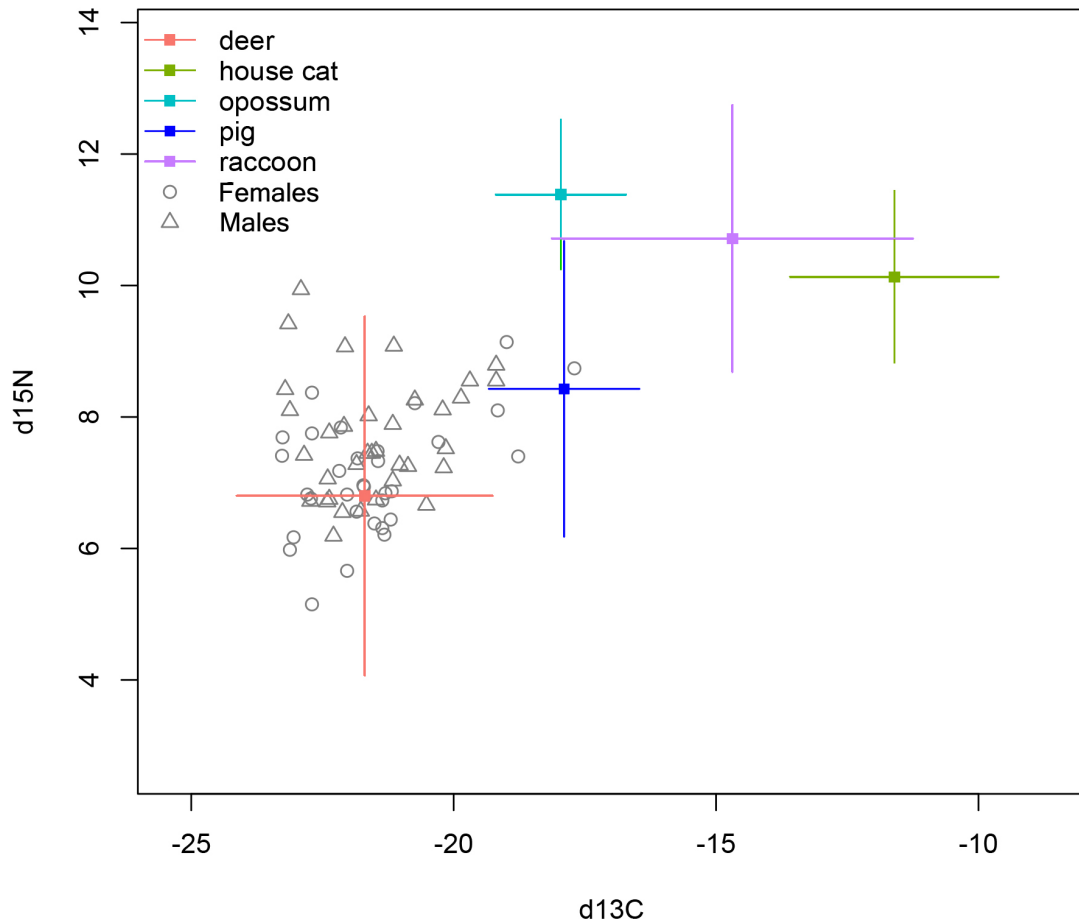
Figure 3.4: Individual puma diet composition by method. Diet A) reconstructed by GPS cluster investigations, and B) using stable isotope analyses. Stable isotope analyses revealed a higher use of small prey items than GPS cluster analyses. For visual clarity, error bars depict standard deviation in only one direction (below the mean).
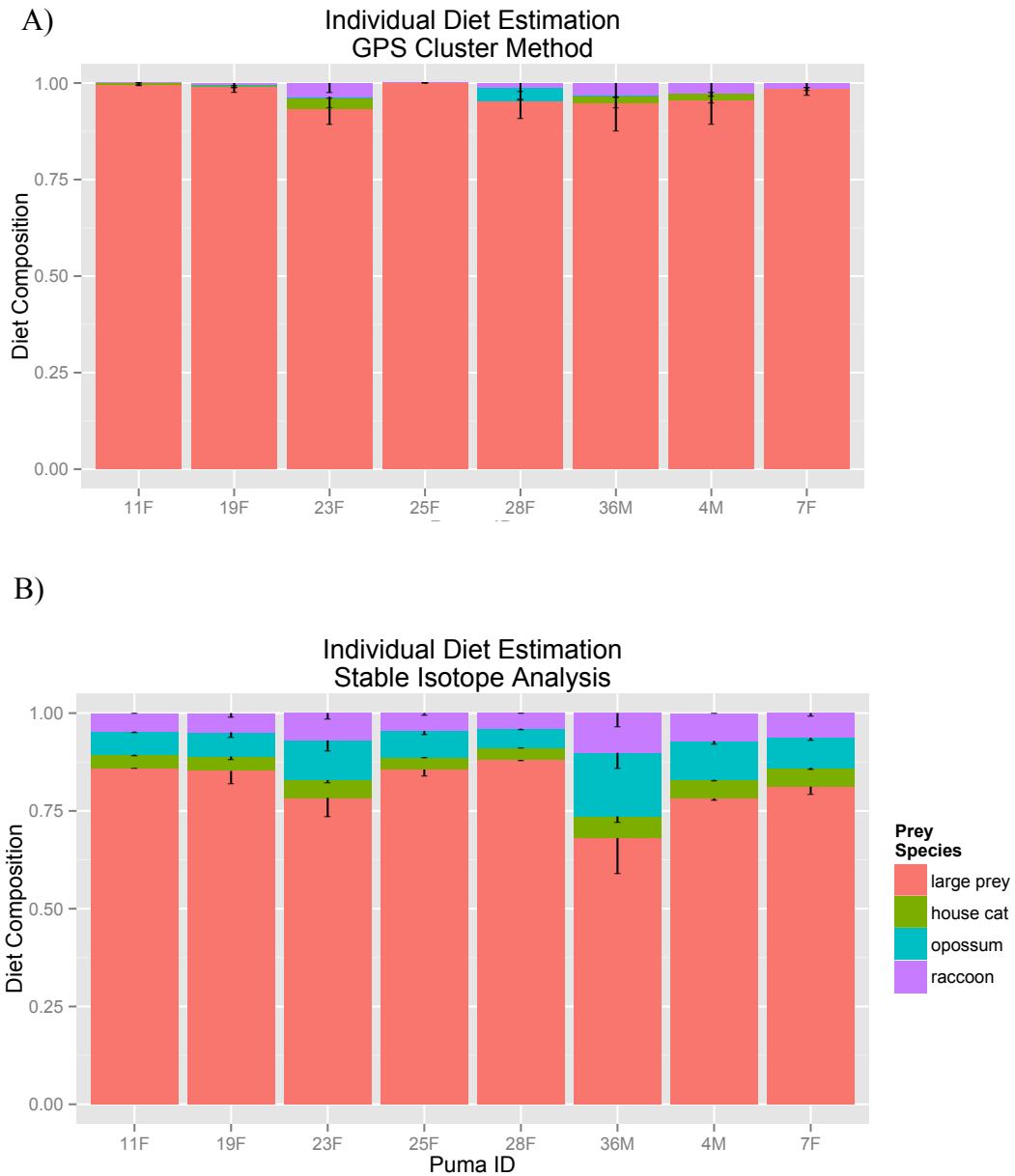
Figure 3.5: Difference between stable isotope prey use and GPS cluster estimates. The bars represent stable isotope estimates subtracted from GPS cluster estimates. Positive values denote higher GPS cluster estimates for the group, while negative values denote higher isotope method estimates. For example, GPS cluster methods overestimated deer consumption in comparison to stable isotope methods. We seldom detected small prey use by males when investigating GPS clusters. Males may have short handling times when consuming small prey items, making it difficult to identify kills with a cluster algorithm. Stable isotope analyses, on the other hand, rely on prey biomass, making them a more suitable method for calculating use of small prey items.
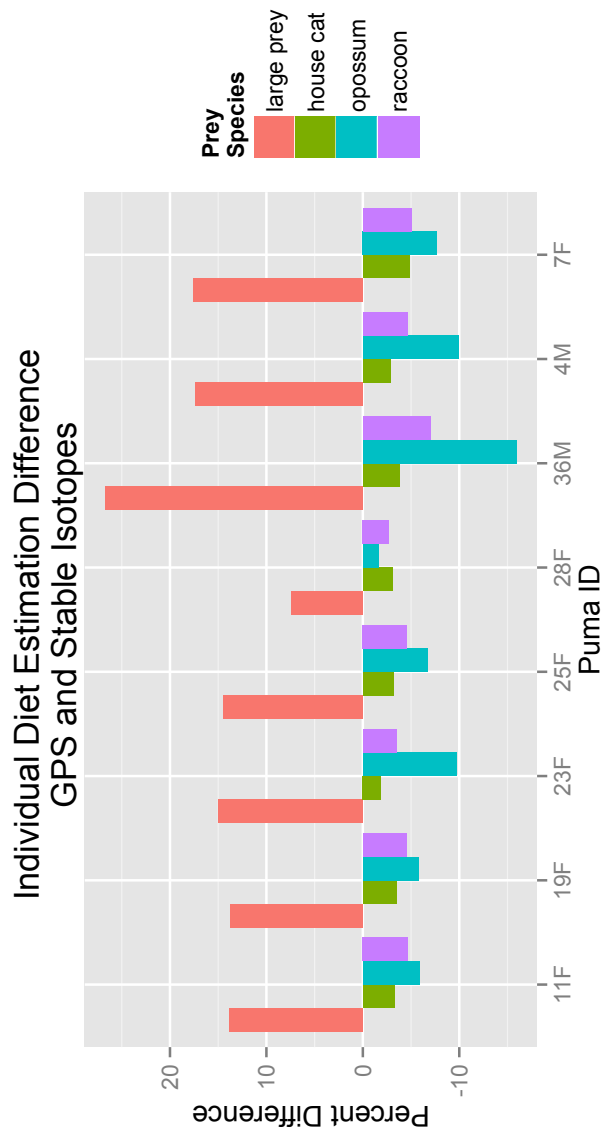
Table 3.1: Mean mass for each prey species as reported in the literature. These numbers were used to calculate total prey biomass identified in feeding sites.

Species	Mean Mass (kg)	Source	kJ per individual	Source
Deer	45	Wittmer et al. 2014	242,139	Laundré 2005
Raccoon	6	Jameson and Peeters 1988	59,574	USDA 2014
Opossum	2.3	Jameson and Peeters 1988	19,577	USDA 2014
House Cat	4.5	Mattern and McLennan 2000	44,200	USDA 2014

Table 3.2: Mean percent diet composition of various prey items for the population, females, and males. The two methods, GPS cluster investigations and stable isotope analyses, provided statistically indistinguishable diet estimates for each species measured. Large prey includes deer and feral pigs.

Prey Species	GPS						Isotopes					
	Males		Females		Population		Males		Females		Population	
	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean
Large Prey	3.5	97.2	5.5	97.3	5.9	97.4	6.4	92	4	95.1	4.4	94.9
Opossum	0.2	0.09	1.2	0.48	0.7	0.15	3.3	4.37	2.1	2.53	2.2	3.03
Raccoon	1.3	1.88	1.8	1.54	2.1	1.88	1.9	2.23	1.2	1.37	1.1	1.24
House Cat	0.9	0.83	0.8	0.71	1	0.62	1.2	1.45	0.8	0.96	0.7	0.8

Table 3.3: Trophic enrichment factors for each prey species. Sample means were calculated from hair collected from puma feeding sites. The trophic enrichment factors allow us to convert between isotopes in hair samples and tissue, and were taken from the literature.

	δ C13		δ N15		Trophic Enrichment Factor		Source
Prey Type	Mean	Std Dev	Mean	Std Dev	C13	N15	
Deer	-25.48	1.16	2.89	1.49	-1.6	0	Codron et al. 2007
Raccoon	-18.69	1.64	6.62	1.01	-1.5	0	Newsome et al. 2015, Roth and Hobson 2000
Opossum	-21.96	0.37	7.66	1.22	-1.5	0	Newsome et al. 2015, Roth and Hobson 2000
Pig	-21.50	1.25	4.86	1.54	-1.9	0	Nardoto et al. 2006
House Cat	-15.60	0.86	6.03	0.64	-1.5	0	Newsome et al. 2015

Table 3.4: Individual diet estimation method comparisons. When we compared GPS cluster methods versus stable isotope analyses we found significant prey use differences for every individual and for nearly each prey species. It should be noted that this analysis was conduced with small sample sizes; further research may help fine-tune these results. Significant relationships are denoted by an asterisk.

Puma ID	Prey Species	GPS Clusters Mean	SE	Stable Isotopes Mean	SE	
4	large prey	95.6	4.4	78.2	0.4	*
	opossum	0.0	0.0	9.9	0.6	*
	raccoon	2.5	2.5	7.1	0.0	*
	house cat	1.9	1.9	4.8	0.2	*
7	large prey	98.7	0.9	81.2	1.1	*
	opossum	0.0	0.0	7.7	0.4	*
	raccoon	1.3	0.9	6.3	0.4	*
	house cat	0.0	0.0	4.8	0.3	*
11	large prey	99.7	0.3	85.9	0.0	*
	opossum	0.0	0.0	5.9	0.2	*
	raccoon	0.0	0.0	4.7	0.0	*
	house cat	0.3	0.3	3.5	0.2	*
19	large prey	99.0	0.7	85.2	2.3	*
	opossum	0.4	0.4	6.2	0.9	*
	raccoon	0.4	0.4	4.9	0.8	*
	house cat	0.2	0.2	3.7	0.6	*
23	large prey	93.4	2.1	78.4	3.5	*
	opossum	0.5	0.2	10.1	2.0	*
	raccoon	3.5	1.3	7.0	1.1	*
	house cat	2.6	1.3	4.5	0.4	
25	large prey	100.0	0.0	85.6	1.0	*
	opossum	0.0	0.0	6.7	0.6	*
	raccoon	0.0	0.0	4.6	0.3	*
	house cat	0.0	0.0	3.2	0.1	*
28	large prey	95.5	2.7	88.0	0.2	*
	opossum	3.3	1.7	4.9	0.2	
	raccoon	1.2	1.2	4.0	0.0	*
	house cat	0.0	0.0	3.1	0.1	*
36	large prey	94.8	4.1	68.0	6.5	*
	opossum	0.3	0.3	16.2	2.9	*
	raccoon	3.2	2.1	10.2	2.5	*
	house cat	1.8	1.8	5.6	1.1	*

Appendix 1. Resource selection function model variable descriptions. These are the variables that were included in the scrape resource selection function, how we measured and defined each one.

Habitat Variable		Description	Measurement
Vegetation	Grassland Forest Shrub	California GAP data	Category
Roads	<35mph	Arterial roads	Distance (meters)
	≥35mph	Neighborhood roads or fire roads	Distance (meters)
Water sources	Waterbody	Standing water, reservoirs, lakes, ponds	Distance (meters)
	River	Seasonal or perennial rivers	Distance (meters)
	Water	Any water source (waterbody and river combined)	Distance (meters)
Puma scrapes	Community	3 or more scrapes within 3 meters of each other	Distance (meters)
Landscape	Elevation	Meters	Sampled at point
	Slope	Degrees	Determined by using nearest neighbors
	Aspect- Northness	Degrees	Determined by using nearest neighbors
	Aspect- Eastness	Degrees	Determined by using nearest neighbors

Appendix 2. Nursery resource selection function estimated parameter coefficients and p-values (n=23). Significant values are highlighted with bold text. Anthropogenic development was the only habitat variable that played a significant role in determining nursery site selection. Females strongly selected for undeveloped sites when choosing where to establish a nursery.

Habitat Variable	Coefficient	p-value
Elevation	-0.1034	0.661
Slope	0.0204	0.929
Aspect:		
Northness	0.0076	0.973
Eastness	-0.1553	0.502
Undeveloped Housing Density	**3.305**	**0.002**
Distance to:		
Roads ≥35mph	-0.0150	0.948
Water Body	0.3235	0.136
Rivers	0.1978	0.369

REFERENCES

Ackerman, B., F. Lindzey, and T. Hemker. 1986. Predictive energetics model for cougars. Cats of the world: biology, conservation, and management. National Wildlife Federation and Caesar Kleberg Wildlife Research Institute, Washington, DC and Kingsville, TX:333-352.

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology **74**:1313-1325.

Alig, R. J., J. D. Kline, and M. Lichtenstein. 2004. Urbanization on the US landscape: looking ahead in the 21st century. Landscape and urban planning **69**:219-234.

Allen, M. L., H. U. Wittmer, and C. C. Wilmers. 2014. Puma communication behaviours: understanding functional use and variation among sex and age classes. Behaviour **151**:819-840.

Allen, M. L., H.U. Wittmer, P. Houghtaling, J. Smith, L.M. Elbroch, and C.C. Wilmers. 2015. The role of scent marking in mate selection by female pumas (Puma concolor). PLoS One.

Anderson, C. R. and F. G. Lindzey. 2003. Estimating cougar predation rates from GPS location clusters. Journal of Wildlife Management 67:307-316.

Ashman, D. L., G. C. Christensen, M. L. Hess, G. K Tsukamoto, and M. S. Wichersham. 1983. The mountain lion in Nevada. Nevada Department of Wildlife Report W-48-15, Reno, USA

Augustine, D. J. and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: Herbivore selectivity and plant tolerance. Journal of Wildlife Management 62:1165-1183.

Bacon, M. M., G. M. Becic, M. T. Epp, and M. S. Boyce. 2011. Do GPS clusters really work? carnivore diet from scat analysis and GPS telemetry methods. Wildlife Society Bulletin 35:409-415.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. lme4: Linear mixed-effects models Eigen and S4. R package version 1.1-9: https://CRAN.R-project.org/package=lme4.

Beier, P., D. Choate, and R. H. Barrett. 1995. Movement patterns of mountain lions during different behaviors. Journal of Mammalogy:1056-1070.

Bell, S., E. D. McCoy, and H. R. Mushinsky. 2012. Habitat structure: the physical arrangement of objects in space. Springer Science & Business Media.

Ben-David, M. and E. A. Flaherty. 2012. Stable isotopes in mammalian research: a beginner's guide. Journal of Mammalogy 93:312-328.

Benhaiem, S., M. Delon, B. Lourtet, B. Cargnelutti, S. Aulagnier, A. J. M. Hewison, N. Morellet, and H. Verheyden. 2008. Hunting increases vigilance levels in roe deer and modifies feeding site selection. Animal Behaviour 76:611-618.

Bergelson, J. and M. Crawley. 1992. The effects of grazers on the performance of individuals and populations of scarlet gilia. Oecologia 90:435-444.

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

Beschta, R. L. and W. J. Ripple. 2012. The role of large predators in maintaining riparian plant communities and river morphology. Geomorphology 158:88-98.

Beschta, R. L. and W. J. Ripple. 2013. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade: comment. Ecology 94:1420-1425.

Bierwagen, B., J. Thomas, C. Pyke, D. Theobald, A. Choate, J. Cohen, and P. Groth. 2009. Land-Use Scenarios: National-Scale Housing-Density Scenarios Consistent with Climate Change Storylines. Environmental Protection Agency.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modeling 157:281-300.

Baruch-Mordo, S., C. T. Webb, S. W. Breck, and K. R. Wilson. 2013. Use of patch selection models as a decision support tool to evaluate mitigation strategies of human‚Äìwildlife conflict. Biological Conservation 160:263-271. Breck, S., P. Clark, L. Howery, D. Johnson, B. Kluever, S. Smallidge, and A. Cibils. 2012. A perspective on livestock-wolf interactions on western rangelands. Rangelands 34:6-11.

Cardillo, M., A. Purvis, W. Sechrest, J. L. Gittleman, J. Bielby, and G. M. Mace. 2004. Human population density and extinction risk in the world's carnivores. PLoS Biol **2**:e197.

Caro, T. and P. W. Sherman. 2012. Vanishing behaviors. Conservation Letters **5**:159-166.

Chavez, A.S., 2002. Assessing the potential, actual, and perceived risk that gray wolves, Canis lupus, pose to livestock in northwestern Minnesota.Crawley, M. J. 2012. The R book. John Wiley & Sons.

Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology **16**:488-502.

Cronon, W. 1996. The trouble with wilderness: or, getting back to the wrong nature. Environmental History:7-28.

Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A Stage-Based Population Model for Loggerhead Sea Turtles and Implications for Conservation. Ecology 68:1412-1423.

Cummings, J. and D. Smith. 2000. The line-intercept method: A tool for introductory plant ecology laboratories. Tested studies for laboratory teaching 22:234-246.

Darimont, C. T., P. C. Paquet, and T. E. Reimchen. 2007. Stable isotopic niche predicts fitness of prey in a wolf–deer system. Biological Journal of the Linnean Society 90:125-137.

DeCesare, N. J., M. Hebblewhite, H. S. Robinson, and M. Musiani. 2010. Endangered, apparently: the role of apparent competition in endangered species conservation. Animal Conservation 13:353-362.

De Jager, N. R. and J. Pastor. 2010. Effects of simulated moose Alces alces browsing on the morphology of rowan Sorbus aucuparia. Wildlife Biology 16:301-307.

Dickman, A. J. 2010. Complexities of conflict: the importance of considering social factors for effectively resolving human–wildlife conflict. Animal Conservation 13:458-466.

Elbroch, L. M., M. L. Allen, B. H. Lowrey, and H. U. Wittmer. 2014. The difference between killing and eating: ecological shortcomings of puma energetic models. Ecosphere 5:1-16.

Estes, J. A. and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. Science 185:1058-1060.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, and J. B. C. Jackson. 2011. Trophic downgrading of planet earth. Science 333:301-306.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics:487-515.

Fenn, M. E., J. S. Baron, E. B. Allen, H. M. Rueth, K. R. Nydick, L. Geiser, W. D. Bowman, J. O. Sickman, T. Meixner, D. W. Johnson, and P. Neitlich. 2003.

Ecological Effects of Nitrogen Deposition in the Western United States. BioScience 53:404-420.

Fleiss, J. L., B. Levin, and M. C. Paik. 2013. Statistical methods for rates and proportions. John Wiley & Sons.

Ford, A. T., J. R. Goheen, T. O. Otieno, L. Bidner, L. A. Isbell, T. M. Palmer, D. Ward, R. Woodroffe, and R. M. Pringle. 2014. Large carnivores make savanna tree communities less thorny. Science 346:346-349.

Frazer, G. W., C. Canham, and K. Lertzman. 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York 36.

Gehrt, S. D., Seth P. D. Riley, Brian L. Cypher, Editors. 2010. Urban carnivores: Ecology, conflict, conservation. John Hopkins University Press, Baltimore, MD, USA.

Getz, W. M., S. Formann-Roe, P. C. Cross, A. J. Lyons, S. J. Ryan, and C. C. Wilmers. 2007. LoCoH: nonparameteric kernel methods for constructing home ranges and utilization distributions. PLoS One:e207.

Gill, R. M. A. 1992. A Review of Damage by Mammals in North Temperate Forests: 1. Deer. Forestry 65:145-169.

Gibbons, J. W., D. E. Scott, T. J. Ryan, K. A. Buhlmann, T. D. Tuberville, B. S. Metts, J. L. Greene, T. Mills, Y. Leiden, and S. Poppy. 2000. The Global Decline of Reptiles, Déja Vu Amphibians Reptile species are declining on a global scale. BioScience 50:653-666.

Gogan, P. J. P. and R. H. Barrett. 1995. Elk and deer diets in a coastal prairie-scrub mosaic, California. Journal of Range Management 48:327-335.

Gittleman, J. L. 2013. Carnivore behavior, ecology, and evolution. Springer Science & Business Media.

Hebblewhite, M. and E. Merrill. 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. Journal of Applied Ecology 45:834-844.

Hebblewhite, M., E. H. Merrill, and T. L. McDonald. 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk predator-prey system. Oikos **111**:101-111.

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

Hinam, H. L. and C. C. S. Clair. 2008. High levels of habitat loss and fragmentation limit reproductive success by reducing home range size and provisioning rates of Northern saw-whet owls. Biological Conservation **141**:524-535.

Hosmer Jr, D. W. and S. Lemeshow. 2004. Applied logistic regression. John Wiley & Sons.

Hovel, K. A. and H. M. Regan. 2008. Using an individual-based model to examine the roles of habitat fragmentation and behavior on predator-prey relationships in seagrass landscapes. Landscape Ecology **23**:75-89.

Iverson, S. J., C. Field, W. Don Bowen, and W. Blanchard. 2004. Quantitative fatty acid signature analysis: a new method of estimating predator diets. Ecological Monographs 74:211-235.

IUCN. 2012. The International Union for Conservation of Nature Red List of Threatened Species. Version 2012. <http://www.iucnredlist.org>. Downloaded on 26 November 2015.

Jameson, E. W. and H. J. Peeters. 1988. California mammals. Univ of California Press.

Jenkins, S. H. 1979. Seasonal and year-to-year differences in food selection by beavers. Oecologia 44:112-116.

Johnson, C. J. and M. P. Gillingham. 2005. An evaluation of mapped species distribution models used for conservation planning. Environmental Conservation 32:117-128.

Johnson, A. R., J. A. Wiens, B. T. Milne, and T. O. Crist. 1992. Animal movements and population-dynamics in heterogenous landscapes. Landscape Ecology **7**:63-75.

Knopff, K. H., A. A. Knopff, M. B. Warren, and M. S. Boyce. 2009. Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. The Journal of Wildlife Management 73:586-597.

Laundré, J. W. 2005. Puma energetics: A recalculation. Journal of Wildlife Management 69:723-732.

Legendre, P. and L. Legendre. 1998. Numerical ecology: second English edition. Developments in environmental modelling 20.

Lima, S. L. and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640.

Lindenmayer, D. B. and H. A. Nix. 1993. Ecological Principles for the Design of Wildlife Corridors. Conservation Biology **7**:627-630.

Linnell, J. D., E. J. Solberg, S. Brainerd, O. Liberg, H. k. Sand, P. Wabakken, and I. Kojola. 2003. Is the fear of wolves justified? A Fennoscandian perspective. Acta Zoologica Lituanica 13:34-40.

Logan, K. A. and L. L. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. 2nd edition. Kluwer Academic Publishers, Boston.

Martin, P. S. and C. R. Szuter. 1999. War zones and game sinks in Lewis and Clark's west. Conservation Biology:36-45.

Mattern, M. Y. and D. A. McLennan. 2000. Phylogeny and Speciation of Felids. Cladistics 16:232-253.

McConnaughey, T. and C. McRoy. 1979. Food-web structure and the fractionation of carbon isotopes in the Bering Sea. Marine Biology 53:257-262.

McGinley, M. A. and T. G. Whitham. 1985. Central Place Foraging by Beavers (Castor canadensis): A Test of Foraging Predictions and the Impact of Selective Feeding on the Growth Form of Cottonwoods (Populus fremontii). Oecologia 66:558-562.

McKinney, M. L. 2002. Urbanization, Biodiversity, and Conservation The impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. BioScience 52:883-890.

McNaughton, S. J., F. F. Banyikwa, and M. M. McNaughton. 1997. Promotion of the Cycling of Diet-Enhancing Nutrients by African Grazers. Science 278:1798-1800.

Miller, J. R. 2015. Mapping attack hotspots to mitigate human-carnivore conflict: approaches and applications of spatial predation risk modeling. Biodiversity and Conservation:1-25.

Nardoto, G. B., P. B. d. Godoy, E. S. d. B. Ferraz, J. P. H. B. Ometto, and L. A. Martinelli. 2006. Stable carbon and nitrogen isotopic fractionation between diet and swine tissues. Scientia agricola 63:579-582.

Newsome, T. M., J. A. Dellinger, C. R. Pavey, W. J. Ripple, C. R. Shores, A. J. Wirsing, and C. R. Dickman. 2015. The ecological effects of providing resource subsidies to predators. Global Ecology and Biogeography **24**:1-11.

Noss, R. F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conservation Biology **10**:949-963.

Oftedal, O. T. and J. L. Gittleman. 1989. Patterns of energy output during reproduction in carnivores. Pages 355-378 Carnivore behavior, ecology, and evolution. Springer.

Ohgushi, T. 2005. Indirect interaction webs: Herbivore-induced effects through trait change in plants. pp81-105 Annual Review of Ecology Evolution and Systematics. Annual Reviews, Palo Alto.

Ordeñana, M. A., K. R. Crooks, E. E. Boydston, R. N. Fisher, L. M. Lyren, S. Siudyla, C. D. Haas, S. Harris, S. A. Hathaway, and G. M. Turschak. 2010. Effects of urbanization on carnivore species distribution and richness. Journal of Mammalogy 91:1322-1331.

Paine, R. T. 1969. A note on trophic complexity and community stability. American Naturalist:91-93.

Parnell, A. C., R. Inger, S. Bearhop, and A. L. Jackson. 2010. Source partitioning using stable isotopes: coping with too much variation. PLoS One **5**:e9672.

Parng, E., A. Crumpacker, and C. M. Kurle. 2014. Variation in the stable carbon and nitrogen isotope discrimination factors from diet to fur in four felid species held on different diets. Journal of Mammalogy 95:151-159.

Peckarsky, B. L., P. A. Abrams, D. I. Bolnick, L. M. Dill, J. H. Grabowski, B. Luttbeg, J. L. Orrock, S. D. Peacor, E. L. Preisser, O. J. Schmitz, and G. C. Trussell. 2008. Revisiting the classics: Considering nonconsumptive effects in textbook examples of predator-prey interactions. Ecology **89**:2416-2425.

Perilli, M. L. L., F. Lima, F. v. H. G. Rodrigues, and S. M. C. Cavalcanti. 2016. Can Scat Analysis Describe the Feeding Habits of Big Cats? A Case Study with Jaguars (Panthera onca) in Southern Pantanal, Brazil. PLoS One 11:e0151814.

Phillips, D. L., S. D. Newsome, and J. W. Gregg. 2005. Combining Sources in Stable Isotope Mixing Models: Alternative Methods. Oecologia **144**:520-527.

Power, M. E. 1990. Effects of fish in river food webs. Science(Washington) 250:811-814.

Prange, H. D., J. F. Anderson, and H. Rahn. 1979. Scaling of Skeletal Mass to Body Mass in Birds and Mammals. The American Naturalist 113:103-122.

Pressey, R. L., M. Cabeza, M. E. Watts, R. M. Cowling, and K. A. Wilson. 2007. Conservation planning in a changing world. Trends in Ecology & Evolution **22**:583-592.

Rankin, D. 2007. Resolving the tragedy of the commons: the feedback between intraspecific conflict and population density. Journal of evolutionary biology **20**:173-180.

Riley, S. P. D., L. E. K. Serieys, J. P. Pollinger, J. A. Sikich, L. Dalbeck, R. K. Wayne, and H. B. Ernest. 2014. Individual Behaviors Dominate the Dynamics of an Urban Mountain Lion Population Isolated by Roads. Current Biology **24**:1989-1994.

Ripple, W. J. and R. L. Beschta. 2012. Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. Biological Conservation 145:205-213.

Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D. Wallach, and A. J. Wirsing. 2014. Status and Ecological Effects of the World's Largest Carnivores. Science **343**.

Ripple, W. J., T. M. Newsome, C. Wolf, R. Dirzo, K. T. Everatt, M. Galetti, M. W. Hayward, G. I. Kerley, T. Levi, and P. A. Lindsey. 2015. Collapse of the world's largest herbivores. Science Advances **1**:e1400103.

Rudzitis, G. 1999. Amenities increasingly draw people to the rural west. Rural Development Perspectives **14**:9-13.

Sand, H., B. Zimmermann, P. Wabakken, H. Andrén, and H. C. Pedersen. 2005. Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. Wildlife Society Bulletin 33:914-925.

Sarasola, J. H., J. I. Zanón-Martínez, A. S. Costán, and W. J. Ripple. 2016. Hypercarnivorous apex predator could provide ecosystem services by dispersing seeds. Scientific Reports 6:19647.

Sargeant, G. A., D. H. Johnson, and W. E. Berg. 1998. Interpreting carnivore scent-station surveys. The Journal of Wildlife Management:1235-1245.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature **413**:591-596.

Schmitz, O. J., P. A. Hamback, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: A review of the effects of carnivore removals on plants. American Naturalist 155:141-153.

Schoener T W. 1993. Mutualism and Community Organization: Behavioral, Theoretical and Food-Web Approaches, eds Kawanabe, Cohen, Iwasaki (Oxford Univ. Press, New York), pp 365–411

Sih, A., A. Bell, and J. C. Johnson. 2004. Behavioral syndromes: an ecological and evolutionary overview. Trends in Ecology & Evolution **19**:372-378.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? Biological Conservation 83:247-257.

Slabbekoorn, H. and E. A. P. Ripmeester. 2008. Birdsong and anthropogenic noise: implications and applications for conservation. Molecular Ecology **17**:72-83.

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

Springer, A. M., J. A. Estes, G. B. van Vliet, T. M. Williams, D. F. Doak, E. M. Danner, K. A. Forney, and B. Pfister. 2003. Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? Proceedings of the National Academy of Sciences 100:12223-12228.

Swift, C. E., M. K. Gross. 2014. Preventing Deer Damage, Fact Sheet No. 6.520. Natural Resource Series | Wildlife. Colorado State University Extension http://www.ext.colostate.edu/pubs/natres/06520.html, accessed March 2014.

Taber, R. D. and R. F. Dasmann. 1957. The dynamics of 3 natural populations of the deer. Ecology 38:233-246.

Terborgh, J. and J. A. Estes. 2010. Trophic cascades: predators, prey, and the changing dynamics of nature. Island Press. Covelo. 488pp.

Theobald, D. M. 2005. Landscape Patterns of Exurban Growth in the USA from 1980 to 2020. Ecology and Society **10**:32.

Treves, A., R. R. Jurewicz, L. Naughton-Treves, R. A. Rose, R. C. Willging, and A. P. Wydeven. 2002. Wolf Depredation on Domestic Animals in Wisconsin, 1976-2000. Wildlife Society Bulletin 30:231-241.

Treves, A. and K. U. Karanth. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. Conservation Biology 17:1491-1499.

Tyler, C. M., F. W. Davis, and B. E. Mahall. 2008. The relative importance of factors affecting age-specific seedling survival of two co-occurring oak species in southern California. Forest Ecology and Management 255:3063-3074.

Tyler, C. M., B. Kuhn, and F. W. Davis. 2006. Demography and recruitment limitations of three oak species in California. The quarterly review of biology 81:127-152.

U.S. Department of Agriculture, Agricultural Research Service. 2014. USDA National Nutrient Database for Standard Reference, Release. Nutrient Data Laboratory Home Page, http://www.ars.usda.gov/nutrientdata

Vallano, D. M. and J. P. Sparks. 2008. Quantifying foliar uptake of gaseous nitrogen dioxide using enriched foliar $\delta15N$ values. New Phytologist 177:946-955.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. Science **277**:494-499.

Votier, S. C., S. Bearhop, A. MacCormick, N. Ratcliffe, and R. W. Furness. 2003. Assessing the diet of great skuas, Catharacta skua, using five different techniques. Polar Biology 26:20-26.

Vucetich, J. A., M. Hebblewhite, D. W. Smith, and R. O. Peterson. 2011. Predicting prey population dynamics from kill rate, predation rate and predator-prey ratios in three wolf-ungulate systems. Journal of Animal Ecology 80:1236-1245.

Wang, Y. 2014. Using Novel Technologies To Confront Challenges In Predator Conservation, Community Ecology, and Citizen Science. University of California, Santa Cruz.

Wang, Y., M. L. Allen, and C. C. Wilmers. 2015. Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. Biological Conservation **190**:23-33.

Wang, Y., J. Smith, C. C. Wilmers. *In press*. Anthropogenic development influences puma behavior, movement, and energetics. Biological Conservation.

Woodroffe, R. 2000. Predators and people: using human densities to interpret declines of large carnivores. Animal Conservation **3**:165-173.

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

Wilmers, C. C., R. L. Crabtree, D. W. Smith, K. M. Murphy, and W. M. Getz. 2003. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. Journal of Animal Ecology 72:909-916.

Wilmers, C. C., B. Nickel, C. M. Bryce, J. A. Smith, R. E. Wheat, and V. Yovovich. 2015. The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. Ecology 96:1741-1753.

Wilmers, C. C. and E. Post. 2006. Predicting the influence of wolf-provided carrion on scavenger community dynamics under climate change scenarios. Global Change Biology 12:403-409.

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

Wittmer, H. U., Forrester, T.D., Allen, M.L., Marescot, L. & Casady, D.S. 2014. Black-tailed deer population assessment in the Mendocino National Forest, California. Report to the California Department of Fish and Wildlife.

Zimmermann, B., P. Wabakken, H. Sand, H. C. Pedersen, and O. Liberg. 2007. Wolf Movement Patterns: a Key to Estimation of Kill Rate? The Journal of Wildlife Management 71:1177-1182.

Zuur, A. F., E. N. Ieno, G. M. Smith. 2007. Analyzing Ecological Data. Springer Science and Business Media, LLC, New York, NY.