Title

Using Novel Technologies To Confront Challenges In Predator Conservation, Community Ecology, and Citizen Science

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USING NOVEL TECHNOLOGIES TO CONFRONT CHALLENGES IN PREDATOR CONSERVATION, COMMUNITY ECOLOGY, AND CITIZEN SCIENCE

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by

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USING NOVEL TECHNOLOGIES TO CONFRONT CHALLENGES IN PREDATOR CONSERVATION, COMMUNITY ECOLOGY, AND CITIZEN SCIENCE

Yiwei Wang

ABSTRACT

Habitat fragmentation and loss is the primary driver of mammalian carnivore extinctions across the world. In the Santa Cruz Mountains of California, native carnivores navigate daily through a landscape highly impacted by human development and activities. The puma (*Puma concolor*) is the apex predator of this habitat, but it is susceptible to both direct and indirect influences of expanding human populations. Smaller predators are not only affected by anthropogenic disturbances, but also by intraguild competition with the more dominant pumas.

My dissertation utilizes new technologies to study the ecology and behavior of carnivores in a human dominated environment. In my first chapter, I catalogued puma behaviors in the wild using measurements recorded by accelerometers attached to the animals. I found that I could clearly distinguish movement from non-movement behavior, and that predation events had distinctive accelerometer signatures. The second chapter describes how I used movement data recorded by GPS (Global Positioning System) collars to evaluate puma behavioral responses to increasing development. Pumas primarily traveled nocturnally, and moved more often and further in areas of higher housing development. The increase in activity in human dominated landscapes could have major repercussions on the energetic expenditure of pumas living in fragmented areas. My third chapter addresses the impacts of human

development and activities on the entire carnivore community. Combining passive and experimental observations using motion-detecting camera traps, I studied the spatiotemporal behavior of predators across a gradient of human influences. Mesopredator activity was restricted temporally in areas of high human use, and certain predators (e.g., pumas and foxes) were more sensitive to increasing development.

Lastly, education and outreach is an important component of carnivore conservation. In my fourth chapter, I describe results from a Facebook game I developed with collaborators. Players earned points by identifying wildlife species from camera trap photographs. I found that agreement among players was the most important determinant of accuracy, and that untrained Internet users could identify many wildlife species. The Internet is an emerging tool for outreach, and I hope my work encourages other ecologists to think creatively about incorporating citizen scientists into their research through social media.

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INTRODUCTION

In a groundbreaking essay from 1995, William Cronon asked whether the conventional concept of wilderness has allowed people to partition off the “natural” world as a place separate from and unspoiled by human influence. As a species that primarily resides in urban areas, people imagine wilderness as something that must be sheltered from human exploitation through laws and physical boundaries. While such protection is often necessary and has helped save millions of acres of land from development, it has also created the false dichotomy that the places we dwell are wholly unnatural and thus unworthy of our protection or interest. Due to this perceived separation of “places for nature” and “places for us”, many people have become increasingly isolated from the natural world to the detriment of conservation efforts.

However, these imagined barriers between our world and the natural world are broken constantly, from the domestic cat that wanders into the forest to hunt migrating birds, to the puma that travels to an exurban neighborhood to hunt raccoons and house cats. Nature is just as much a part of the anthropogenic landscape as we are a part of its ecological community. My motivation for conducting this dissertation research is to help bridge this divide between nature and people because I believe that we cannot and will not preserve something that we don’t love and understand. I used advanced remote-sensing technologies to study carnivore species living in a human-dominated environment, and I employed social media to promote ecological awareness in the general public. By recognizing that natural and anthropogenic communities are often intertwined, I hope that people will find that wilderness is not something they have to drive to go see or fence off to protect, but rather, that it is a part of their everyday lives.

The four chapters of my dissertation primarily focus on the ecology and behavior of pumas (*Puma concolor*) and other predators living in the Santa Cruz Mountains of California. Chapter one describes the methods I developed to predict puma behavior in the field based on measurements from onboard accelerometers. Wild pumas were outfitted with collars with onboard accelerometers, which measured the continuous three-dimensional displacement of the animals. I used video recordings of captive pumas wearing accelerometer collars to generate a Random Forest model, which was then used to predict the behaviors of wild pumas from their accelerometer measurements. I also identified characteristics of accelerometer recordings that indicated potential predation events. I concluded that accelerometers are a valuable tool for monitoring animals that are not easily observed in the wild and that future studies with accelerometer will shed more light on the hunting and feeding behaviors of pumas

Chapter two describes and reports my analyses of the impacts of housing development on puma behavior. I used fine-scale location data from GPS (Global Positioning System) collars deployed on 22 pumas to evaluate how puma movements and activities were affected by housing development. I found that pumas were more active and traveled further in developed areas in the nighttime and showed the opposite pattern in the daytime. These results suggest that increased development in puma habitat may lead to higher energetic costs for pumas since the amount of calories they burn is directly related to their movement activities. I also found that energetic predictions based on GPS movement data underestimated the calories expended by more than 50% when compared with measurements calculated from accelerometer data, suggesting that pumas may need to hunt prey at a much higher rate than previously predicted.

My third chapter evaluated how human development and activities influenced the spatiotemporal relationships among the carnivore community. I used motion-detecting camera traps at 50 locations along a gradient of human development to assess how carnivore activities shifted as human development and use increased. I found that pumas were less likely to occupy an area as development increased, and that this resulted in a lower probability of detecting smaller carnivores like foxes but a higher probability of detecting coyotes. I also found that carnivores experience more temporal overlap in areas with higher human use because they reduced their nocturnal activity to avoid people. Additionally, I conducted an experiment to test whether puma activity and housing development influenced scavenger use of resources at 49 bait sites. I added puma urine and feces to 25 sites to mimic puma presence and used camera traps to monitor scavenging activity at each bait. I found that bobcats behaved differently at sites treated with puma urine and feces and that foxes avoided baits used by coyotes. I also showed that bobcats and foxes were less likely to visit baits in more developed areas.

Chapter four describes a Facebook game I created as a citizen science project. Players in the game viewed photographs of wildlife captured by my camera traps and identified the species in those photos. I tested whether Internet users could accurately categorize species and found that agreement among players was the most important factor in determining accuracy. I recommended that ecologists consider using the Internet as a new way of conducting outreach and recruiting citizen scientists, especially to help with large data sets of wildlife photographs from camera traps. Because the Internet is quickly becoming the most convenient and reliable form of global communication, it represents an impressive tool for ecologists looking to involve people in research.

At the end of his essay, Cronon suggests that when we realize that nature is all around us and not just locked up in national parks, we will be more inclined to cherish and protect it. Through the results of my research, I hope to impart a similar message that although wild animals leave behind only shadowy glimpses of their existence, they nonetheless tread the same ground as we do and are both directly and indirectly impacted by our actions. Perhaps by recognizing both the familiar and the awesome in the wilderness around us, we can begin exploring Michael Rozensweig's idea of "reconciliation ecology" and work towards a world that enhances our existence without diminishing those of other species.

Chapter 1

Movement, resting and attack behaviors of wild pumas are revealed by tri-axial accelerometer measurements

Abstract:

Accelerometers are a promising tool for biologists seeking to gain a deeper understanding of the daily behavior of cryptic species. We describe a new method to monitor behaviors of animals that are difficult or impossible to observe in the wild. We attached GPS and tri-axial accelerometer equipped collars (sampling continuously at 64 Hz) to twelve pumas (*Puma concolor*) in the Santa Cruz Mountains from 2010-2012. We implemented Random Forest classification models to classify behaviors in wild pumas based on training data from observations and measurements of captive puma behavior.

We applied these models to accelerometer data collected from wild pumas and identified mobile and non-mobile behaviors in captive animals with an accuracy rate of greater than 96%. Accuracy remained above 95% even after downsampling our accelerometer data to 16Hz. We had difficulty predicting non-movement behaviors due to the small size of our training dataset. We were further able to predict low-acceleration movement behavior (e.g. walking) and high-acceleration movement behavior (e.g. running) with 93.8% and 92% accuracy, respectively. Lastly, we used field and model-vetted predation events to quantify acceleration characteristics of puma attacks on large prey.

These results demonstrate that accelerometers are a useful tool for classifying animal behavior in their natural habitat and can help scientists gain deeper insight into how behavior is impacted by sex, breeding status, and the physical environment. We also show how accelerometer measurements can provide novel insights on the energetics and predation behavior of wild animals.

Introduction

One of the major challenges to studying animal behavior remains our inability to continuously observe free-ranging animals (Wilson et al. 2008). While recent technological achievements in the design and versatility of bio-logging devices (e.g., Global Positioning System (GPS) collars) have substantially improved monitoring of animals, our ability to document behavior through time and space remains limited (Cagnacci et al. 2010). For example, when studying the impacts of habitat fragmentation on large carnivores, we would like to know how landscape variables influence fine scale animal movement, resting, and hunting patterns. Accurately discerning such fine scale behavior is almost impossible from information on location data alone, but critical to informing conservation management decisions (Cooke 2008).

In the last decade, accelerometer sensors have emerged as a promising tool for remotely monitoring animal behavior (Nathan et al. 2012; Shamoun-Baranes et al. 2012). By continuously measuring body movement and posture, accelerometers allow scientists to infer the behavior and energy expenditure of the instrumented individual (Shepard et al. 2010). Accelerometers have been used to study a wide range of behavioral and physiological aspects of animals including foraging behavior in wild (Gallon et al. 2013; Goldbogen et al. 2006; Iwata et al. 2012; Kato et al. 2006; Shepard et al. 2011; Tanoue et al. 2012; Watanabe & Takahashi 2013; Weimerskirch et al. 2005) and domestic subjects (Moreau et al. 2009), reproduction (Tsuda et al. 2006; Whitney et al. 2010), activity budgets (Grunewalder et al. 2012; Laich et al.

2010; Nathan et al. 2012; Ropert-Coudert et al. 2004; Whitney et al. 2007), energy budgets (Byrnes et al. 2011; Fossette et al. 2012; Green et al. 2009; Murchie et al. 2011; Shepard et al. 2010; Wilson et al. 2012), and locomotion in cursorial, volant, and aquatic animals (Bundle & Dial 2003; Byrnes et al. 2011; Gleiss et al. 2011; Kato et al. 2006; Le Vaillant et al. 2012; O'Toole et al. 2010; Okuyama et al. 2012). While accelerometry has been used successfully to differentiate behaviors across a variety of taxa, most accelerometer-based behavioral studies have focused on marine animals including marine mammals, sea turtles, sharks, and seabirds. To date, there are few studies using accelerometers to study behavior in wild terrestrial animals.

Watanabe et al. (2005) first demonstrated the potential applicability of accelerometer technology for studying terrestrial animal behavior using a domestic cat. By combining direct observations with five parameters extracted from a single-axis accelerometer, they were able to successfully categorize different behaviors of the cat as it roamed freely. In a larger study, Shepard et al. (2010) deployed tri-axial accelerometers on twelve species ranging from marine sharks to terrestrial carnivores and concluded that locomotive activities can generally be accurately identified from accelerometers measurements. However, behaviors that are non-locomotive or non-repetitive, such as feeding and grooming, were more difficult to resolve, as their accelerometer signatures were generally complex and nuanced or obscured by noisy measurements.

Accelerometer measurements are generally deconstructed into static and dynamic components (Shepard et al. 2010). Static acceleration relates to the inclination of the accelerometer with respect to the earth's gravitational field, and thereby reflects the posture of the animal. Measurements of this component can be impacted by where and how the accelerometer is affixed to the individual. For example, an accelerometer mounted in a collar worn by an animal may not reflect the true posture of the animal if the collar position shifts. Additionally, animals may not always maintain the same posture when performing similar behaviors (e.g., sleeping on side versus on back). Dynamic acceleration relates to changes in velocity resulting from patterns of locomotion and generally reflects the movement of the animal. Similar to static acceleration, dynamic acceleration measurements may also be obscured by noisy measurements given a loosely secured or placed collar.

Accelerometer measurements can supplement GPS-positioning data to help scientist better understand animal movement and behavior. Wilson et al. (2013) recently used a combination of comprehensive tri-axial accelerometer measurements and extremely fine scale GPS data to uncover unprecedented insights about hunting behavior in cheetahs. The authors were able to continuously quantify the mechanics, acceleration, and positions that defined every footstep of the hunt. While Wilson et al. (2013) demonstrated the potential of accelerometry, the current cost-prohibitive budget of using such state-of-the-art technologies likely means that most accelerometer related studies will be more modest. Nevertheless, other recent projects on cheetahs and oystercatchers have indicated that our understanding of animal behavior in the field is greatly enhanced by even simple and limited accelerometer data compared to GPS data alone (Grunewalder et al. 2012; Shamoun-Baranes et al.

2012). Both of these studies used short temporal segments (i.e., a few seconds) of accelerometer measurements and field observations to predict behavior between successive GPS locations. However, many animals cannot be observed easily in the wild and sampling behavior at periodic intervals does not necessarily reflect the animal's primary activity during that time segment. Here we demonstrate how we used raw accelerometer measurements and observations of captive animals to predict behavior in wild pumas.

Our objective in this study was to use continuous accelerometer measurements (sampling at 64 times a second), in combination with periodic GPS readings, to distinguish different behaviors in free-roaming wild pumas (*Puma concolor*). Like most large felids, pumas lead solitary and secretive lives, and are infrequently observed in their natural environment (Logan & L. 2001). This creates difficulties for researchers aiming to gain a fine-scale understanding of the behavioral patterns of free-ranging pumas. To overcome this limitation, we paired observations of captive pumas performing activities including resting, feeding, moving, and grooming with accelerometer measurements to build a classification algorithm to categorize those behaviors in the wild animals. We also tested predictions generated using six accelerometer sampling frequencies to determine the appropriate frequency for categorizing different behaviors.

By outfitting wild pumas with collars equipped with custom-built accelerometers and GPSs, we constructed continuous activity budgets over multi-day periods for individual pumas as they moved through their natural habitats. We first segregated each animal's activity into mobile and non-mobile periods and built a second model to categorize the animal's movement behaviors into low acceleration (e.g., walk) and high acceleration (e.g., trotting and running) movements, and the non-movement behaviors into resting, eating, and grooming behaviors. Pumas generally walk at a slow speed and hunt using quick bursts of movement, so we located sustained periods of high acceleration to determine whether these were linked to predatory behavior.

The methods we describe in this paper should be applicable to the study of continuously monitored behaviors of other medium and large-sized terrestrial mammals across the globe moving across a variety of environments. This increased understanding of activity budgets and predatory behavior could then provide greater insight into the energetic costs and gains experienced by wild animals in their natural habitat.

Results

Behavioral measurements

From 2010-2011, we outfitted 12 pumas (5 males, 7 females) with GPS collars and accelerometer sensors (Table 2). Due to mechanical or software failure in the onboard accelerometer sensors or SD cards, we removed six individuals from analyses entirely and extracted 4-26 days of accelerometer data from the remaining individuals (Table 2). From the two captive pumas we outfitted with an accelerometer collar, we documented 2142 discrete behavioral observations, including walking, grooming, resting, feeding, and fast movement (Table 3).

Mobility model

The mobility model correctly classified movements 96.17% of the time. Amp M was identified by our model as the most important variable in predicting mobility, followed by DFZ and SDM (refer to Table 1 for variable descriptions). Results from our regression model showed that our model predictions of mobility were highly correlated with the distance traveled ($\beta = 5.245$, standard error = 0.174, $p < 0.001$), adding further support to the accuracy of movement model determinations. Random effects were not significant.

Behavior model

Our behavior model predicted pumas resting, low and high acceleration movement with 96.8%, 93.8%, and 92% accuracy, respectively. The model predicted feeding behavior with 65.7% accuracy but failed to detect grooming (0%) (Table 4). The model identified SDM, DFZ, and SDZ as the most important variables for classification. The 24-hour behavioral budget we generated using the model resulted in biologically unreasonable predictions, such as feeding behavior interspersed with movement. This is likely due to the fact that feeding behavior generated accelerometer readings that are intermediate between movement and resting activities. In addition, all of our observations of feeding behavior were limited to one feeding session by the captive female puma. Her feeding behavior signature is likely not representative of the wider spectrum of feeding behaviors that may be exhibited by wild pumas.

As predicted, we observed peaks of high acceleration movements either within one GPS sampling interval of the start of a predation event or in the first quartile of the event (Fig. 2). When compared to all high acceleration clusters, which may not necessarily be associated with predation events, 4 of our 6 potential predation events were ranked among the top 10% for cluster size and 3 of 6 for maximum magnitude (Fig. 3). 5M's predation event did not feature an exceptionally high magnitude range, but his prey was a 6-month-old fawn, so it is possible that he did not have to struggle too hard. The two predation events for puma 16M were also exceptions, but it is reasonable to assume that he did not need to expend much effort or time to catch his prey since they were both one month old fawns.

From the limited predation incidents we analyzed, we noted that the amount of time it took to dispatch animals was related to their age and size. Based on the duration of the high acceleration cluster, two one-month-old fawns were dispatched by 16M in 10 and 12 seconds and one six-month-old fawn was killed by 5M in one minute. It appears that male lions were able to kill juvenile prey fairly quickly. In contrast, 7F took 2 minutes to kill a 4-year-old buck and 2F killed a 10-year-old buck in 4.5 minutes. 2F also engaged in a 10 minute long predation sequence to kill an unknown animal.

Movement Activity budgets

Our 24-hour activity budgets for individual pumas show a general pattern of decreased movement activity in the daytime and increased activity at night (Fig. 4). This is in line with our understanding of puma behavior from previous studies with

GPS data (Cooley et al. 2008; Sweanor et al. 2008). Males were far more active than females, and regularly spent more than 50% of time moving during hourly increments. In contrast, females were much more sedentary. However, even for pumas of the same sex, individuals exhibited quite a bit of variability in their activity. For example, 2F and 7F, both females with kittens, moved very little even during dawn and dusk, whereas 28F, a female without kittens, was much more active and even moved regularly throughout the daytime. 5M, a territorial male, exhibited one peak in activity around midnight whereas the two other males experienced a dip in activity around midnight. When detailed GPS information was available, the actual distance traveled by pumas strongly corroborated the proportion of time we predicted movement (Figs. 5, 6).

Discussion and Conclusion

Our aim in this study was to use accelerometer measurements taken on captive animals as a proxy to classify behavior in wild animals. Using Random Forest models, we were able to accurately predict periods of non-movement, low acceleration (e.g., walking), and high acceleration movements (e.g., trotting and running) in unobservable wild animals. This insight allowed us to better document puma movement patterns and activity levels throughout the day and to identify individual and sex differences.

Our model identified Amp M, DFZ, and SDM as the top ranked predictors of puma mobility. The first two variables are strongly tied to the periodicity of the movement since Amp M is the dominant power spectrum of the magnitude and DFZ is the dominant frequency of the Z-axis. Movement behavior results in cyclic accelerometer patterns that are dominated by one frequency because the accelerations are primarily produced by footfalls and body movements (Fig. 1). These dominant frequencies correspond to footfall frequencies and can be used for dead reckoning and energetics analyses (Williams et al., in prep). The third parameter identified is the standard deviation of the magnitude, which is higher during mobile than non-mobile behaviors. Taken together, these parameters can clearly distinguish movement behavior, which is characterized by higher acceleration and periodicity, from non-movement activities. The tight association between footfall frequency and the dominant frequency of the accelerometer measurements bodes many promising avenues for calculating daily energetic expenditure (see Williams et al., in prep.).

Most current research on animal movement uses GPS or radio-telemetry collars, which only allow researchers to measure locations sporadically throughout each day. In contrast, accelerometer collars take continuous measurements, thus providing a complete diary of the time period over which the instrument is activated. This enhanced dataset allowed us to gain more nuanced insights about animal behavior. For example, we observed that male pumas were more active than females and exhibited stronger crepuscular and nocturnal activity preferences. In contrast, females were active throughout both day and night, although their overall activity rate was much lower than males. Additionally, our movement activity budgets revealed that the two female pumas with kittens were far less active than the female without kittens (Fig. 4), although these observations were from a relatively short time period.

We were also able to identify attack signatures of pumas taking down their prey using the behavioral model. Although high acceleration clusters occurred throughout the day, the events which we classified as kills had raw accelerometer readings with sizes and magnitudes that were generally longer and larger compared to other events (Figs. 2, 3). Additionally, there were several other prolonged high acceleration clusters of similar or even larger magnitudes that were not associated with identified kills. These events may have been unidentified kills or unsuccessful hunting attempts.

In our study, accelerometer sensors helped us gain novel insights on the length of the predation events identified by GPS locations. We noted that predation by pumas on prey produced spikes of high acceleration activity. However, while predation by females on adult prey occurred over several minutes and included some of the highest magnitude ranges, events involving larger-bodied male puma and smaller juvenile prey were not as extreme. It is likely that with additional data, we will be able to characterize and identify predation and attempted predation events of medium and large bodied mammals using paired accelerometer and GPS data and corroborating these predictions with field visitations. In future accelerometry studies, we can design collars with GPS sensors that work synergistically with accelerometer sensors such that if a collar detects high acceleration behavior, it automatically records additional GPS locations. Combining such detailed locational and acceleration information can reveal the duration, energetic expenditure, and chase sequence of puma predation events and help scientists gain more insight about the hunting behavior of pumas.

Data derived from accelerometers can be used to assess how animals respond to anthropogenic influences. For example, pumas may transition between resting and moving more often or spend more time traveling in landscapes with more human disturbances than undisturbed habitats, changing their overall activity levels and hunting patterns and impacting their caloric demands. Additionally, caloric expenditure by pumas can be calculated more accurately using our predicted activity budgets and footfall frequencies derived from accelerometer data than from GPS information alone. Such information, paired with data from predation events can allow researchers to determine where pumas are gaining and depleting calories in relation to the built environment.

Our behavior model was weak at predicting feeding events and was not able to predict grooming behaviors. This is most likely due to the complexity of identifying non-locomotive motion and to the relatively few instances of these behaviors observed in the captive pumas. While grooming is a relatively unimportant behavior to identify, accurately predicting feeding events is crucial in understanding behavior and energetics. We believe these issues can be overcome in the future through a variety of innovative strategies. Studies on oystercatchers and cheetahs have used accelerometers to identify feeding bouts with some success (Grunewalder et al. 2012; Shamoun-Baranes et al. 2012). However, both studies were able to observe the collared individual engaging in these behaviors and use that information to classify additional events. While we are unable to observe pumas in the wild, we may be able to record their feeding behavior using cameras placed at bait sites or fresh carcasses. Using this information, we could then identify accelerometer sequences that correspond with feeding in the field and then use that to identify future feeding events. Additionally, we could perform more feeding trials with captive pumas using whole deer and raccoon carcasses so as to more closely mimic their dietary habits in our study area.

Accelerometer technology has great potential for animal behavioral research. Although our first generation accelerometers suffered from limited longevity, we are working to resolve these issues for the next generation of accelerometer-equipped collars. We expect that onboard microSD cards will be capable of storing up to 2 years worth of accelerometer data, depending on how often they are programmed to collect data. Additionally, we observed little loss of predictive power down to 16Hz for our mobility model when we down-sampled our accelerometer measurements from 64Hz to 32, 16, 8, 4 and 2 (Fig. 7). Future accelerometer collars can thus potentially operate for longer by sampling at a lower frequency to provide a comprehensive and long-term picture of animal behavior.

As collar and battery technologies continue to improve, we are likely entering a new age of movement behavior research. Smart collars using accelerometers can help reduce battery consumption by only recording GPS data points when the animal is actively moving. In addition, future collars may be equipped with small cameras that could be triggered when the accelerometer identifies high intensity events.

Cameras deployed on animals have already been used to help document cat predation on wildlife (Loyd et al. 2013) and the energetics costs of seals preying on fish (Williams et al., 2004). In wild pumas, cameras paired with accelerometers could potentially catalog and quantify attempted kills and kills of small prey that are not picked up by GPS data alone.

Our project demonstrates that accelerometers can successfully predict movement behaviors in animals that are difficult to observe in the wild. However, more complex behaviors, such as feeding, might only be accurately identified with more observations from captive and wild animals. Our methods are not limited to pumas, but can be used with any terrestrial mammal to create a complete activity budget, catalogue behaviors, including predatory ones, and potentially measure energetic expenditure as well as foraging efficiency. We believe this ability to link behavior, spatial location, and energy expenditure has the potential to provide novel insights into how landscape structure influences the allocation of energy to different behaviors. Such information would be valuable for conservation and management issues by revealing the detailed responses of individual animals to their surrounding landscape.

Methods

Study species and area

Pumas are territorial, apex predators that live in diverse habitats throughout the Americas (Hornocker & Negri 2009). Individuals are primarily nocturnal and solitary, although females will typically raise and accompany cubs for 15-21 months after birth. In our study area in the Santa Cruz Mountains of California, pumas primarily feed on black-tailed deer (*Odocoileus hemionus columbianus*) but occasionally on other species, including wild boars (*Sus scrofa*), raccoons (*Procyon lotor*) and cats (*Felis catus*) (Wilmers et al. 2013).

Our 17,000 km^2 study area encompasses a diverse landscape ranging from dense, urban development to large tracts of intact and relatively undisturbed native vegetation. It is bisected by a large freeway and further crisscrossed by numerous smaller roads providing access to rural houses and developments. The climate is Mediterranean, with precipitation concentrated between November and April. Elevation ranges from sea level to 1155m.

Data collection

Captive Animals

We used custom-built collars (Rutishauser et al., 2011) equipped with a tri-axial accelerometer sampling continuously at 64Hz to monitor behavior in captive and wild pumas. Captive pumas were housed and trained by the Colorado Parks and Wildlife (Division of Wildlife Foothills Wildlife Research Facility) (Williams et al., in prep.). We outfitted one male and one female puma with a test accelerometer collar during training sessions. We observed the collared animals and recorded their behaviors both manually and with a video camera. We conducted 1-2 trials per animal during two different visits. At the end of each visit, we retrieved the collar and downloaded the data.

Wild Animals

We outfitted wild pumas (5 males, 7 females) from 2010-2012 by capturing them using trailing hounds, cage traps, or leg hold snares as described in Wilmers et al. (2013). Each animal was tranquilized using Telazol and outfitted with an off-the-shelf GPS/VHF collar (Vectronics Aerospace GPS PLUS model) combined with the custom-built archival 3-axis accelerometer tag (Rutishauser et al. 2011), which was incorporated into the battery casing. The tri-axial accelerometer was mounted such that the x-, y-, and z- axes were parallel to the anterior-posterior, the transverse, and the dorsal-ventral planes of the animal, respectively. Data collected by the accelerometer were recorded in an onboard 8GB microSD card, which is capable of storing more than 200 days of accelerometer measurements.

We programmed each collar to acquire a GPS fix every 4 hours. Prior to April 2011, we programmed accelerometers to record at a duty-cycle of 2 weeks on, 4 weeks off commencing immediately upon capture. While accelerometers were recording, the collars were programed to acquire additional GPS fixes at 5-minute intervals between 8 and 9PM local time for one week (GPS intensive sampling period). After April 2011, we programmed accelerometers to operate two consecutive days every week beginning 5 days after the animal was captured. Concurrently, we acquired GPS locations every 15 minutes during a 24-hour period from noon to noon (GPS intensive sampling period). We retrieved all collars either during a recapture of the animal (n=8) or following its death (n=4). The Animal Care and Use Committee at UC Santa Cruz approved all animal-handling procedures.

Data processing

Captive Animals

We reviewed all recordings of captive pumas and categorized behaviors into mobile (e.g., normal movement, fast movement) or non-mobile (e.g., resting, feeding, grooming) activities. We divided observations into 2-second segments encompassing only one behavior type and extracted the corresponding accelerometer data (Fig. 1). We chose 2 second segments because the length of the test track for videotaping was approximately 20 m to accommodate 1-2 full strides of the animals within the camera field.

To compare across collars we converted all accelerometer data into units of *g* (1 *g* = 9.8 m s^{-2}) using tag specific calibration values derived prior to deployment. The process of calibrating the accelerometers consists of gently tumbling the collar and measuring the body-frame output of the accelerometer triad (Gebre-Egziabher et al. 2006). In the case of a perfectly calibrated accelerometer, the locus of points would all be attached to a sphere centered at the origin with a radius of 1*g*. Due to null shift errors, the sphere is centered off the origin, and scale factor errors transform the sphere into an ellipsoid. We developed a custom MATLAB 8.0 (The MathWorks, Inc., Natick, Massachusetts, United States) script to extract the null shift and scale factor errors by fitting an ellipse to the data two axes at a time, and combining the resultant parameters.

Wild Animals

We downloaded all available accelerometer data and removed the first 24 hours of data following anesthesia. We then converted accelerometer data into units of *g* as described in the previous section.

Modeling

From each 2-second segment of accelerometer measurements, we extracted 16 predictor variables from the three-accelerometer axes and the magnitude (see Table 1). Most of the predictors have been used and described in previous studies (Nathan et al. 2012; Shamoun-Baranes et al. 2012; Watanabe et al. 2005). We used parameters associated with dynamic acceleration but not static acceleration, because static acceleration is dependent upon collar placement on the animal and is influenced by changes to the animal's posture. We also applied a Fast Fourier Transform to accelerometer measurements to extract the dominant frequency and dominant power spectrum values of the behavior.

We selected Random Forests (RF) (Breiman 2001) as our modeling tool to predict unobserved behaviors in wild animals based on measurements of observed behaviors in captive animals. RF is a relatively novel and powerful machine learning tool that works well for non-linear and complex ecological data not easily fitted by traditional methods such as generalized linear models (Cutler et al. 2007). Compared to a classification tree, which creates a set of decision rules to classify data, RF achieves higher prediction accuracy because it combines predictions made by numerous classification trees (Strobl et al. 2009). Another benefit of using RF compared to other classification methods lies in its ability to make accurate predictions from datasets with correlated variables and to compare conditional variable importance measures, which identify the extent to which specific predictor variables influence classification accuracy (Cutler et al. 2007). A higher measure of variable importance indicates that the variable exerts greater influence on the response relative to other predictors with lower values (Strobl 2009).

Our first model (mobility model) segregated mobile from non-mobile behavior. To build our model using RF, we fit 500 classification trees to a randomly selected subsample (without replacement) of the original data using a random subset of 5 predictor variables for each split in the tree (Breiman et al. 1984; Strobl et al. 2009). Predictions made by all trees for each observation were then tallied, with a classification assigned by the majority result and ties decided randomly. Model prediction accuracies were calculated by comparing predicted and actual classifications. We then obtained unbiased variable importance estimates using a permutation procedure described in Strobl (2009). We built our second model (behavior model) using the same methodology to predict five classes of behaviors: low acceleration movement (e.g., walking), high acceleration movements (e.g. trotting, running), resting, eating, and grooming. We fit all of our models and calculated variable importance estimates using the Party package (Hothorn et al. 2006) in the R statistical program (vers. 2.15.1) (R Development Core Team 2013).

We created down-sampled datasets of accelerometer data at 32, 16, 8, 4, and 2 Hz to test how reducing sampling frequency affects model prediction accuracy. Using the down-sampled datasets, we built additional mobility models and assessed model accuracy as described previously.

Model Application

We applied our mobility model and behavior model to all data from puma collars which yielded >1 day of accelerometer and GPS intensive sampling data. Because we could not observe behavior in wild animals, we tested the accuracy of our mobility model's predictions by fitting a linear mixed effects model to GPS data using the lme4 package (Bates & Sarkar 2007). We did this both for the full mobility model and for the mobility models created using down-sampled accelerometer data. We used the distance between successive GPS points as our response variable and treated the percentage of time spent moving as a fixed effect and puma ID as a random effect. We expected that longer-distance GPS movement would be correlated with a higher percentage of time dedicated to movement behavior, and that this relationship might vary by individual pumas. For example, during a 15-minute gap between successive GPS points, we made 450 predictions at 2-second intervals. If we mostly predicted movement, we would expect the distance between the two GPS points to be generally larger than if we mostly predicted non-movement.

We constructed 24-hour movement budgets for all pumas to document the proportion of time pumas spent moving throughout the day. To determine the proportion of time spent moving for each one-hour period (e.g., 1AM to 2AM), we calculated the number of increments during which we predicted mobile activity and divided that by the total number of predictions we recorded between those time periods. From our behavior model, we generated 24-hour behavioral budgets for our five behavior classes.

Using the results from our behavior model, we tested whether prediction events are correlated with clusters of high acceleration movement. We used six known feeding events by four pumas on five deer and one unknown species to examine the corresponding high accelerometer activity. When feeding, pumas generally remain with the carcass over several GPS acquisitions. We used this information to estimate the duration of the feeding event as the interval of time between the first and last GPS location at the kill site. We also appended the four-hour interval prior to the first GPS location associated with the site to the feeding duration since it is possible that the puma made a kill during this period of time.

Five of these feeding events were visited and verified by field personnel, and one was classified as a kill with 80% probability using a predation model developed by Wilmers et al. (2013). From observations of captive puma behavior, we know that faster and more intense movements, such as running and jumping, lead to accelerometer readings with ranges spanning 3-5 g or more. We expected that predation events would involve several of these high acceleration readings as pumas attack and wrestle with their prey. For each of the four pumas, we identified clusters of high acceleration behaviors with a magnitude range exceeding 3.4 *g,* or two standard deviations above the average and calculated the duration and the maximum magnitude of the event. We defined a cluster to be two or more successive high acceleration behaviors separated by no more than three minutes between consecutive behaviors. We expected that if high acceleration movements were associated with predation events, we would see a prolonged cluster of these types of movements in the first quartile of each predation event. Compared to non-predation high acceleration clusters, we also expected the size and maximum magnitude of the cluster representing a potential predation event to be in the top 10% of those measurements across all clusters.

Acknowledgements

We thank the California Department of Fish and Wildlife, Cliff Wylie and Dan Tichenor for their expertise in capturing pumas with hounds and Paul Houghtaling, Veronica Yovovich, Yasaman Shakeri, and Joseph Kermish-Wells for additional field support. L. Wolfe and the staff and animals at the Colorado Parks and Wildlife (Fort Collins, CO) were invaluable for the collar calibration tests. We also thank Caleb Bryce for his help with classifying captive puma behavior from videos. Funding was provided by NSF grant #0963022, as well as by the Gordon and Betty Moore Foundation, The Nature Conservancy, Midpeninsula Regional Open Space District, UC Santa Cruz and the Felidae Conservation Fund.

Table 1.1. Parameter labels and explanations for Random Forest model.

Parameter	**Label**	**Definition**
Axes	X, Y, Z	X, Y, Z axes
Magnitude	M	Square root of the sums of squares of the acceleration in the X, Y and Z axes
Dynamic body acceleration (in g)	ODBA X, ODBA Y, ODBA Z,	Mean of dynamic acceleration value along X, Y, and Z axes
Overall dynamic body acceleration	ODBA	Sum of ODBA X, ODBA Y, ODBA Z
Dominant power spectrum (Hz)	Amp X, Amp Y, Amp Z, Amp M	Amplitude of dominant frequency
Dominant frequency (Hz)	DFX, DFY, DFZ, DFM	Frequency at dominant power spectrum
Standard Deviation of dynamic body acceleration and magnitude	SDX, SDY, SDZ, SDM	Standard Deviation of dynamic acceleration and magnitude in window

Table 1.2. Total accelerometer and GPS data gathered for pumas from 2010-2011.

Puma ID	Sex	Accelerometer Days Sampled	GPS Available
2	F	26.72	Yes
4	M	8.23 **	Yes
5	M	14	Yes
7	F	9.42	Yes
11	F	0.66	No
13	F	20.35 *	Yes
16	M	16	Yes
17	M	14	Yes
20	F	11.2	No
27	M	0	Yes
28	F	4	Yes
30	F	NA**	Yes

*only two axes accurately measured ** date/time inaccurately recorded

Table 1.3. Total 2 second observations (N) of captive puma behaviors classified by mobility class and behavior class.

Mobility	**Behavior**	**N**
Yes	Low acceleration movement	564
Yes	High acceleration movement	50
No	Resting	1167
No	Eating	284
No	Grooming	77

Table 1.4. Cross-validation of actual (rows) and predicted (columns) behaviors of captive animals as categorized by the behavior model. High and low represent high and low acceleration movements.

	Feed	**Groom**	**Rest**	**High**	**Low**	**Percent Accurate**
Feed	179	0	67	0	38	63.7
Groom	20	0	54	0	1	0
Rest	26	1	1130	0	10	96.8
High	0	0	0	46	4	92
Low	24	0	9	2	529	93.8

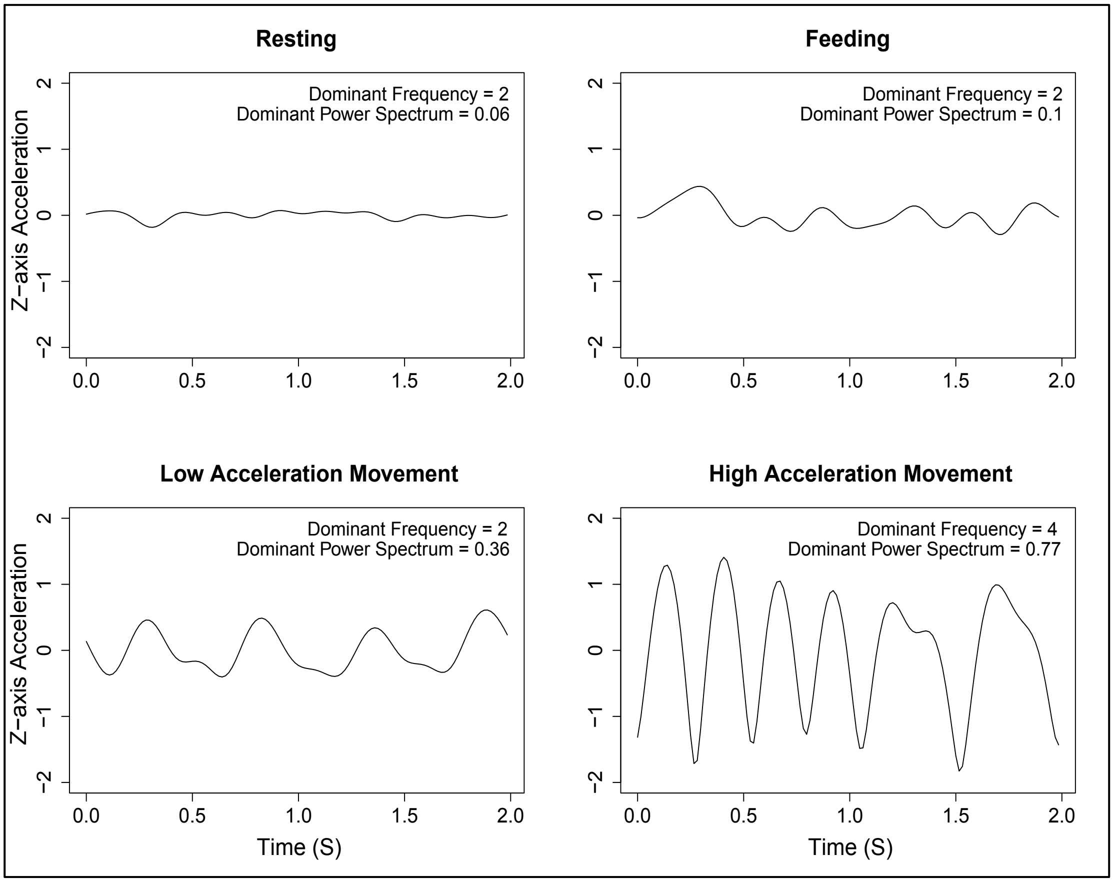
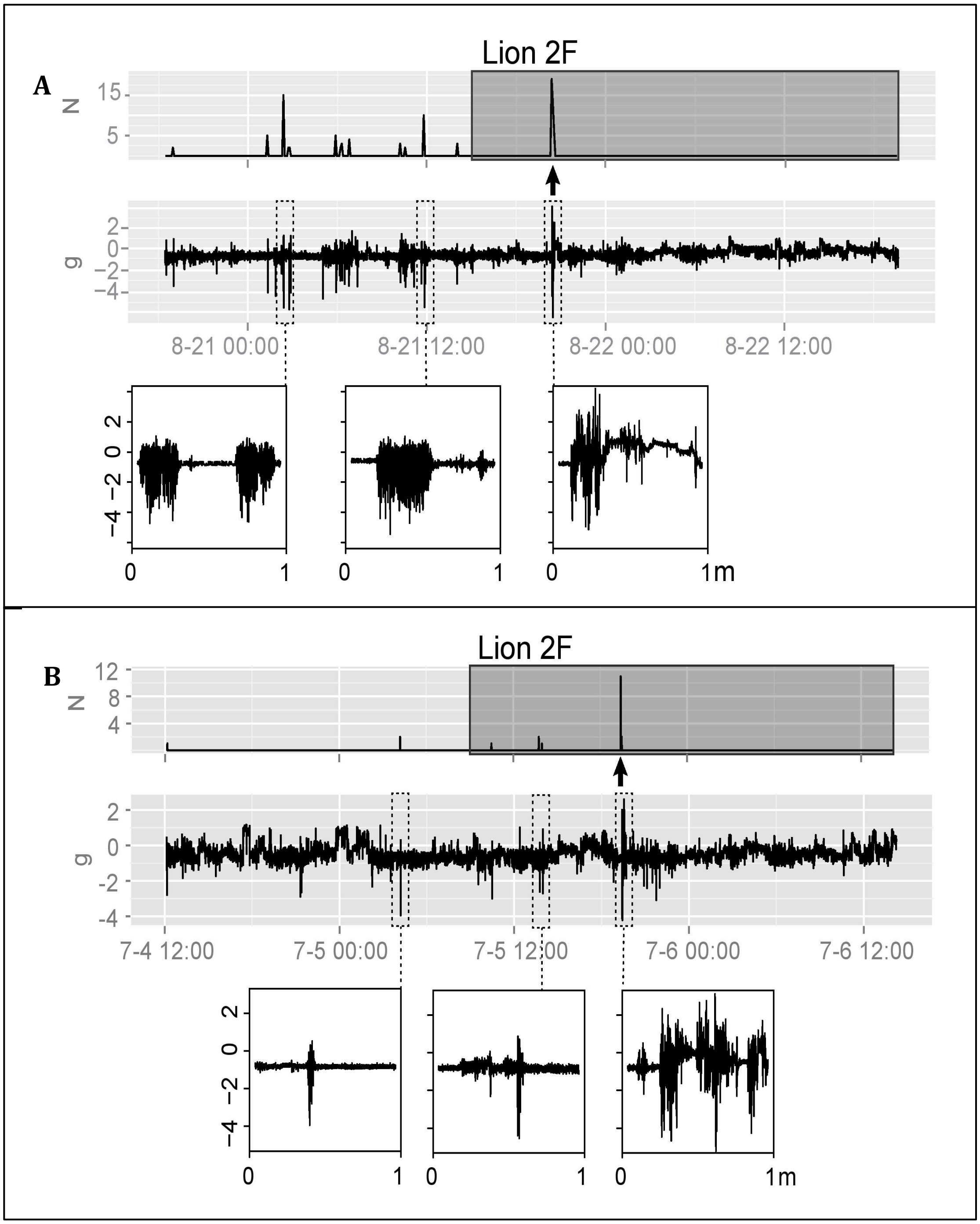


Figure 1.1. Two-second windows of Z-axis acceleration for four behaviors with associated dominant frequencies and dominant power spectrums.


A
Lion 2F
N
15
5
g
2
0
−2
−4
8-21 00:00
8-21 12:00
8-22 00:00
8-22 12:00
2
0
−2
−4
0
1
0
1
0
1m
B
Lion 2F
N
12
8
4
g
2
0
-2
-4
7-4 12:00
7-5 00:00
7-5 12:00
7-6 00:00
7-6 12:00
2
0
−2
−4
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1
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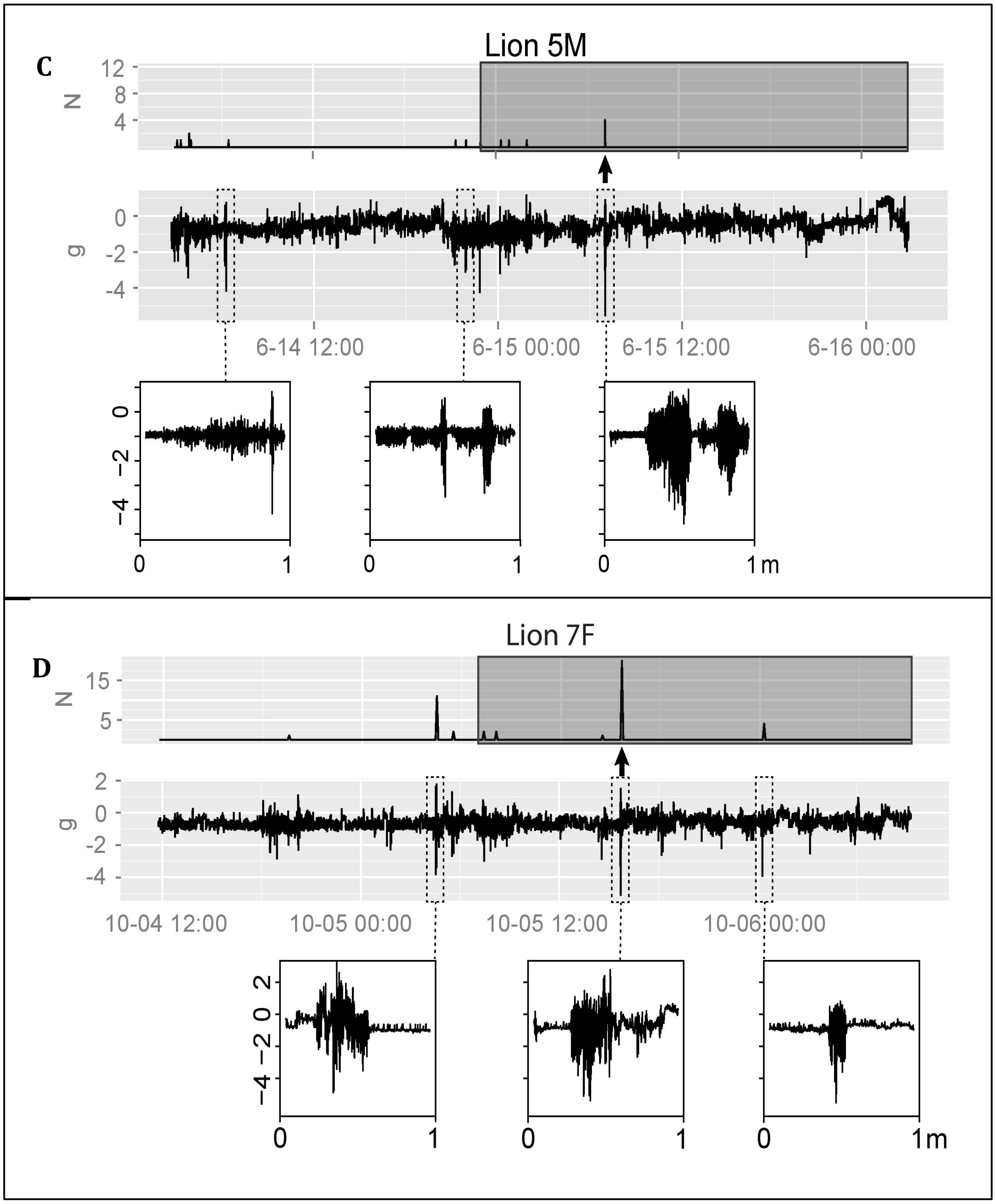
0
1m


C
Lion 5M
N
12
8
4
g
0
-2
-4
6-14 12:00
6-15 00:00
6-15 12:00
6-16 00:00
0
−2
−4
0
1
0
1
0
1 m
D
Lion 7F
N
15
5
g
2
0
-2
-4
10-04 12:00
10-05 00:00
10-05 12:00
10-06 00:00
−4 −2 0 2
0
1
0
1
0
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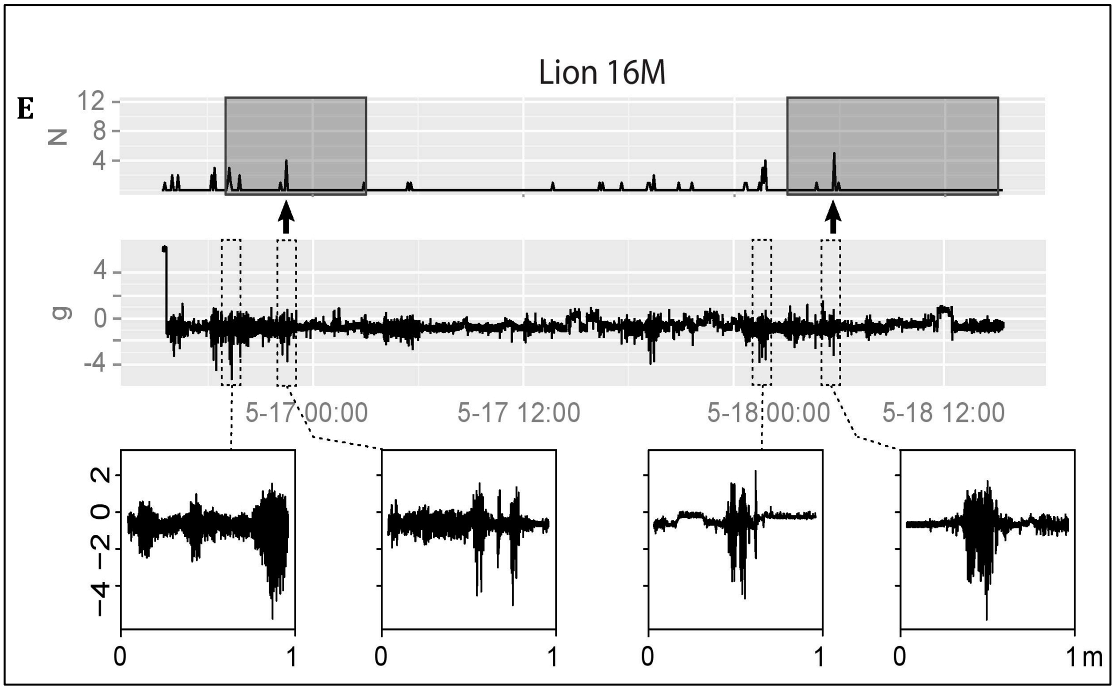
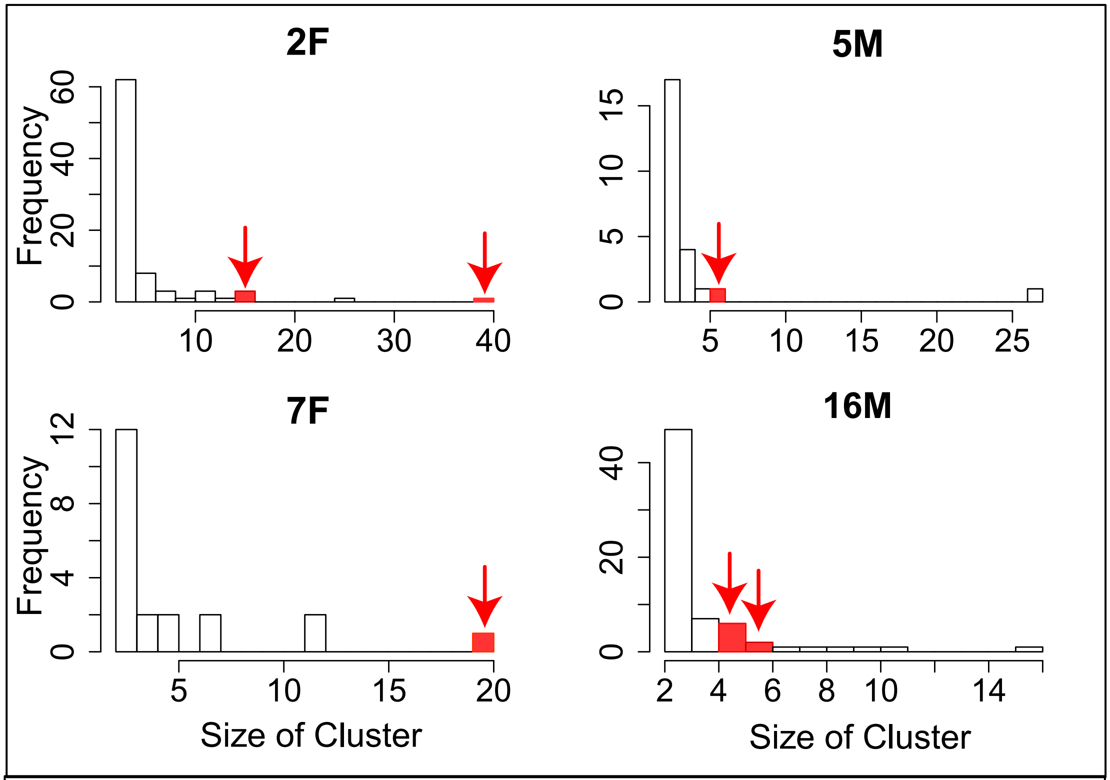
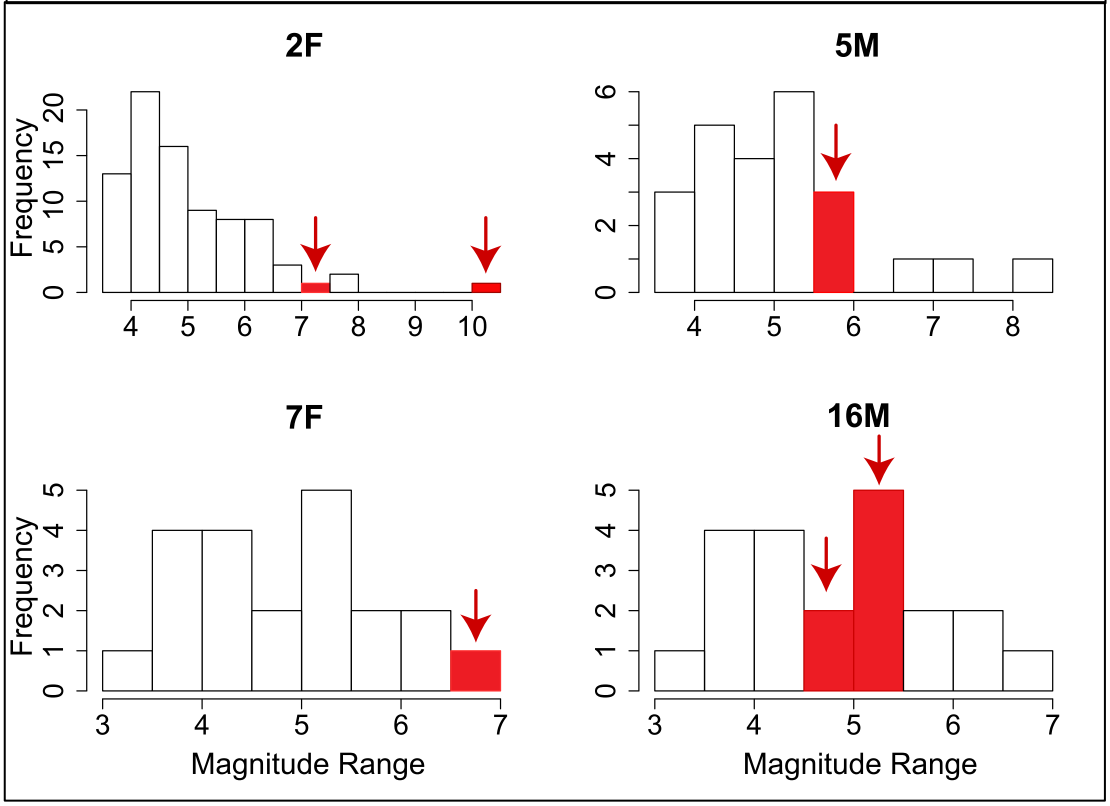


Figure 1.2. Plots of predation events by pumas a. and b.) 2F, c.) 5M, d.) 7F, and e.) 16M. The top panel for each plot illustrates the number (N) of high acceleration movements per minute over a period of two days. The dark grey rectangle highlights the period of time associated with the predation event as verified independently from field visits to clusters of GPS locations. The bottom panel shows the raw accelerometer measurements in units of gravity *g* for the Z-axis. The bottom inserts magnify a one-minute period of accelerometer measurements from selected large clusters to show the magnitude and duration of the acceleration during those high acceleration events. The arrow indicates when we hypothesize the kill event to have occurred.



2F
5M
7F
16M
Frequency
Size of Cluster
0
20
40
60
10
20
30
40
0
5
10
15
5
10
15
20
25
0
4
8
12
5
10
15
20
0
20
40
2
4
6
8
10
14



2F
5M
7F
16M
Frequency
Magnitude Range
0
5
10
15
20
4
5
6
7
8
9
10
0
2
4
6
4
5
6
7
8
0
1
2
3
4
5
3
4
5
6
7

Figure 1.3. Histograms of the number of predicted high acceleration movements in each cluster (top) and magnitude range (bottom) for pumas 2F, 5M, 7F and 16M. Bins containing values corresponding to verified predation events are highlighted in red and accented by an arrow. Kills by 2F and 7F at the far right of the histogram were of adult deer whereas those of 16M and 5M in the center of the histogram were of fawns.

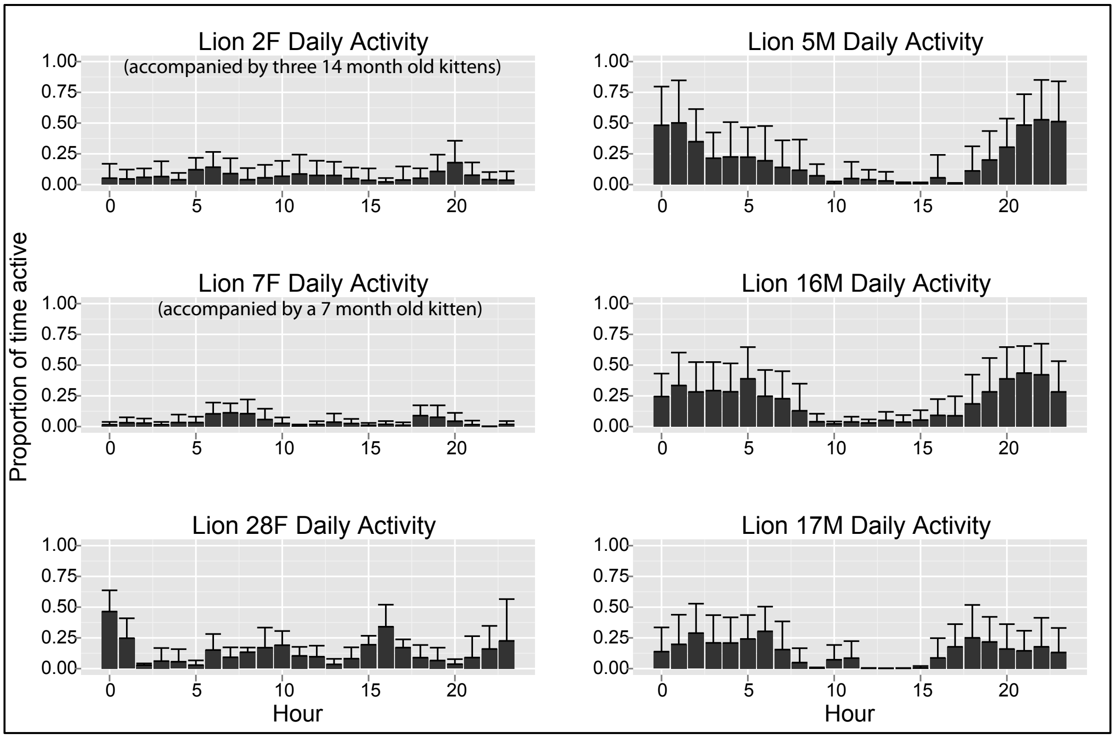


Figure 1.4. Predicted hourly activity across a 24-hour period for all pumas (+ 1 SD). These behavioral dairies are averaged over 25.64 days (2F), 13 days (5M), 8.42 days (7F), 13 days (17M), 16 days (16M) and 4 days (28F).

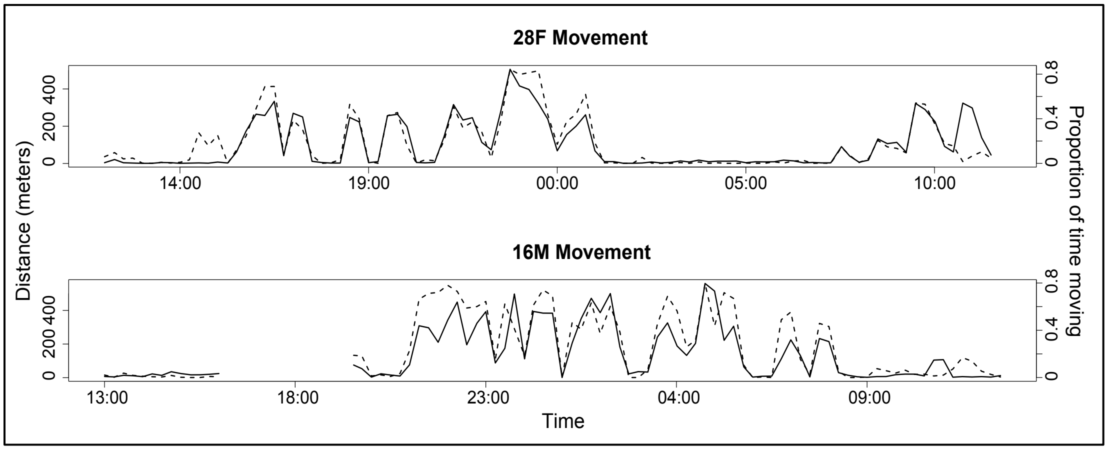


Figure 1.5. 15-minute movement distances measured directly from subsequent GPS locations (solid) and associated predicted movement activity based on accelerometry (dashed) for pumas 28F and 16M. While we would not expect activity levels to be perfectly correlated with linear movement distances, the level or correspondence between these two measures provides a field-based assessment of the ability of accelerometer measurements to predict movement activity.

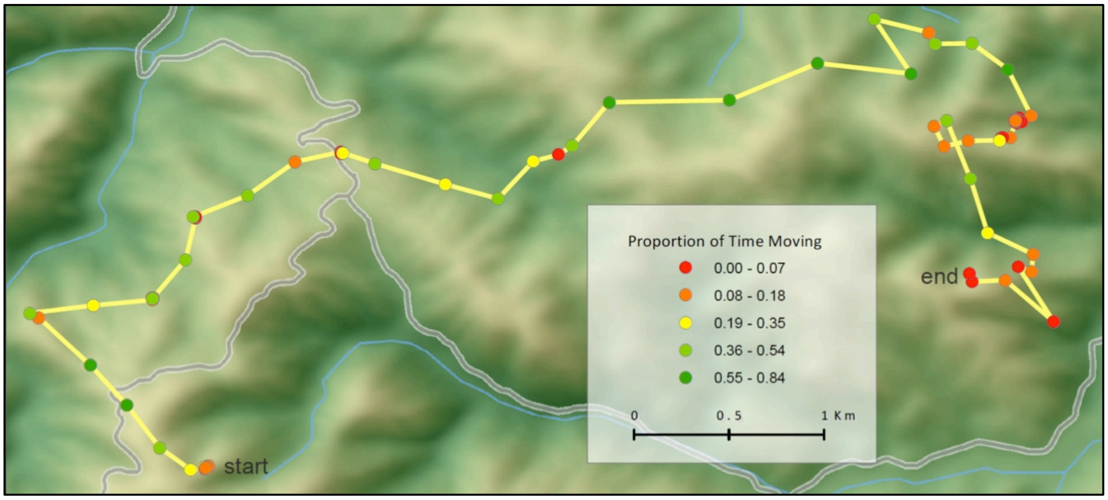


Figure 1.6. 15 minute GPS locations and associated predicted movement activity for 28F.

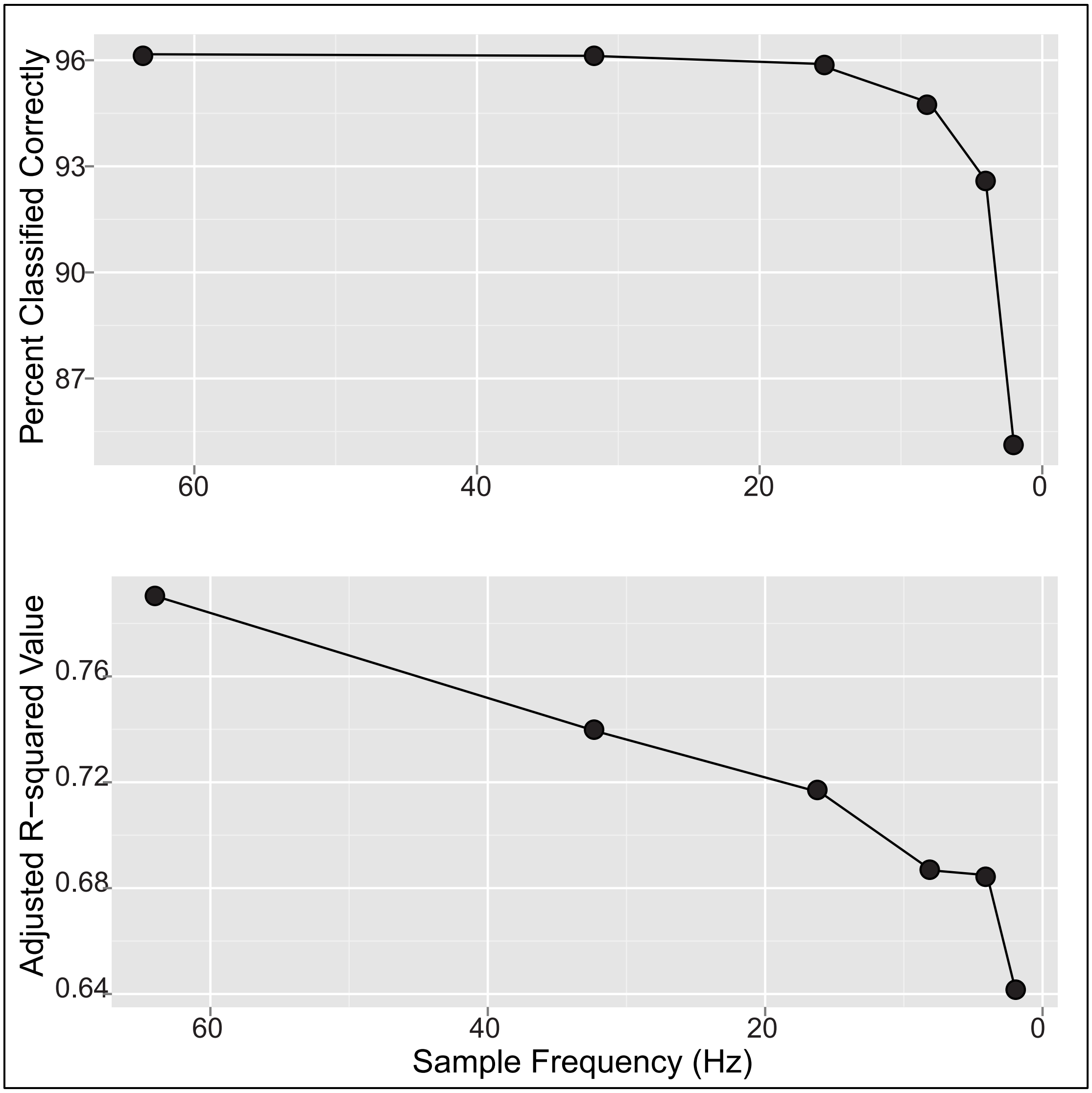


Figure 1.7. The accuracy of predictions by the mobility model remains high until the data is sampled past 8 Hz (top graph). The correlation between the mobility model predictions and the distance traveled declines steadily as the data is down-sampled (bottom graph).

Chapter 2

Anthropogenic development influences on puma behavior, movement, and energetics in a fragmented landscape

Abstract

Human development has strongly influenced large carnivore survival and persistence globally. Changes in behavior are often the first measureable responses to human disturbances, and can have dramatic ramifications on animal populations. Understanding how apex predators respond to anthropogenic changes can greatly inform management and conservation of apex predators. We used 3 years of GPS location data for pumas in the Santa Cruz Mountains to study how their movements and behaviors were affected by human development. We used log-linear analyses to examine how habitat, time of day, and proximity to housing influenced the activity patterns of male and female pumas. We also used 15-minute GPS sampling points to evaluate how development density affected the average distances pumas traveled and calculated their daily energetic expenditures. We compared energetic estimates obtained from GPS movement data with Overall Dynamic Body Acceleration (ODBA) measurements recorded by onboard accelerometers. We found that pumas responded to development differently depending on the time of day. Pumas generally were more active and moved further when they were in developed areas at night. In contrast, during the day, pumas either did not change their activity or moved less in developed areas. Energetic estimates obtained from ODBA measurements suggest

that energetic requirement estimates based on our GPS movement data are 4-5 times lower than true values. Our integration of energetic and movement models indicates that pumas have higher energetics costs and requirements in human-dominated habitats. We recommend that future conservation work consider the ramifications of behavioral shifts on animal energetic costs and fitness.

Introduction

The disciplines of animal behavior and conservation have increasingly coalesced over the past four decades (Caro 1999), culminating in the new field of conservation behavior (Blumstein & Fernandez-Juricic 2004). Conservation behavior aims to stem biodiversity loss by applying insights gained through investigating the proximate and ultimate causes of animal behavior (Berger-Tal et al. 2011). Already, application of these lessons has aided the success of many applied conservation efforts including translocations, reintroductions, and captive breeding programs (Bennett et al. 2013; Moore et al. 2008). In addition to aiding active conservation programs, understanding animal behavior is also critical to identifying conservation needs (Wilmers et al. 2013). Indeed, some biologists have argued that preserving behavioral diversity should be an important focus for conservation biologists, on par with maintaining genetic diversity in populations (Caro & Sherman 2012).

Despite the growing recognition that the study of animal behavior is an integral component in conservation biology, the applicability of behavioral knowledge to conservation remains tenuous and interdisciplinary collaborations between the two fields rare (Angeloni et al. 2008). This mismatch partially stems from the emphasis placed on theoretical understanding in animal behavior and the immediate practical needs of conservation practitioners (Caro 2007). To bridge this divide, behavioral studies can focus on species in threatened habitats or on questions of conservation significance, such as behavioral responses to anthropogenic influences.

Behavioral changes often provide the first measurable indication that individuals are responding to human-induced environmental alterations (Ordiz et al. 2012; Tadesse & Kotler 2012; Tuomainen & Candolin 2011) such as habitat fragmentation, the primary anthropogenic driver of species extinction (Czech et al. 2000). Fragmentation alters the size, shape, connectivity, and structure of habitats, thus impacting many important behaviors (e.g., foraging, mating, and movement) (Magle & Angeloni 2011) and transforming species interactions (Batary & Baldi 2004). Even in undeveloped areas and especially in edge habitats, human activities (e.g., recreation) and the activities of companion animals may also influence the behaviors of native animals (George & Crooks 2006; Reed & Merenlender 2008). These behavioral responses can potentially increase or decrease individual fitness for different species, leading to population level changes and possibly even to shifts in species communities as some species are extirpated from the landscape. In a meta-analysis, Preisser et al. (2005) concluded that trait-mediated effects were equally or more important than direct demographic effects for prey species. Identifying these changes can be critical to recognizing and predicting conservation need, but has thus far been difficult to achieve in the wild.

Large carnivores are often the first to disappear as anthropogenic influences begin to transform the landscape (Woodroffe 2000). Despite this, comparatively little is known about the behavioral responses of predators to urbanization that could eventually lead to their extirpation from the landscape (Crooks 2002). In most human-influenced ecosystems, humans are the apex predators and are capable of hunting or extirpating large predators (Frid & Dill 2002; Woodroffe & Ginsberg 1998). Carnivores, such as wolves (*Canis lupus*), grizzlies (*Ursus arctos*) and pumas (*Puma concolor*), in these systems may respond to human disturbance and persecution through behavioral modifications much like prey species respond to predators (Ordiz et al. 2012). For example, Dickson et al (2005) found that radio-collared pumas (*Puma concolor*) avoided paved roads and moved swiftest through urbanized landscapes compared to 8 other habitat types, potentially indicating discomfort near humans. As human development continues to fragment previously intact landscapes, it becomes increasingly vital to understand how species adjust their behavior in response to these perturbations. Only by better understanding the behavioral ecology of these animals, can we implement protective policies that can ensure their continued existence in the face of rising human influence (Caro & Sherman 2011).

Our inability to directly observe wild carnivores has greatly constrained our previous understanding of their behavior. Much of our data on predators come from indirect evidence (i.e. scats, photographs from camera traps, hairs) or sporadic location points (i.e. radio telemetry or GPS) (Cooke et al. 2004; Rowcliffe & Carbone 2008). Recent technological developments have provided researchers with new opportunities to monitor animal behavior at a much finer scale and with greater accuracy than previously had been possible. In the Santa Cruz Mountains of California, we have been using accelerometers and GPS collars to document detailed puma movement and behavior in a fragmented landscape. Thus, while we cannot directly observe the behavior of our study animals, we can use accelerometer and GPS readings to infer how their daily activity patterns may be influenced by human development.

Previous studies have found that pumas will sometimes use habitats in close proximity to humans (Dickson et al. 2005; Wilmers et al. 2013). Based on the risk-disturbance hypothesis, we expect that pumas might alter their behaviors to manage the risk of moving through anthropogenic landscapes (Frid & Dill 2002). Proximity to anthropogenic structures can affect the amount of time pumas spend active rather than resting and also increase the number of times they switch between the two behavioral states. These behavioral differences translate into differential energetic costs that progressively accumulate over time, which may have lasting impacts on individual fitness. Our study's goals were to further the understanding of how human development impacts the behavior and energetics of large carnivores. Determining how anthropogenic influences mediate puma activities and energetics is invaluable to creating suitable conservation strategies that preserve structural patterns of habitat to reduce costly behavioral adaptations.

In this study, we used Markov Chains to test how human dominated habitats impact the movement and resting patterns of wild pumas. In order to enrich our inference on activity data derived from GPS collars, we evaluated the relationship between fine- and course-scale activity patterns using both GPS and accelerometer technologies. We expected pumas closer to development structures would spend more time active than when further away. Expanding upon the work done by Dickson et al.

(2005) on puma movement, we examined whether habitat type and time of day influenced how pumas responded to human development. We also evaluated how human development affected the daily movement patterns and caloric expenditures of pumas using fine-scale GPS tracks. While Dickson et al. (2005) found that pumas preferred energetically conservative travel paths, we expected that individual pumas traversing through more human dominated habitats would expend more kilocalories (kcals) and travel further as they navigated through more developed habitats. By exploring how puma behavior might be influenced by development, we hope to illustrate the usefulness of behavior studies for advancing our understanding of human impacts on large carnivores.

Methods

Study species and area

Pumas are territorial, apex predators which live throughout diverse habitats in the Americas (Hornocker & Negri 2009). Individuals are primarily nocturnal and solitary, although females will typically raise and accompany cubs for up to 15-21 months after birth. In our study area in the Santa Cruz Mountains of California, pumas predominantly feed on mule deer (*Odocoileus hemionus*) but occasionally on other species, including wild boars (*Sus scrofa*), raccoons (*Procyon lotor*) and house cats (*Felis catus*) (Wilmers et al. 2013).

Our 17,000 km^2 study area encompasses a diverse landscape ranging from dense, urban development to large tracts of intact and relatively undisturbed native vegetation. The vegetation structure is primarily comprised of forested (e.g., woodlands, hardwood and conifer forests) and shrubland (e.g., scrub and chaparral) habitats. It is bisected by a large freeway and further crisscrossed by numerous other smaller roads providing access to rural houses and developments. The climate is Mediterranean, with precipitation concentrated between November and April, and elevation ranges from sea level to 1155m.

Data Collection

We captured 22 wild pumas (11 males, 11 females) from June 2010 - March 2013 using trailing hounds, cage traps, or leg hold snares. More detailed information on capture and handling methods can be found at Wilmers et al. (2013). Each animal was tranquilized using Telazol at a concentration of 100mg/mL and outfitted with an off-the-shelf GPS/VHF collar (Model GPS Plus 1D, Vectronics Aerospace, Berlin, Germany). Six of the 22 animals were also equipped with a custom-built archival 3-axis accelerometer sampling continuously at 64Hz when activated (Rutishauser et al. 2011). The tri-axial accelerometer was mounted such that the x-axis is parallel to the anterior-posterior plane of the animal, the y-axis the transverse plane, and the z-axis the dorsal-ventral plane. Data collected by the accelerometer are recorded in an onboard 8GB microSD card, which is capable of storing more than 200 days of accelerometer measurements.

Accelerometers on pumas were programmed to record at a duty-cycle of 2 days on and five days off to maximize battery life. The GPS collars were also programmed at two different fix rates to maximize both fine scale spatial coverage and battery life. We programmed all collars to acquire GPS locations every 15 minutes during a 24-hour intense sampling period from noon to noon one day a week and every 4 hours for the remainder of the week. The Animal Care and Use Committee at UC Santa Cruz approved all animal-handling procedures. We retrieved all GPS information either through a remote download, cell phone tower transmission, or through a direct download after we collected the collar from the field.

Data Processing

During each 15-minute GPS sampling interval, we assigned one behavioral state (active or inactive) to each collared individual and considered these states to be mutually exclusive. Because GPS measurements can err by 10-20 meters regularly, we used accelerometer measurements to determine the distance cutoff between activity states. We used a random forest algorithm described in Wang et al. (*in review*) to categorize 2-second increments of accelerometer measurements into mobile or non-mobile behaviors. These were then aggregated into 15-minute observation periods to match the GPS sampling periods. After inspecting the data visually, we identified 10% activity (i.e., 10% of accelerometer measurements categorized as mobile out of 15 minutes) as the cutoff between active and inactive periods. Because of the strong linear relationship between accelerometer defined activity and the distance traveled between GPS points, 10% activity recorded by accelerometers corresponded to roughly 70 meters between GPS points. Therefore, we considered any distance greater than 70m between successive 15 minute GPS points to be an active period, and a distance smaller than 70m to be an inactive period.

Environmental and anthropogenic measurements

Our study animals inhabit a landscape primarily comprised of forested or shrubland habitats interspersed with developed areas. To examine how human development and habitat type impacted puma behavior, we collected spatial information on buildings and vegetation structure surrounding each puma GPS location. Using the Geographic Information Systems program ArcGIS (v.10, ESRI, 2010), we digitized house and building locations manually from high-resolution satellite imagery for rural areas and with a street address layer provided by the local counties for urban areas. For each GPS position recorded, we calculated the distance in meters to the nearest house. We then placed circular buffers with 150m radii around each GPS location and used the California GAP analysis data (US Geological Survey 2011) to categorize the local habitat as either predominantly forested or shrubland. We also classified the time each GPS location was recorded as diurnal or nocturnal based on sunset and sunrise times.

Markov Chains

We modeled puma behavior sequences as discrete-time Markov chains, which are used to describe activities that depend on previous ones (Caswell 2001). Here, we used first-order Markov chains to model a dependent relationship between the succeeding behavior and the preceding behavior. First-order Markov chains have been successfully used to describe sex differences in beaver behavior (Rugg & Buech

1990), behavioral responses to predators by dugongs (Wirsing & Heithaus 2012), and impacts of tourism on cetacean behavior (Christiansen et al. 2013; Lusseau 2003). Because we were modeling behavior transitions with respect to location characteristics, we recorded the states of the puma (active or inactive) in the 15 minutes prior to and succeeding each GPS acquisition. We populated a transition matrix using these preceding and succeeding behaviors and examined whether proximity to anthropogenic features influenced the transition frequencies between preceding and succeeding behavior states.

We built multi-way contingency tables to evaluate how sex (*S),* time of day (*T*), proximity to house (*H*), and habitat type (*L*) affected the transition frequency between preceding (*B*) and succeeding behaviors (*A*). Because high-dimensional contingency tables become increasingly difficult to interpret, we first used log linear analyses to evaluate whether sex and habitat type influenced puma behavior patterns using two three-way contingency tables (Before × After × Sex). Log linear analyses specifically test how the response variable is influenced by independent variables (e.g., sex and habitat) by using Likelihood Ratio Tests to compare hierarchical models with and without the independent variable (Caswell 2001). We used the R statistical program (v. 3.0.2, R Core Team, 2013) for all analyses. We found that there were strong sex differences in activity patterns because adding *S* to the model greatly increased the fit compared to the null model (ΔG^2=159.8, d.f. = 1, p<.0001), which assumed that succeeding behaviors only depend on preceding ones. Therefore, we evaluated data from male pumas separately from those of female pumas.

We then used another three-way contingency table for each sex to evaluate whether behavior patterns differed between habitats (*L*). We found that including habitat type significantly improved model fit for male (ΔG^2=7.9, df=1, P<.005) but not female pumas (ΔG^2 = 3.18, df=1, P=.0744). Thus we evaluated three sets of data: all females, males in forests, and males in shrublands. For each dataset, we created four-way contingency tables (Before × After × House × Time) to evaluate how anthropogenic factors and time of day affected behavioral transitions using the likelihood ratio methods described above.

We considered puma traveling within 150 m of a building as impacted by anthropogenic influences because that distance was the scale that best described the influence of housing density on puma movement (Wilmers et al. 2013). Our null model (*BA, BHT*) is built such that succeeding behaviors (*A*) are only affected by behaviors in the previous time steps (*B*) and independent of proximity to houses and time of day (Figs. 1-3). We tested whether including additional factors (proximity to house and time of day) improved model fit by comparing the null model with hierarchically more complex models. For example, the effects of proximity to housing on succeeding behaviors are evaluated by comparing the goodness-of-fit (G^2) values for the null model and the model containing an interaction between succeeding behaviors and houses (*BAH, BHL*). We also tested the interaction between proximity to houses and time of day by comparing the saturated model (*BAHT*), which fits the data fully, to a less complex model without the interaction term (*BAH, BAT, BHT).*

Finally, we selected the best fitting model by minimizing the Akaike Information Crtierion (AIC) estimate.

Behavioral budgets

We tested whether transition matrices differed when pumas were close to houses or roads using the Z test for proportions (Fleiss 1981). Transition matrices are the probabilities that pumas remain in a behavioral state (active or inactive) or transition from one behavior state to another. We also estimated the amount of time pumas spent in each behavioral state by conducting an eigenanalysis on the transition matrix. Because Markov chains are ergodic matrices, we used the left eigenvector of the transition matrix to estimate the proportion of time pumas spent in each state (Caswell 2001). We compared these values using a Z test of proportions and calculated 95% confidence intervals using the Wilson's score test (Newcombe 1998).

Puma travel and energetic costs

For each puma, we identified all 24-hour intensive sampling periods during which GPS points were recorded every 15 minutes. At a fix rate of 4 times an hour, up to 96 GPS points are recorded throughout the day, equating to a total of 95 travel segments (straight lines between consecutive points). We removed any days from analyses that were missing more than 10% (i.e., 9 points) of potential GPS points. We determined the linear length of all travel segments and calculated the total daily distance (*D*) traveled by pumas by summing all travel segments and correcting for any missing GPS fixes using the formula,

D_{total} (km) = D_{summed} (km) × (95 travel segments/day)/(actual segments recorded). (1)

Next, we calculated the minimum cost of transport (*COT*) expended daily for each puma by adapting the equation developed by Taylor et al. (1982):

$$COT\ (\text{W/kg}) = \sum_i^n 10.7 \times wt^{-0.316}\ (\text{kg}) \times v_i\ (\text{m/s}) + 6.03 \times wt^{-0.303}\ (\text{kg}), \quad (2)$$

in which *wt* is the weight of the animal when captured and v_i is the velocity of travel between consecutive GPS points. *COT* has the units Watts/kg, which can then be converted to kcal/kg by applying the conversion factor 4.1868 Watt = 1 cal/s. We did not account for the additional energetic expenses of raising kittens for female pumas because we did not have full information on kitten survival and numbers.

Lastly, we estimated the minimum number of deer needed to sustain each puma given their daily minimum *COT*. We calculated the daily deer biomass (*DB*) needed to fulfill each puma's prey requirements using equation 3 (Ackerman et al. 1986):

$$DB\ (\text{kg/day}) = COT\ (\text{kcal}) / (1890\ (\text{kcal/kg}) \times 0.86 \times 0.94). \quad (3)$$

1890 kcal represents the caloric content in each kg of wet deer tissue (Laundre 2005), and this value is then modified by multiplying it by the conversion efficiency (0.86) and the proportion of deer in a puma's diet - here estimated as 94% (Martins et al. 2011). We finally used equation 4 to converted the daily deer biomass into an estimate of the yearly deer requirements (Ackerman et al. 1986):

$$Deer/year = ((DB\ (\text{kg/day}) \times 365\ \text{days}) / 36.5\ \text{kg}) / 0.79, \quad (4)$$

in which 36.5 kg is the average weight of a black-tailed deer doe (Dasmann & Taber 1956) and 0.79 is the edible proportion of the deer (Laundre 2005).

It is broadly understood that the energetic estimates generated using the equation developed by Taylor et al. (1982) are the minimum estimates for *COT*. Even at 15-minute GPS sampling intervals, animals can deviate greatly from straight-line travel paths, thus expending many more kcals than we estimated. In contrast, Overall Dynamic Body (ODBA) acceleration measurements recorded by accelerometer collars may provide a more precise measurement of energetic expenditure because it takes measurements at a rate of 64Hz. Williams et al. (in prep) recently used accelerometer measurements of captive pumas to generate a predictive regression equation to estimate field COT using ODBA values. We used methods outlined by Qasem et al. (2012) to extract ODBA values from our accelerometer measurements for two pumas, a male and female, whose accelerometers were active during concurrent to GPS intensive sampling periods. Using those values, we used linear regression to evaluate the correlation between *COT* estimates from ODBA measurements and those estimated using velocities generated from intensive GPS sampling by the Taylor et al. (1982) equation.

Development influences on puma movement

To quantify puma exposure to human development, we used ArcGIS (v. 10.1, ESRI, 2012) to create buffers of 500m around all GPS points within each 24-hour intensive GPS sampling period. We then calculated the number of houses encompassed within each buffer polygon and also recorded the time of day. For each day, we recorded the average housing density individual pumas were exposed to during nocturnal and diel periods and the average distance pumas traveled between successive GPS locations. We expected that pumas would move faster and further through areas with more houses in order to minimize their exposure to development (Beier et al. 1995; Wilmers et al. 2013). However we also expected that this relationship might be affected by the time of day because pumas may prefer to stay hidden if they are in more developed areas during the day. We only evaluated development influences on puma movement because energetic estimates are directly calculated from the distance traveled.

We performed a linear mixed effects analysis using restricted maximum likelihood estimation with the average diurnal and nocturnal distance traveled between successive GPS points as the dependent variable. To select the best model, we followed the protocol outlined in Zuur et al. (2009) and started by fitting a linear model that included the full complement of fixed effects terms. For fixed effects, we used sex of the puma (male coded as 1 and female as 0), time of day (day coded as 1 and night as 0), the log-transformed average number of houses, and the interactions between sex and time of day and time of day and housing. Puma identity was included as a factor in the model to allow for random intercepts. We used AIC to compare the two models to determine the optimal model structure.

After determining the optimal model structure, we sequentially removed any fixed effects terms that were not significant at the P=0.05 level. We then compared the reduced model to the full model using likelihood ratio tests. In order to compare models using likelihood ratio tests, we first re-estimated all models using maximum likelihood estimation. We iterated this process until we arrived at a model that only included significant fixed effects. We examined the residuals for our final model visually to identify any obvious deviations from normality. All analyses were performed in R using the package *nlme* (Pinheiro et al. 2012).

Results

Log linear analyses

We recorded 78,242 GPS locations for 22 pumas, including 6967 transitions for males in shrubland habitats, 11379 transitions for males in forested habitats, and 21977 transitions for females in all habitats. Log linear analyses revealed that both proximity to houses and time of day influenced puma behavior, but this effect differed by sex and habitat type for males. Proximity to houses and time of day had a significant effect on the behavior transitions of male pumas in forests (Fig. 1). However, for males in forests, support for the interaction term was ambiguous because the two models had a ΔAIC less than 0.2, indicating that the models were statistically indistinguishable (Burnham and Anderson 2002). AIC comparison revealed that the best models for all female pumas and males in shrublands included the proximity to houses, time of day, and an interaction between the two (Figs. 2, 3). This indicates that puma responses to houses differed by time of day.

Behavioral Budgets

All puma behavioral transitions showed contrasting responses to housing depending on the time of day (Fig. 4). At night, all pumas regardless of sex or habitat were less likely to remain inactive, more likely to remain active, and more likely to transition between behavioral states near houses. In contrast, male and female pumas were more likely to stay inactive near houses during the daytime. However, male pumas in forests were also less likely to remain active near houses in the forest during the day whereas male pumas in shrublands were unaffected.

Both male and females pumas spent most of their time in an inactive state regardless of the time of day, and were far more active at night. We calculated and compared the behavioral budgets of pumas near and far from houses in daytime and nighttime (Fig. 5). We found that male pumas near houses at night were active 26.9% and 21.1% of the time in forested and shrubland habitats, respectively, compared with 17.2% and 13.2% when they weren't close to human structures. Females were only active 13.3% of the time when near houses at night, compared with 7.5% when further away. In the daytime, puma activity was generally low, with females and males in forests exhibiting no difference in activity level when close to houses. However, males in shrubland habitats were less likely to be active near houses (2.8%) than when far from houses (8%).

Energetic costs

We used 19 pumas (10 males and 9 females) to evaluate movement activities and energetics over 377 24-hour intense sampling periods (218 for females and 159 for males) (Table1). Male pumas, averaging 53.3 kg ± 7.82kg (SD), traveled 7.33 km ± 4.63 km daily and expended 2275 kcal ± 346 kcal. Females, averaging 39.8 kg ± 2.73 kg, were more sedentary and traveled 4km ± 2.58 km daily and expended 1748 ±

106 kcal. If a puma only subsisted on a diet of black-tailed deer, we calculated that a male puma would need to kill an average minimum of 18 does/year and that a female puma would need to kill 14 does/year.

Our *COT* estimates based on ODBA measurements from accelerometers for pumas 16M and 28F showed that our energetic expenditure estimates based off GPS movement data greatly underestimated caloric intake. Applying the *COT* formula from Taylor et al. (1982) to the intensive GPS sampling period, we estimated that 16M expended 2492 and 2296 kcals over two days and that 28F expended 1793 kcals. In contrast, our *COT* estimates from ODBA for the same three days were about 2-2.5 higher at 6079 and 5492 kcals, and 3608 kcal, respectively. However, there was a positive correlative relationship (R^2 = 0.5) between the *COT* values calculated using GPS and ODBA measurements.

Development influences on puma movement

We found that the model structure that included random intercepts for Puma ID minimized AIC values and fit the data better compared to a fixed-effects model (ΔAIC = 25)t. The final model included all original fixed effects terms for sex (β = 0.747, df=17, *t*=6.83, *P*<0.001), time (β = 0.199, df = 942, *t*=2.05, *P*=0.043), the log-transformed number of houses (β = 0.16, df=942, *t*=6.64, *P*< 0.001), and the interactions between sex and time (β = -0.52, df=942, *t*=-5.23, *P*< 0.001) and time and number of houses (β = -0.25, df=942, *t*=-7.27, *P*< 0.001). As expected, males moved further on average than females between GPS points at both nocturnal and diurnal hours (Fig. 6). However, the influence of increasing housing on puma movement differed depending on time of day, with pumas moving further distances between GPS points in higher development areas in nocturnal hours and exhibiting the opposite pattern during diurnal hours.

Discussion

Our study explored how anthropogenic structures influence puma behavior in a fragmented landscape by quantifying how pumas altered their behaviors in relation to human development. From the log linear analyses, we saw a clear effect of proximity to anthropogenic buildings on puma behavioral state. However, this effect was modulated by the time of day, with pumas in the nighttime more likely to be active and remain active when within 150m from houses. We also found that pumas were more likely to transition between states when close to houses, indicating that they may be shifting between behavioral states more often. These activity shifts may reflect their discomfort with being in close proximity to humans and domestic animals.

Like other large carnivores living in more developed areas, pumas moved far more at night than during the day in our study. Interestingly, pumas exhibited similar levels of low activity whether near or far from houses during the day. This could be because pumas in the Santa Cruz Mountains have limited their overall diurnal activity to cope with human activities. Reduced daytime activity has been recorded in other large carnivores such as wolves (Hebblewhite & Merrill 2008), tigers (*Panthera tigris*) and grizzlies (Ordiz et al. 2012) around humans. Even in undeveloped areas in our study area, there is a great deal of open space available for recreational activities such as hiking or biking, thus increasing human presence in the areas juxtaposing development.

Our study generated simplified activity budgets using GPS data corroborated by accelerometer measurements. The activity levels of our study animals were relatively low compared to Beier et al.'s (1995) estimates of 25% diel activity for Southern Californian pumas. Our discrepancies may be due to methodological differences; Beier et al. (1995) classified any distance above 50m between two locations as an active period, whereas we limited activity to distances above 70m based on corroborations from our accelerometer data. Beier et al. (1995) also used the radio-telemetry to estimate the locations of animals, which may have led to more misclassifications of movement due to the lowered precision of radio-telemetry. However, our activity values are comparable to activity levels of other carnivores, including African lions, which are active about 9% of the day (Schaller 1972). We also found that male pumas were more likely to be active in forested habitats at night, which aligns with Dickson et al.'s (2005) finding that pumas moved more slowly hrough shrubby habitats compared to woodland habitats. This is potentially because pumas prefer to hunt in shrubby habitats, where there is more horizontal cover.

More studies are beginning to investigate the effects of human development on large carnivores behaviors (Ordiz et al. 2012; Valeix et al. 2012). Previous studies on pumas have found that pumas will readily kill prey in human-influenced habitats (Sweanor et al. 2008; Wilmers et al. 2013). However, it is possible that female pumas feeding close to structures, which would be classified as inactive by our model, may transition to an active state and leave their kills if disturbed. This type of behavior has been documented in tigers, who were more likely to abandon their kills when disturned by humans (Kerley et al. 2002).

Currently, we are only able to identify two states from our GPS and accelerometer data. However, as predictive capabilities increase with better accelerometer algorithms, we can incorporate feeding as an additional state. Once we can determine feeding behavior, we can use similar log linear analyses to examine how the proportion of time spent feeding is impacted by proximity to human structures. For example, Amur tigers responded negatively to human disturbance by abandoning their kills, which compounded energetic costs because they not only were unable to finish feeding but also had to expend extra energy hunting again (Kerley et al. 2002). Identifying feeding bouts for pumas will more explicitly link how behavioral changes due to human disturbances might translate into fitness consequences.

Our estimates for puma energetics (average of 1748 kcal for females and 2275 kcal for males) were lower that those of Laundré (2005) (average of 2420 kcal for females and 3144 kcal for males). However, our pumas also traveled less than half as far (4-7 km/day compared to 14-17 km/day) as those monitored by Laundré. Pumas tracked in our study have some of the lowest travel distances of any pumas studied, but are similar to those followed by Beier et al. (1995). Our estimates for minimum deer consumption (14 deer/yr for females without kittens and 18 deer/yr for males) are comparable to those produce d by Laundré (2005) (14.9 deer/yr for females and

19.4 deer/yr for males) despite the decreased caloric expenditures of our study animals. This discrepancy is mostly attributable to the smaller weight of the black-tailed deer in our study area compared to the larger-bodied mule deer (avg. wt 46kg) found in Utah and Idaho. Pumas in our study also feed on a number of small animals (e.g. raccoons, house cats), but deer biomass still comprises the vast majority of their diet.

Since pumas do not always feed at a carcass to completion and may lose portions of the carcass to scavengers or abandon their kill due to disturbances, it is likely that pumas actualy kill substantially more deer than what we estimated. Additionally, pumas who kill deer close to areas of higher human development or activity might spend less time feeding and move further away from their kills between feeding spurts, decreasing their energetic gains from each kill. We were not able to evaluate the energetic requirements of females with kittens, although almost all of our females had kittens during a portion of the study. Because we did not track kitten survival, we could not conclusively measure the length of time females traveled with kittens or the number of kittens they were raising. However, Laundré (2005) found that females with kittens in his study required about twice as many deer per year than males and more than 2.5 times more than females without kittens.

We also found that our *COT* calculations based on distances between successive GPS points were much lower than those generated from ODBA measurements using accelerometer collars. Puma females in our study area may actually be expending around 3500 kcals a day and males may be using 5000 kcal.

Factoring in these adjustments, we expect that the minimum number of deer required by pumas in our study area to survive is likely at least 2-3 times higher than our estimates and may be 4-5 times higher for females with kittens. Because of our underestimation of carnivore energetic needs from GPS movement data, we have likely been under-predicting the amount of prey to which predators need access. This increased energetic demand may lead to pumas to venture into neighborhoods to access alternate prey, such as goats and house cats, and increasing potential conflicts with humans.

Male pumas in our study moved an average of 3 km/day more than females in the area. However, we also observed considerable individual variation in distance traveled; for example, the mean daily distance traveled by males ranged from 4km/day to 10.6 km/day. As we predicted, there was a significant relationship between distance traveled and the number of houses surrounding each puma's travel path. Dickson et al. (2005) found that pumas moved most through urbanized landscapes, although they did not have enough information to compare daytime versus nighttime movement patterns. Our study revealed that the relationship between movement distance and housing was positive at nighttime and negative during the daytime, providing further evidence that puma response to development was strongly influenced by the time of day (Fig. 6). Pumas moved faster through developed areas during nocturnal hours, but they reduced their movement in developed areas during diurnal hours.

Because the distance traveled determines the kcals expended and the number of deer required per year, we also inferred that pumas in more developed areas will generally expend more kcals and require more kills than those in undeveloped areas. Although pumas only increased their movement near houses at night, we believe this still translates to increased energetic costs since pumas primarily travel nocturnally. During the day, pumas may have reduced travel opportunities to access preferred hunting locations if they are staying in one location in order to reduce detection by humans.

Conservation Implications

Although pumas in our study area are not hunted, they do suffer human-caused mortalities through depredations and vehicle collisions. In our population, "predation" by humans is the leading cause of death for collared pumas (unpublished data), thus providing pumas strong incentives to alter their behaviors to minimize contact with humans. Even when large tracts of land are protected from development, other non-lethal human disturbances can also affect puma behavior. Responses to non-lethal human activities or disturbances (e.g., development, hunting pressure) have been demonstrated in many large carnivores, including brown bears and lions. For example, bears in Sweden changed their daily movement patterns during hunting season, with solitary males and females expecially shifting their activity towards nocturnal hours (Ordiz et al. 2012). African lions also moved more quickly when closer to cattle posts, likely to reduce the amount of time spent in dangerous territories (Valeix et al. 2012).

Our study provides additional evidence of trait-mediated large predator responses to human disturbance. Although pumas generally select against more developed areas, they are unable to completely avoid them in the Santa Cruz Mountains (Wilmers et al. 2013). We found that pumas moved more often and further in developed areas during nocturnal hours, with measurable impacts to their energetic expenditure. Female with kittens are especially vulnerable to development, because of their higher energetic demands. Kittens older than 6 months will follow their mothers to kill sites to feed (Laundre & Hernandez 2008); if these locations are close to development, it is possible that their feeding times will be more restricted to avoid disturbances by humans or domestic animals. Additionally, females may choose daytime resting locations further away from a kill site in a developed area, thus reducing the energetic gains the kittens will receive from the carcass. Although we could not track kitten survival during our study, we know that most of the female pumas had kittens and lived in home ranges which encompassed developed areas. Future studies with collared kittens will give us a better idea of the potential added energetic and survival costs of raising kittens near developed areas.

Currently, exurban or low density development is the fastest growing type of land-use change in the United States (Radeloff et al. 2005). As low density development fragments previously intact landscapes, it could pose significant challenges to puma survival due to increased non-lethal human disturbances. Changes in movement activity and behavior can provide the first indications of predator responses to development. Further research can explore how pumas behave at their feeding sites in developed versus unfragmented areas. For example, accelerometers can measure footfall frequencies of animals (Wang et al. *in review*), which will allow us to ascertain whether pumas move more swiftly and often when closer to human influences. Apex carnivores like pumas occupy pivotal roles in ecosystems, and human-induced changes to their behaviors can lead to demographic impacts that reverberate throughout the ecological community. For all large predators, accounting for human-induced behavioral changes should play a larger role in any conservation management strategies.

Acknowledgments

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Table 2.1. Average daily distanced traveled, daily caloric expenditure, and yearly deer requirements of 9 female (F) and 10 male (M) pumas.

Puma ID	Daily distance (m)	Daily kcal/kg	Deer/year
7F	3236.41	42.65	18.51
11F	3977.36	44.50	17.34
18F	10176.25	44.67	17.25
19F	4531.16	43.20	18.65
23F	4304.47	43.83	18.46
24F	3789.70	44.77	17.11
25F	9951.82	44.43	17.89
28F	4397.31	45.24	16.83
29F	3782.99	45.44	17.50
16M	4641.39	43.54	25.89
17M	6500.21	41.81	20.54
22M	6771.44	41.94	26.88
26M	3847.31	44.85	19.75
27M	5587.89	43.29	21.65
31M	5728.27	41.73	23.87
34M	6503.50	40.72	24.68
35M	4461.17	42.54	19.65
36M	7114.24	42.41	25.47
37M	6030.743254	42.50	25.04

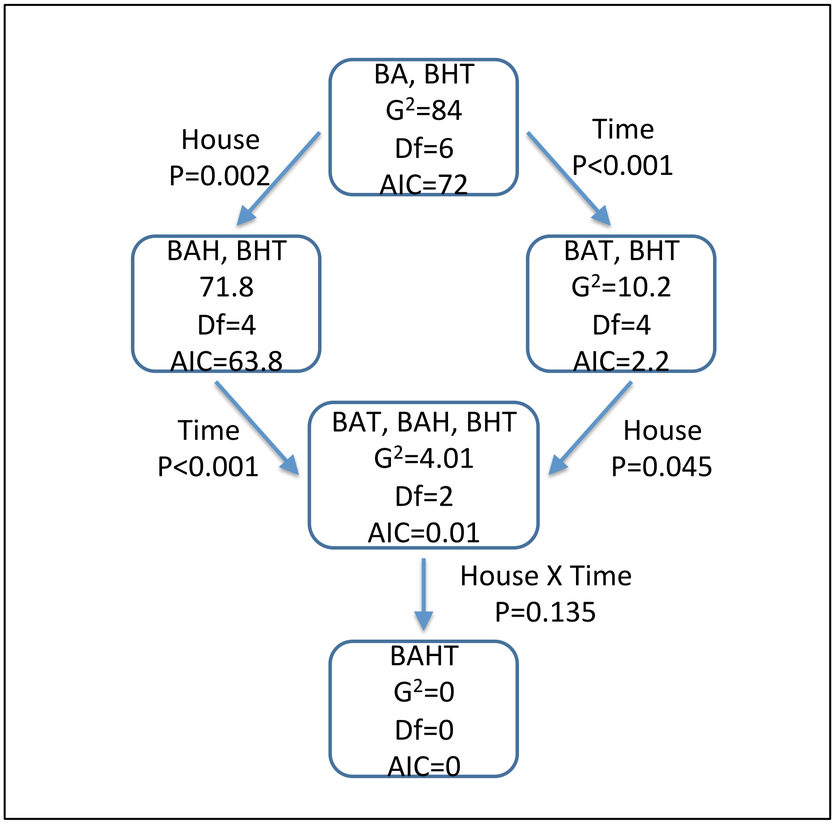


Figure 2.1. Tests of the effects of proximity to housing (H) and time of day (T) on male puma behavior transitions in forests using log linear analyses. Models and their respective goodness-of-fit (G^2) statistics, degrees of freedom (Df), and Akaike Information Crtierion (AIC) values are shown in boxes. Terms added are displayed next to arrows, with *P* values indicating the significance of including the term based on likelihood ratio tests.

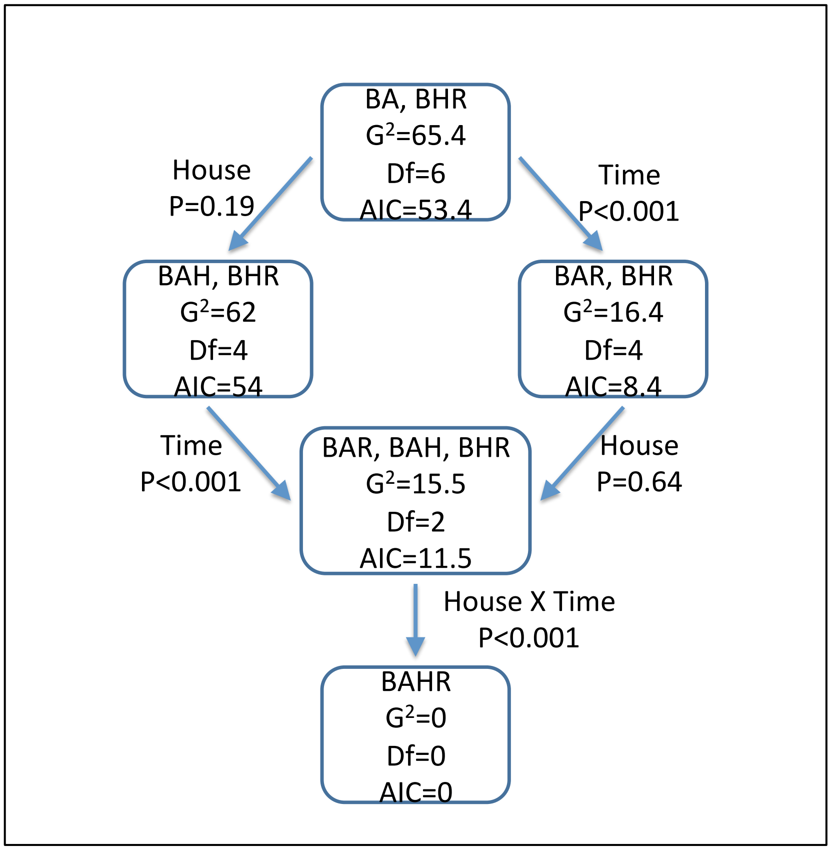


Figure 2.2 Tests of the effects of proximity to housing (H) and time of day (T) on male puma behavior transitions in shrublands using log linear analyses. Models and their respective goodness-of-fit (G^2) statistics, degrees of freedom (Df), and Akaike Information Crtierion (AIC) values are shown in boxes. Terms added are displayed next to arrows, with *P* values indicating the significance of including the term based on likelihood ratio tests.

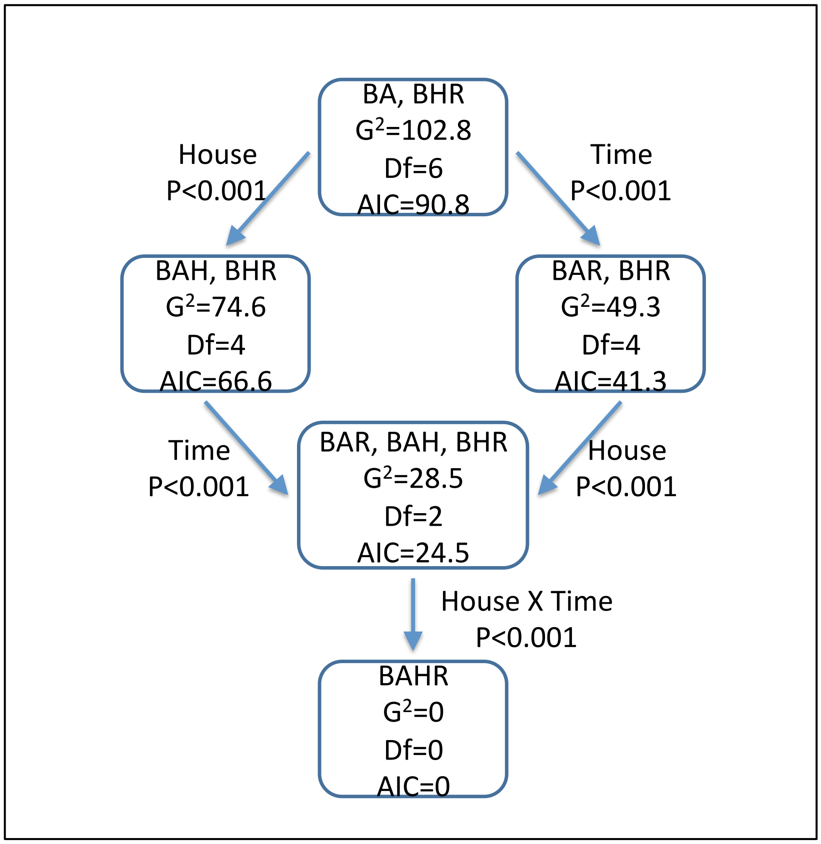


Figure 2.3. Tests of the effects of proximity to housing (H) and time of day (T) on female puma behavior transitions using log linear analyses. Models and their respective goodness-of-fit (G^2) statistics, degrees of freedom (Df), and Akaike Information Crtierion (AIC) values are shown in boxes. Terms added are displayed next to arrows, with *P* values indicating the significance of including the term based on likelihood ratio tests.

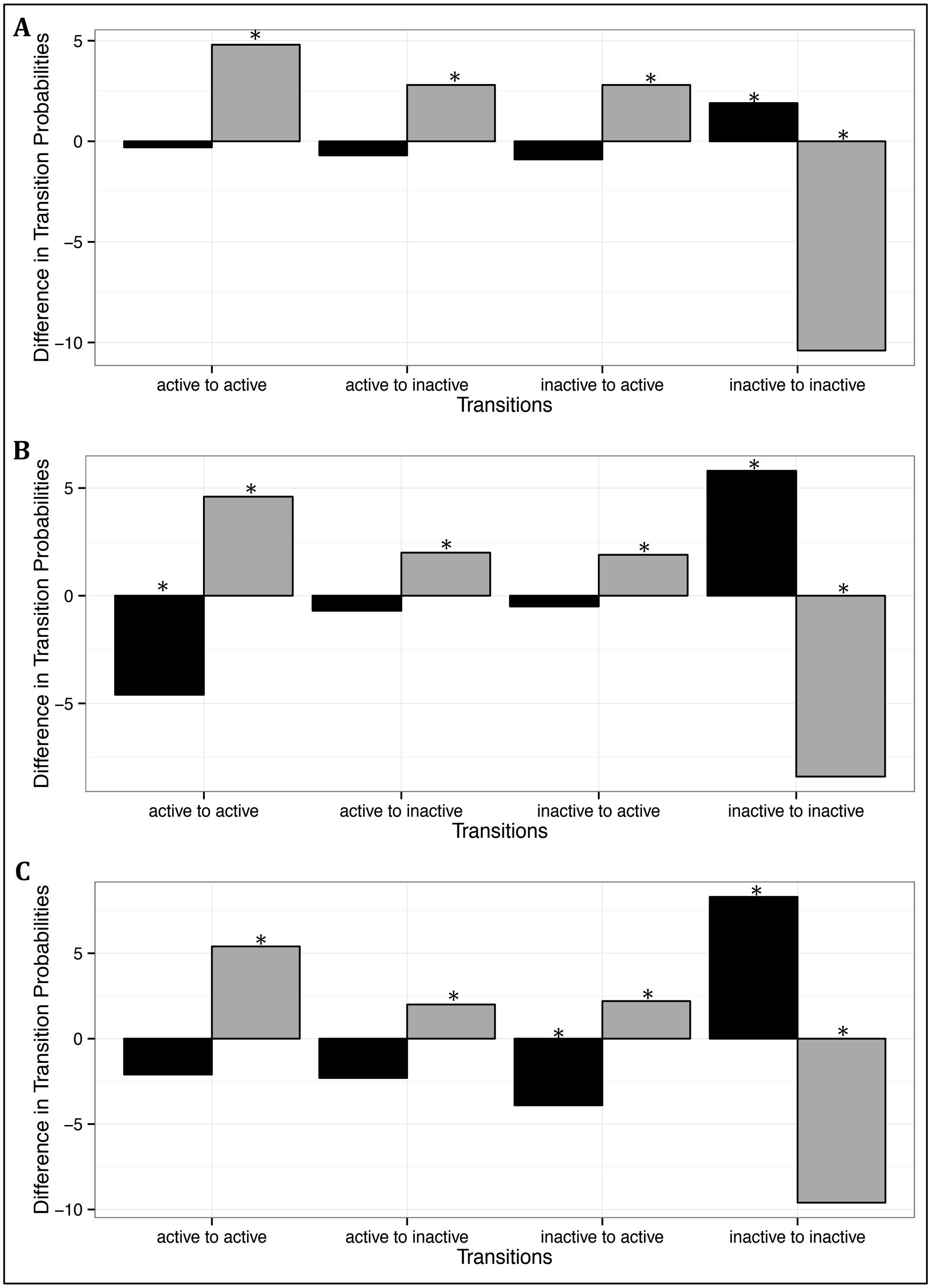
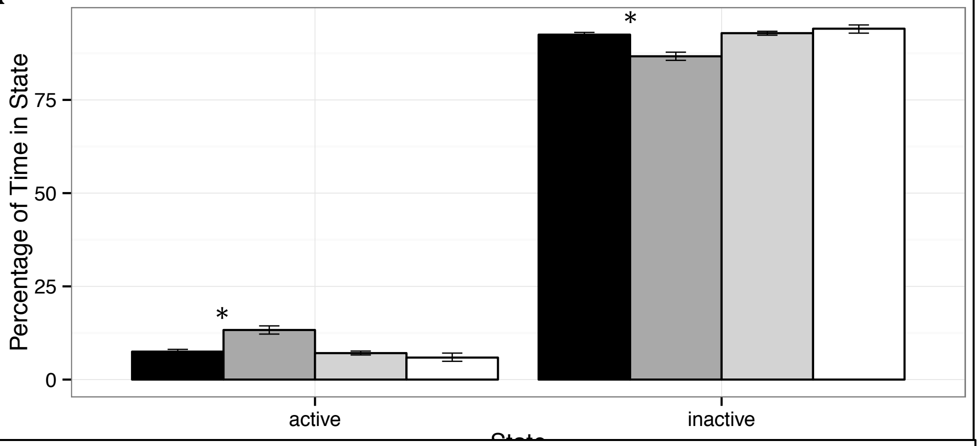

A
Difference in Transition Probabilities
5
0
−5
−10
active to active
active to inactive
inactive to active
inactive to inactive
Transitions
B
Difference in Transition Probabilities
5
0
−5
active to active
active to inactive
inactive to active
inactive to inactive
Transitions
C
Difference in Transition Probabilities
5
0
−5
−10
active to active
active to inactive
inactive to active
inactive to inactive
Transitions

Figure 2.4. Effect of proximity (≤150m) to houses on the transition probabilities between activity states for a.) female pumas, b.) male pumas in forested areas, and c.) male pumas in shrubland habitats in daytime (grey bars) and nighttime (black bars). Difference in transition probabilities is calculated as probability of transitioning between states (>150m from houses) – probabillity of transitioning between states (≤150m from houses). Asterisks above columns represent a significant differences ($P < 0.05$).

A


Percentage of Time in State
0
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50
75
*
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active
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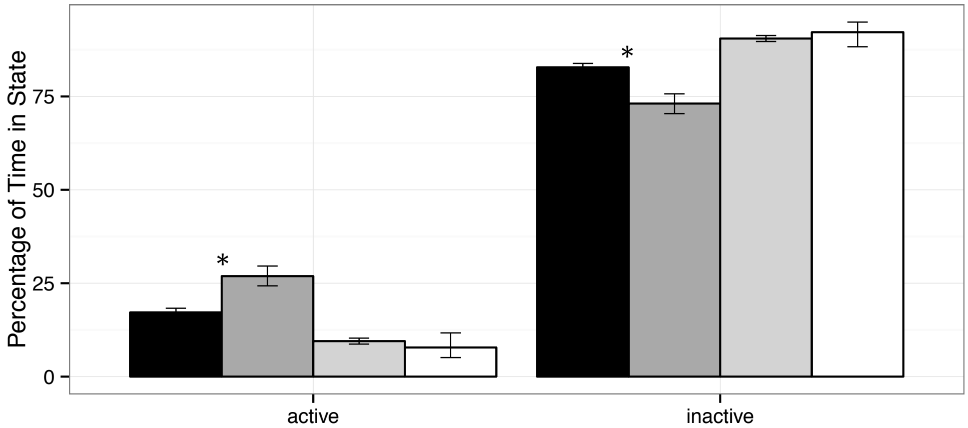
State

B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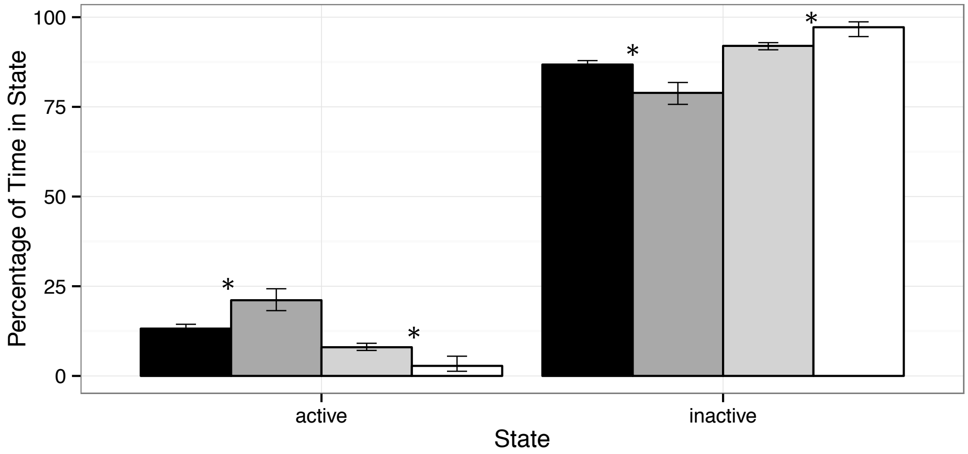
Percentage of Time in State
0
25
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100
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*
active
inactive
State

Figure 2.5. Proportion of time spent active and inactive for a.) female pumas, b.) male pumas in forests, and c.) male pumas in shrublands. Bars are color-coded to represent nighttime far from houses (>150m, black), nighttime near houses (≤150m, grey), daytime far from houses (light grey), and daytime near house (white). Asterisks above paired columns represent significant differences between activity levels near houses and far from houses ($P < 0.05$). Error bars represent 95% confidence intervals.

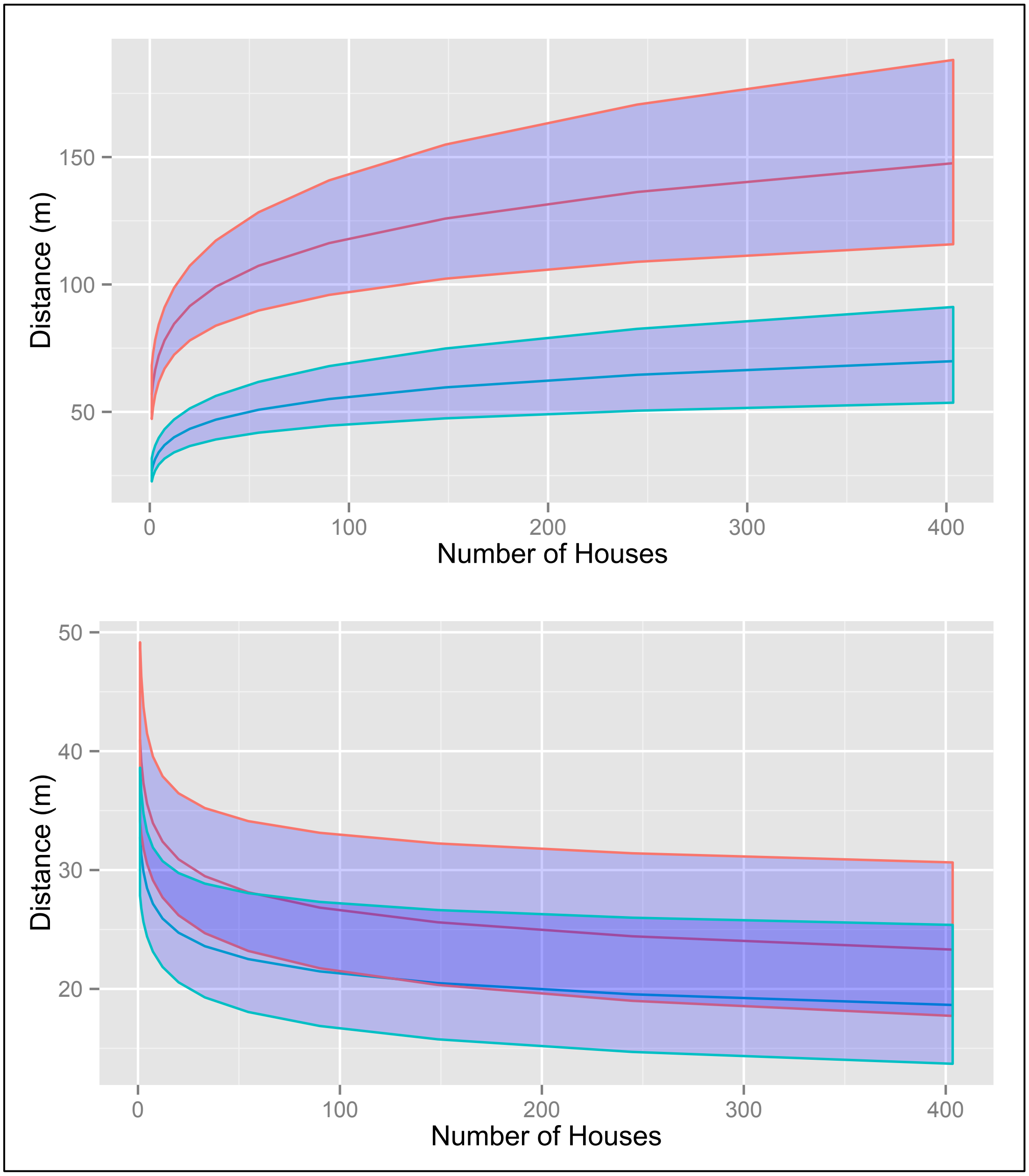

Figure 2.6. Predicted curves and 95% confidence bands for male (red) and female (blue) pumas relating the average distance traveled between 15 minute GPS points and the average number of houses in a 500m radius around locations in a.) nighttime and b.) daytime.

Chapter 3

Context dependent spatiotemporal influences of human disturbance on predator interactions

Abstract

Human-driven decline of apex predators can trigger widespread impacts throughout ecological communities. Reduced top predator activity or presence can release mesopredators from intraguild competition, with unknown repercussions on the prey community. However, mesopredators are also impacted by anthropogenic influences and some species may benefit from human subsidies. Our study used motion-detecting camera traps to examine spatial and temporal patterns of mesopredator and puma activity and occupancy in a fragmented landscape in California. We found reduced puma occupancy with higher development but no influence of development on the occupancy of mesopredators. However, species detection differences suggest a potential intraguild cascade among pumas, coyotes, and grey foxes. We also found that locations with higher human activities led to reduced opportunities for temporal niche partitioning among mesopredators. Lastly, an experimental scavenging study revealed that bobcats delayed visiting bait sites treated with puma sign and that foxes avoided visiting baits fed on by coyotes. Our results suggest that the varying influences of human development and activity in this heterogeneous landscape may alter predator community structure. Effective conservation of an intact carnivore community requires an understanding of how mesopredators respond to varying levels of top predator and anthropogenic influences.

Keywords: Mesopredator, *Puma concolor,* occupancy, carnivore community, development

Introduction

Apex predators often drive the population dynamics of their prey and shape the structure of biological communities through top-down effects (Ripple et al. 2014). However, the anthropogenic-driven extirpation of many apex predators worldwide has profoundly affected local ecosystems, as the effects resulting from their loss are propagated through the foodweb. These trophic cascades have been documented in diverse ecosystems over the past half century (Estes et al. 2011) and generally progress through two pathways: 1.) releasing herbivores from predation and 2.) releasing mesopredators from intraguild predation and competition. Herbivores freed from predation can initiate large-scale habitat changes, and mesopredators released from competition with larger consumers can disproportionately reduce their favored prey species and diminish community diversity.

As both predators and competitors of mesopredators (Palomares & Caro 1999; Polis & Holt 1992), top predators limit mesopredators through consumptive (density mediated) and non-consumptive (trait-mediated) effects. However the relative influence of density mediated versus trait-mediated effects are unknown, although a meta-analysis on the subject suggests that a majority of the influence exerted by predators on prey is through trait-mediated rather than density-mediated effects (Preisser et al. 2005). Mesocarnivores, as behaviorally plastic individuals, are thus incentivized to limit potentially costly interactions with dominant competitors through spatiotemporal partitioning of habitat (Gehrt & Clark 2003; Wilson et al. 2010). However, within a guild, top predators can also benefit smaller ones by suppressing larger-bodied mesopredators (Berger & Conner 2008; Elmhagen et al. 2010). For example, Levi and Wilmers (2012) demonstrated an intraguild cascade in which wolves (*Canis lupus*) suppressed coyotes (*Canis latrans*), thus releasing foxes (*Vulpes vulpes, Urocyon cinereoargentus, and Vulpes velox*). In addition, carrion provided by top predators can serve as an important source of food for mesopredators and smaller predators such as grey foxes (*U. cinereoargenteus*), raccoons (*Procyon lotors*), striped skunks (*Mephitis mephitis*), western spotted skunks (*Spilogale gracilis*) and Virginia opossums (*Didelphis virginiana*; hereafter opossums) (Ruth & Murphy 2009; Selva et al. 2005). Thus, the true relationship between dominant and smaller predators may reflect a complex balance of risk-avoidance and energetic needs, all of which may be influenced by anthropogenic subsidies and disturbances.

Mammalian predators are among the most vulnerable species in ecological communities to anthropogenic influences, but may differ in their actual sensitivities to humans disturbances (Crooks 2002). Globally, human activities have generally prompted the extirpation of large carnivores and facilitated the introduction or proliferation of mesopredators such as raccoons and domestic cats (*Felis catus*) (Crooks & Soulé 1999; Prugh et al. 2009). Due to their requirement for vast tracts of land and potential conflicts with humans and domestic animals, apex predators are especially vulnerable to habitat changes, human persecution, and automobile collisions (Gill 2009). In contrast, mesocarnivores sometimes benefit from urbanization because they may gain a degree of protection from dominant predators and access to additional food resources, such as garbage, domestic animals, and human commensals (Ritchie & Johnson 2009). The combined extirpation of top predators and release of mesopredators has been repeatedly identified as a possible cause for the decline or extinction of songbirds and small mammals, prey disproportionately preferred by mesopredators (Crooks & Soulé 1999; Johnson et al. 2007; Ritchie & Johnson 2009). Such changes to the predator guild can greatly alter ecological networks, with lasting effects manifested throughout the foodweb (Levi & Wilmers 2012; Noss et al. 1996; Pace et al. 1999; Polis & Holt 1992). By understanding how larger predators and mesopredators respond to varying levels of human influences, we can better manage for the coexistence of a diverse carnivore community alongside human populations.

When human populations expand outwards from cities, this wildland-urban interface (WUI) becomes the leading edge of environmental conflicts where human activities are juxtaposed with natural landscapes (Radeloff et al. 2005). These disturbances lead to habitat fragmentation and altered resources, which can then indirectly restructure ecological relationships among predators in the surrounding communities (Gehrt et al. 2010). Recreation (e.g., hiking and biking) is also a popular activity in many open spaces preserves and private lands in or near the WUI, but human activity can disturb the temporal patterns and interspecific interactions of animals (George & Crooks 2006; Reed & Merenlender 2008). While nature recreation is important for establishing conservation ethos in people (Zaradic et al. 2009) and parks protect land from development, those benefits need to be balanced with any negative potential ecological impacts resulting from human and companion animal use. Despite the potential negative repercussions of living near humans, coexistence between predator species and human communities have been documented in India and the Serengeti (Carter et al. 2012; Schuette et al. 2013). This cohabitation is facilitated by both the behavioral adaptations of carnivore species and the explicit conservation ethos and actions of the local community. As the WUI continues to expand with growing human populations, it is crucial that we continue to understand how human pressures alter the composition of predator communities and the interaction web between those species in order to inform conservation and management goals.

Our study examined how spatiotemporal interactions between mammalian mesopredators and an apex predator, the puma (*Puma concolor*), were impacted by urbanization and human activity in the Santa Cruz Mountains of California. This region has a legacy of preserving large tracts of open space, with 24% of the surrounding San Francisco Bay area held in some form of public land trust or conservation easement (Rissman & Merenlender 2008). Significant portions of this public land are available for a wide variety of recreational activities, including biking, hiking, horseback riding, and dog walking. There are also many large private landholdings, which may be managed for resource extraction activities, such as logging and mining, but are not open to the public for recreation. In other parts of the region, exurban and suburban communities continue to persist and expand, reducing wildlife habitat and increasing the area of the WUI. In many developing areas across the United States, coyotes have replaced larger carnivores as the top predator. These shifts in carnivore community structure and alterations to their interaction webs may reverberate across the ecological community through unknown impacts upon smaller guild members and prey species. To conserve and manage species and their interactions across this diverse landscape as the human footprint continues to expand, it is important to quantify how different facets of anthropogenic influences impact wildlife communities.

We hypothesized that 1.) Top predator (puma) occupancy would be primarily driven by anthropogenic pressures (e.g., development and activity) because large carnivores are particularly sensitive to human activities. 2.) Smaller predators would respond differently to human development and coyote activity in the presence and absence of dominant predators (pumas). In the absence of pumas, smaller predators (e.g., grey foxes) may experience more competitive pressures from coyotes and human associated species (e.g. raccoons) may be better able to exploit anthropogenic resources if they no longer need to avoid top predators. 3.) Species pairs in which one species is the aggressor and the other the receiver of intraguild predation (e.g., coyotes and foxes) would exhibit low temporal overlap, but this overlap would increase in places with higher human activity. Temporal partitioning is a common way for competing species to minimize conflict, but diurnal human activities will likely constrict the activity period of wildlife. 4.) Mesopredators would reduce their usage of carrion when fresh puma signs were nearby, but this avoidance would disappear at higher levels of human disturbance. We expected that mesopredators would generally avoid sharing space with a more dominant competitor, but that their fear would be decoupled as their interactions with pumas are reduced in more developed habitats.

Methods

We used digital motion-detecting cameras to observe human and animal activity at fine spatial and extended temporal scales in their natural environment. We monitored a suite of predator species along a gradient of human development and varying levels of human activity to quantify how top carnivores, human development, and human activities affect mesopredator behavior and spatiotemporal partitioning. Specifically, we used two-species occupancy models to parse out how mesopredator occupancy and detection is influenced by top predators and humans disturbances. We also examined temporal partitioning between carnivore species at disparate levels of human activity using a coefficient of overlap developed by Ridout and Linke (2009). Lastly, we used a field experiment to test how mesopredators would respond to top predator sign at baited locations across a gradient of human development.

Study Site

We conducted our study in the southern part of the Santa Cruz Mountains in west-central California. The study area is encompassed within Santa Cruz, Santa Clara and San Mateo counties (Fig. 1). The Santa Cruz Mountains includes a diverse collection of habitats ranging from intact wilderness to urban regions, providing a gradient of environmental conditions to study the impacts of development on interspecific interactions. The urban municipalities of Santa Cruz and the South Bay Area juxtapose the borders of our study site, and several small suburban and exurban mountain communities are contained within our study area. Many large tracts of undeveloped lands, both privately and publicly owned, also exist in the Santa Cruz Mountains. A major highway bisects our study region, and numerous arterial (> 35mph), neighborhood (<35mpg) and unpaved roads also mark the landscape.

The Santa Cruz Mountains experiences a dry season from May to October and a wet season from November to April. Small to large-sized mammalian carnivores that occur in the Santa Cruz Mountains include: pumas, bobcats (*Lynx rufus*), coyotes, grey foxes, red foxes (*V. vulpes*), raccoons, striped skunks, opossums, western spotted skunks, and American badgers (*Taxidea taxus*). Two domestic carnivores, cats and dogs (*Canis lupus familiaris*), also inhabit the mountains and are generally associated with humans.

Camera trap survey

We placed cameras (Bushnell Trail Scout Digital; Bushnell Corp., Overland Park, KS, USA) at 50 locations throughout the study site between May 2011 and June 2013 (Fig. 1). Our goal was to monitor animal activity across a gradient of human development from undeveloped to exurban neighborhoods. We measured human development from building structures identified from high-resolution satellite imagery. We digitized structures manually in exurban and low development landscapes and used address points to locate houses in suburban and urban areas to create a development layer in ArcGIS (v. 10.0, ESRI 2010). We used the kernel density tool in ArcGIS with a radius of 400 meters and grid size of 30mX30m to summarize the building density of the study area. The tool works by placing a smoothed surface of volume one and radius *h* over each house. At each raster cell in the grid, we generated a housing density value by summing all values of kernel surfaces overlaying the cell.

With development mapped, we then randomly selected 10 locations each along a stratified development gradient of approximately 0, 0-0.5, 0.5-1, 1-1.5, and 1.5-2 houses per hectare for a total of 50 cameras locations. We further restricted potential camera locations to within 100 meters from a road or trail and at least 1 km away from the next closest camera. We traveled to each randomly generated location and placed a camera along the closest animal movement trail, recreational trail, or road to the location. If we could not secure permission from the landowner to place a camera at the randomly generated site, we placed it in a nearby location of comparable housing density.

We programmed the cameras to take three photographs when triggered with a one minute delay between successive image sets. We excluded data collected by cameras when they were heavily obscured by fallen or growing vegetation or when interference by humans or animals altered the camera angle or field of visibility. We visited all cameras to replace batteries and download memory cards either monthly or every two months, depending on the amount of activity at the site.

Spatial activity analyses

We compiled a detection history for all carnivore species for a full year from October 2011 to October 2012. We demarcated each survey period as a full week beginning Monday at 10AM PST for a total of 53 surveys. We assumed that our cameras were closed to occupancy changes over the one-year period because the species we targeted for monitoring live several years in the wild and maintain generally stable home ranges (Riley 2006). For each survey, we recorded whether a species was present or absent based on whether it was captured by the camera trap. Upon completion of our camera-trapping study, we had enough data to model occupancy for 8 predators: pumas, coyotes, bobcats, grey foxes, raccoons, striped skunks, opossums, and domestic cats.

We examined species co-occurrence patterns between pumas and all subordinate carnivore species pairs using single season, two species occupancy models. Occupancy models improve upon traditional methods of examining spatial patterns of species occurrence because they provide unbiased estimates of species occurrence by explicitly accounting for imperfect detection(MacKenzie et al. 2004; MacKenzie et al. 2002). Occupancy models also allow habitat and survey covariates to be incorporated when estimating both occupancy and detection through a logit link (MacKenzie et al. 2004; MacKenzie et al. 2002). We used two-species occupancy models to test whether the occupancy and detection of mesopredators were influenced by the occupancy of the dominant species. We also tested whether the subordinate predators responded to habitat and anthropogenic factors differently in sites occupied and not occupied by pumas. Lastly, we incorporated coyote activity and detection as covariates to test whether they influenced the occupancy and detection of subordinate mesopredators.

We used the program PRESENCE 5.9 (United States Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland; MacKenzie et al. 2006), which utilizes a maximum-likelihood-estimation modeling approach to compare all models. We used the conditional parameterization of the two-species occupancy model as outlined in Richmond et al. (2010) for our analyses because we wanted to examine interactions between pairs of dominant and subordinate carnivores. Under this model structure, estimates of occupancy ψ^A and detection p^A probabilities for species A (pumas) are not influenced by the presence of species B (mesopredators). Because species A is the dominant competitor, we did not expect either the occupancy or detection of species B to influence those of species A. In contrast, the conditional parameterization allowed us to explicitly test whether the estimates for the occupancy (ψ_B) and detection (p^B, r^B) probabilities of species B, the subordinate competitor, are conditional upon those of species A. We did not test whether the detection of species B was influenced by the detection of species A (i.e., we set $r^{BA} = r^{Ba}$) because of limited data due to the infrequent detection of pumas. The full set of parameters and covariates utilized by the models and their descriptions is listed in Table 1.

Our occupancy covariates for native predators were human development and percent forest habitat. For domestic cats, we used human development as the sole occupancy covariate because we expected their occupancy to be primarily tied to the presence of humans on the landscape. We derived our development covariate using the kernel density tool to calculate housing density from the GIS housing layer at radii (*h*) of 100m, 300m, and 500m. We found that a radius of 500m minimized model Akaike Information Criterion (AIC) and therefore used that scale for our development covariates. We classified forest habitat by placing a circular buffer with radius 500m above the camera location. We then extracted vegetation data from the California GAP Analysis Project (Lennartz et al. 2008) and calculated percentage forest cover by dividing the area classified as forest or woodland by the total area of the circular buffer. We used human development, as defined above, for our detection covariate. For subordinate mesopredators (i.e., not coyotes), we also included coyote activity and the interaction between coyote activity and development as occupancy and detection covariates. We expected that high coyote activity might deter inferior competitors from occupying a habitat and reduce their activity at the site. Coyote activity was defined as the average number of coyote photos taken at each site per 100 days. We z-transformed all forest cover, development, and coyote activity covariates.

As pointed out by Richmond et al. (2010), the candidate model set for the conditional two-species parameterization is very large due to all the potential combinations of model parameters. To simplify the *a priori* size of the candidate model set, we carried out a multi-step modeling approach. First, we identified the best occupancy and detection model for species A by fitting 8 one species, single season models to the puma data with all combinations of occupancy, detection and site-specific covariate parameters (Appendix 1). We used AIC rankings to identify the best single species occupancy models for pumas and used the resulting top model in all subsequent two-species co-occurrence occupancy analyses.

Using the best occupancy and detection covariates for pumas, we then modeled co-occurrence between pumas and all subordinate species (coyotes, grey foxes, bobcats, raccoons, domestic cats, striped skunks and opossums). For each species pair, we first held ψ^B constant and compared the conditional and unconditional detection models for species B ($\text{i.e.}, p^B \neq r^B$ vs. $p^B = r^B$). For all puma-mesopredator pairs, the conditional model was the better model, so we used it to evaluate candidate covariates (i.e., development, coyote detection). We compared 25 candidate models to evaluate the influence of coyote activity and development on mesopredator detection probabilities and to test whether covariates affected detection differently based on whether pumas occupied the site. We discarded models from further inference if they were within ≤2 ΔAIC of the top ranked model and contained uninformative parameters as identified by Arnold (2010). For example, a model that has a higher AIC while hierarchically more complex than the top ranked model would not be considered for inference. We used AIC rankings to determine the best model.

Once we identified the top detection model, we held that portion of the model constant and fit occupancy parameters for Species B in addition to it. Bobcats, coyotes, raccoons and striped skunks were common across the landscape (occupancy rates >83%) so we did not model the effects of puma occupancy or any covariates on their probability of occupancy. For domestic cats, we only compared models with and without human development as an occupancy covariate since we did not expect puma occupancy to affect cat presence. For all other species pairs, we compared conditional occupancy models ($\psi^{BA} = \psi^{Ba}$) to the unconditional ones ($\psi^{BA} \neq \psi^{Ba}$) with all combinations of occupancy covariates. We followed the same protocol as with the detection models and discarded any models including uninformative parameters from comparison (Arnold 2010). Finally, we used AIC to rank all models for comparison.

Temporal activity analyses

For each photograph from our study, we recorded the date, time, camera site ID, and species. To ensure sample independence, we did not record photos of animals of the same species if they occurred within 30 minutes of a previous photo. If the camera captured two or more individuals of the same species in one photograph, we treated this as one time data point.

We examined whether species activity patterns differed between sites with disparate levels of human activity by separating our data into photographs that were captured at sites with high human use and those with low human use. We defined high human use sites as all those in which the cameras captured an average of 14 or more photos of humans weekly and low-use sites as those with fewer than 14 photos a week. We identified this threshold by visually examining the distribution of human activity data and identifying a natural break at about 2 photos day. This resulted in 31 sites being classified as high use and 19 sites as low use sites.

We used the non-parametric kernel density estimation procedure described in Ridout and Linkie (2009) and Linkie and Ridout (2011) to compare whether species offset their temporal activity at the two different human activity levels. We first converted all times to radians and used kernel density estimation to generate a probability density distribution of each species' activity pattern at each human activity level (Ridout & Linkie 2009). Next, we calculated the overlap term $\hat{\Delta}$, which is defined as the area under the curve formed by taking the smaller of two density functions at each time point (Ridout & Linkie 2009). In other words, $\hat{\Delta}$ represents the temporal activity overlap, ranging from 0 to1, between species activity times at regular and low human use sites. If species did not change their temporal activity patterns at regular human use sites, then we would expect an overlap value ($\hat{\Delta}$) close to 1, whereas if species altered their activity greatly, then we would expect $\hat{\Delta}$ values closer to 0. Ridout and Linkie (2009) outlined three methods for estimating $\hat{\Delta}$ and suggested using $\hat{\Delta}_1$ for small sample sizes (n<50) and $\hat{\Delta}_4$ for larger sample sizes, which we follow. Thus we calculated ($\hat{\Delta}_4$) for 11 species (pumas, deer, bobcats, coyotes, grey foxes, opossums, striped skunks, raccoons, domestic cats, dogs, and humans) to evaluate whether their temporal activity shifted between regular and low human use sites. To test whether temporal overlap between species pairs increased at sites of regular human use, we also compared $\hat{\Delta}_4$ at regular versus low use sites for 15 species pairs (Table 4). Finally, we obtained 95% confidence intervals for these estimates from 1000 bootstrap samples. All statistics were analyzed using the "overlap" package in R (v.2.15.1: the R Development Core Team, 2010).

To compare how human activity and development might impact temporal overlap between mesopredator species pairs on a continuous scale, we used the same method outlined above to calculate $\hat{\Delta}$ between species pairs at each camera station.

For these analyses we focused on temporal partitioning among three mesopredators pairs for which we had the most data: coyotes, grey foxes and bobcats. We then used multiple regression to determine how forest cover, development, and human activity affected the amount of temporal overlap between species. Our covariates for forest cover and development are described in full in the previous section. We calculate human activity by log-transforming the average number of humans photographed at each camera location. We started with the full model:

$$\hat{\Delta} = \beta_0 + \beta_1(Human\ Activity) + \beta_2(Development) + \beta_3(Forest\ Cover),$$

and used likelihood-ratio tests to compare model fit results with reduced models to determine the best model.

Bait experiment

While camera traps allowed us to passively assess interactions between pumas and mesopredators, we wanted to explicitly test whether puma presence might influence mesopredator use of a resource. To accomplish this, we used a field experiment to evaluate whether mesopredators responded to signs of puma occupancy in the context of human-altered landscape. We placed 49 baits between February and April 2012 along a gradient of human development in the same locations as the camera traps whenever possible. For a few locations, we placed the bait in a location of similar development density but not at the camera site due to lack of permission from landowners or unsuitable conditions (e.g., in a neighborhood).

We used defrosted hind legs of road-kill deer for our baits and weighed each leg to ensure that it was at least 10 pounds. We tied baits to trees or posts to prevent mesopredators from dragging away baits, at least initially. We treated 25 of 49 baits with puma feces (placed one meter away from the bait) and 4 mLs of puma urine, distributed evenly on all four sides of the bait. We obtained the feces from a captive puma in a nearby sanctuary and urine from In Heat Scents (Kinston, AL, USA). One motion-detecting infrared camera was secured to a tree or post directly facing the bait to monitor the fate of the deer leg. Cameras were set to capture one picture at a time with no more than mechanical delay between photos. Each bait was monitored for two full weeks by the cameras.

For each bait, we recorded all species that visited, time to first visit by a mesopredator, start time of each visit, and the duration of each visit. We used generalized linear models (GLMs, log link and binomial error distribution) in R to compare how puma treatment, housing development, and local forest cover affected which species visited baits. Puma treatment was coded as a binary variable, with 1 representing treatment and 0 control. For mesopedators that were not coyotes, we also included coyote presence as a binary predictor variable. We defined local forest cover as the percentage of forest in a circular area of radius 100m around the site. We used a kernel density estimator and computed the level of housing development at 6 scales surrounding the bait site (h = 50m, 100m, 200m, 300m, 400m, and 500m). We first used univariate analyses to identify important covariates and retained models that significantly differed from the null model based on a likelihood ratio test. For development, we picked the *h* value that minimized model AIC. We also tested models including interaction terms (puma x development, puma x forest cover, coyote x development, coyote x forest cover) because we suspected that scavenging behavior might be impacted by top predators differently depending on the surrounding environment. Finally, we evaluated the combined effects of all significant factors and interaction terms and used likelihood ratio tests to determine whether they were significantly better than reduced models.

We also evaluated whether behavior at the bait was impacted by either puma treatment, forest cover, or housing density. Specifically, we looked at time until a species first visited the bait, the cumulative time spent at the bait over the two-week period, and the average time spent per visit. Preliminary analyses revealed no effect of forest cover or housing density on bobcats, coyotes or grey fox behavior at the bait. We thus used one-tailed Welch's t-tests to determine whether puma treatment influenced arrival time at bait. We used the one-tailed Kolmogorov-Smirnov 2-sample test to compare the amount of time spent at the treated and control bait stations.

Results

Cameras operated for 21950 cumulative trap nights at over 50 sites. From recorded phototographs, we identified at least 68 unique species of animals from 193815 photo sets. All carnivores, except for domestic dogs, were primarily active at night, with some species, such as grey foxes, opossums and striped skunks, almost exclusively so (Table 2).

Our bait experiments attracted 564 visits from mesopredators, of which 28719 photos were taken. A total of 36 unique species visited the baits, including 8 mesopredators: coyotes, bobcats, grey foxes, striped skunks, raccoons, opossums, domestic cats and dogs. Pumas also visited four of the baits. We focused our analyses on bobcats, coyotes and grey foxes because they were the most prevalent scavengers, having visited 24, 22, and 13 of the baits, respectively.

Single-species occupancy models for pumas

All 8 one species single-season occupancy models for pumas are listed in Appendix 1. The top model for pumas identified development as an influential negative occupancy covariate ($\beta = -1.518$, SE = 0.474). The best models ($\Delta AIC<2$) included development as an occupancy variable and all models including development as an occupancy covariate had a cumulative AIC weight of greater than 0.99. Development ($\beta = -0.515$, SE = 0.188) was also negatively associated with detection probabilities of pumas in the best model, and the cumulative AIC weight all models including development as a detection covariate was greater than 0.98.

Two-species occupancy modeling

We modeled 7 pairs of species interactions between the dominant predator and 7 subordinate predators for a one-year period. Top models ($\Delta AIC<2$) for each species pair are summarized in Appendix 2. The conditional co-occurrence models for opossums had slightly more support (0.46 vs 0.44 model weight) than the unconditional co-occurrence models, indicating that their occupancy rate was influenced by puma occupancy. Under the top ranked model, opossum occupancy was higher (75% ± 8% SE vs 55% ± 13% SE) in sites where pumas were present, holding all covariates constant. Opossums were also more likely to occupy sites with increased coyote activity (β =1.05, SE = 0.69) and higher forest cover (β =0.58, SE = 0.38). There was ambiguous evidence that grey fox occupancy was affected by puma occupancy because the unconditional and conditional occupancy models had almost equivalent AIC scores (ΔAIC =0.1). Under the conditional model, which had the lowest AIC, grey fox occupancy was 40% (±18.5% SE) at puma-absent sites and 84.9% (±7%) at puma-present sites. With the unconditional model, grey fox occupancy was predicted at 83.5% (±7.5%) across the entire region. We identified no other informative covariates that influenced grey fox occupancy. Domestic cat occupancy showed the opposite pattern to that of pumas and was positively correlated with development (β =0.594, se=0.317).

All subordinate species' detection probabilities were affected by the presence of pumas independent of covariates ($\text{i.e.}, p^B \neq r^B$). In general, bobcats, grey foxes, opossums and striped skunks were more likely to be detected at sites with pumas whereas raccoons and coyotes were less likely to be detected (Figs. 2, 3, 4). The probability of detecting domestic cats showed a more complicated response to puma presence. Higher development was correlated with increased striped skunk and raccoon and decreased bobcat and coyote detections independent of puma occupancy (Figs. 3, 4). Opossums, domestic cats and grey foxes responded to development differently depending upon whether sites were occupied by pumas (Fig. 3). Opossum detection was positively correlated with human development at puma-occupied sites and negatively correlated with development at sites without pumas. At sites occupied by pumas, grey fox detection was negatively correlated with higher development whereas domestic cat detection increased with development.

Subordinate species detections were also influenced by coyote activity, although some species responded to coyotes differently depending upon puma occupancy status. Bobcats were more likely to be detected and opossums less likely to be detected at sites with increased coyote activity (Figs 3). Grey fox detection exhibited the most negative response to coyote activity, but only at sites occupied by pumas. At sites without pumas, grey fox detection was near zero and showed no relationships with any of the covariates. Skunk detections were negatively impacted by coyote activity whereas cat detections were positively influenced by coyote activity at sites with no pumas. Finally, raccoon detections decreased with coyote activity at sites not occupied by pumas.

Temporal interactions

Pumas and coyotes shifted their activity patterns in sites with more regular human activity by increasing nighttime trail activity and reducing daytime and especially morning activity (Fig. 5). Bobcats exhibited similar activity peaks and valleys at both levels of human use, but with overall lower daytime activity and higher nighttime activity levels. Grey fox activity patterns shifted little in sites with higher human activity, most likely because grey foxes were almost exclusively active nocturnally. Opossums, striped skunks and raccoons all had very similar activity patterns to grey foxes and were primarily nocturnal as well. Black-tailed deer

(*Odocoileus hemionus*) were not impacted by increased human activity and maintained a strong crepuscular pattern. Humans and dogs in regular human use areas were more active in mornings and less active in afternoons. This perhaps reflects a bias towards morning recreation in parks.

Coyotes and smaller mesopredator species (grey fox, opossum, raccoon, and striped skunks) showed the highest temporal segregation of all species pairs in both low (45.4%-54.5% overlap) and regular (65.3-73.9%) human use areas (Table 4). All $\hat{\Delta}_4$ (overlap) values between coyotes and smaller mesopredators increased by more than 15% in higher human use sites with non-overlapping confidence intervals. Coyote and domestic cat temporal overlap also increased by 19.9% from 70.4%to 90.3%. Pumas exhibited the lowest temporal overlap with deer, opossums, and coyotes. Interestingly, while overlap increased between pumas and the two aforementioned mesopredators increased at regular human use locations, overlap between deer and pumas actually decreased 8.7% at higher human use. From our fine scale analyses of temporal segregation and human activity, we observed that overlap between all three mesopredator species pairs (bobcat and grey fox, coyote and grey fox, and bobcat and coyote) significantly increased with human activity and overlap between bobcats and coyotes significantly increased with both human activity and development (Table 3).

Bait experiment

Puma treatment did not affect the probability of bobcats ($\chi^2 = 0.507, p = 0.476$), coyotes ($\chi^2 = 1.05, p = 0.307$), or grey foxes ($\chi^2 = 0.295, p = 0.587$)

visiting baits. We found a negative relationship between the probability of bobcats visiting a bait and housing density ($\chi^2 = 6.93, p = 0.0085$), evaluated at h = 100m, but no other variables or interaction terms were significant. Grey fox presence was negatively influenced by the presence of coyotes ($\chi^2 = 8.13, p = 0.0043$) at the baits and higher housing density ($\chi^2 = 10.46, p = 0.0012$), evaluated at h = 500m. Coyote presence at the baits was not significantly associated with any of the covariates or interaction terms.

We found no differences in grey fox or coyote arrival and behavior at baits treated by puma sign. However, we did find that bobcats arrived 3.6 days later on average to treated baits than untreated ones ($t = 2.661, p = 0.0076$). Bobcats stayed longer during individual visits ($Kolmogorov - Smimov\ test, p = 0.008$) and across all visits ($K.S.test, p = 0.02$) at control baits compared to treated ones.

Discussion

Anthropogenic and top predator influences on spatial patterns of predator activity

As we expected, pumas were sensitive to development, and their occupancy and detection probabilities decreased as housing density increased. Thus, it appears the influence of pumas as top predators on smaller ones will ebb as development levels increase. Nevertheless, we found that pumas often shared space with humans at a very fine spatiotemporal scale. Pumas visited sites with moderate to high levels of human development, particularly if these locations were at the edges of undeveloped lands. This supports the conclusions drawn by Wilmers et al. (2013), who found that while pumas preferred to use undeveloped habitats, they still regularly traveled and hunted throughout human-dominated landscapes. Interestingly, despite the puma's generally shy disposition, we sometimes detected pumas traveling along well-used trails in parks during hours when people and dogs were active.

Bobcats, coyotes, raccoons and striped skunks were present throughout all levels of exurban development and occupied more than 83% of the sites throughout the study area. While coyotes, raccoons, and striped skunks are behaviorally plastic species known to tolerate or even benefit from anthropogenic ecosystems (Prange & Gehrt 2004), some previous studies have found that bobcat presence and abundance have generally declined with increased development (Riley 2006). For example, Crooks (2002) found bobcats to be intermediate between pumas and smaller mesopredators in their sensitivities to development. However, we observed bobcats at all but one of our sites, including several sites in relatively dense neighborhoods. Our results align with those from a meta-analysis of camera trap data from Southern California, which also found that bobcats were prevalent across the landscape even though their presence declined with urbanization (Ordenana et al. 2010). One reason we did not observe declining bobcat occupancy across our development gradient might be because we capped our upper development limit to 2 houses per hectare due to the logistical concerns of camera trapping in higher density neighborhoods (e.g., theft, privacy concerns). The prevalence of large connected habitats in the Santa Cruz Mountains may also contribute as a rich source of bobcats, which then migrate into exurban mountain communities or out into surrounding suburbs.

Domestic cats were the only mesopredator whose occupancy was influenced by development, and they exhibited the opposite relationship to human development as pumas. Because they are pets, domestic cats were rarely observed in undeveloped sites unless these areas were adjacent to houses. Opossum occupancy was positively influenced by both puma occupancy and coyote activity. This appears counterintuitive, since opossums are inferior competitors to coyotes and pumas and are sometimes eaten by them (Wilmers et al., unpublished data). We are uncertain what mechanisms may have caused this, but speculate that this relationship may be due to the indirect influence of an unmeasured variable. For example, opossums were regular scavengers at our bait sites and may benefit from scavenging coyote and puma kills. Higher forest cover was also associated with increased opossum occupancy, which might be because they prefer wooded areas for shelter and den sites (Prange & Gehrt 2004).

Although our study found limited evidence that top predators or human development influenced the presence of subordinate mesopredators on the landscape, we did find that predator and development covariates affected the patterns of detection for mesopredators (Figs. 2, 3, 4). As expected, detection probability increased for raccoons and striped skunks in locations with higher human development. In contrast, bobcat and coyote detections decreased with development, suggesting that while development pressures did not negatively influence their occupancy, bobcats and coyotes may utilize developed areas on the landscape less frequently. Coyote detections decreased to a lesser degree with higher development than bobcat detections, indicating that bobcats are perhaps the more sensitive of the two species to development. Grey fox detections responded even more negatively to development than coyotes and bobcats. While Bidlack (2007) and Riley (2006) concluded that grey foxes were capable of persisting in small urban patches, our results aligned more with the meta-analysis of camera-trap studies from southern California, which found grey foxes to be sensitive to urban development (Ordenana et al. 2010). It is also possible that grey foxes may be detected more in small urban patches that are not occupied by coyotes, but we did not monitor any such sites. Opossum detection probabilities increased the most at higher development sites occupied by pumas. This indicates the existence of potential unmeasured environmental site characteristics that make these locations more attractive to both species, despite the anthropogenic disturbances. Alternately, opossums may be benefitting from reduced activity of raccoons due to puma occupancy of these sites.

Detection changes by mesopredators in response to the occupancy of a superior competitor may reflect behavioral avoidance (Richmond et al. 2010), and we found that coyote and raccoon detection probabilities were the most negatively influenced by puma occupancy. Pumas are known intraguild predators of coyotes (Logan & Sweanor 2001), and raccoons were the second most common prey item in the diets of pumas in this region (Wilmers, unpublished data). Thus, coyotes and raccoons may have minimized their activity in sites occupied by pumas to avoid encountering the dominant predator. In contrast, bobcats, grey foxes and striped skunks were all detected more often at sites with pumas, suggesting that the three mesopredators can successfully avoid confrontations with pumas or, alternatively, benefit from suppressed activity of coyotes and raccoons.

Coyote activity also influenced the detection of smaller mesopredators, but its effect sometimes differed depending on puma occupancy (Fig 3). Striped skunk and grey fox detections decreased with increased coyote activity, but only at sites occupied by pumas. This is likely due to the low detection rate of both skunks and foxes at sites without pumas and the subsequent lack of influence of coyote activity on detection. Raccoon detections, in contrast, only exhibited a relationship with coyote activity at sites without pumas. Both pumas and coyotes will kill raccoons, but it is possible that raccoon detection was more strongly influenced by pumas than coyotes at sites occupied by pumas. Bobcats were detected more often at all sites with higher coyote activity, suggesting that the two mesopredators coexist at a fine scale. In contrast, opossums were detected less often at all locations with higher coyote activity. This supports findings from Crooks and Soulé (1999), who concluded that coyote abundance was negatively related to opossum abundance, while seeming to contradict our finding of a positive relationship between opossum occupancy and coyote activity. One potential explanation is that opossums may avoid coyotes at fine scales, both temporally and spatially, but that both species might be selecting for similar habitats.

Domestic cats presented the most complex responses to covariates and puma occupancy (Fig 3). Cat detection was low and positively correlated to development at sites without pumas. Domestic cats were also detected more with increased coyote activity at sites with pumas. This is contradictory to what we expected since both coyotes and pumas are known predators of domestic cats (Crooks & Soulé 1999); Wilmers et al. unpublished data). Our complex results from the two-species model may be due to two possibilities: spurious correlations between parameters or invalid a priori model formulations. To test the results of our two-species conditional occupancy models, we compared the results from two-species models with one-species occupancy models for domestic cats in which we included human development, coyote activity and puma occupancy as covariates. Results from our one species models revealed a positive relationship between cat detection and puma occupancy and increased development and a negative relationship with coyote activity. Thus, the one-species model confirms the association between puma occupancy and higher domestic cat detection probabilities and lends more support towards a general positive relationship with development and a negative one with coyotes. The second possible explanation, that the results arise from invalid model formulation, is due to the fact that pumas, development, and coyotes may not be primary drivers of domestic cat detection rates. Instead, because most domestic cats are people's pets, they might not have properly modulated fear responses to predators. Since there is no selective pressure for domestic cats to exhibit behavioral avoidance of predators, cats are not expected to respond appropriately to the activity of dominant predators.

Anthropogenic influences on temporal patterns of predator activity

Many previous studies have observed that top predators will alter their temporal patterns to avoid human activities (Carter et al. 2012; Riley et al. 2003; Schuette et al. 2013). Our study corroborated those findings and showed that pumas reduced their morning activity and increased their nighttime activity between midnight and 6AM, potentially to avoid conflicts with humans and dogs at sites of regular human use (Fig. 3). This shift in activity may reduce their hunting success in high human use areas since deer activity peaks in the early morning. Deer in our study did not shift their activity times at differing levels of human disturbance, contrary to the findings from George and Crooks (2006), which concluded that deer were detected less during the daytime at places with higher human activity. It is possible that deer in our study area have become habituated to human disturbances after numerous generations of living in areas of sustained human recreation.

Mesopredators also adjusted their behavior to reduce overlap with humans in the daytime. Coyotes in low disturbance areas were very active in the mornings and early evenings, but became more nocturnal at high disturbance locations (Fig. 3). Bobcats were more nocturnal than coyotes generally, but also decreased their diurnal activity in high human activity locations. Similar to pumas, coyotes and bobcats likely shifted their behavior to avoid humans and dogs, who were very active in the morning. Our results support findings from previous studies from Southern California, which also concluded that bobcats and coyotes adjusted their behavior to increase nocturnal activity to facilitate coexistence with humans (Riley et al. 2003).

Grey foxes, opossums, raccoons, and striped skunks exhibited almost exclusively nocturnal behavior at all locations, and were rarely observed on trails or roads during daylight. Temporal partitioning between coyotes and smaller predators was evident at sites with sporadic human activity, and may be a useful evolutionary strategy employed by subordinate species to avoid encountering and being killed by a larger competitor (Gehrt & Prange 2007; Hayward & Slotow 2009; Palomares & Caro 1999; Schuette et al. 2013). Alternatively, striped skunks, opossums and raccoons may have adopted a more nocturnal schedule to avoid conflicts with people as they adapted to living alongside humans. Higher levels of human activity intensified temporal overlap between smaller mesopredators and the more dominant coyotes, potentially augmenting interspecific conflict between competing predators.

Our fine scale analyses of bobcat, coyote, and grey fox temporal interactions further revealed that higher human activity was associated with increased overlap between all carnivore species pairs on a site-by-site basis. We also found higher development was significantly correlated with greater bobcat and coyote overlap levels. Most of this increase is likely due to coyotes and bobcats shifting their patterns to become more nocturnal (Fig. 3). While bobcats and coyotes were still regularly spotted in locations with heavy foot traffic (upwards of over 100 people a day), they likely reduced their daytime activity to avoid confrontation with people and their dogs. Alternatively, they may have shifted their activity off roads and trails during daylight hours, which may increase their energetic expenditures. These behavioral shifts by bobcats and coyotes may cascade through the food web to influence grey foxes, prey species and plant communities. For example, if coyotes are not as active in the daytime, they may disproportionately target nocturnally active prey species and release more diurnal prey from predation. Higher temporal overlap between grey foxes and coyotes may also lead to more interspecific competition and foxes may have to adopt a more conservative hunting strategy to avoid encountering coyotes at night.

Mesopredator behavior at baits

Bobcats, coyotes, and grey foxes were the most prominent mammalian scavengers at our baits, followed by opossums, striped skunks, and raccoons. Interestingly, although raccoons are widely acknowledged to be prevalent scavengers of disturbed ecosystems (DeVault et al. 2011; Olson et al. 2012), we only observed them visiting 7 baits but did not observe them feeding on any of them. This discrepancy could be partially due to raccoons trying to avoid dominant mesopredators, such as coyotes and bobcats, and to the widespread availability of anthropogenic food sources. Opossums, normally considered subordinate to raccoons, did feed at baits, and even shared the same resource with bobcats and grey foxes through temporal partitioning. Bobcats sometimes fed on the same bait as coyotes and grey foxes, but temporally staggered their consumption with that of the other predators'. We also recorded an encounter between bobcats and coyotes during which coyotes usurped the bait from the bobcat feeding on it. Our results indicate that while interspecific competition exists at carrion resources between some species, temporal partitioning may facilitate resource sharing between several mesopredators.

Contrary to our expectations, baits treated with puma sign did not reduce or influence the probability of visitation for bobcats, coyotes and grey foxes. Instead, our results indicate that development may influence whether mesopredators show up at the bait because bobcats and grey fox presence at the bait was negatively correlated to development levels. Alternatively, grey foxes and bobcats may simply avoid baits near development to reduce encounters with domestic dogs. Surprisingly, bobcats were less sensitive to development (h = 100m) than grey foxes (h = 500). This is contrary to findings from previous studies, which found that grey foxes were more tolerant of high levels of habitat fragmentation compared to bobcats (Bidlack 2007; Crooks 2002; Crooks & Soulé 1999). Grey foxes were also sensitive to coyote presence at the bait, and avoided baits visited by the dominant predator. Since dietary overlap between grey foxes and coyotes is high (Neale & Sacks 2001), this fine scale spatial avoidance by foxes likely contributes to their spatial co-existence.

We did not see any influence of puma sign on the behavior of coyotes and grey foxes at baits. Bobcats were an exception to this pattern, as they arrived later to feed at baits treated with puma sign and stayed for shorter periods on average and cumulatively. Pumas occasionally kill and eat both bobcats (Hass 2009) and coyotes (Palomares & Caro 1999), but we did not find that puma sign deterred coyotes from feeding on baits. As the only other native felid in the ecosystem, it is possible that bobcats were more sensitive to puma sign than the other scavengers were. Several studies have documented temporal partitioning between cohabiting felid species (Di Bitetti et al. 2009; Harmsen et al. 2009), although Hass (2009) found no evidence of spatial avoidance of pumas by bobcats in Arizona. While pumas are widespread across much of the Santa Cruz Mountains, the probability of encountering them at any one location is very low because they have such large home ranges and occur at low densities. It appears that in this system, mesopredators may be more motivated by the reward of scavenging than by the fear of encountering the top predator. Previous fieldwork from our research lab supports this idea because we have observed numerous mesopredator species feeding on baits also visited by pumas.

Implications for wildlife communities in developing landscapes

Exurban development is the fastest growing form of land use change in the United States, and can irreversibly alter ecosystem stability (Hansen et al. 2005). At the edges of urban habitats, land-use change often occurs at a rate far out-stripping that of population growth and can influence ecological communities for miles outside of urban centers (Gehrt et al. 2010). These anthropogenic influences can disrupt predator interaction webs and alter the traditional ecological roles served by these species. Despite these disturbances in the Santa Cruz Mountains, our study site supported a diverse complement of mammalian carnivores, including 8 native and 4 non-native species. Habitats with moderate amounts of human development and high levels of human activity were still occupied and used by pumas. Bobcats and coyotes were ubiquitous across the landscape, even in highly developed mountain communities. Grey foxes were commonly observed at lower development sites, but also at a few high development locations. We only evaluated locations where development did not exceed 2 houses/hectare, so it is likely that the carnivore community will continue to be transformed as human pressure increases. Previous research revealed grey fox tolerance of highly fragmented habitats, so it is possible that grey foxes do occupy highly disturbed environments if and when higher development pressures reduce coyotes from the landscape. We also found human-associated mesopredators (striped skunks, opossums) occupying undisturbed landscapes with low human use. Taken together, this suggests the carnivore community in our study area was generally very adaptable to contrasting levels of anthropogenic disturbances, although some species were clearly more sensitive to humans than others.

We observed regular mesopredator usage of sites with high human activity (as documented by photo-captures of humans at camera sites) by species considered more sensitive to humans and dogs (e.g., bobcats, coyotes, and grey foxes). We originally included human activity as another detection covariate, but we removed it due to its negative correlation with development; sites with high human use were generally in open space preserves, which serve the dual purposes of protecting habitats from development and promoting outdoor recreation. Some of these sites were used by 20 to over 100 people a day, but were still regularly visited by mesopredators at night. This is in stark contrast to previous research of mesopredator responses to human activity in California, which concluded that carnivores were detected less often in protected areas open to recreation than those that were not (George & Crooks 2006; Reed & Merenlender 2008). Some, but not all, of this discrepancy may be due to methodological differences (e.g. counts versus presence/absence). While we did not measure abundance of native carnivores, we did observe them regularly sharing parks with people on a weekly basis. Other studies have demonstrated fine-scale coexistence between tigers and humans within park boundaries and in the surrounding lands (Carter et al. 2012). In addition, Burton et al. (2012) found that West African carnivore species did not always respond negatively to human influences, including hunter activity. Our results and those of other studies suggest that carnivore communities, even in close geographical proximity, may have vastly different responses to anthropogenic disturbances.

In a heterogenous landscape such as the Santa Cruz Mountains, it is important to understand how different land-uses might impact the entire carnivore guild and the ecological community. Relatively developed exurban mountain communities and city edges do not generally support pumas, but often still host coyotes and bobcats. Changes in top predator membership and human development can influence the foodweb by altering relationships between predator guild members (Levi & Wilmers 2012). For example, our results suggest a potential among-predator cascade involving pumas, coyotes and grey foxes. Taken separately, we found evidence that grey foxes were detected less where coyote activity was high, and that coyotes were detected less frequently at sites occupied by pumas. Grey fox detection probability was very low at sites not occupied by pumas (regardless of coyote detection), and they may also be more likely to occupy sites also occupied by pumas, although the evidence is more ambiguous. However, because coyotes were present at most sites, it appears that they do coexist with pumas and grey foxes at least on a coarse spatial scale. Instead, coyotes and grey foxes may practice more fine-scale avoidance to circumvent their more dominant competitors. For example, coyotes might rarely visit sites occupied by pumas while grey foxes might reduce their activity or avoid certain trails in areas when coyotes are also present. Such fine-scale spatial partitioning, paired with some temporal avoidance, may facilitate spatial coexistence of competing predators in this landscape. If puma presence is reduced in more developed areas, then coyotes may suppress grey foxes more, thus releasing some small mammals from predation. Small mammals are known reservoir hosts of many zoonotic diseases, including Lyme disease, and are hunted more effectively by grey foxes than coyotes. Predator guild compositional shifts will also occur as domestic predators enter the landscape. In this paper, we did not deeply explore the potential influence of dogs on wildlife, although a previous study on dogs in Northern California parks observed higher native carnivore abundances in locations where dogs and people were not allowed (George & Crooks 2006). Free roaming domestic cats, as a potential prey species, might also influence top predator activity by attracting them to neighborhoods.

Many habitats in the Santa Cruz Mountains continue to support a diverse assemblage of native predator species, although increasing development pressure will test management effectiveness in years to come. Both large privately owned parcels and vast open space preserves are invaluable for providing relatively undisturbed habitats for top carnivores. Parks serve the dual purposes of protecting the land from development and creating opportunities for nature recreation for humans. People, and especially children, who participate in outdoor recreational activities in natural spaces feel more connected to nature and are more likely to develop a conservation ethic (Zaradic et al. 2009). However, intensive use of parks by people could also pose significant challenges to the management of carnivore species living in those parks. Species in these locations experienced more limitations to their daily activity, resulting in higher interspecific temporal overlaps. The consequences of reduced temporal niche partitioning on species interactions and prey species are unknown and need to be further explored. The primary objective of most protected areas is to maintain intact ecological communities while accommodating reasonable human activities. If human recreation is indeed adversely affecting a subset of predator species, then we may need to balance the benefits and costs of human use through some form of management (e.g., limiting human activities either temporally or spatially).

Even in relatively high development exurban habitats, we still observed use by multiple carnivore species, including pumas. It is likely that predators were retained in these human dominated systems because much of the exurban development we studied bordered large natural preserves. Residents who live in these types of development should be targeted for education to reduce conflicts between their domestic animals and native wildlife. For example, free-roaming outdoor domestic cats and raccoons may attract coyotes and pumas from neighboring wilderness areas. By securing pets and food at night, some of these problems can be reduced with benefits to both wildlife and domestic animals. As anthropogenic influences continue to expand, studies like ours can help elucidate the context-dependent spatiotemporal responses of mesopredators to human disturbances to better inform management options and future research directions.

Acknowledgments

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Table 3.1. List of parameters and covariates used in occupancy models

Parameter or Covariate	**Description**
$\boldsymbol{\psi^{A}}$	Probability of site occupancy for species A
$\boldsymbol{\psi^{BA}}$	Probability species B occupies site given species A occupies the site
$\boldsymbol{\psi^{Ba}}$	Probability species B occupies site given species A does not occupy the site
$\boldsymbol{p^{A}}$	Probability of detection for species A, independent of presence of species B
$\boldsymbol{p^{B}}$	Probability of detection for species B, given species A is absent
$\boldsymbol{r^{B}}$	Probability of detection for species B, given species A and B are present
Development (D)	Kernel housing density estimates with a radius of 500 meters
Forest (F)	Percent forested habitat in the surrounding area with 500 meter radius
Coyote Activity (C)	Average coyote activity per 100 days

Table 3.2. Summary statistics for the top 11 species captured by the camera traps

Species	**Number of captures**	**Camera Detections (out of 50 cameras)**	**Percentage of nighttime captures**
Bobcat	4223	49	70.38
Domestic Cat	1429	25	75.44
Coyote	2241	47	58.28
Deer	16354	50	46.63
Dog	9650	44	8.15
Grey Fox	2464	34	94.58
Human	142616	50	8.80
Opossum	986	34	96.55
Puma	217	33	80.65
Raccoon	1065	47	90.70
Striped Skunk	3024	49	94.01

Table 3.3. Top models describing the influence of covariates (human activity and development) on species temporal overlap.

Model	***p-value***	**Adj. R^2**
$\widehat{\Delta}_{fox,coyote} = \mathbf{0.487 + 0.139}(\boldsymbol{Human\ Activity})$	<0.019	0.417
$\widehat{\Delta}_{bobcat,fox} = \mathbf{0.689 + 0.065}(\boldsymbol{Human\ Activity})$	<0.013	0.269
$\widehat{\Delta}_{bobcat,coyote} = \mathbf{0.701 + 0.073}(\boldsymbol{Development}) + \mathbf{0.074}(\boldsymbol{Human\ Activity})$	<0.001	0.323

Table 3.4: Overlap values ($\hat{\Delta}_4$) between species pairs in areas of low and regular human use. Bolded lines indicated 95% confidence intervals that do not overlap for low compared with regular human use sites.

Species Pair	**Low Human Use $\hat{\Delta}_4$ (95% CI)**	**Regular Human Use $\hat{\Delta}_4$ (95% CI)**	**Difference**
Bobcat, Coyote	**0.851 (0.799 – 0.875)**	**0.915 (0.889 – 0.945)**	**0.064**
Grey Fox, Coyote	**0.543 (0.479 – 0.555)**	**0.701 (0.665 – 0.727)**	**0.158**
Bobcat, Grey Fox	**0.675 (0.630 – 0.699)**	**0.771 (0.745 – 0.788)**	**0.114**
Puma, Fox	0.775 (0.697 – 0.852)	0.806 (0.733 – 0.891)	0.031
Puma, Coyote	0.708 (0.621 – 0.782)	0.837 (0.764 – 0.908)	0.129
Puma, Bobcat	0.748 (0.649 – 0.813)	0.851 (0.777 – 0.921)	0.103
Coyote, Raccoon	**0.545 (0.485 – 0.557)**	**0.739 (0.681 – 0.781)**	**0.194**
Coyote, Opossum	**0.454 (0.389 – 0.464)**	**0.653 (0.594 – 0.672)**	**0.199**
Coyote, Skunk	**0.52 (0.465 – 0.530)**	**0.732 (0.695 – 0.764)**	**0.212**
Coyote, Cat	**0.704 (0.641 – 0.726)**	**0.903 (0.858 - 0.944)**	**0.199**
Puma, Deer	0.682 (0.600 – 0.767)	0.614 (0.512 – 0.664)	-0.068
Puma, Raccoon	0.793 (0.774 – 0.937)	0.844 (0.725 – 0.866)	0.051
Puma, Opossum	0.659 (0.554 – 0.730)	0.771 (0.680 – 0.850)	0.112
Puma, Skunk	0.749 (0.674 – 0.825)	0.836 (0.776 – 0.930)	0.087
Puma, Cat	0.800 (0.706 – 0.869)	0.817 (0.745 – 0.896)	-0.017

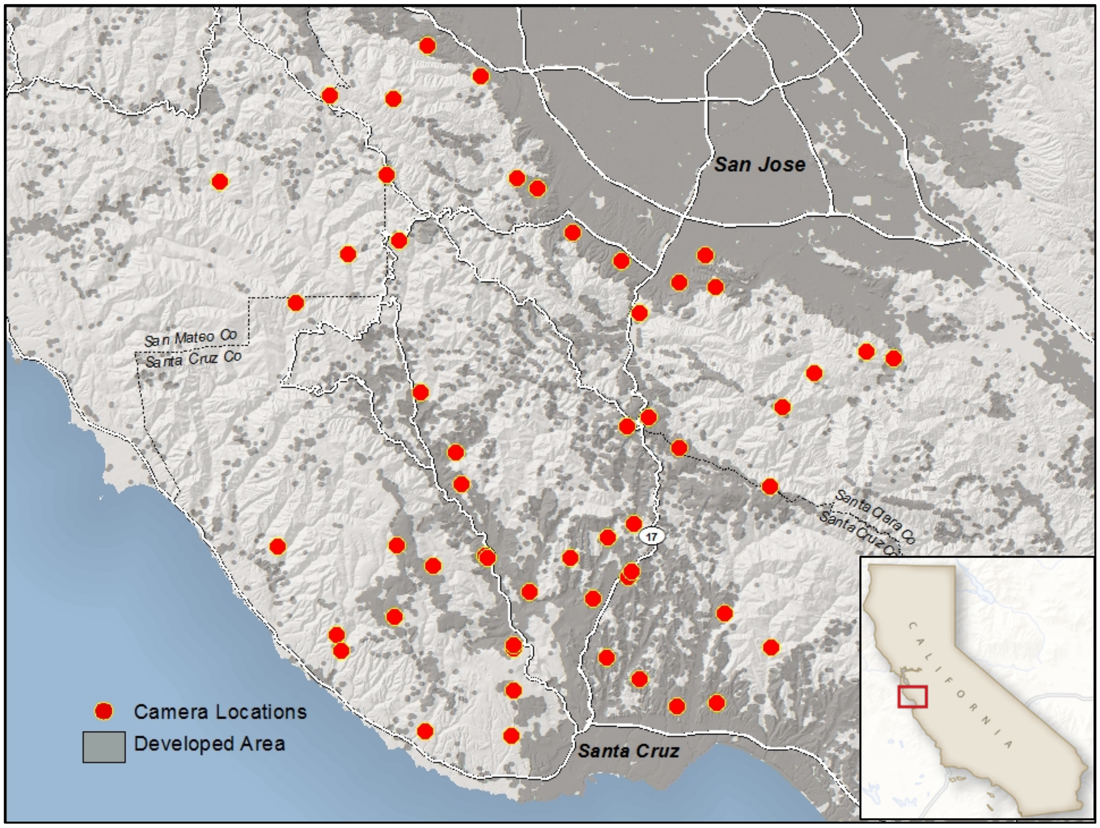


Figure 3.1. Map of study area with camera locations marked with red dots and housing development areas represented by grey. Inset marks location of the Santa Cruz Mountains in California.

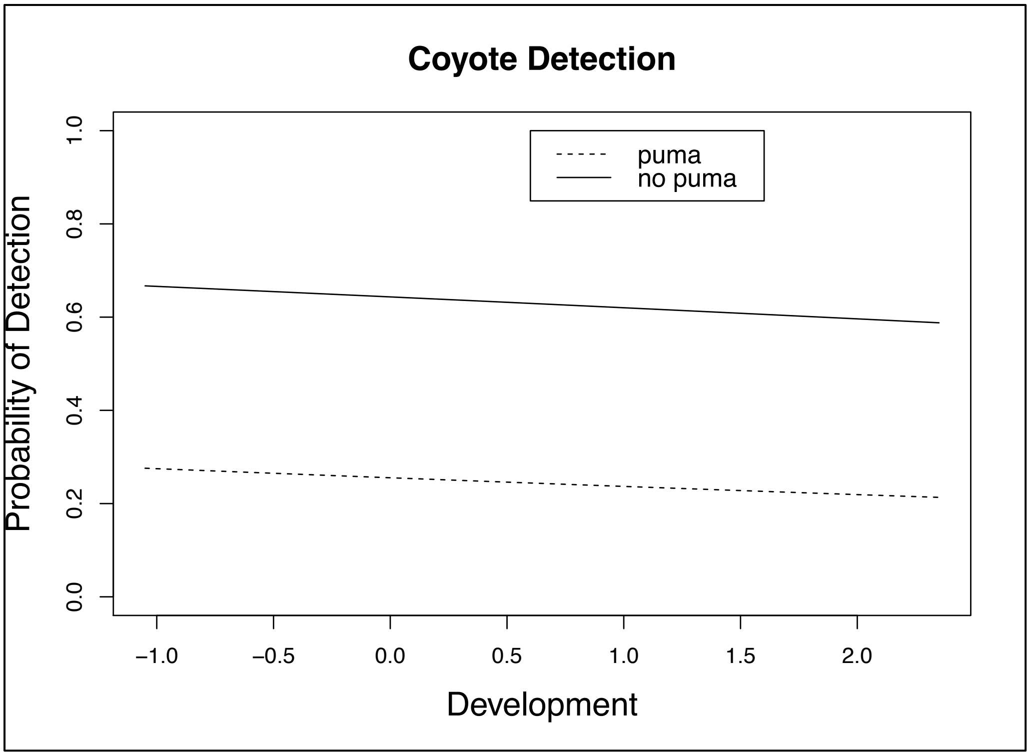
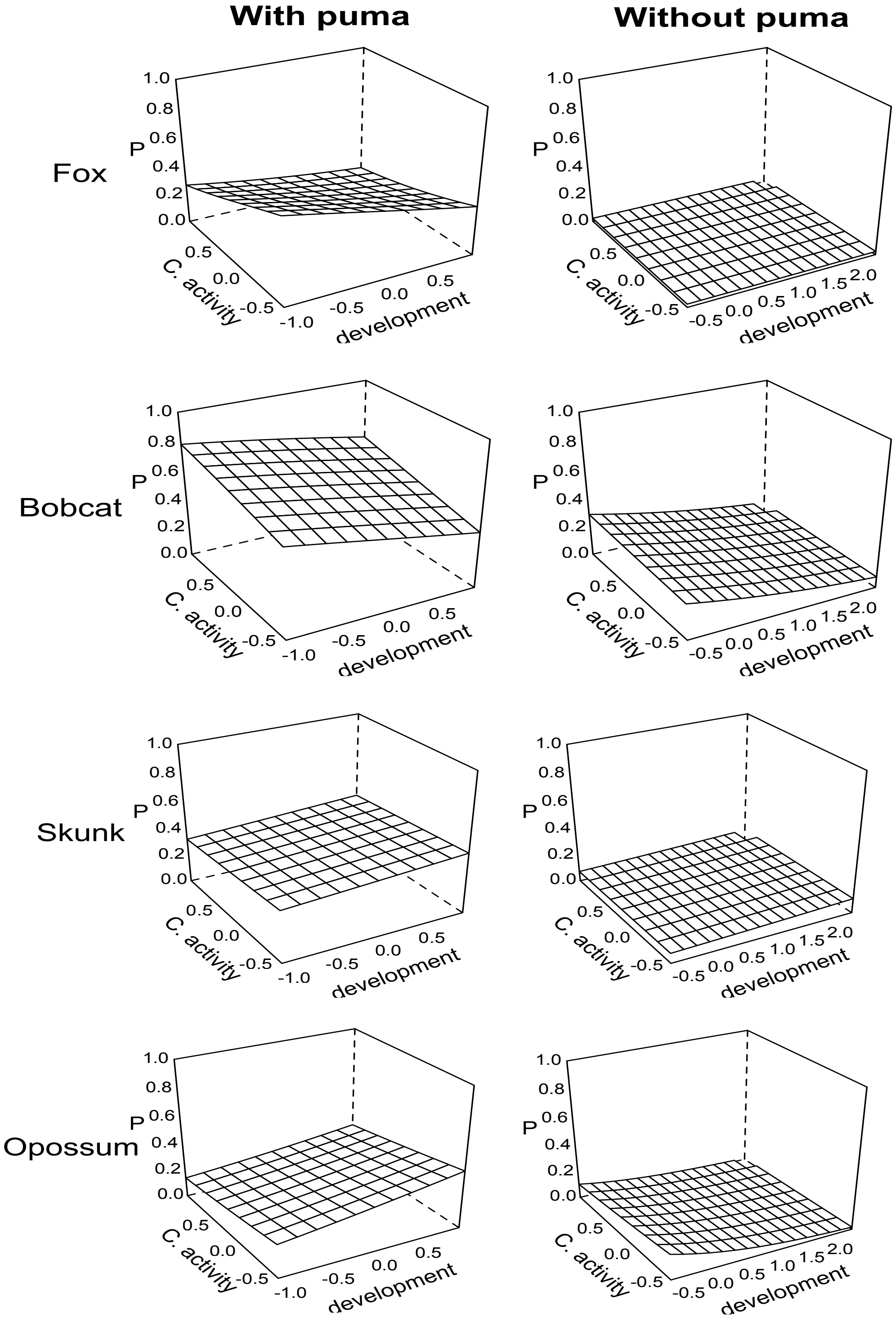


Figure 3.2. Influence of puma occupancy and human development on detection probabilities of coyotes. Development values have been z-transformed.


With puma
Without puma
Fox
Bobcat
Skunk
Opossum
P
1.0
0.8
0.6
0.4
0.2
0.0
C. activity
0.5
0.0
-0.5
development
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0

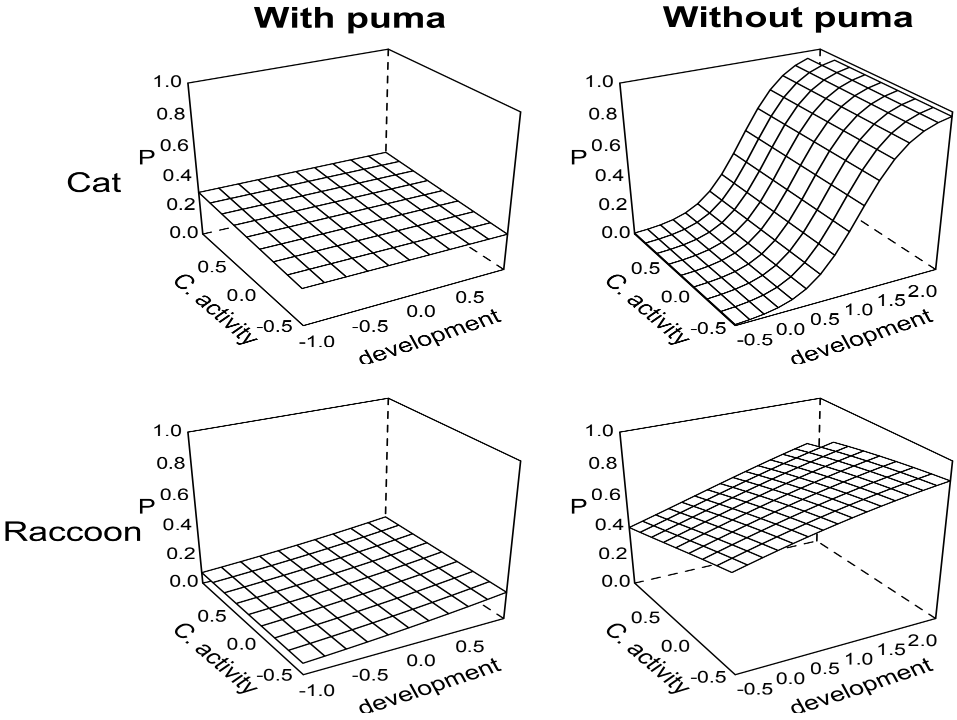


Figure 3.3. Estimated detection probabilities (P) for 6 mesopredator species as a function of puma occupancy, coyote activity (C. activity), and human development. Development and coyote activity values have been z-transformed.

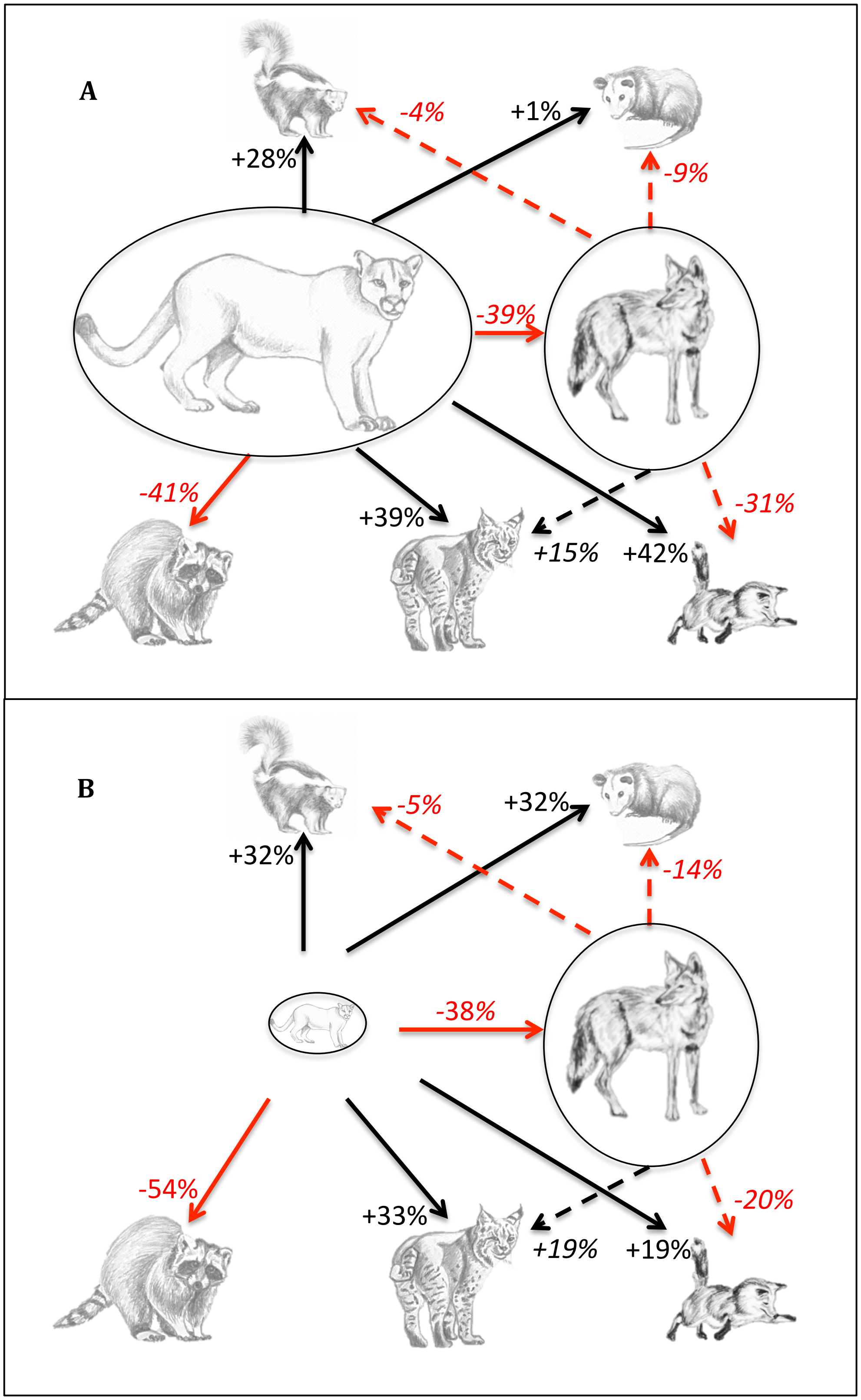

A
-4%
+1%
+28%
-9%
-39%
-41%
+39%
+15%
+42%
-31%
B
-5%
+32%
+32%
-14%
-38%
-54%
+33%
+19%
+19%
-20%

Figure 3.4. Percent differences in mesopredator detection probabilities with puma occupancy and coyote activity in low (a.) and high (b.) development sites. Low development is represented by a development z-score of -1 and high development by 1. Solid arrows originating from pumas represent the differences in mesopredator detection probabilities at sites occupied by pumas compared to sites unoccupied by pumas. A positive value means the species is more likely to be detected when pumas are present and a negative value means the species is less likely to be detected. Dashed arrows originating from coyotes represent the differences in mesopredator detection probabilities at sites with low coyote activity (z-score = -0.5) and sites with high coyote activity (z-score = 1). The size of the puma represents how its occupancy changes from low to high development.

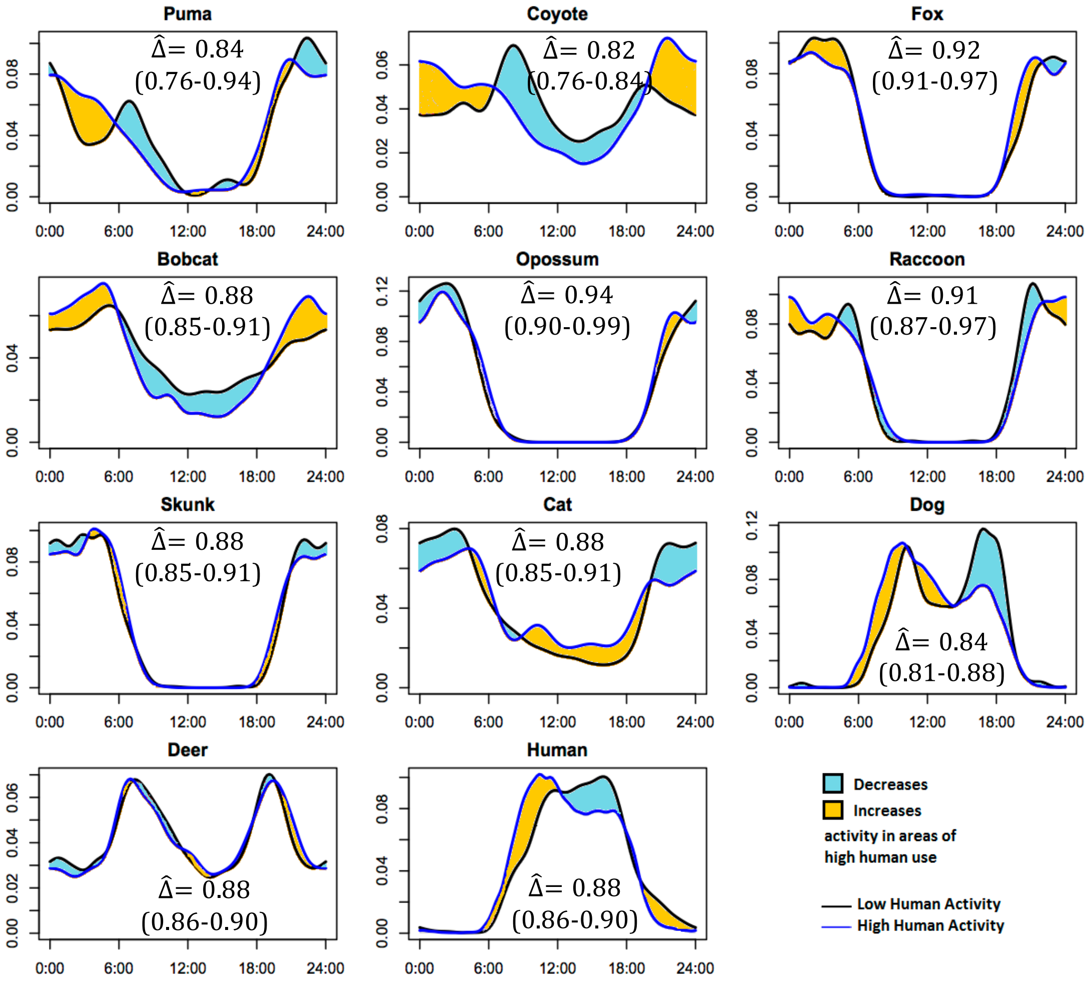


Figure 3.5. Kernel density estimates of daily activity patterns of 10 animal species and humans in areas of high (blue lines) and low (black lines) human use in the Santa Cruz Mountains. Temporal activity shifts for species are represented by $\hat{\Delta}$, with $\hat{\Delta}$=1 representing no temporal shifts between low and high human use areas and $\hat{\Delta}$=0 representing complete activity shift. Light blue colors indicate a decrease in activity and yellow colors represent an increase in activity in areas of higher human use.

Chapter 4

Validating citizen science generated data from Wildlife Tracker, an online game with a purpose

Abstract

Citizen science programs are increasingly popular with ecologists seeking to broaden their public outreach by involving people in scientific research. However, data validation among traditional citizen science programs has sometimes been difficult. Here, we describe Wildlife Tracker, a Facebook game we created which had players identify wildlife species captured by motion-detecting cameras, and discuss our data validation methods. We found that players accurately identified 88% of species in photographs and that the percentage agreement among players was the best predictor of accuracy.

Keywords: citizen science, data validation, Facebook, remote cameras

Introduction

Citizen science can be considered the progenitor of all scientific research since most historical discoveries were made by amateur scientists (Silvertown 2009). Whereas the citizen scientists of the past were limited to an elite group of mostly wealthy and male members with the means to pursue a scientific hobby, the opportunities for citizen scientists today are far more egalitarian and widespread (Couvet et al. 2008). Modern citizen science programs provide the dual benefit of increasing the scientific literacy of participants and amassing data on a vast spatiotemporal scale for scientists with limited funding. Organizations such as the Cornell Lab of Ornithology and the National Phenology Network have already trained thousands of volunteers across the United States to collect scientific data for their projects (Evans et al. 2005; Schwartz & Hanes 2010). People who participate in these citizen science programs volunteer many hours of their time to receive training, travel to field sites to collect data, and record and submit their data to scientists. This learning strategy is termed experiential education and is intended to help individuals learn through completing and participating in activities (Brossard et al. 2005). While this type of experiential learning has been well-received by scientists and the public alike, these opportunities are not available to everyone, as many individuals do not have the time or finances to participate citizen science outside their homes.

With the advent of social media and the growing reach of Internet resources, opportunities for citizen scientists continue to expand in the 21st century. More than 2 billion people are now connected to the Internet and over 5.3 billion people have access to a mobile network (International Telecommunication Union 2010). As this level of connectivity continues to rise, ecologists are beginning to recognize the extraordinary opportunities the Internet offers as a vehicle for engaging the general public in scientific endeavors (Pace et al. 2010). A first wave of scientific projects are now enlisting people around the world to help them sort through large amounts of data (e.g., photos of galaxies or wild animals from trail cameras) through programs such as Zooniverse and Serengeti Snapshot (Bowler 2013). By using the Internet to reach volunteers, scientists can now eliminate some hurdles associated with participating in traditional citizen science projects such as transportation to field site, accessing equipment (e.g., binoculars, GPS), and time commitments.

In this paper, we introduce Wildlife Tracker, an experiential online education game developed as part of our ongoing ecological study of pumas (*Puma concolor*) and other wildlife of the Santa Cruz Mountains in California. An advantage of operating a research study in a semi-urban area is our ability to reach and interact with a large number of local residents. As part of our community outreach plan for the Santa Cruz Puma Project, we implemented an environmental education strategy incorporating many Web 2.0 features (e.g., blogs, social media) in order to encourage sustained public interest and participation. We developed Wildlife Tracker to test the effectiveness of new media tools as vehicles for public involvement. Because our volunteers participated through a game, we term them “players”. Game players view photographs of wildlife captured from motion-detecting cameras and work with a partner to identify species for scientific research. As an Internet application, Wildlife

Tracker differs from traditional citizen science programs (e.g. Christmas Bird Count) because it allows volunteers to contribute to data collection on their own schedule and without previous training.

Wildlife Tracker is modeled after Games with a Purpose (GWAP), which are social media tools developed by Luis Von Ahn that incentivize users to generate useful data through playing online games (Von Ahn & Dabbish 2008). GWAPs have been very popular, attracting up to tens of thousands of unique players in a single month (von Ahn et al. 2006). As a GWAP, Wildlife Tracker provides the general public with opportunities to contribute to scientific research and a game-like experience in which to observe biodiversity. All data produced by players are then recorded and available for further verification by scientists.

With this proliferation of Web 2.0 technologies comes the need to understand and scrutinize their effectiveness in producing usable data. While social media allows more people to participate in science, the inherent openness of the technology presents new challenges as well. Many traditional citizen science programs have been criticized for lacking accountability and relatively few have directly compared data generated from non-scientists with those from professionals (Belt & Krausman 2010). Here, we evaluate the accuracy of data collected by a pilot test of Wildlife Tracker to test whether data generated by anonymous Internet volunteers can be reliably used by scientists. Since maintaining and initiating citizen science programs require a significant commitment by scientists, it is important to assess the value of the data generated as early as possible.

Methods

Wildlife Tracker Game Structure

To implement Wildlife Tracker, we developed an online game using modern web technologies through the Facebook API (Application Platform Interface). We selected Facebook because it is one of the largest social media networks in the world, with one billion users and growing. The interface of the game features photographs of wildlife captured by motion detecting cameras distributed across the Santa Cruz Mountains and tags that players can use to categorize animals (Fig. 1). A full list of potential species identification choices are listed in Table 1. We uploaded the game onto Facebook in June 2013 and the app is currently viewable through apps.facebook.com/wildlifetracker/. The app also includes a "Field Guide" that provides hints to players who are interested in improving their wildlife identification skills.

Wildlife Tracker is an output agreement game, in which a team of two randomly selected players are provided with the same input (photograph) and asked to submit an output (species categorization) that matches(Von Ahn & Dabbish 2008). Two-player teams work together to identify 10 photographs in 90 seconds. In order to encourage accuracy, players also receive bonus points for matching their selections. The main server uses node.js (v 0.10.26) and socket.io (v 0.9.6) to allow partners to work together, and the picture data is organized and stored using MongoDB (v 2.4) to allow for flexibility as the game continues to evolve. Each photograph can be tagged by multiple teams of players, and all species classifications by each player are recorded. To facilitate data validation, we extracted the identifications generated by players for each photograph into a database for analyses.

Validation

Wildlife photographs used for the game were viewed and classified to species by biologists associated with our project. Thus, we had a dataset generated by biologists that we could compare to one produced by game players. For each photograph, we recorded the accuracy of responses provided by volunteers by checking whether the species classification selected by the majority of players matched that of the biologists. We used a binary indicator (0 for not matching and 1 for matching) to signify the accuracy of the identification. Any time a photograph received 50% or fewer agreement by players, we automatically considered that a mismatch (0). We then tallied the total number of people who had tagged the photograph and the percentage agreement for the identification. For example, a dataset of (1, 6, 67) indicates that this photograph was identified correctly (1), tagged by 6 people, and 67% of the players agreed upon the majority answer.

We applied a multiple logistic regression (eq. 1) using a logit link to determine the probability that a photograph is labeled correctly given three predictor variables: number of individuals who have tagged it, the strength of the consensus, and an interaction term.

$$\ln\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_1 x_2 \qquad (1)$$

The above equation describes the log odds of obtaining the right answer given the intercept β_0, coefficients, β_1, β_2 and β_3, and the data, where x_1 represents the number of players who tagged the photo and x_2 the proportion of players who agreed upon the majority answer. All analyses were conducted in R (v.2.15.1: the R Development Core Team, 2010).

Results

We recorded 1996 guesses by 70 players for 433 photographs. Some players were undergraduates from the University of California Santa Cruz who were recruited to play the game, but a portion of players were anonymous Facebook volunteers. On average 4.6 players viewed each photograph and 88.9% of species in photographs were identified correctly. All species were categorized with higher than 85% accuracy except in cases when no animal was visible in the photograph or when biologists were also unable to identify the animal (e.g. “unknown”).

Results from the multiple logistic regression suggested that percentage agreement among players was the only significant predictor of whether a species was classified correctly ($\beta = 0.208, S.E. = 0.067, P < 0.002$). In contrast, having more players view the photograph did not significantly impact the prediction accuracy ($\beta = 0.95, S.E. = 1.01, P < 0.35$). There was high agreement among players for most species classifications, except for photographs categorized as “unknown” or “no animal” by biologists (Fig. 2). The lack of agreement for these photographs is likely due to the poor quality of the photographs and the inconsistent use of “unknown” versus “no animal” tags by players.

Discussion

Ecologists are increasingly turning to citizen scientists to help sort and analyze a growing body of data. Specifically, the advancement of digital camera-traps have now made it possible for research teams to collect hundreds of thousands of photographs of wildlife over a period of months to years. Sorting through this data can be very time consuming, and citizen scientists are potentially an important resource for data analysis. Equally as important, the nature of the data lends itself to validation, as identifications generated by citizen scientists are easily comparable to those made by biologists.

Most traditional (i.e., non web-based) citizen science research projects rely on trained volunteers to individually produce data from their observations (Belt & Krausman 2010). In some cases, it was possible to directly compare data collected by biologists to those collected by individual observers. However, these studies have had to deal with observation errors from volunteers and professionals alike. In contrast, we have very little uncertainty in our data because our biologists were able to correctly identify almost all visible animals in our photographs and determine which photographs were of too poor quality to categorize. Therefore, we were able to fully document the accuracy rate of Wildlife Tracker players.

Current computer programs are not advanced enough to automate wildlife identifications; instead, Internet volunteers can provide a potential labor resource for processing large numbers of wildlife photographs. Generally, we found that players were very good at identifying photographs to species or taxa (e.g., for birds) and their accuracy was strongly predicted by percentage agreement among all players who tagged a given photograph (Fig. 3). This suggests that citizen scientists can effectively generate data for wildlife monitoring programs employing motion-detecting cameras.

The accuracy of groups of untrained players of Wildlife Tracker rivaled that of biologists, demonstrating the enormous potential awaiting to be unlocked in the citizen science world. Most photographs that were not successfully identified by players were also not identified by trained biologists. Instead of sorting through every single photograph, biologists employing this method could instead focus on validating species classifications that did not exceed a predetermined threshold of majority support. For example, photographs with 80% classification agreement among players have an 85% chance of being identified correctly, whereas those with 70% agreement have only a 55% chance. In our study, 19% of photos fell below 80% agreement, suggesting that scientists would only need to validate 83 of 433 photos. Alternatively, biologists could simply remove those photographs from analyses since they represented a relatively small amount of useful data.

Most ecologists recognize that public communication should be an important aspect of their research, but few understand how to successfully frame and publicize their issues to the general public in a meaningful format (Lubchenco 1998; Nisbet 2009). As increasing numbers of people receive their news and information from the Internet (Purcell et al. 2011), the web may provide a platform on which scientists can communicate and share their findings with the public. An emerging outreach strategy is to generate interactive web content designed to both engage and educate the public by providing Internet users with the ability to participate in citizen science programs. Although Wildlife Tracker did not explicitly represent itself as a citizen science game, it did offer opportunities for players to learn more about wildlife and the research project that supplied all the photographs (the Santa Cruz Puma Project).

Wildlife Tracker capitalizes on people's natural interest in playing online games to generate useful data for researchers while exposing players to the biodiversity of the Santa Cruz Mountains. Incentives written into the game can potentially encourage players to learn more about wildlife identification in order to improve their scores. As online games, Wildlife Tracker and other similar applications remove many hurdles that traditionally prevented people from participating in fieldwork. Instead, these games allow unprecedented access to scientific data and information to a potential pool of billions of people through the Internet. In addition, by hosting these applications on social media sites such as Facebook, we can collect anonymous demographic information on users that can be further analyzed for educational purposes.

However, there are novel challenges associated with reaching citizen scientists through social media websites. Creating online apps or games is computationally difficult and requires collaborations with computer scientists or game designers. Finding individuals to participate or play online games is also difficult and requires a great deal of thought and effort. Wildlife Tracker was designed as a two-player game in order to incentivize accurate identification, but the two-player design of the game compounded the difficulties of soliciting players. Future games may benefit from allowing a one-player option and validating datasets generated from one and two-player games separately. Despite these difficulties, the enormous potential of the Internet as an environmental educational tool cannot and should not be ignored. Now that funding agencies such as the National Science Foundation require grant-holders to implement project-based outreach (Silvertown 2009), games such as Wildlife Tracker could prove a useful framework for ecologists to emulate as a tool for incorporating citizen scientists.

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Table 4.1. List of available tags in Wildlife Tracker and corresponding scientific names.

Tags	**Scientific Name**
Puma	*Puma concolor*
Bobcat	*Lynx rufus*
Coyote	*Canis latrans*
(Grey) Fox	*Urocyon cinereoargenteus*
Brush Rabbit	*Sylvilagus bachmani*
Black-tailed Deer	*Odocoileus hemionus columbianus*
Striped Skunk	*Mephitis mephitis*
Raccoon	*Procyon lotor*
(Virginia) Opossum	*Didelphis virginiana*
Cow	*Bos taurus*
Wild Pig	*Sus scrofa*
Domestic Dog	*Canis lupus*
Domestic Cat	*Felis catus*
Ground Squirrel	*Spermophilus beecheyi*
Tree Squirrel	*Sciurus griseus* or *Sciurus carolinensis*
Woodrat	*Neotoma fuscipes*
Mouse	NA – includes all small mice species
California Quail	*Callipepla californica*
Turkey	*Meleagris gallopavo*
Other Bird	NA
Skip	NA
Unknown	NA
No Animal	NA

Table 4.2. Summary of player identification accuracy by species.

Species in Photograph	**Percent identified Correctly**	**Number of photographs**
bobcat	90	88
coyote	100	6
deer	95	96
domestic cat	100	2
domestic dog	100	29
grey fox	87	15
no animal	32	19
opossum	100	2
other bird	88	82
puma	100	4
rabbit	86	7
raccoon	100	1
skunk	94	54
squirrel	91	23
unknown	40	5

02–14–2012 19:54:24

Image 1 of 10

Timer 61

Guesses Remaining 15

Current Streak 7

Our Score 15400

Figure 4.1. Screenshot of game displaying motion-detecting camera photograph and available species classification tags.

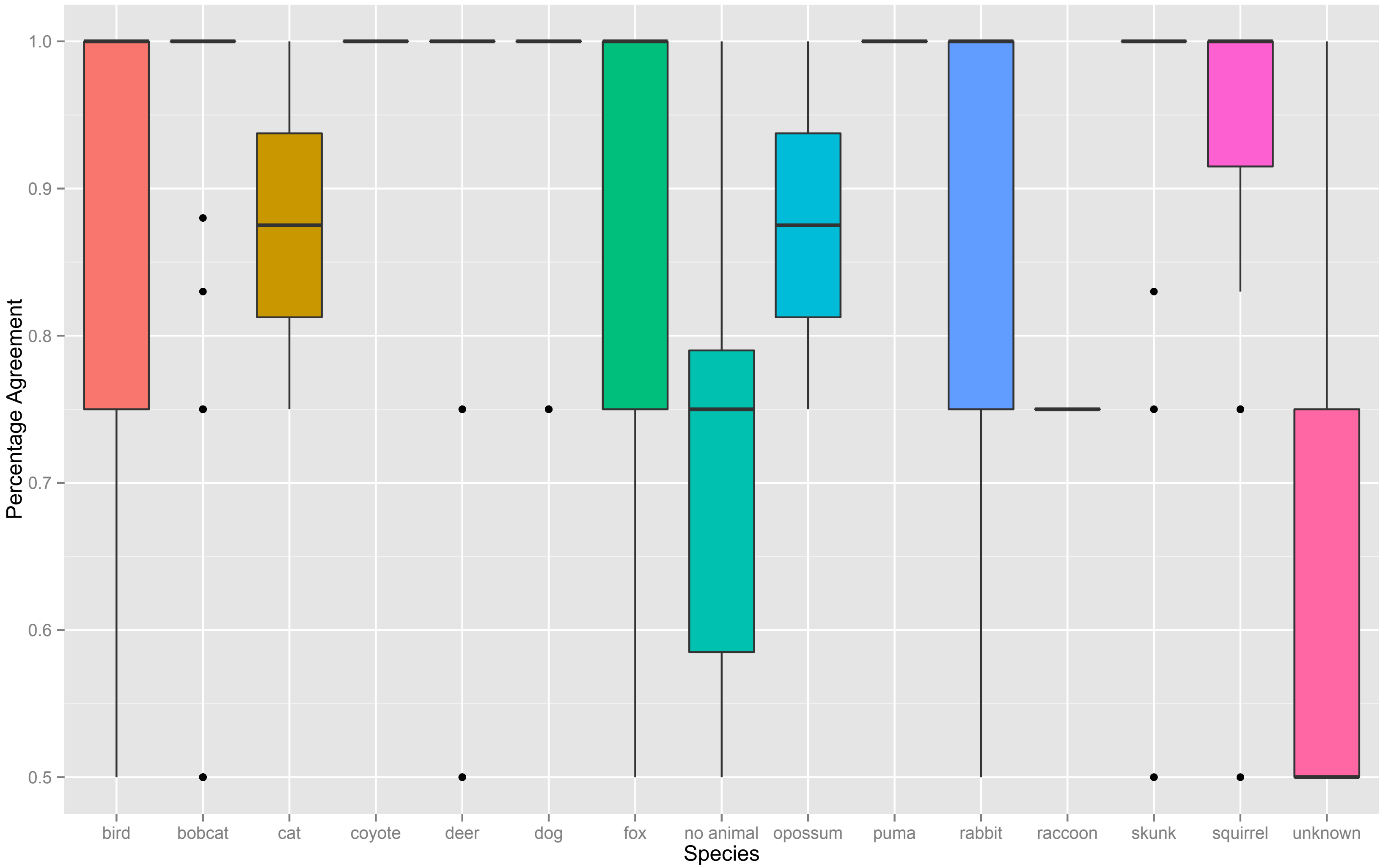

Figure 4.2. Boxplots showing percentage agreement reached among players by species

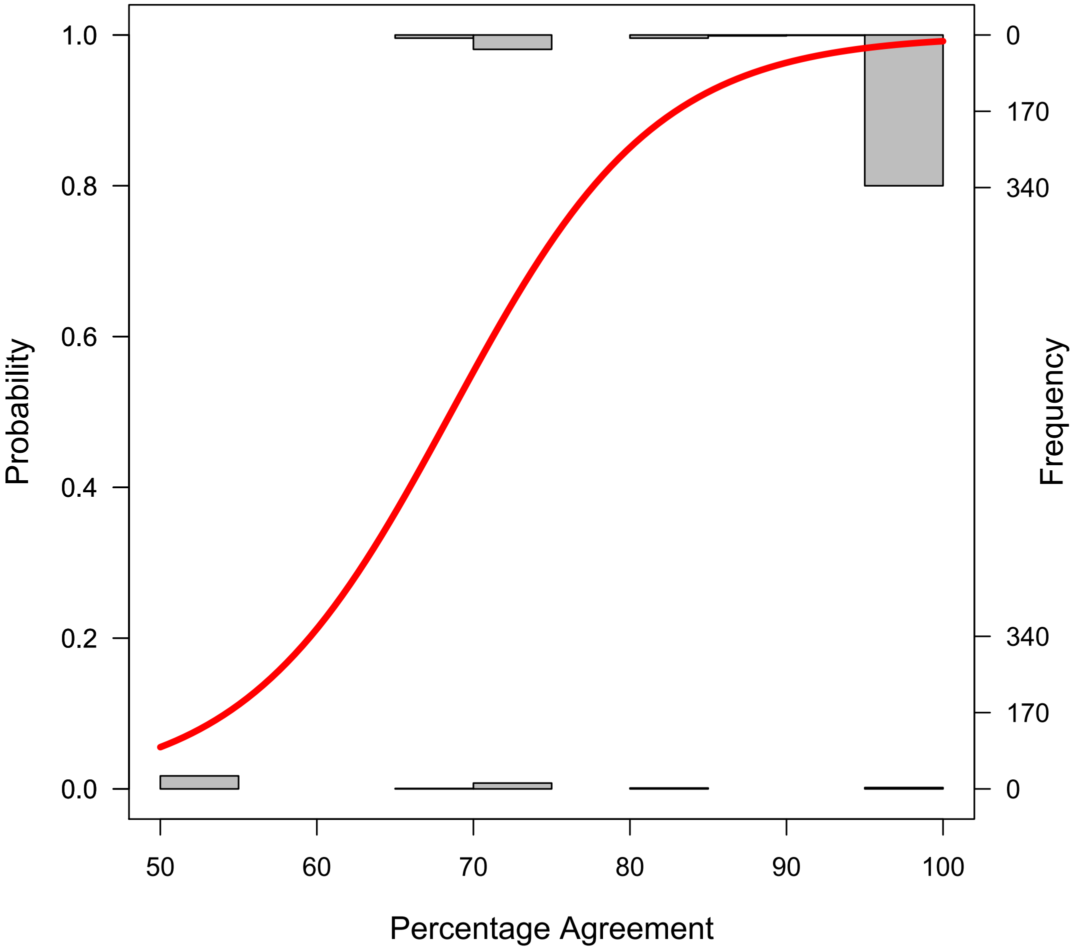

Figure 4.3. Fitted logistic regression curve showing the probability that a species is identified correctly as a function of the percentage agreement among players. The observed data is represented by histograms.

Appendices

Appendix 1. All single species occupancy models for pumas. Covariate abbreviations are D=Human development, F= Percentage forest cover, and H = Human activity.

Model	AIC	ΔAIC	AIC weight	Model Likelihood	Number of Parameters	Deviance
Ψ(D),p(D)	711.26	0	0.516	1	4	703.26
Ψ(D,F),p(D)	711.49	0.23	0.46	0.891	5	701.49
Ψ(D),p(.)	719.35	8.09	0.009	0.0175	3	713.35
Ψ(D,F),p(.)	719.53	8.27	0.0083	0.016	4	711.53
Ψ(.),p(D)	720.58	9.32	0.0049	0.0095	3	714.58
Ψ(F),p(D)	722.54	11.28	0.0018	0.0036	4	714.54
Ψ(.),p(.)	737	25.74	0	0	2	733
Ψ(F),p(.)	737.9	26.64	0	0	3	731.9

Appendix 2: Top-ranked species co-occurrence models. Covariate abbreviations are D=Human development, F= Percentage forest cover, and C=Coyote activity. If unique covariate parameters were estimated, they are designated numerically (e.g., D1 and D2).

Species B	Model	AIC	ΔAIC	AIC weight	Model Likelihood	Number of Parameters	Deviance
Grey Fox	ΨA(D),ΨBA,ΨBa,pA(D),pB,rB(D,C)	1982.98	0	0.51	1	10	1962.98
	ΨA(D),ΨB,pA(D),pB,rB(D,C)	1983.08	0.1	0.49	0.95	9	1965.08
Bobcat	ΨA(D),ΨB,pA(D),pB(C1,D),rB(C2,D)	3120.47	0	0.26	1	10	3100.47
	ΨA(D),ΨB,pA(D),pB(D),rB(C,D)	3121.07	0.6	0.20	0.74	9	3103.07
	ΨA(D),ΨB,pA(D),pB(C1),rB(C2,D)	3121.39	0.92	0.17	0.64	10	3101.39
	ΨA(D),ΨB,pA(D),pB(C1,D1),rB(C2, D2)	3121.53	1.06	0.16	0.58	11	3099.53
	ΨA(D),ΨB,pA(D),pB(D1),rB(,C,D2)	3121.94	1.47	0.13	0.48	10	3101.94
Domestic Cat	ΨA(D),ΨB(D),pA(D),pB(D),rB(C)	1761.43	0	0.38	1	10	1741.43
	ΨA(D),ΨB,pA(D),pB(D),rB(C)	1762.86	1.43	0.18	0.48	9	1744.86
	ΨA(D),ΨB,pA(D),pB(D),rB	1763.23	1.8	0.15	0.41	8	1747.23
Opossum	ΨA(D),ΨBA(C,F),ΨBa(C,F),pA(D), pB(C,D1),rB(C,D2)	1990.45	0	0.14	1	13	1964.45
	ΨA(D),ΨB(C,F),pA(D),pB(C,D1), rB(C,D2)	1990.69	0.24	0.13	0.89	12	1966.69
	ΨA(D),ΨBA(C),ΨBa(C),pA(D), pB(C,D1),rB(C,D2)	1991.06	0.61	0.10	0.74	12	1967.06
	ΨA(D),ΨB(C),pA(D),pB(C,D1),rB(C,D2)	1991.85	1.4	0.07	0.5	11	1969.85
	ΨA(D),ΨB(F),pA(D),pB(C,D1),rB(C,D2)	1991.97	1.52	0.07	0.47	11	1969.97
	ΨA(D),ΨB(),pA(D),pB(C,D1),rB(C,D2)	1992.4	1.95	0.05	0.38	10	1972.4

Raccoon	ΨA(D),ΨB,pA(D),pB(C,D),rB(D)	2157.62	0	0.45	1	9	2139.62
	ΨA(D),ΨB,pA(D),pB(C,D1),rB(D2)	2159.62	2	0.16	0.37	10	2139.62
Striped Skunk	ΨA(D),ΨB,pA(D),pB(D),rB(C,D)	3164.41	0	0.33	1	9	3145.08
	ΨA(D),ΨB,pA(D),pB(C,D),rB(C,D)	3165.46	1.05	0.20	0.59	9	3147.7
Coyote	ΨA(D),ΨB,pA(D),pB(D),rB(D)	2969.4	0	0.31	1	8	2953.37
	ΨA(D),ΨB,pA(D),pB,rB	2970.06	0.69	0.22	0.71	7	2956.06
	ΨA(D),ΨB,pA(D),pB,rB(D)	2970.12	0.75	0.21	0.69	8	2954.12
	ΨA(D),ΨB,pA(D),pB(D),rB	2971.12	1.75	0.13	0.42	8	2955.12
	ΨA(D),ΨB,pA(D),pB(D1),rB(D2)	2971.17	1.8	0.12	0.41	9	2953.17

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