Landscape and Urban Planning 192 (2019) 103648

Contents lists available at ScienceDirect

Landscape and Urban Planning

journal homepage: www.elsevier.com/locate/landurbplan

Research Paper

Effects of land-use change and prey abundance on the body condition of an obligate carnivore at the wildland-urban interface

Courtney A.C. Coon[a,*], Bradley C. Nichols[a], Zara McDonald[a], David C. Stoner[a,b]

[a] Felidae Conservation Fund, 110 Tiburon Blvd. Ste. 3, Mill Valley, CA 94941, United States
[b] Utah State University, Department of Wildland Resources, 5230 Old Main Hill, Logan, UT 84322-5230, United States

ARTICLE INFO

Keywords:
Animal health
Body condition
Camera trap
Land-use change
Puma concolor
Urban carnivore

ABSTRACT

Land-use change represents a primary driver of carnivore population declines, yet some large carnivore species have acclimated and persist within anthropogenically altered landscapes. Previous attention has been focused on the genetic and behavioral implications of land-use changes, but few studies have investigated how human development impacts animal physiology and health. Here we examined how body condition scores of a widely distributed North American carnivore, the puma (*Puma concolor*), are affected by anthropogenic habitat modification. For this study we collected 252 puma camera trap events across a land-use gradient in the San Francisco Bay Area. We found that pumas in this region generally had body condition scores within a healthy range. However, pumas in areas with marginal development (e.g., parks, golf courses, low-density residences) had significantly higher body condition scores than conspecifics in areas defined as highly developed (urban) or undeveloped (wilderness). Notably, detections of black-tailed deer (*Odocoileus hemionus columbianus*) showed the same patterns. Additionally, puma body condition was significantly and positively correlated with detection frequency of small prey like raccoons and squirrels. Taken together, our findings show that pumas are present in developed environments, and suggest that puma body condition may reflect relative prey abundance across land-use types. We suggest that in mixed-use landscapes where public tolerance of large carnivores is sufficient, management efforts should integrate non-wilderness lands into conservation plans for pumas. However, in areas defined by low tolerance or high conflict potential, management should focus on public education and control of food resources that attract pumas to those areas.

1. Introduction

Anthropogenic activity has led to extensive loss, degradation and fragmentation of wildlife habitats worldwide (Fahrig, 1997; Williams et al., 2016), significantly altering ecological processes for remaining wildlife (Chace & Walsh, 2006; Lewis et al., 2015; McKinney, 2008; Shochat, Warren, Faeth, McIntyre, & Hope, 2006). As such, the question of how land-use change affects the movement (Ditchkoff, Saalfeld, & Gibson, 2006), survival (Sala et al., 2000) and health (Acevedo-Whitehouse & Duffus, 2009) of wildlife species is a major focus of applied ecological research (Magle, Hunt, Vernon, & Crooks, 2012). Many of the impacts of land-use change have been borne by species with narrow habitat ranges or highly specialized niche requirements (Aizen, Sabatino, & Tylianakis, 2012; Munday, 2004). However, land-use change has also had significant negative influences on habitat generalists like some large mammalian predators (Fahrig, 2003) because these animals are constrained to live at low densities by their high trophic status (Duncan, Nilsen, Linnell, & Pettorelli, 2015; Hatton et al., 2015; Stoner et al., 2018). The high energetic demands of large carnivores necessitates extensive daily and seasonal movements to assimilate sufficient food resources (Gittleman & Harvey, 1982). This characteristic requires large home ranges which can be difficult to realize in fragmented landscapes where high edge-area ratios makes them vulnerable to increased contact with humans (Woodroffe & Ginsberg, 1998).

An oft overlooked aspect of land-use change, is that developed landscapes may provide reliable and diverse food resources for predators (Ditchkoff et al., 2006), such as garbage, roadkill, livestock and pets (Baruch-Mordo et al., 2014) as well as urban-tolerant prey species like rodents, rabbits and squirrels which may occur at higher densities than in adjacent wildland habitats (Crooks & Soulé, 1999; Prange & Gehrt, 2004). For some species, these benefits lead to lower mortality and higher population densities near urban areas as compared to wildlands (Bateman & Fleming, 2012; Boutin, 1990; Oro, Genovart,

---

[*] Corresponding author.
E-mail address: courtneycoon@felidaefund.org (C.A.C. Coon).

https://doi.org/10.1016/j.landurbplan.2019.103648
Received 3 January 2018; Received in revised form 12 June 2019; Accepted 27 August 2019

Tavecchia, Fowler, & Martínez-Abraín, 2013; Riley & Manski, 1998). On the other hand, anthropogenic food subsidies can have negative impacts on wildlife health by increasing exposure to toxins, pathogens or high risk habitats, i.e., areas where vehicle strikes or poisoning are more likely (Bateman & Fleming, 2012; Becker, Streicker, & Altizer, 2015; Cook & Blumstein, 2013; Iriarte, Franklin, Johnson, & Redford, 1990; Oro et al., 2013; Treves & Karanth, 2003).

Wildlife habitat is becoming increasingly disturbed, to such an extent that if predators are able to persist in human-modified landscapes then their exploitation of food resources in urban or suburban areas will likewise continue to escalate (Beckmann & Berger, 2003; Valeix, Hemson, Loveridge, Mills, & Macdonald, 2012; Woodroffe & Ginsberg, 1998). For these reasons, and because predators play important roles in ecosystems, it is critical to understand if and how they can persist within human-modified landscapes. Here we investigated the effects of land-use and prey abundance on fat deposition in a large, obligate carnivore – the puma (*Puma concolor*).

Although pumas are habitat generalists with broad dietary niches (Iriarte et al., 1990), during the past 300 years they have undergone severe range contractions stemming from habitat loss, prey depletion and overexploitation (Chapman & Feldhamer, 1982; Šálek, Drahníková, & Tkadlec, 2015; Wolf & Ripple, 2017). Thus, although pumas use wildland habitats adjacent to major metropolitan and recreational areas (Beier, Riley, & Sauvajot, 2010; Sweanor, Logan, & Bauer, 2008), they tend to exhibit a general avoidance of direct contact with humans by altering activity times (Crooks, 2002; Kertson, Spencer, & Grue, 2011; Ordenana et al., 2010; Wang, Allen, & Wilmers, 2015). Puma diets can also be affected by land-use such that individuals near urban habitats eat more urban-tolerant wildlife species (Kertson et al., 2011; Moss, Alldredge, & Pauli, 2016) and exhibit higher kill rates, likely due to disturbance at cache sites (Smith et al., 2015). Indeed, one California study suggests that pumas may perceive humans as a threat, given the frequency and speed with which they flee feeding sites in response to recorded human speech (Smith et al., 2017). Nevertheless, the species appears capable of persisting in anthropogenically altered environments, perhaps due to the consistent abundance of prey in human-disturbed habitats (Conover, 1995; Kertson et al., 2011).

To evaluate one aspect of the question on how puma health varies with respect to anthropogenic environments, we quantified puma body condition scores across a land-use gradient spanning urban areas to wilderness in the San Francisco Bay Area (California, USA). Body condition scores are a categorical measure of fat deposition (Morfeld, Meehan, Hogan, & Brown, 2016). In other species, body condition scores have been correlated with physiological metrics of animal health and condition. For example, fertility and offspring success correlates with body condition in female red deer (*Cervus elaphus*; Audigé, Wilson, & Morris, 1998). Compared to other species, felids are relatively resilient to inter-annual variation in weight (Yom-Tov, Kjellander, Yom-Tov, Mortensen, & Andrén, 2010). Instead, between-individual variation in body condition is largely due to differences in resource availability during the growing period (birth to 2 years) for most wild felids. In support, a study following puma populations after a decline in the abundance of their primary prey (mule deer, *Odocoileus hemionus*) found that pumas were in poorer physical condition, had lower adult survival rates, and showed declines in kitten survival to independence, but only after a 4 year lag (Laundré, Hernández, & Clark, 2007). Hence, body condition scores are likely repeatable within individual adult pumas, and variation in this metric can be considered an index of long-term food availability and nutrient assimilation.

In this study we compare the impact of habitat and prey on puma health by examining the relationships between body condition scores and prey detection, anthropogenic infrastructure and human activity. We formulated and tested two competing hypotheses: (H_1) that puma body condition scores would be positively associated with prey detection, which may be higher in human-altered habitats and (H_2) that puma body condition would be negatively impacted by human disturbance (Woodroffe, 2000) leading to lower body condition scores in areas with more human infrastructure and activity.

2. Methods

2.1. Study sites

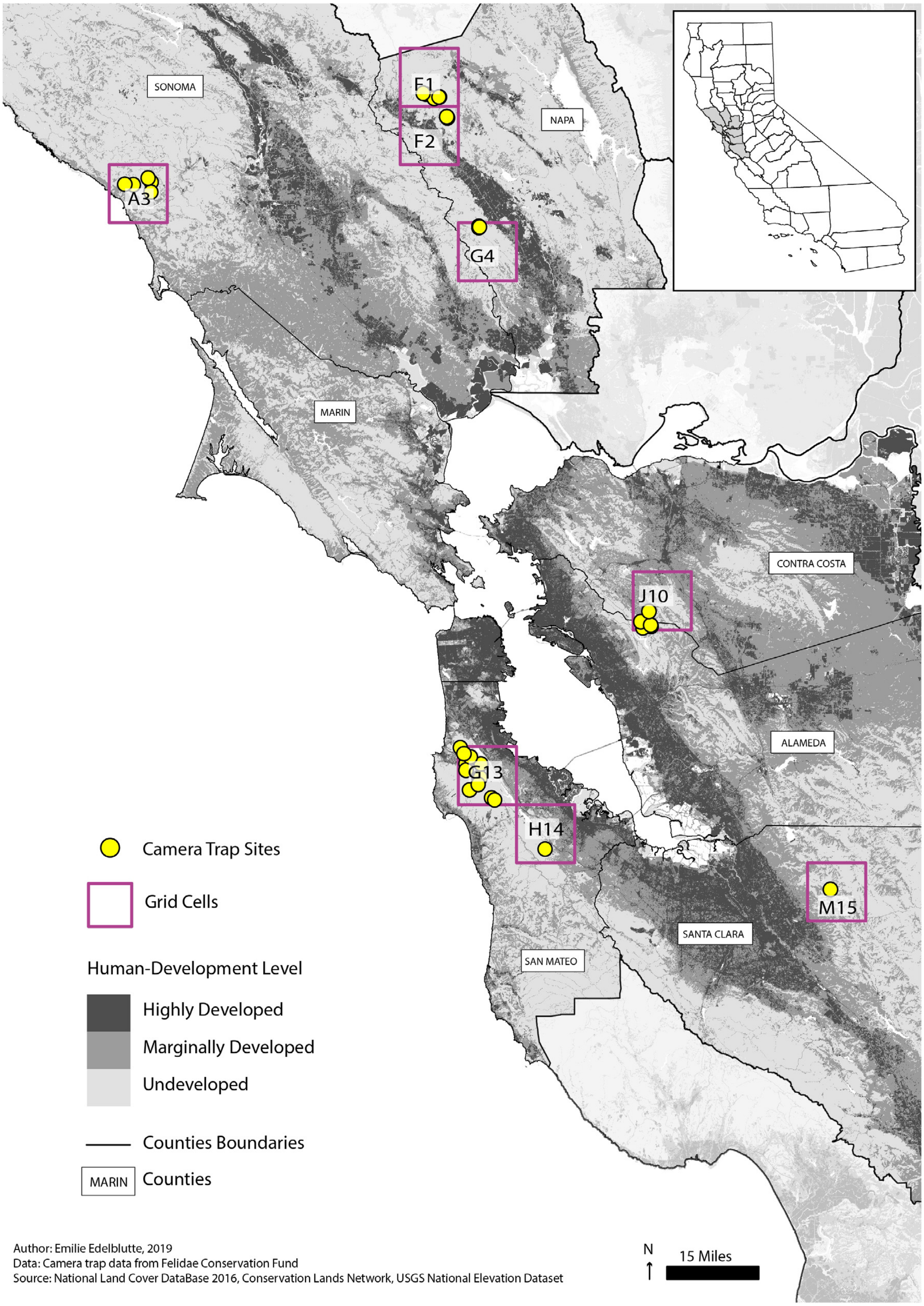
The greater San Francisco Bay Area in California, USA is one of the most fragmented and anthropogenically influenced landscapes still occupied by pumas in North America. Within the Bay Area, pumas are typically associated with relict native habitat patches within a matrix of suburban or agricultural lands (Beier et al., 2010). Our study area included land in 5 counties: Napa, Sonoma, San Mateo, Contra Costa and Santa Clara. Climate in the area is strongly seasonal with rain falling primarily between October and May and peaking in January or February. This is followed by seasonal drought which begins in April or May and lasts through October or November. Precipitation is variable in space, with coastal environments and higher elevations receiving more moisture than lowland and inland sites (range: ~1000 mm in Napa; ~1200 mm in Sonoma; ~600 mm in San Mateo; ~600 mm in Contra Costa; and ~500 mm in Santa Clara County; https://www.usclimatedata.com/, 2017). Average temperatures in the region range from 2 °C to 18 °C in the winter and from 10 °C to 33 °C in the summer (https://www.usclimatedata.com/, 2017). Temperatures on the coast are less variable (between 14 and 22 °C year-round) than those inland. Frosts are infrequent but increase with elevation and distance from the coast. Climate is correlated with plant communities and productivity, which likewise may affect the movement, health or density of both predator and prey species. Major plant communities in the region include oak woodlands, grasslands, chapparal scrub as well as redwood forests in the coastal fog zone.

2.2. Species monitoring

For this study, we stationed motion-triggered, wildlife camera traps throughout the study area between March 2012 and January 2017 (Fig. 1). Cameras were placed in Sonoma County (North Bay) from 2016 through 2017; in Napa County (North Bay) from 2012 through 2017; in Contra Costa County (East Bay) between 2013 and 2015; in Santa Clara County (South Bay) between 2014 and 2015; and in San Mateo County (SF Peninsula) from 2012 through 2017. A total of 90 camera sites collected images of pumas or deer and were included in this study. Camera placements lasted 303 days on average (range: 28–1469 days). Because cameras were unevenly distributed over space and time, we pooled and averaged data from cameras into 10x10km^2 grid cells by month (see 'Data Summarization and Statistical Analyses' section below). The numbers of active cameras during each month of the study are listed in Supplementary Table 1.

Cameras were placed on trails in National, State, County, Regional and City parks, water districts, and on private properties within or near wildlands or open spaces. Sites varied in human-use and species diversity. Camera locations were chosen generally based on property access, and then more specifically based on the presence of suitable wildlife habitat: areas with suitable cover and identifiable prey or carnivore sign (scat, tracks, biologist sighting). We used Bushnell Trophy or Natureview cameras (95%), and a few Reconyx Hyperfire and Moultrie M-class brand cameras. Motion detection sensors were set to auto or low sensitivity depending on surroundings (e.g., areas with lots of grass had cameras set to lower sensitivity to minimize misfires).

Cameras were attached to trees or posts 90–120 cm from the ground, and angled down a trail to photograph or video medium to large quadrupeds. Upon set-up, GPS coordinates were recorded, and each camera was set to film 10–20 s videos at 720 p resolution, or take a burst of 3 photos (hereafter "picture set") at 8 + megapixels. Trigger speeds and delays between bursts were less than 1 s. Latency between motion sensor re-triggers ranged from 15–30 s but all pumas captured



Author: Emilie Edelblutte, 2019
Data: Camera trap data from Felidae Conservation Fund
Source: National Land Cover DataBase 2016, Conservation Lands Network, USGS National Elevation Dataset

Fig. 1. Study area map. Wildlife camera traps were placed throughout the greater San Francisco Bay area between 2012 and 2017. Dots indicate cameras that were arranged into grid cells. Grid cells were grouped by region for analyses. Disturbance levels of the habitats are also shown.

in a 1 hr period were considered a single event to reduce potential for double-counts unless photos or videos contained two adult cats simultaneously (Reilly, Tobler, Sonderegger, & Beier, 2017).

Photo sets and videos were initially categorized for species identification using Camerabase software (The Botanical Research Institute of Texas; http://www.atrium-biodiversity.org/tools/camerabase/). By using picture sets or videos we were able to get several angles of every individual scored in the study which allowed for sufficient visualization of soft tissue deposits (Fernando, Janaka, Ekanayaka, Nishantha, & Pastorini, 2009; Prosser et al., 2016). Photos and videos that were blurry, or those in which animals were > 5 m from the camera were discarded.

2.3. Body condition scoring

We used a body condition scoring system as an index of fat deposition. Evidence suggests that scores of fat deposition are correlated with metrics of health in both domestic animals and wildlife (Audigé et al., 1998; Ezenwa et al., 2009; Soares & Dryden, 2011). Many fat scoring systems use palpation, but this is not often feasible. Hence, visual scoring of body condition (Ferguson, Azzaro, & Licitra, 2006; Negretti, Bianconi, Bartocci, Terramoccia, & Verna, 2008) is increasingly being used with wildlife (Bastin, Loker, Gengler, Sewalem, & Miglior, 2010; Fernando et al., 2009; Marshal, Krausman, & Bleich, 2008; Prosser et al., 2016; Ramesh, Kalle, Sankar, & Qureshi, 2011) and for domestic animals when palpation is not physically or numerically practical (Azzaro et al., 2010). A number of these body condition scoring systems have demonstrated utility in predicting animal health in a wide range of species (Altmann, Schoeller, Altmann, Muruthi, & Sapolsky, 1993; Kitaysky, Wingfield, & Piatt, 1999; Millette, Sauther, & Cuozzo, 2015; Pulliainen, Lindgren, & Tunkkari, 1995; Wijeyamohan, Treiber, Schmitt, & Santiapillai, 2015). For example, visual scores of body condition predict triglyceride levels in Asian elephants (*Elephas maximus*; Morfeld, Lehnhardt, Alligood, Bolling, & Brown, 2014; Morfeld et al., 2016; Wijeyamohan et al., 2015) and resource availability and reproductive status in wild lemurs (Millette et al., 2015).

Our categorical system estimates fat deposition in the neck, between the shoulders, above the hind legs, at the base of the tail, or around the midsection, depending on the angle and movement of the animal in front of the camera. Although sex could potentially affect fat deposition location, it is not possible to consistently distinguish between sexes in camera trap photographs/videos (Pulliainen et al., 1995). We circumvented this problem by considering three regions on the body of each animal when giving body condition scores, including at least one non-abdominal region which is where sex-specific body fat deposition is most likely to occur. Likewise, age may also affect deposition so only adult animals (> 1 yr) were scored. All videos and picture sets were evaluated by two researchers (CACC and BCN) on a 1–9 scale (Fig. 2) based on the visual scoring system developed for African lions by the Association of Zoos and Aquariums (AZA, 2012). The correlation of consistency between the two observers (i.e., inter-rater reliability) was above 0.7 using both a Pearson's correlation (0.726) and a Spearman's Rank correlation (0.712) and therefore deemed acceptable (Stemler, 2004). The six scores (2 researchers scoring 3 body regions) were averaged to create a single body condition score per puma observation.

We assume that scores between 3 and 7 indicate varying degrees of good health in wild pumas, with higher scores in that range (i.e., 5, 6 or 7) indicating higher quality or quantity of food availability during the growth periods and over the long-term period of adulthood (Yom-Tov et al., 2010). We likewise assume animals with scores < 3 to be underweight and those above 7 to be obese.

2.4. Predictor variables

In order to test the importance of prey availability on puma body condition, we used a list of focal prey species based on a puma dietary study conducted nearby in an ecologically similar site in northern California (Allen, Elbroch, Casady, & Wittmer, 2015). Focal prey species included: mule deer (aka black-tailed deer; *O. h. columbianus*), squirrels (family *Sciuromorpha*), rabbits (family *Leporidae*), raccoons (*Procyon lotor*) and foxes (*Urocyon cinereoargenteus*). Relative detection for each species was calculated by summing the number of camera capture events of each species in a 10x10km^2 grid cell each month, and then dividing by the number of cameras operating in that grid cell during the month (Jenks et al., 2011). We also developed this metric for humans as a measure of human activity to complement our other measures of anthropogenic disturbance, described below. Our cameras were placed on trails rather than randomly within our study system; therefore, our relative detection metric is not a measure of absolute abundance since many wildlife species are known to travel throughout their habitat matrix rather than specifically on trails, and species may vary in their willingness to use trails based on a number of environmental factors (Lenth, Knight, & Brennan, 2008; Wearn, Rowcliffe, Carbone, Bernard, & Ewers, 2013). However, pumas preferentially use trails within their habitats (Gloyne & Clevenger, 2001; Harmsen, Foster, Silver, Ostro, & Doncaster, 2010; Sweanor et al., 2008), which makes our metric similar to a relative prey encounter rate for pumas.

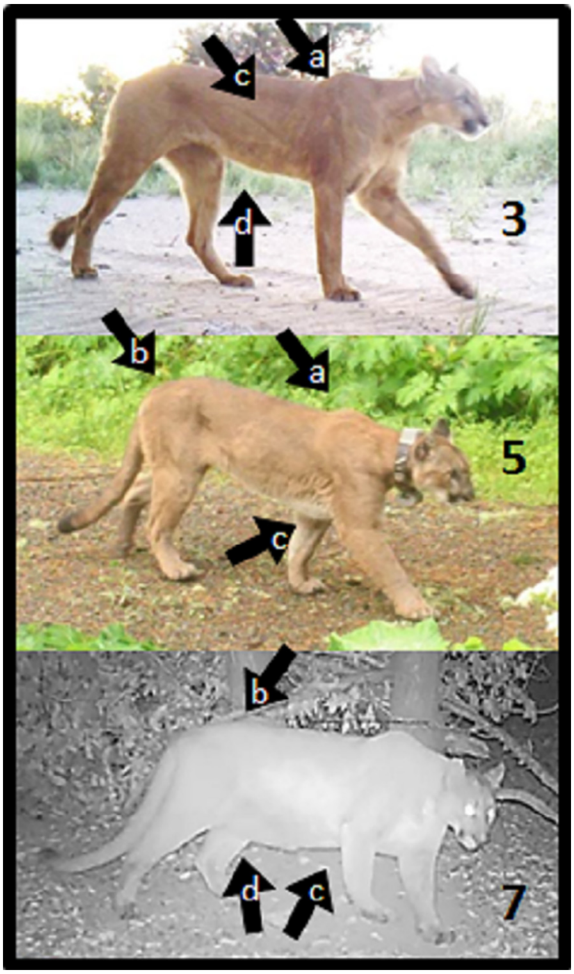


Fig. 2. Body condition scoring guide. We modified a 1–9 visual body condition scoring system developed for African lions for use in pumas. Scores were based on fat deposition (a) between the shoulders; (b) above and on the hind legs; (c) chest; and (d) midsection. At least two body regions were used to determine a score. The top animal was given a score of 3 (below average) because of the tightness of its midsection, visible ribcage, protruding shoulder blades and thinness of the hind legs. The middle animal was given a score of 5 (average) because of the smooth shoulders and rump, and loose skin on the hind legs and chest. The bottom animal was given a score of 7 (above average) because of the depth of the midsection and chest, the roundness of the rump, and loose skin on the hind legs.

In addition to our metric of human trail use, we created three categories of disturbance based on land cover attributes in the National Land Cover Database (Homer et al., 2015) in order to evaluate the relationship between puma body condition and anthropogenic land-uses. Our "undeveloped" land-use category included forests and chaparral; our "marginally disturbed" category included pastures, low intensity development (impervious surfaces account for 20–49% of total cover) and open space such as parks, cemeteries, golf courses, etc.; and our “highly developed” category included medium and high intensity development (50–79 and 80–100% of total cover, respectively), and intensive agriculture. The percent of cover for each category in every grid cell was used in the analyses. In addition, the sum total kilometers of roads for each grid cell was used as an additional metric of anthropogenic disturbance.

2.5. Data summarization and statistical analyses

Though some photographed animals were individually recognizable , animals were not marked by our research group and consequently could not be identified to individual. To minimize the potential for pseudo-replication that comes from scoring the same individual several times on one or multiple nearby cameras, we divided the greater study region into $10 \times 10\,\text{km}^2$ grid cells (Fig. 1). We then averaged body condition scores to one significant digit from all photos collected each month within the grid cell. This method is perhaps overly-conservative as it reduces total variability. However, it was a simple solution for removing potential bias. Additionally, it helped to control for spatial and temporal variation in camera placement.

The grid cell size was chosen because it is a conservative estimate of puma home range size ($\sim 100\,\text{km}^2$) for our urban edge population. Other studies of pumas in the western USA have found home ranges to be between $16\,\text{km}^2$ and $608\,\text{km}^2$ with urban and suburban individuals tending to have ranges on the small end of that spectrum (Dickson & Beier, 2002; Grigione et al., 2002; Laundré & Loxterman, 2007; Smith et al., 2015).

We tested two competing hypotheses in addition to a null hypothesis. H_1 predicted that prey resources would be more important predictors of puma body condition scores, such that prey would be most strongly and positively correlated with body condition. Models testing H_1 used standardized, relative camera encounter rate of focal prey species. H_2 predicted that variables describing human disturbance would be the most important factor explaining puma body condition scores, with pumas closer to anthropogenic disturbance in worse condition. Variables used for testing H_2 included one of three land cover variables (percent of undisturbed, marginally disturbed, and highly disturbed adjacent lands), relative camera encounter rate of humans, or the standardized summed length of roads. The null hypothesis, H_0, tested the importance of potentially confounding variables such as the number of photos or videos, specifically the number of videos, photo sets and total puma detection events used to determine body condition.

To test these hypotheses, we first z-score standardized all variables (subtracting the mean and dividing by the standard deviation) so that we could compare variable estimates between models. We used individual general linear models (GLMs) where each GLM used body condition scores averaged per grid cell and month as the dependent variable; and one of the variables described above. By using standardized variables and separate GLMs, we were able to compare and rank the importance of variables via their model estimates, despite the fact that some predictors were correlated (Dormann et al., 2013) (Supplementary Table 2). All statistics were performed in R version 3.4.3 (R Core Team, 2013) with P-values < 0.05 considered significant.

3. Results

For this study we collected puma body condition scores from 252 camera events (85 videos and 167 still photo sets) from 8 grid cells. After averaging by month there was a total of 88 grid cell – months used in analyses. Overall mean puma body condition score was 4.8 (range: 3–7; SD: 0.8) with the average grid cell – month mean being 4.9 (range: 4–7; SD: 0.7).

With respect to our hypotheses, relative prey detection rate (H_1) was more strongly correlated with puma body condition scores (BCS) than human disturbance (H_2) or any potentially confounding variables (H_0), given that 3 of the 4 strongest models, based on values of the standardized estimates, had prey as the predictor: raccoons, squirrels and rabbits, in that order ($\text{estimate}_{\text{raccoon-BCS}} = 3.582$, $\text{estimate}_{\text{squirrel-BCS}} = 0.983$ and $\text{estimate}_{\text{rabbit-BCS}} = 0.465$; $\text{P-value}_{\text{raccoon-BCS}} < 0.001$, $\text{P-value}_{\text{squirrel-BCS}} < 0.001$ and $\text{P-value}_{\text{rabbit-BCS}} = 0.821$; Table 1). Prey was always positively correlated with puma body condition scores. High anthropogenic disturbance was also important based on values of the standardized estimate but unlike prey, it was negatively correlated with puma body condition score ($\text{estimate}_{\text{high-BCS}} = -1.237$, $\text{P-value}_{\text{high-BCS}} < 0.001$; Table 1). Interestingly, undisturbed habitats were also negatively correlated with puma body condition ($\text{estimate}_{\text{undist-BCS}} = -0.423$, $\text{P-value}_{\text{undist-BCS}} < 0.001$), whereas marginal human disturbance was positively correlated with puma body condition ($\text{estimate}_{\text{marg-BCS}} = 0.418$, $\text{P-value}_{\text{undist-BCS}} < 0.001$; Table 1).

Table 1

Ranked predictors of puma body condition. We used separate GLMs on standardized variables to compare the importance of anthropogenic disturbance, relative detection rates of prey, or potential confounding factors on average puma body condition scores. Results suggest that relative detection of small mammal prey is the most important predictor of puma body condition score in the San Francisco Bay Area.

Ranked predictors of puma body condition score	Estimate	Standard error	t-value	P-value
Raccoons detected	3.582	0.461	7.774	< 0.001***
High anthropogenic disturbance	−1.237	0.227	−5.441	< 0.001***
Squirrel detected	0.983	0.255	3.851	< 0.001***
Rabbit detected	0.465	2.046	0.227	0.821
Undisturbed	−0.423	0.111	−3.806	< 0.001***
Marginal anthropogenic disturbance	0.418	0.065	6.444	< 0.001***
Deer detected	0.332	0.066	4.993	< 0.001***
Foxes detected	0.170	0.100	1.691	0.094•
Kilometers of roads	0.097	0.140	0.692	0.491
Number of active cameras	0.077	0.052	1.475	0.144
Number of puma videos	−0.055	0.051	−1.083	0.282
Number of puma videos + stills	−0.034	0.025	−1.350	0.181
Number of puma stills	−0.034	0.032	−1.041	0.301
Humans detected	−0.006	0.030	−0.208	0.835

Significance is indicated as: < 0.001***, < 0.1•.

Follow-up GLMs indicated that the percentage of marginal disturbance within a grid cell was positively correlated with relative raccoon, squirrel, rabbit and deer detection rates ($\text{estimate}_{\text{marg-raccoon}} = 0.102$, $\text{P-value}_{\text{marg-raccoon}} < 0.001$; $\text{estimate}_{\text{marg-squirrel}} = 0.106$, $\text{P-value}_{\text{marg-squirrel}} < 0.001$; $\text{estimate}_{\text{marg-rabbit}} = 0.005$, $\text{P-value}_{\text{marg-rabbit}} = 0.204$; Fig. 2 and Supplementary Table 3). In contrast, both the percentages of undisturbed and high anthropogenic disturbance were negatively associated with the detection of those same species (except that rabbits were positively, but not significantly, correlated with high disturbance; $\text{estimate}_{\text{undist-raccoon}} = -0.132$, $\text{P-value}_{\text{undist-raccoon}} < 0.001$; $\text{estimate}_{\text{high-raccoon}} = -0.132$, $\text{P-value}_{\text{high-raccoon}} = 0.004$; $\text{estimate}_{\text{undist-squirrel}} = -0.089$, $\text{P-value}_{\text{undist-squirrel}} = 0.055$; $\text{estimate}_{\text{high-squirrel}} = -0.362$, $\text{P-value}_{\text{high-squirrel}} < 0.001$; $\text{estimate}_{\text{undist-rabbit}} = -0.010$, $\text{P-value}_{\text{undist-rabbit}} = 0.121$; $\text{estimate}_{\text{high-rabbit}} = 0.002$, $\text{P-value}_{\text{high-rabbit}} = 0.904$; Fig. 2 and Supplementary Table 3). Foxes were positively correlated with the percentage of undisturbed habitat ($\text{estimate}_{\text{undist-fox}} = 0.224$, $\text{P-value}_{\text{undist-fox}} = 0.076$) and negatively correlated with percentages of the two disturbed habitat types ($\text{estimate}_{\text{marg-fox}} = -0.067$, $\text{P-value}_{\text{marg-fox}} = 0.424$; $\text{estimate}_{\text{high-fox}} = -0.352$, $\text{P-value}_{\text{high-fox}} = 0.205$), though none of the test statistics were significant. This is compared to human detections, which were negatively correlated with the percentage of undisturbed habitat ($\text{estimate}_{\text{undist-human}} = -1.110$; $\text{P-value}_{\text{undist-human}} = 0.010$) and positively correlated with the percentages of two disturbed habitat types

($\text{estimate}_{\text{marg-human}} = 0.360$, $\text{P-value}_{\text{marg-human}} = 0.208$; $\text{estimate}_{\text{high-human}} = 1.605$, $\text{P-value}_{\text{high-human}} = 0.091$), as expected. Together, these data indicate a decreasing fox detection rate but an increasing human detection rate on trails in more disturbed habitats.

4. Discussion

Our results indicate that puma body condition scores are most strongly and positively predicted by encounter rate with prey (H_1), especially small mammals, in the San Francisco Bay Area. Although three environmental disturbance variables also had strong and significant model estimates (H_2), specifically the percentages of each land-use category, other metrics of anthropogenic disturbance – detection of humans on camera and density of roads – were unimportant. This is likely explained by the fact that the land-use metrics we used include more information about habitat than just human disturbance. We suggest that the importance of the land-use variables in our analyses is because these areas accommodate differing amounts of potential prey. Indeed, we found that the amount of marginal anthropogenic disturbance (i.e., areas containing golf courses, cemeteries, urban parks and low-density housing) was positively correlated with both puma body condition scores and detection of the four most important prey species (raccoons, squirrels, rabbits and mule deer; Fig. 3). Conversely, the amount of undisturbed (wilderness) and highly disturbed (urban) areas were negatively correlated with puma body condition scores and detection rates of the same four prey species.

Previous research on puma demography and habitat-use in human modified habitats is mixed. Some researchers have proposed that coexistence of pumas and humans in these environments may be possible when adequate food resources exist or when management policy is favorable (Linnell, Swenson, & Anderson, 2001), while others suggested that pumas are strongly and negatively impacted by humans in these same environments (Beier et al., 2010; Burdett et al., 2010; Kertson, Spencer, & Grue, 2013; Knopff, Knopff, Boyce, & St. Clair, 2014; Moss et al., 2016; Sweanor et al., 2008; Wilmers et al., 2013). In one study, Woodroffe (2000) found that very low human densities (< 15 people/km^2) were associated with extirpation of pumas and other large carnivores. In another, Ripple and Beschta (2006) argued that pumas had abandoned otherwise suitable habitat in Zion National Park in Utah, USA due to the influx of tourism and associated human activity. Our results, however, lend greater support to the former hypothesis: habitats with abundant prey resources have pumas, regardless of human activity. Furthermore, pumas with access to these habitats appear to be in better physical condition than their counterparts near highly developed or undisturbed areas. Whether this translates to higher fertility or offspring survival is unknown, but critical for determining the overall impact of land-use change on puma demography.

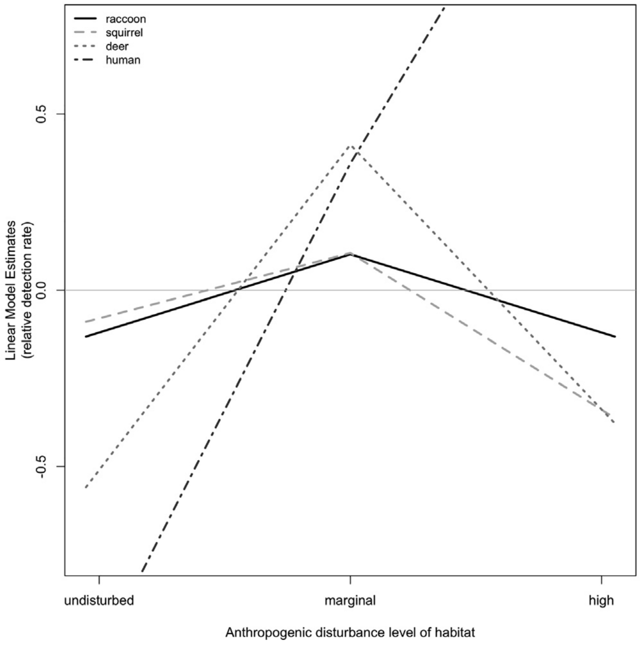


Fig. 3. Human and prey detection rates by habitat type. Habitats in our study system varied in regards to amount of human-disturbance. Hence, we have classified habitats into three categories: (1) undeveloped; (2) marginal disturbance, which included open space, grasslands, pastures and low intensity development; and (3) high disturbance, which included medium and high intensity development and intensive agriculture. Models were run to examine the relationship between habitat category percentage of each grid cell (Fig. 1) and detection rates of focal prey species as well as humans. Estimates from these models are graphed for all but two of our focal prey species, rabbits and foxes, which did not show strong variation between habitats (Supplementary Table 3). Raccoons, squirrels and mule deer were most positively correlated with intermediate levels of disturbance and, as expected, estimates for humans increased with increasing disturbance level.

Interestingly, though our study corroborates that deer are a significant food resource for pumas (Allen et al., 2015; Iriarte et al., 1990), we found puma body condition scores exhibited stronger correlations with squirrel and raccoon detection rates than with mule deer, suggesting that, in addition to deer, these species may be important subsidies, especially in developed landscapes. This is consistent with a study on kill rates of 6 collared pumas in northern California where non-ungulate prey accounted for 5–45% of all prey mass with the majority of the non-ungulate prey being small mammals (Allen et al., 2015). Likewise, non-ungulate prey, especially smaller mammals, made up the bulk of prey in the diets of pumas nearer to residential development as compared to those individuals hunting in wildland areas in Washington state (Kertson et al., 2011).

The inconsequential effect of humans (i.e., road density and human detections) in predicting puma body condition scores came as some surprise since both have been shown to affect puma movement and habitat-use in other studies (Crooks, 2002; Kertson et al., 2011; Mattson, 2007; Ordenana et al., 2010; Wang et al., 2015). Previous research indicates that large carnivores exhibit lower survival rates in landscapes with high road densities because high edge-area ratios and crossing frequencies make them vulnerable to both exploitation and vehicle collisions (Stoner et al., 2013; Vickers et al., 2015). Moreover, under certain traffic volumes, roads can sever demographic connectivity thereby leading to population isolation and the formation of metapopulations (Beier et al., 2010; Crooks, 2002; Vickers et al., 2015). That said, there may be nutritional benefits associated with roads as native prey are drawn to ruderal plant communities, which in turn may lead to predictable concentrations of live prey as well as carrion and scavenging opportunities (Bauer, Logan, Sweanor, & Boyce, 2005). In sum, we found no evidence for a negative response of puma body condition scores to roads, so hypotheses about puma occupancy or habitat-use that hinge on subtle, indirect effects of roads should be viewed with caution.

If prey encounter rate, rather than anthropogenic disturbance, is indeed the primary determinant of body condition in pumas in other disturbed habitats, and prey species are attracted to areas of marginal habitat modification, then the question remains as to what determines the association between prey and marginally modified environments. Previous research in California chaparral ecosystems suggests that deer, in particular, select disturbance-prone habitats that support early successional plant communities (Cates & Orians, 1975). Mule deer depend on high-quality, succulent forage during fawning, and in this region, native vegetation is at its nutritional low when females are lactating (Sommer et al., 2007). In some developed environments, anthropogenic water subsidies maintain highly consistent and predictable forage growing conditions. Thus, lightly disturbed but irrigated anthropogenic landscapes mimic valuable habitats, with the primary difference being that the growing season is artificially long relative to surrounding wildlands (Krehbiel, Jackson, & Henebry, 2016). The effects of water subsidies on growing season length have been demonstrated by Buyantuyev and Wu (2010) in which they measured phenological variability across an urban to wildland gradient in the Sonoran Desert. Their findings suggested that growth of managed vegetation (i.e., landscaping) was decoupled from precipitation and completely unsynchronized with native vegetation. Similarly, deer attraction to golf courses has been noted in parts of the San Francisco Bay Area (Elliot, 1996; McCullough, Jennings, Gates, Elliott, & DiDonato, 1997). In the Mojave Desert, bighorn sheep with access to a city park exhibited higher fecundity and less movement than their wildland conspecifics (Longshore, Lowrey, & Cummings, 2016). Therefore, mule deer that exploit irrigated or artificially maintained landscapes (e.g., parks and golf courses) have access to more high-quality forage for a longer growing season, much of which overlaps parturition and lactation; the period when energetic demands are highest. Year-round availability of surface water and succulent vegetation likely make deer and other prey movements and habitat-use highly predictable for native predators that depend on them as a food resource (Longshore et al., 2016).

With these issues in mind, our results have several practical implications for the management of pumas in both modified and undeveloped habitats. First, given that our results suggest pumas use marginally developed landscapes, future models of puma connectivity and conservation should employ a broad definition of habitat suitability – one that incorporates some level of anthropogenically modified habitat (Dickson, Roemer, McRae, & Rundall, 2013; Kertson et al., 2013; Moss et al., 2016). However, the inclusions of such mixed-use, small or poorly connected habitat patches into puma conservation landscapes will necessitate greater human tolerance and active management. Therefore, sufficient public education will be needed in places where the potential for human-wildlife conflict is high. Similarly, managers and land-use planners should not assume that pumas will abandon or avoid otherwise productive (i.e., prey-rich) habitats in response to human activity. This is particularly relevant for development that modifies native habitats through irrigation and horticultural improvements, as these changes may be attractive to deer, especially during the seasonal or long-term droughts that characterize the climate of the western USA (Potter, 2015). Lastly, in undeveloped habitats food availability may be more variable than in environments with anthropogenic subsidies. For this reason, pumas in wildland habitats may be prone to domestic animal depredation, especially when fawn production is low (Stoner, Sexton, Nagol, Bernales, & Edwards Jr., 2016).

Our results suggest that puma body condition is positively correlated with puma-prey encounter rates. Future research in this area should also consider puma population density since body condition scores are likely density-dependent and temporal trends in this index may be indicative of intraspecific competition, and movement constraints. For example, if home range sizes are smaller in disturbed areas, either due to landscape fragmentation or because of higher food abundance, then animals may expend less energy during hunting activities, which could permit pumas to maintain higher body condition. Previous research on pumas suggests that home range size is affected by urbanization (Burdett et al., 2010) but it is currently unclear how intraspecific competition may be affected by various types of anthropogenic disturbance. Additionally, while there is sufficient evidence to liken fat deposition to measures of health in other species, it would be useful to link the body condition scores developed here to metrics of health, reproductive output and /or survival of pumas specifically. These future studies would ideally include longitudinal measures on marked, chipped or collared individuals; something that was not feasible with the non-invasive study described here.

5. Conclusions

Our findings demonstrate puma body condition is correlated with prey availability or rates of prey encounter, even in human-modified habitats. This supports the developing hypothesis that pumas are flexible in their habitat selection in response to anthropogenic development (Knopff, Knopff, Boyce, & St. Clair, C. C. , 2014) and that conservation of this species may not hinge entirely on wilderness habitats.

Acknowledgements

We would like to thank the Felidae Conservation Fund team - Ally Nauer, Geno DeRango and countless volunteers - for assistance with the data collection for this research. Joe Acampora and Emilie Edelblutte assisted this project through their expertise with GIS and map development. We thank Ginger Thomson, Adrienne Sussman and the FCF board for their thoughtful comments on this manuscript and support throughout its completion. This project was funded by Disney Conservation Fund (Grant #5104364160),National Geographic Society (Grant #154409), Coypu Foundation (2015), Thornton S. Glide, Jr. and Katrina D. Glide Foundation (2013, 2016), East Bay Zoological Society (2012, 2103), Norcross Wildlife Foundation (2014), Patagonia Environmental Grants program (2013), Marine Ventures Foundation (2104), Bob and Michelle Friend, Sharon Osberg, and Susan Pritzker.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.landurbplan.2019.103648.

References

Acevedo-Whitehouse, K., & Duffus, A. L. J. (2009). Effects of environmental change on wildlife health. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 364*(1534), 3429–3438.

Aizen, M. A., Sabatino, M., & Tylianakis, J. M. (2012). Specialization and rarity predict nonrandom loss of interactions from mutualist networks. *Science, 335*(6075), 1486–1489.

Allen, M. L., Elbroch, L. M., Casady, D. S., & Wittmer, H. U. (2015). Feeding and spatial ecology of mountain lions in the Mendocino National Forest. *California. California Fish and Game, 101*(1), 51–65.

Altmann, J., Schoeller, D., Altmann, S. A., Muruthi, P., & Sapolsky, R. M. (1993). Body size and fatness of free-living baboons reflect food availability and activity levels. *American Journal of Primatology, 30*(2), 149–161.

Audigé, L., Wilson, P. R., & Morris, R. S. (1998). A body condition score system and its use for farmed red deer hinds. *New Zealand Journal of Agricultural Research, 41*(4), 545–553.

AZA (2012). AZA Lion Species Survival Plan, Lion Care Manual. (A. of Z. and Aquariums, Ed.). Silver Spring, MD.

Azzaro, G., Caccamo, M., Ferguson, J. D., Battiato, S., Farinella, G. M., Guarnera, G. C., ... Licitra, G. (2010). Objective estimation of body condition score by modeling cow body shape from digital images. *Journal of Dair Science, 94*, 2126–2137.

Baruch-Mordo, S., Wilson, K. R., Lewis, D. L., Broderick, J., Mao, J. S., & Breck, S. W. (2014). Stochasticity in natural forage production affects use of urban areas by black bears: Implications to management of human-bear conflicts. *PloS One, 9*(1), e85122.

Bastin, C., Loker, S., Gengler, N., Sewalem, A., & Miglior, F. (2010). Genetic relationships between body condition score and reproduction traits in Canadian Holstein and Ayrshire first-parity cows. *Journal of Dairy Science, 93*(5), 2215–2228.

Bateman, P. W., & Fleming, P. A. (2012). Big city life: Carnivores in urban environments. *Journal of Zoology, 287*, 1–23.

Bauer, J. W., Logan, K. A., Sweanor, L. L., & Boyce, W. M. (2005). Scavenging behavior in puma. *The Southwestern Naturalist, 50*(4), 466–471.

Becker, D. J., Streicker, D. G., & Altizer, S. (2015). Linking anthropogenic resources to wildlife–pathogen dynamics: A review and meta-analysis. *Ecology Letters, 18*(5), 483–495.

Beckmann, J. P., & Berger, J. (2003). Rapid ecological and behavioural changes in carnivores: The responses of black bears (Ursus americanus) to altered food. *Journal of Zoology, 261*(2), 207–212.

Beier, P., Riley, S. P. D., & Sauvajot, R. M. (2010). Mountain lions (Puma concolor). *Urban Carnivores: Ecology, Conflict, and Conservation* (pp. 141–156). .

Boutin, S. (1990). Food supplementation experiments with terrestrial vertebrates: Patterns, problems, and the future. *Canadian Journal of Zoology, 68*(2), 203–220.

Burdett, C. L., Crooks, K. R., Theobald, D. M., Wilson, K. R., Boydston, E. E., Lyren, L. M., ... Boyce, W. M. (2010). Interfacing models of wildlife habitat and human development to predict the future distribution of puma habitat. *Ecosphere, 1*(1), 1–21.

Buyantuyev, A., & Wu, J. (2010). Urban heat islands and landscape heterogeneity: Linking spatiotemporal variations in surface temperatures to land-cover and socioeconomic patterns. *Landscape Ecology, 25*(1), 17–33.

Cates, R. G., & Orians, G. H. (1975). Sucessional status and the palatability of plants to generalized herbivores. *Ecology, 56*(2), 410–418.

Chace, J. F., & Walsh, J. J. (2006). Urban effects on native avifauna: A review. *Landscape* *and Urban Planning, 74*(1), 46–69.

Chapman, J. A., & Feldhamer, G. A. (1982). Wild mammals of North America: biology, management, and economics.

Conover, M. R. (1995). What is the urban deer problem and where did it come from? In J. B. McAninch (Ed.). *Urban deer: A Manageable Resource? Proceedings of the 1993 Symposium of the North Central Section of the Wildlife Society* (pp. 11–18). .

Cook, T. C., & Blumstein, D. T. (2013). The omnivore's dilemma: Diet explains variation in vulnerability to vehicle collision mortality. *Biological Conservation, 167*, 310–315.

Crooks, K. R. (2002). Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology, 16*(2), 488–502.

Crooks, K. R., & Soulé, M. E. (1999). Mesopredator release and avifaunal extinctions in a fragmented system. *Nature, 400*(6744), 563.

Dickson, B. G., & Beier, P. (2002). Home-range and habitat selection by adult cougars in southern California. *The Journal of Wildlife Management,* 1235–1245.

Dickson, B. G., Roemer, G. W., McRae, B. H., & Rundall, J. M. (2013). Models of regional habitat quality and connectivity for pumas (Puma concolor) in the southwestern United States. *PloS One, 8*(12), e81898.

Ditchkoff, S. S., Saalfeld, S. T., & Gibson, C. J. (2006). Animal behavior in urban ecosystems: Modifications due to human-induced stress. *Urban Ecosystems, 9*(1), 5–12.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., ... Leitão, P. J. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography, 36*(1), 27–46.

Duncan, C., Nilsen, E. B., Linnell, J. D. C., & Pettorelli, N. (2015). Life-history attributes and resource dynamics determine intraspecific home-range sizes in Carnivora. *Remote Sensing in Ecology and Conservation, 1*(1), 39–50.

Elliot, B. (1996). Challenges of managing urban black-tailed deer in northern Monterey County, California. *Transactions of the Western Section of the Wildlife Society, 32*, 46–47.

Ezenwa, V. O., Jolles, A. E., O'Brien, M. P., Wern, J. G. E., Ambu, L. N., & Goossens, B. (2009). A reliable body condition scoring technique for estimating condition in African buffalo. *African Journal of Ecology, 47*(4), 476–481.

Fahrig, L. (1997). Relative effects of habitat loss and fragmentation on population extinction. *The Journal of Wildlife Management,* 603–610.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics, 34*(1), 487–515.

Ferguson, J. D., Azzaro, G., & Licitra, G. (2006). Body condition assessment using digital images. *Journal of Dairy Science, 89*(10), 3833–3841.

Fernando, P., Janaka, H. K., Ekanayaka, S. K. K., Nishantha, H. G., & Pastorini, J. (2009). A simple method for assessing elephant body condition. *Gajah, 31*, 29–31.

Gittleman, J. L., & Harvey, P. H. (1982). Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology, 10*(1), 57–63.

Gloyne, C. C., & Clevenger, A. P. (2001). Cougar Puma concolor use of wildlife crossing structures on the Trans-Canada highway in Banff National Park, Alberta. *Wildlife Biology, 7*(2), 117–124.

Grigione, M. M., Beier, P., Hopkins, R. A., Neal, D., Padley, W. D., Schonewald, C. M., & Johnson, M. L. (2002). Ecological and allometric determinants of home-range size for mountain lions (Puma concolor). *Animal Conservation Forum: Vol. 5*, (pp. 317–324).

Harmsen, B. J., Foster, R. J., Silver, S., Ostro, L., & Doncaster, C. P. (2010). Differential use of trails by forest mammals and the implications for camera-trap studies: A case study from Belize. *Biotropica, 42*(1), 126–133.

Hatton, I. A., McCann, K. S., Fryxell, J. M., Davies, T. J., Smerlak, M., Sinclair, A. R. E., & Loreau, M. (2015). The predator-prey power law: Biomass scaling across terrestrial and aquatic biomes. *Science, 349*(6252), aac6284.

Homer, C., Dewitz, J., Yang, L., Jin, S., Danielson, P., Xian, G., ... Megown, K. (2015). Completion of the 2011 National Land Cover Database for the conterminous United States–representing a decade of land cover change information. *Photogrammetric Engineering & Remote Sensing, 81*(5), 345–354.

https://www.usclimatedata.com/. (2017). U.S. Climate Data. Retrieved from www.usclimatedata.com.

Iriarte, J. A., Franklin, W. L., Johnson, W. E., & Redford, K. (1990). Biogeographic variation of food habits and body size of the America puma. *Oecologia, 85*(2), 185–190.

Jenks, K. E., Chanteap, P., Kanda, D., Peter, C., Cutter, P., Redford, T., ... Leimgruber, P. (2011). Using relative abundance indices from camera-trapping to test wildlife conservation hypotheses–an example from Khao Yai National Park, Thailand. *Tropical Conservation Science, 4*(2), 113–131.

Kertson, B. N., Spencer, R. D., & Grue, C. E. (2011). Cougar prey use in a wildland-urban environment In Western Washington. *Northwestern Naturalist, 92*(3), 175–185.

Kertson, B. N., Spencer, R. D., & Grue, C. E. (2013). Demographic influences on cougar residential use and interactions with people in western Washington. *Journal of Mammalogy, 94*(2), 269–281.

Kitaysky, A. S., Wingfield, J. C., & Piatt, J. F. (1999). Dynamics of food availability, body condition and physiological stress response in breeding black-legged kittiwakes. *Functional Ecology, 13*(5), 577–584.

Knopff, A. A., Knopff, K. H., Boyce, M. S., & St. Clair, C. C. (2014). Flexible habitat selection by cougars in response to anthropogenic development. *Biological Conservation, 178*, 136–145.

Krehbiel, C. P., Jackson, T., & Henebry, G. M. (2016). Web-Enabled Landsat Data time series for monitoring urban heat island impacts on land surface phenology. *IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing, 9*(5), 2043–2050.

Laundré, J. W., Hernández, L., & Clark, S. G. (2007). Numerical and demographic responses of pumas to changes in prey abundance: Testing current predictions. *Journal of Wildlife Management, 71*(2), 345–355.

Laundré, J. W., & Loxterman, J. (2007). Impact of edge habitat on summer home range size in female pumas. *The American Midland Naturalist, 157*(1), 221–229.

Lenth, B. E., Knight, R. L., & Brennan, M. E. (2008). The effects of dogs on wildlife communities. *Natural Areas Journal, 28*(3), 218–227.

Lewis, J. S., Logan, K. A., Alldredge, M. W., Bailey, L. L., VandeWoude, S., & Crooks, K. R. (2015). The effects of urbanization on population density, occupancy and detection probability of wild felids. *Ecological Applications, 25*(7), 1880–1895.

Linnell, J. D. C., Swenson, J. E., & Anderson, R. (2001). Predators and people: Conservation of large carnivores is possible at high human densities if management policy is favourable. *Animal conservation forum: Vol. 4*, (pp. 345–349). Cambridge University Press.

Longshore, K., Lowrey, C., & Cummings, P. (2016). Foraging at the wildland–urban interface decouples weather as a driver of recruitment for desert bighorn sheep. *Wildlife Society Bulletin, 40*(3), 494–499.

Magle, S. B., Hunt, V. M., Vernon, M., & Crooks, K. R. (2012). Urban wildlife research: Past, present, and future. *Biological Conservation, 155*, 23–32.

Marshal, J. P., Krausman, P. R., & Bleich, V. C. (2008). Body condition of mule deer in the Sonoran Desert is related to rainfall. *The Southwestern Naturalist, 53*(3), 311–318.

Mattson, D. J. (2007). Mountain Lions of the Flagstaff Uplands: 2003-2006 Progress Report.

McCullough, D. R., Jennings, K. W., Gates, N. B., Elliott, B. G., & DiDonato, J. E. (1997). *Overabundant deer populations in California. Vol. 25*, Wildlife Society Bulletin478–483.

McKinney, M. L. (2008). Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems, 11*(2), 161–176.

Millette, J. B., Sauther, M. L., & Cuozzo, F. P. (2015). Examining visual measures of coat and body condition in wild ring-tailed lemurs at the Bezà Mahafaly Special Reserve, Madagascar. *Folia Primatologica, 86*(1–2), 44–55.

Morfeld, K. A., Lehnhardt, J., Alligood, C., Bolling, J., & Brown, J. L. (2014). Development of a body condition scoring index for female African elephants validated by ultrasound measurements of subcutaneous fat. *PloS One, 9*(4), e93802.

Morfeld, K. A., Meehan, C. L., Hogan, J. N., & Brown, J. L. (2016). Assessment of body condition in African (Loxodonta africana) and Asian (Elephas maximus) elephants in North American zoos and management practices associated with high body condition scores. *PloS One, 11*(7), e0155146.

Moss, W. E., Alldredge, M. W., & Pauli, J. N. (2016). Quantifying risk and resource use for a large carnivore in an expanding urban–wildland interface. *Journal of Applied Ecology, 53*(2), 371–378.

Munday, P. L. (2004). Habitat loss, resource specialization, and extinction on coral reefs. *Global Change Biology, 10*(10), 1642–1647.

Negretti, P., Bianconi, G., Bartocci, S., Terramoccia, S., & Verna, M. (2008). Determination of live weight and body condition score in lactating Mediterranean buffalo by Visual Image Analysis. *Livestock Science, 113*, 1–7.

Ordenana, M. A., Crooks, K. R., Boydston, E. E., Fisher, R. N., Lyren, L. M., Siudyla, S., ... Keith Miles, A. (2010). Effects of urbanization on carnivore species distribution and richness. *Journal of Mammalogy, 91*(6), 1322–1331.

Oro, D., Genovart, M., Tavecchia, G., Fowler, M. S., & Martínez-Abraín, A. (2013). Ecological and evolutionary implications of food subsidies from humans. *Ecology Letters, 16*(12), 1501–1514.

Potter, C. (2015). Assessment of the immediate impacts of the 2013–2014 drought on ecosystems of the California Central Coast. *Western North American Naturalist, 75*(2), 129–145.

Prange, S., & Gehrt, S. D. (2004). Changes in mesopredator-community structure in response to urbanization. *Canadian Journal of Zoology, 82*(11), 1804–1817.

Prosser, N. S., Gardner, P. C., Smith, J. A., Wern, J. G. E., Ambu, L. N., & Goossens, B. (2016). Body condition scoring of Bornean banteng in logged forests. *BMC Zoology, 1*(8).

Pulliainen, E., Lindgren, E., & Tunkkari, P. S. (1995). Influence of food availability and reproductive status on the diet and body condition of the European lynx in Finland. *Acta Theriologica, 40*(2), 181–196.

R Core Team (2013). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.r-project.org/.

Ramesh, T., Kalle, R., Sankar, K., & Qureshi, Q. (2011). Assessment of wild Asiatic elephant (Elephas maximus indicus) body condition by simple scoring method in a tropical deciduous forest of Western Ghats, Southern India. *Wildlife Biology in Practice, 7*(2), 47–54.

Reilly, M. L., Tobler, M. W., Sonderegger, D. L., & Beier, P. (2017). Spatial and temporal response of wildlife to recreational activities in the San Francisco Bay ecoregion. *Biological Conservation, 207*, 117–126.

Riley, S. P. D., & Manski, D. (1998). Population density, survival and rabies in raccoons in an urban national park. *Canadian Journal of Zoology, 76*, 1153–1164.

Ripple, W. J., & Beschta, R. L. (2006). Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. *Biological Conservation, 133*(4), 397–408.

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., ... Kinzig, A. (2000). Global biodiversity scenarios for the year 2100. *Science, 287*(5459), 1770–1774.

Šálek, M., Drahníková, L., & Tkadlec, E. (2015). Changes in home range sizes and population densities of carnivore species along the natural to urban habitat gradient. *Mammal Review, 45*(1), 1–14.

Shochat, E., Warren, P. S., Faeth, S. H., McIntyre, N. E., & Hope, D. (2006). From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology & Evolution, 21*(4), 186–191.

Smith, J. A., Suraci, J. P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L. Y., & Wilmers, C. C. (2017). Fear of the human "super predator" reduces feeding time in large carnivores. *Proceedings Of The Royal Society B-Biological Sciences, 284*(1857).

Smith, J. A., Wang, Y., ... Wilmers, C. C. (2015). Top carnivores increase their kill rates on prey as a response to human-induced fear. *The Royal Society, 282*(1802), 20142711.

Soares, F. S., & Dryden, G. (2011). A body condition scoring system for Bali cattle. *Asian-*

Australasian Journal of Animal Sciences, 24(11), 1587–1594.

Sommer, M., Barboza, R., Botta, R., Kleinfelter, E., Schauss, M., & Thomson, J. (2007). *Habitat Guidelines for mule deer California woodland and chaparral ecoregion.* Sacramento, California, USA: Western Association of Fish and Wildlife Agencies.

Stemler, S. E. (2004). A comparison of consensus, consistency, and measurement approaches to estimating interrater reliability. *Practical Assessment, Research & Evaluation, 9*(4), 1–19.

Stoner, D. C., Sexton, J. O., Choate, D. M., Nagol, J., Bernales, H. H., Sims, S. A., ... Edwards, T. C., Jr. (2018). Climatically driven changes in primary production propagate through trophic levels. *Global Change Biology, 24*, 4453–4463.

Stoner, D. C., Sexton, J. O., Nagol, J., Bernales, H. H., & Edwards, T. C., Jr. (2016). Ungulate reproductive parameters track satellite observations of plant phenology across latitude and climatological regimes. *PLOS ONE, 11*(2), e0148780.

Stoner, D. C., Wolfe, M. L., Rieth, W. R., Bunnell, K. D., Durham, S. L., & Stoner, L. L. (2013). De facto refugia, ecological traps and the biogeography of anthropogenic cougar mortality in U tah. *Diversity and Distributions, 19*(9), 1114–1124.

Sweanor, L. L., Logan, K. A., & Bauer, J. W. (2008). Puma and human spatial and temporal use of a popular California State Park. *The Journal of Wildlife Management, 72*(5), 1076–1084.

Treves, A., & Karanth, K. U. (2003). Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology, 17*(6), 1491–1499.

Valeix, M., Hemson, G., Loveridge, A. J., Mills, G., & Macdonald, D. W. (2012). Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. *Journal of Applied Ecology, 49*(1), 73–81.

Vickers, T. W., Sanchez, J. N., Johnson, C. K., Morrison, S. A., Botta, R., Smith, T., ... Boyce, W. M. (2015). Survival and Mortality of Pumas (Puma concolor) in a Fragmented, Urbanizing Landscape. *PLOS ONE, 10*(7), e0131490.

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

Wearn, O. R., Rowcliffe, J. M., Carbone, C., Bernard, H., & Ewers, R. M. (2013). Assessing the status of wild felids in a highly-disturbed commercial forest reserve in Borneo and the implications for camera trap survey design. *PLoS One, 8*(11), e77598.

Wijeyamohan, S., Treiber, K., Schmitt, D., & Santiapillai, C. (2015). A visual system for scoring body condition of Asian elephants (Elephas maximus). *Zoo Biology, 34*(1), 53–59.

Williams, M., Zalasiewicz, J., Waters, C. N., Edgeworth, M., Bennett, C., Barnosky, A. D., ... Haff, P. K. (2016). The Anthropocene: A conspicuous stratigraphical signal of anthropogenic changes in production and consumption across the biosphere. *Earth's Future, 4*(3), 34–53.

Wilmers, C. C., Wang, Y., Nickel, B., Houghtaling, P., Shakeri, Y., Allen, M. L., ... Williams, T. (2013). Scale dependent behavioral responses to human development by a large predator, the Puma. *PLoS One, 8*(4), e60590.

Wolf, C., & Ripple, W. J. (2017). Range contractions of the world's large carnivores. *Royal Society Open Science, 4*(170052).

Woodroffe, R. (2000). Predators and people: Using human densities to interpret declines of large carnivores. *Animal Conservation Forum: Vol. 3*, (pp. 165–173).

Woodroffe, R., & Ginsberg, J. R. (1998). Edge effects and the extinction of populations inside protected areas. *Science, 280*(5372), 2126–2128.

Yom-Tov, Y., Kjellander, P., Yom-Tov, S., Mortensen, P., & Andrén, H. (2010). Body size in the Eurasian lynx in Sweden: Dependence on prey availability. *Polar Biology, 33*(4), 505–513.