INVESTIGATING THE EFFECTS OF URBANIZATION ON COUGAR FORAGING ECOLOGY ALONG THE WILDLAND-URBAN GRADIENT OF WESTERN WASHINGTON

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Abstract

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Humans have historically altered ecosystem structure through landscape manipulation, leaving "remnants," or refuge patches of suitable habitat amidst inhospitable terrain. Large carnivores are especially vulnerable to such habitat modification because they tend to have low population densities and reproductive rates as well as wide-ranging behavior to satisfy high food requirements. Cougars (*Puma concolor*), by contrast, are highly resilient and have demonstrated a tolerance for fragmented and managed landscapes. The temporal influence of landscape development on cougar foraging behavior, however, is not well understood. Accordingly, I compared cougar diets assessed during two different time periods, 2004 – 2008 (Study period 1) and 2013 – 2016 (Study period 2), along a wildland-urban gradient in western Washington to determine how urbanization influences the foraging ecology of this apex predator. Generalized linear mixed model results from this investigation showed that the odds of cougar predation on synanthropic prey increased with urbanization. Ungulate usage by cougars increased over time, and the odds of ungulate predation remained relatively consistent across the wildland-urban gradient, suggesting that cougars were able to maintain similar reliance on ungulates over time and space despite potential differences in ungulate availability. The odds of rodent predation

decreased with increased development, suggesting that urbanization may diminish the quality of riparian habitats in areas where wildlands abut residential landscapes. Individual differences among cougars were a significant predictor of predation on all three prey groups, and the dominant driver of cougar use of synanthrope and ungulate prey (which were primarily black-tailed deer). The variation in cougar diets exhibited in this study suggests that cougar population responses to urbanization, and other forms of human disturbance, are unlikely to be uniform, and therefore, understanding the drivers that cause dietary specialization on certain prey types is a key to predicting how cougar populations will be shaped by anthropogenic landscape modification. Cougar kill locations consistently occurred in areas with low housing density despite an advancing pattern of urban growth in the region since 2004. The residential landscapes used by cougars in western Washington often fall outside city limits, and these areas have undergone limited development as a consequence of Washington state’s approach to managing urban growth. Specifically, in 1990, the Washington state legislature passed the Growth Management Act (GMA), which largely restricted urban-growth to incorporated townships and cities with the aim of protecting wildlife habitat. Washington's GMA has influenced land-use planning in a way that benefits cougars, and could be used as a model for structuring environmental policies beneficial to large carnivores elsewhere. Modeling individual differences in cougar behavior, as I have done with cougar diets in this study, could aid in mitigating cougar-human conflict by helping management agencies to identify individual cougars prone to causing depredations. Lastly, cougar reliance on ungulates has increased over time, and minimizing cougar-human conflict may also require minimizing browse opportunities for deer near residences in an effort to keep foraging cougars away from homes.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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1. INTRODUCTION

Since the onset of plant and animal domestication approximately 12,000 years ago (Diamond 2002, Price and Bar-Yosef 2011), humans have been reshaping ecosystems through landscape modification (Ellis et al. 2010, Moss et al. 2016a). Today, landscape development in the form of agriculture and urbanization are among the greatest drivers of species extinction and biodiversity decline worldwide (Pimm and Raven 2000, Maxwell et al. 2016). Urbanization, and the development of wild landscapes specifically, often happens in the form of residential sprawl, which creates a gradient of human disturbance at the interface of built and natural ecosystems (Radeloff et al. 2005, Conedera et al. 2015). Recent studies have shown that human activities can alter patterns of disturbance and resource availability along such gradients, and that these effects may extend well into rural and even wildland areas (Hendry et al. 2008, Palkovacs et al. 2010, Palkovacs et al. 2012, Alberti 2015, McDonnell and Hahs 2015, Alberti et al. 2017). There remains a need, however, for more studies that explore how species and ecological communities respond to the varying amounts of development that characterize wildland-urban gradients.

Community assemblages along wildland-urban gradients are often shaped by differences in species' capacity to exploit anthropogenic resource subsidies and their tolerance for human proximity and disturbed landscapes (Markovchick-Nicholls et al. 2008, Ordeñana et al. 2010, Newsome et al. 2015b, Marzluff et al. 2016b). For example, urbanization has profoundly affected the diversity of bird communities by influencing reproduction, survival, and breeding dispersal in songbird species in Seattle, WA, USA (Marzluff et al. 2016b, Marzluff et al. 2016a). Namely, sensitive forest species (e.g., Swainson's thrush, *Catharus ustulatus*, Pacific wren, *Troglodytes pacificus*) dispersed from active development to nearby forested areas, resulting in lower annual reproduction, whereas more tolerant species (e.g., song sparrow, *Melospiza melodia*, spotted towhee, *Pipilo maculatus*) adapted to changing landscapes and exhibited higher site fidelity. By implication, studies of how particular species respond to resource changes associated with urbanization are critical to predicting how ecological communities are likely to be shaped by anthropogenic ecosystem transformation.

Large mammalian carnivores are especially vulnerable to human development because they tend to have low reproductive rates and must roam widely in search of prey to meet their demanding energy requirements (Carbon et al. 1999, Cardillo et al. 2004, Cardillo et al. 2005, Ripple et al. 2014). Moreover, these species often come into conflict with humans over livestock depredation and personal safety (Ripple et al. 2014). Consequently, many large carnivores have experienced substantial population declines and range contractions in the face of ongoing anthropogenic landscape development (Laliberte and Ripple 2004, Sandom et al. 2014, Newsome et al. 2016). Some carnivores, however, have shown the ability to adapt to living in human-dominated environments (Tigas et al. 2002, Newsome et al. 2015a). Newsome et al. (2015a), for example, showed that individual variation in movement and diet facilitated the successful establishment of coyotes (*Canis latrans*) in urban Chicago, USA. Additional studies exploring carnivore use of human-modified landscapes could help to build a general framework for predicting which species are likely (and not likely) to exhibit population-level resilience to ecosystem disturbances (Weaver et al. 1996) and potentially aid wildlife managers in mitigating conflicts between humans and wildlife.

Cougars (*Puma concolor*) are solitary, far-ranging felids that are capable of occupying a broad range of habitat types in both temperate and tropical environments (Sunquist and Sunquist 2002). Despite being extirpated from much of the eastern United States through predator removal programs, this large carnivore still retains the largest range of any terrestrial mammal in the Western Hemisphere (Laliberte and Ripple 2004, Ripple et al. 2014). Historically, cougars were associated with wildland environments, but recent studies have revealed that cougars are capable of utilizing areas with extensive human presence (Torres et al. 1996, Beier et al. 2010, Kertson et al. 2011a, Kertson et al. 2011b, Kertson et al. 2013, Wilmers et al. 2013). Though some studies across the western United States and southern Canada have indicated that cougar presence decreases as urbanization intensifies (Knopff et al. 2014, Lewis et al. 2015, Gray et al. 2016), cougars in urban environments have also demonstrated the capacity to adapt by changing their foraging behavior and temporal activity patterns (Knopff et al. 2014, Wang et al. 2015). For example, cougars in west-central Alberta, Canada and west-central California, USA decreased diurnal activity patterns in areas with human activity and showed less avoidance of anthropogenic disturbance at night, as well as increased nocturnal activity (Knopff et al. 2014, Wang et al. 2015). Cougars in urbanized ecosystems have also been found to increase their consumption of non-ungulate prey, which is presumably a byproduct of increased availability due to landscape development (Smith et al. 2015, Moss et al. 2016a, Moss et al. 2016b). As urbanization intensifies, overlap between cougar and human populations will increase, especially in areas where residential development extends into cougar territories and wild landscapes. Thus far, however, only two studies have addressed changes in cougar foraging behavior over time along a wildland-urban gradient that continues to urbanize (Moss et al. 2016a, Moss et al. 2016b). Such studies are crucial to understanding how on-going urbanization functionally changes cougar ecology and for predicting how cougar populations will fare as urbanization increases. Accordingly, I examined changes to cougar foraging behavior over time along a continually urbanizing wildland-urban gradient in western Washington.

In the state of Washington, many cougar populations overlap with exurban and suburban environments, making them ideal for long-term research on predator responses to anthropogenic disturbance. In western Washington at the foothills of the Cascade Mountains, cougars occur throughout a well-defined wildland-urban gradient (0 - >10 residences/ha; Robinson et al. 2005, Kertson et al. 2011a, Kertson et al. 2013). Examination of cougar space-use along this gradient revealed that individuals exhibited similar movement patterns in wildland and residential environments (Kertson et al. 2011b). By inference, cougars in this system have been able to find suitable habitats and resources within a matrix of residential development while keeping interaction rates with humans low (1.6 interactions/1,000 radio days; Kertson et al. 2013). Moreover, Kertson et al. (2011a) demonstrated differential prey use across the gradient, suggesting that urban development in western WA has shaped cougar diets. The relationship between temporal changes to urban development and cougar diets in this system has not been investigated, however. Accordingly, I compared cougar kill location data collected during two study periods – the years 2004 – 2008 (termed hereafter as "study period 1") and 2013 – 2016 (termed hereafter as "study period 2") – in a region where I was also able to quantify increases in development during that time span.

Under the hypothesis that cougars adjust their diets to take advantage of widely available prey (Kertson et al. 2011a, Moss et al. 2016a), I predicted that increasing building density would be associated with an elevated presence of synanthropic species (Moss et al. 2016, Alberti et al. 2017) in cougar diets, and a commensurate decrease in forest-associated ungulates and rodents that are generally taken in wildland portions of the study area (Kertson et al. 2011a). I also expected cougars to exhibit increased use of synanthropic prey and diminished use of ungulates and rodents during study period 2 relative to study period 1 under the assumption that increases in development translate to increases in synanthropic species availability and decreases in the other two prey groups.

2. METHODS

2.1. Study site

I examined cougar kill site locations in a 4,450 km^2 research site encompassing portions of King County, Snohomish County, and Pierce County Washington, USA (590 000 E, 5 260 000 N; Fig. 1). Land ownership within the study site was an amalgamation of state, federal, municipal, and private property. Major landowners included the Washington Department of Natural Resources, the United States Forest Service, City of Seattle, King County, Campbell Global, Hancock Forest Management, and Fruit Growers Supply Incorporated (King County GIS Center, 2016). Major cities and towns within the study area include Bellevue (population 139,820), Redmond (60,598), Issaquah (36,081), Snoqualmie (13,169), Duvall (7,674), and North Bend (6,679), Washington, USA (US Census Bureau 2015).

The study site is topographically complex, and is characterized by a gradual east-west gradient spanning wildland, exurban (< 2.5 residences/ha), suburban (2.5-10 residences/ha), and urban (> 10 residences/ha) environments (Robinson et al. 2005, Kertson et al. 2011b). Private timberland, Washington Department of Natural Resources forest, and United States Forest Service holdings comprise the majority of the eastern portion of the study site. The majority of wildland spaces within the study area consist of temperate coniferous forests typical of the North Cascades eco-region (Franklin and Dyrness 1973). Cougars within the study area primarily prey on black-tailed deer (*Odocoileus hemionus columbianus*), elk (*Cervus elaphus*), beaver (*Castor canadensis*), raccoon (*Procyon lotor*), and mountain beaver (*Aplodontia rufa*; Kertson et al. 2011b, 2013), but their diet can also include mountain goats (*Oreamnos americanus*), coyotes (*Canis latrans*), opossums (*Didelphis virginiana*), river otters (*Lontra canadensis*), mink (*Neovison vison*), black bears *(Ursus americanus),* and domestic species. Domestic species

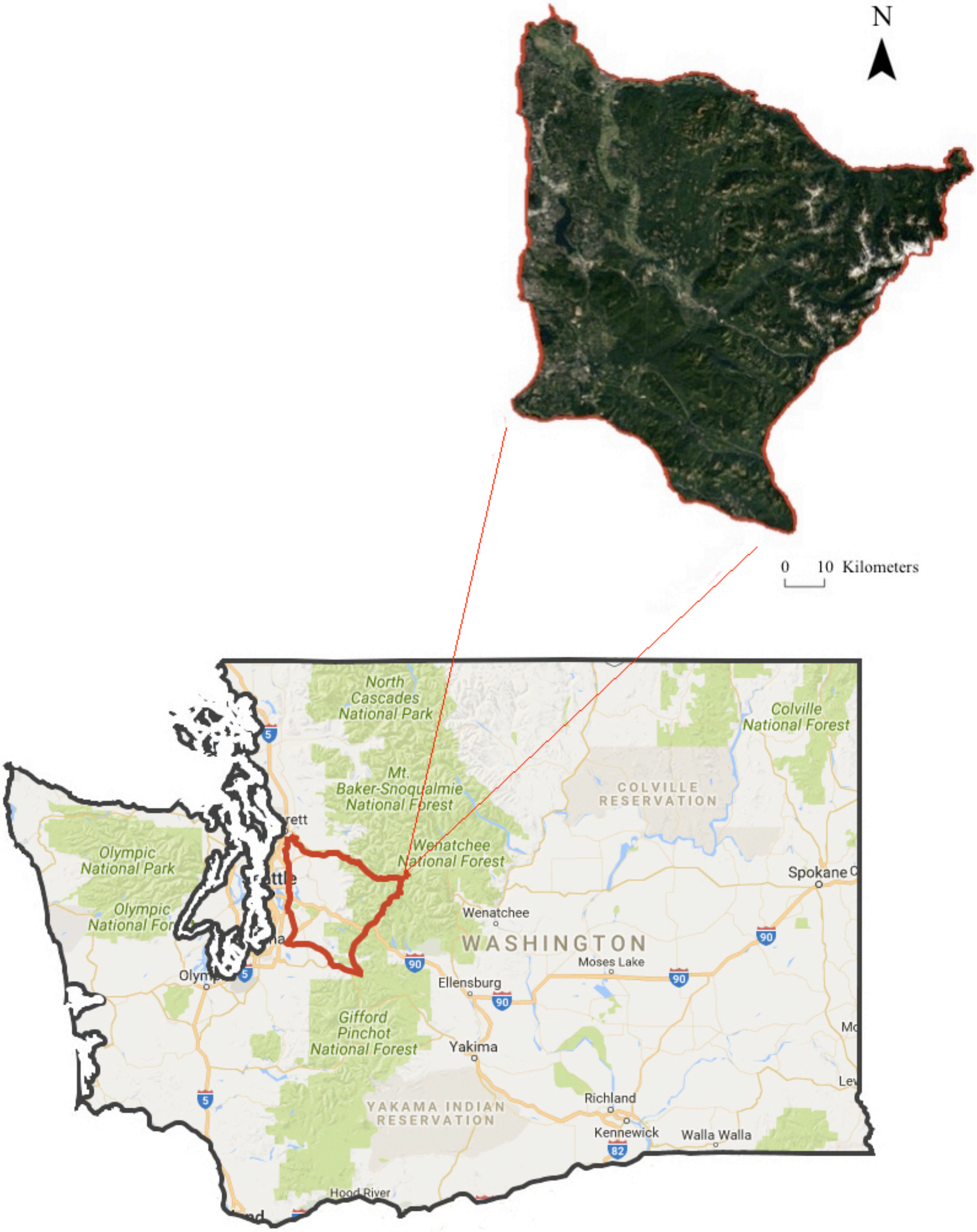

Figure 1. Location of the 4,450 km^2 cougar (*Puma concolor*) study site encompassing portions of King County, Snohomish County, and a small section of wildland in Pierce County (<75 km^2). The study site used by Washington's Department of Fish and Wildlife during period 1 was smaller (3,500 km^2), although King County portions of the study site were identical. Residential and suburban development was concentrated in the western third of the study area with development densities generally decreasing from west to east.

consumed by cougars during this study included llama (*Lama glama*), domestic cat (*Felis catus*), sheep (*Ovis aries*), and chicken (*Gallus gallus domesticus*). The topographic, physiographic, and developmental characteristics of the study site are described at greater length in Kertson et al. (2011b; 2013).

2.2. Radio-tagging and GPS cluster analysis

Washington Department of Fish and Wildlife personnel used trained dogs and cage traps to capture and radio-tag cougars throughout the study site from 2004 to 2008, and again from 2013 to 2016. Once captured, cougars were immobilized, given a physical examination, and outfitted with a global positioning system (GPS) radio-collar equipped with Vhf/Uhf download or Globalstar uplinks (Models Simplex, Televilt, Lindesberg, Sweden and GPS Plus, Vectronic Aerospace, Berlin, Germany). All captured cougars were anesthetized using a 10:1 mixture of Ketamine hydrochloride and Xylazine hydrochloride (Wildlife Pharmaceuticals, Fort Collins, Colorado, USA) at a dosage of 8.8 mg/kg ketamine and 0.88 mg/kg xylazine, and handled in concurrence with University of Washington Institutional Animal Care and Use Committee (IACUC) protocol No. 3077-07 (version 3). All capture methods have been vetted previously and described in detail elsewhere (Kertson and Marzluff 2010, Kertson et al. 2011a, Kertson et al. 2011b, Kertson et al. 2013).

Global positioning system radio-collars were programed to attempt a satellite fix for 180 seconds every 4 hours at 2:00, 6:00, 10:00, 14:00, 18:00, and 22:00 hours. The 4-hour fix interval was chosen to maximize data acquisition and battery life (Cain et al. 2005, Kertson et al. 2011b). Cougars used in this study averaged 1,560 usable fixes (median = 1,528, range = 290 – 3,244; Table 1). I identified potential kill site locations during study period 2 in accordance with the methodology used by Kertson et al. (2011a, 2011b) during study period 1. Namely, I first

Table 1. Cougars used in this analysis (n = 21) with associated identification numbers, sexes, GPS fix numbers, study period designation (2004 to 2008 [study period 1] or 2013 to 2016 [study period 2]), and numbers of kills.

Cougar ID	Cougar Sex	GPS Fixes	Study Period	Total Kills
4	Female	1303	2	33
5	Male	465	2	10
6	Female	2068	2	35
8	Female	2071	2	33
12	Female	1891	2	21
14	Female	1826	2	39
17	Female	3244	2	49
30	Female	1693	2	12
34	Female	1954	2	16
35	Female	1169	2	26
37	Male	1176	2	14
131	Male	1214	1	21
136	Female	2358	1	64
137	Female	745	1	18
309	Male	574	1	10
323	Male	2842	1	78
324	Male	1272	1	43
325	Female	290	1	8
326	Male	1312	1	7
327	Female	1771	1	18
331	Female	1528	1	7

plotted cougar relocations in ArcMap 10.3 and 10.4 (Environmental Systems Research Institute 2014) and Google Earth (Google Inc., Mountain View, California, USA) and then defined location clusters as ≥3 GPS fixes occurring within ≤100m^2 area (methods by Anderson and Lindzey 2003 slightly adapted to account for small prey items). After identifying potential predation sites, I used a handheld GPS receiver and antenna to locate prey remains on the ground (Model Etrex 20, Garmin Ltd., Schaffhausen, Switzerland). Similar to Kertson et al. (2011a), after reaching each GPS location, I searched in concentric circles varying between 5m and 10m apart (depending on visibility) out to the extent of the cluster radius (up to 100m) until I found prey remains. I recorded a GPS location at the kill site if prey remains were found that closely matched the dates during which the cluster was created and if I also found definitive evidence of cougar feeding behavior (e.g., carcass caching behavior, drag marks, hemorrhaging, skeletal remains, and cougar scat; Knopff et al. 2009, White et al. 2011, Kertson et al. 2011a, Wilkens et al. 2015). I attempted to visit potential cougar kill sites within 2-4 weeks of the final GPS fix recorded at the cluster location in order to obtain as much data on each prey item as possible (e.g., sex, age, and relative condition, Cheatum 1949, Ballard 1995).

2.3. Kill site assessment

WDFW personnel assessed kill sites from 2004 – 2008, and I did so from 2013 – 2016 using the same methodology. Namely, after confirming each kill site location based on the presence of prey remains, hair, drag marks, and caching behavior (Beier et al. 1995; Knopff et al. 2009, Wilkens et al. 2015), I adjusted kill site coordinates on-site to correspond to the location of the rumen. In most cases, cougars disembowel their prey, remove the rumen, and consume the heart, lungs, and liver shortly after making the kill. Cougars may cache a carcass 0-80 meters from the predation location during subsequent feeding bouts (Beier et al. 1995). Thus, designating the position of the rumen as the kill location allowed for more consistent assessment of kill site features. If the prey item was a non-ungulate species, I used the presence of intestines and internal organs to record the location of the kill site. Whenever possible, I documented prey species, sex, age, condition, and relative carcass consumption, after the approach employed by Kertson et al. (2011a) during study period 1. I determined prey sex in ungulates based on antler presence or absence, and prey age using dentition and patterns of tooth wear and replacement (Severinghaus 1949). I completed a field-based evaluation of prey physiological condition (on a scale of 1 to 3, poor to high quality, in increments of 0.5) whenever possible using the color and consistency of femur bone marrow (Cheatum 1949, Davis et al 1987). In accord with Ballard (1995), femur bone marrow was only considered a proxy for physiological condition if site visitation occurred within 14 days of the predation event.

2.4. Statistical Analysis

I examined the influence of urbanization on diets of 10 cougars from study period 1 and 11 cougars from study period 2; one cougar spanned both time periods (F137 in study period 1 was also F4 in study period 2). Specifically, I used generalized linear mixed models (GLMMs) to test whether building density, a proxy for urbanization intensity (Theobald 2005, Theobald 2010), had an effect on the occurrence of certain prey items across the wildland-urban gradient. To create a building density predictor variable, I quantified urbanization within the study site using GIS parcel data from King and Snohomish Counties, Washington, USA. Parcel data for years 2007 and 2015 (King County) and 2004 and 2016 (Snohomish County) were acquired through the University of Washington Libraries media archive, along with the associated assessor's tables containing parcel attribute data. I chose these years because they suffered the least amount of data loss following a melding of the assessor's table and parcel layer shapefile (accomplished using the Join tool in ArcToolbox, ArcMap 10.4). All the years selected retained more than 90% of the original data following a fusion of the assessor's table and shapefile. I used the 2007 parcel layer for King County to quantify development during study period 1, and parcel data from 2015 to quantify development during study period 2. I developed land use maps at the parcel scale using information available from present-use codes in the assessor's table for each year (Alberti et al. 2007). Present-use codes identify the property type for each parcel. The present-use codes allowed me to assign parcels a new land-use classification that expanded slightly on the categories used in Alberti et al. (2007) and Robinson et al. (2005). I designated forested and non-forested vegetation (including agricultural land) in accordance with both of the aforementioned studies, however. I removed parcels considered forested and non-forested vegetation (Table 2) when quantifying development (e.g., built environment) because cougars frequently use such land cover types. Indeed, these cover types often contain more forested habitat or pasture than built space, reinforcing the need to remove such parcels from the analysis. The remaining parcels (Land-use ID 1-5, 6-12, 15, 16) included other forms of development such as parking lots, residences, office spaces, shopping centers, major roads, schools, hospitals, and government institutions. Regression models used by Alberti et al. (2007) indicated that land-use and housing density data along Washington's wildland-urban gradient are good predictors of landcover composition and configuration. Using definition query in ArcMap 10.4, I selected these urbanized parcels and assigned each a centroid via the feature-to-point tool in ArcToolbox (Kertson et al. 2011a, ESRI 2014). I then converted each resulting point layer to a raster using the point density tool in the spatial analyst extension of ArcMap 10.4. After raster files were created for both years, I used the minus tool to subtract one raster from another. In this way, I quantified changes in development in King County by subtracting the 2007 raster

Table 2. Land-use classifications used to quantify changes in built parcels in King County and Snohomish, Washington, USA. The categories selected were structured similarly to Robinson et al. (2005) and Alberti et al. (2007) and were created using publicly available King County parcel data. Forested and non-forested vegetation were removed when quantifying development within the study area and are highlighted in bold.

Land Use ID	Land Use Abbreviation	Land use Description
1	SFR	Single-family residential
2	MFR	Multi-family residential
3	MXU	Mixed use (assemblies, storage, theatres, sports facilities, miscellaneous)
4	COM	Commercial (retail, entertainment, services)
5	COH	Heavy use commercial (amusement parks, malls, shopping centers)
6	**AGR**	**Agriculture (farming, husbandry, fisheries)**
7	IND	Industrial and utilities
8	INH	Heavy use industrial
9	OFF	Office
10	OFH	Heavy use office
11	INS	Institutional (cultural centers, community centers, schools, churches, hospitals, government buildings)
12	PKG	Parking
13	**REC**	**Outdoor recreation (trails, camps, parks, hiking and fishing areas)**
14	**OSP**	**Open space (vacant land, timber land, water, wild space)**
15	TRA	Transportation
16	TRH	Heavy use transportation

from the 2015 raster. The resulting heat map indicated where development in the form of built space had increased within the study area during the aforementioned time interval. I evaluated all changes in building density at both the hectare and square kilometer scale, and found that the growth rate for the study site portion of King County was 7.6% (128,733 to 138,506 parcels; Fig. 2). The percent increase in development observed inside the King County portion of the study area is similar to growth rates reported in western Washington previously by Alberti et al. (2009). According to Alberti et al. (2009), urban land cover outside of urban growth boundaries increasing by 7.4%, compared to 3.9% inside urban growth boundaries from 1986 to 2002. Urban Growth Boundaries are landscape delineations inside which urban development is encouraged under Washington State law (GMA; Chapter 36.70A RCW). The similarity between development estimates in this study and those reported previously implies a relatively accurate assessment of development changes within the study site.

To quantify building density at each cougar kill location throughout the study site, I determined the year in which each kill was made and then calculated building density at that location from the most temporally relevant parcel layer (e.g., the King County 2004 parcel layer was used to measure building density at a kill in King County from 2005). Once all kills had a temporally appropriate representation of building density, I used the Extract Values to Points tool in ArcMap 10.4 to extract raster cell values for all kill site locations. The resulting values represented a continuous building density variable at the hectare scale. I also applied the methodology used to quantify built space in the King County portion of the study site to Snohomish parcel data from 2004 and 2016. However, subtracting the 2004 Snohomish raster from the 2016 Snohomish raster file using the minus tool generated an inaccurate assessment of urban growth rates in Snohomish County. Consequently, I did not include the Snohomish

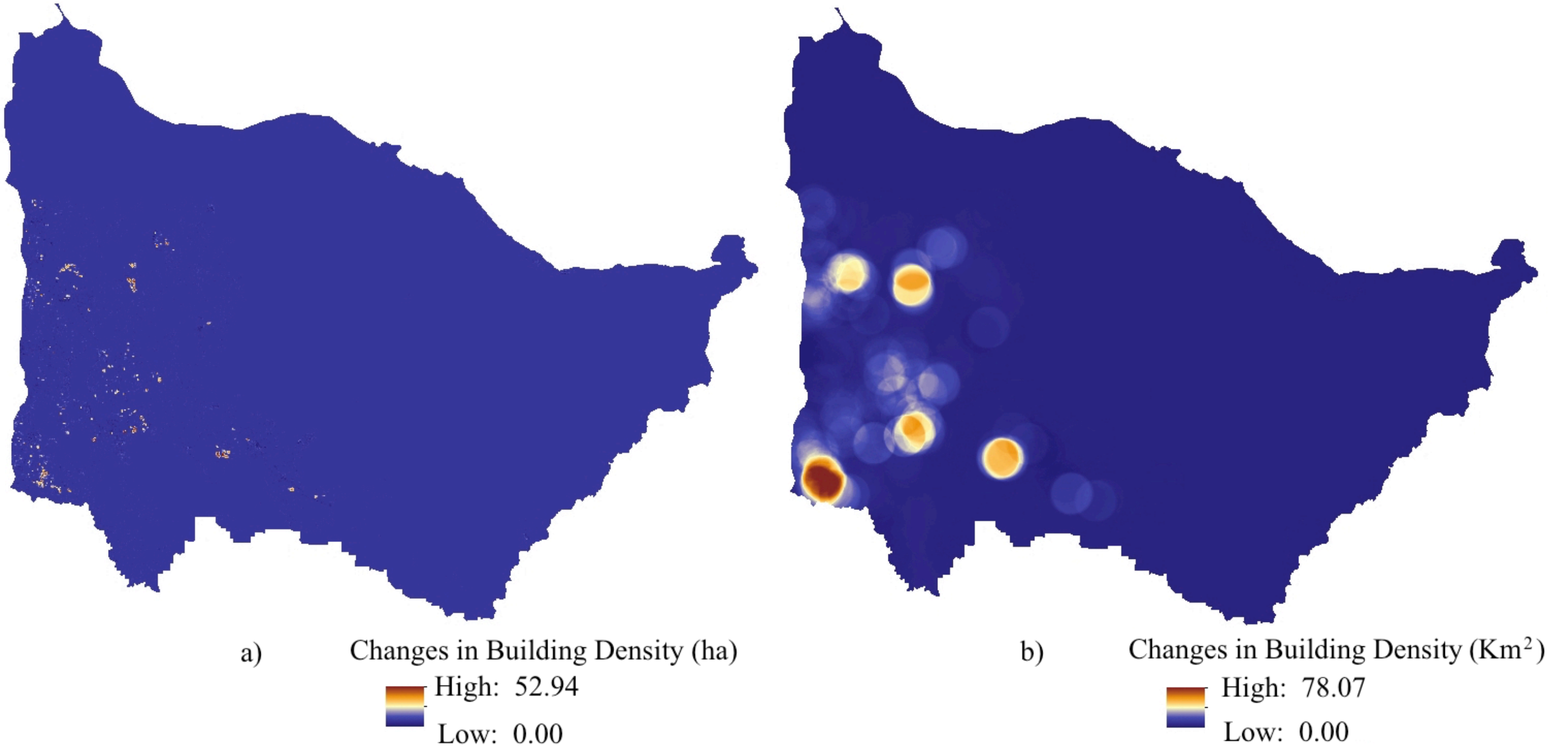

Figure 2. Changes in the density of built structures in the King County (2007 – 2015) portion of the study site at both the hectare (*a*) and square kilometer (*b*) scale. Development along the urban-wildland gradient was concentrated in the western portion of the research site, with King County growing from 128,733 built parcels inside the study area in 2007 to 138,506 in 2015 (7.6% annual growth rate). Many of the development hotspots are located in incorporated townships.

County residential analysis in this thesis; however, using the Extract Values to Points tool in ArcMap 10.4 I was still able to quantify building density for the 29 kill locations that occurred in Snohomish County. All 29 kills in Snohomish County had similar building density values as kills in King County, and thus were retained for analysis. The four kills located in Pierce County all occurred in wildland areas, negating the need to quantify building density for Pierce County kill sites.

To address the hypothesis that building density would affect the occurrence of different prey species, I used GLMMs with multiple ecologically relevant predictors. To achieve sample sizes necessary for modeling of cougar diets, I grouped prey species into three ecologically relevant categories: ungulates (mountain goat, elk, and black-tailed deer), synanthropes (raccoons, coyotes, and domestic species), and rodents (mountain beaver and American beaver). These prey categories closely mirror those used by Moss et al. (2016b), who grouped prey into biologically meaningful categories based on isotopic signatures. The ungulate group in this study consisted of species typically associated with wildland areas in western Washington, specifically black-tailed deer, elk, and mountain goat. Likewise, rodents (American beaver and mountain beaver) are largely wildland obligates in our system. Synanthropic species included coyotes, raccoons, opossums, and domestic species. Grouping prey species into these categories removed multiple low-digit kills from the dataset. I modeled each prey group as a binary response variable, with a kill of the target species within a focal prey category equating to 1 and kills of species in the other two categories equaling 0. I used several fixed predictor variables – cougar sex, study period, and building density – to build a set of candidate models for each prey type response variable. Previous studies in western WA have revealed individual differences in cougar dietary and spatial responses to urbanization (Kertson et al. 2011a, b). Thus, I also included the random effect of cougar ID in all models to account for the possibility of individual differences in dietary responses to urbanization within and between the two time intervals. The random cougar effect allows a separate intercept for each cougar, where the random effects are offsets from the mean fixed intercept and are assumed to be normally distributed with a mean of zero. Including the random cougar effects helps account for correlation among kill types by individual cougars. Null models contained only a single fixed intercept. I considered all possible interaction effects among fixed predictor variables in candidate models for each response, and ranked candidate models based on differences in the small-sample corrected Akaike information criterion (AIC_c) in accordance with Burnham and Anderson (2002). I only considered models with a $\Delta\ AIC_c \leq 2$ relative to the top model to be competitive (Burnham and Anderson 2002), and only considered fixed and random effects significant if 95% confidence intervals for their coefficient estimates did not overlap 0. Profile confidence intervals were used to evaluate the variance of the cougar ID random effect in each top model, and standard Wald confidence intervals were used to determine the strength of fixed effect estimates. To quantify the relative strength of evidence for each candidate model, I calculated model likelihood using the equation

$$\mathcal{L}(g_i|\chi) \propto \exp(-\frac{1}{2}\Delta_i)$$

where "$\propto$" means "is proportional to", and g_i represents the model of interest whereas Δ_i represents its associated AIC_c difference. To better interpret the relative likelihood of each model, I normalized each likelihood outcome to create a set of positive AIC_c weights (Burnham and Anderson 2002). Odds ratios and their associated 95% confidence intervals were extracted in R and used to evaluate the effect magnitude of the fixed and random effects in each of the top models. I built all GLMMs using the glmer and glm functions in the lme4 package in R (Bates et al. 2016). The lme4 package fits linear and generalized mixed-effects models by implementing computational algorithms from the Eigen C++ library (Bates et al. 2016).

3. RESULTS

I evaluated diets from 21 individual cougars to determine if urbanization drove changes in cougar diets spatially (e.g., across the gradient) and temporally (e.g., between study periods). Overall, cougar diets included 15 different prey species (Fig. 3 and 4), with black-tailed deer (407 kills) and American beaver (70 kills) accounting for the majority of cougar food resources based on investigation of GPS clusters. Spatially, the frequency of synanthropic species in cougar diets was positively associated with increases in building density (Table 3), and cougar predation on synanthropic species tended to occur in areas with greater building density than areas associated with rodent and ungulate kills. Temporally, ungulates were the most common cougar prey item in both study periods, and proportional use of ungulates as prey increased in study period 2 relative to study period 1 (Table 4). The distributions of kill site locations from study period 1 and study period 2 were roughly equivalent across the wildland-urban gradient, however, minimizing the likelihood that differences in cougar diets between study periods were a function of differences in sampling effort in residential areas (Table 5). Despite synanthropic species occurring in areas with greater building density, building density changed little among prey groups across time (Fig. 5), and the average residential density at which kill site locations occurred did not vary markedly across all years of the investigation (Fig. 6).

The occurrence of synanthropic species in cougar diets was strongly tied to individual identity as well as the extent of urbanization. Namely, the top synanthrope model included building density as the sole fixed effect and indicated that there was a multiplicative change of 4.77 (95% CI: 1.06, 21.53) in the odds of cougar predation on synanthropic species with every increase in building density of one building per hectare (Table 6).

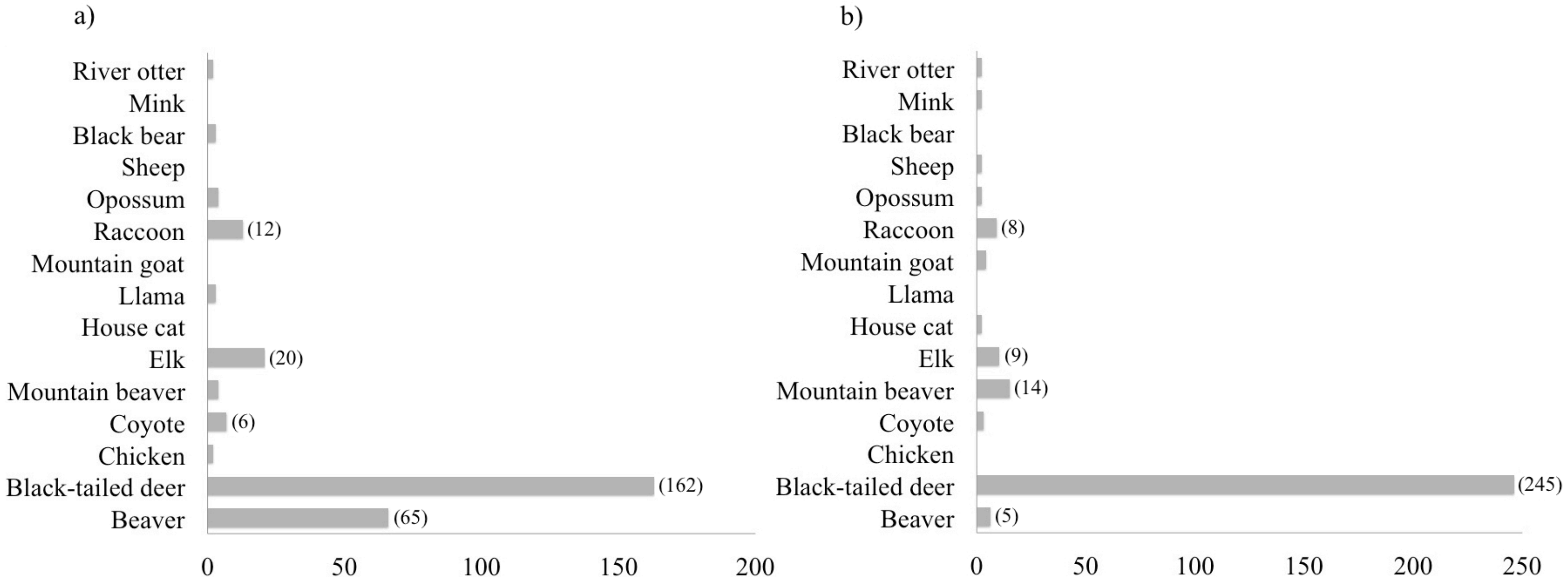

Figure 3. Number of prey species killed during study period 1 (a) and study period 2 (b). Kill numbers ≥5 are indicated in parentheses.

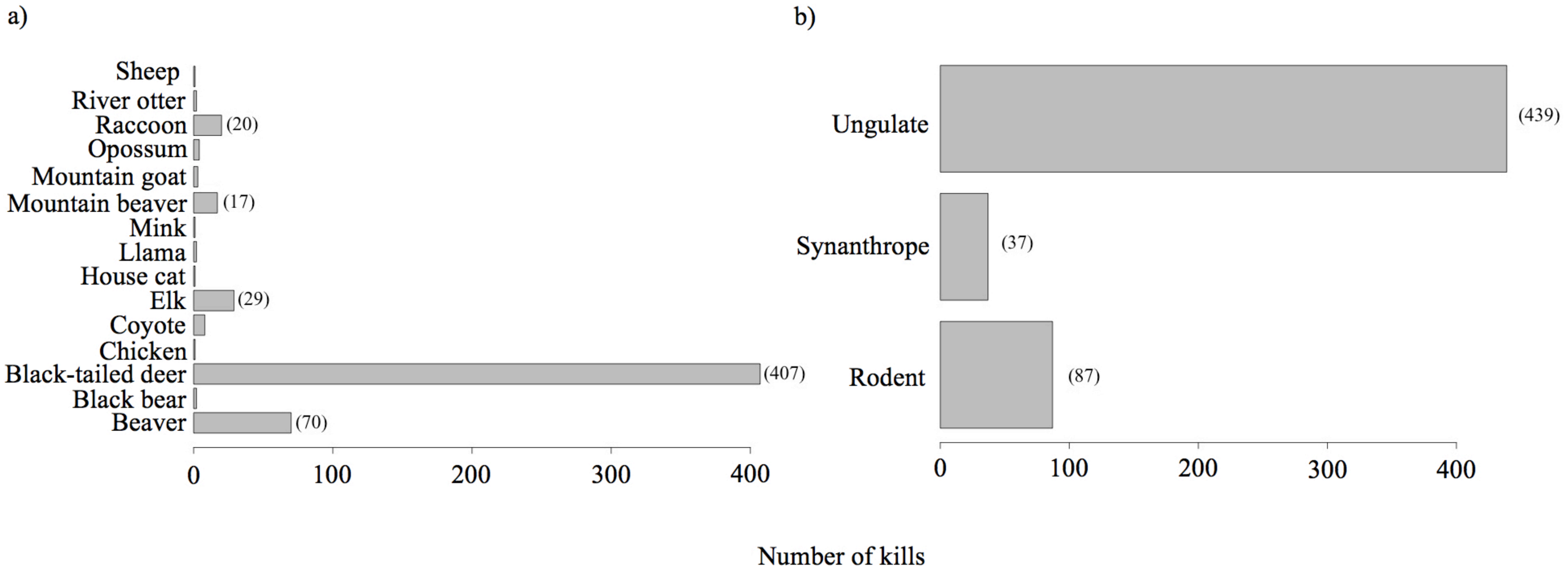

Figure 4. Numbers of prey species killed by cougars (n = 568) across all study years (a) and the number of cougar kills included in each of the three prey categories: Ungulates (black-tailed deer, elk, mountain goat); Rodents (beaver, mountain beaver); Synanthropes (raccoon, coyote, opossum). Two black bear kills, two river otter kills, and one mink kill were removed when grouping prey as these species, while considered wildland mammals, are not rodents or ungulates. Kill numbers for species and prey groups with ≥ 20 kills are indicated in parentheses.

Table 3. The number of kills by prey group made by cougars at three levels of building density. The mean for building density across all kills was 0.05; hence, the three categories of building density were created to correspond with wildland areas, residential densities below the mean, and residential densities above the mean. The proportion of each prey type across building densities is indicated in parentheses

Building density (ha)	**Ungulate**	**Rodent**	**Synanthrope**
0	330 (0.80)	74 (0.18)	8 (0.02)
0 – 0.05	40 (0.77)	5 (0.10)	7 (0.14)
> 0.05	69 (0.70)	8 (0.08)	22 (0.22)

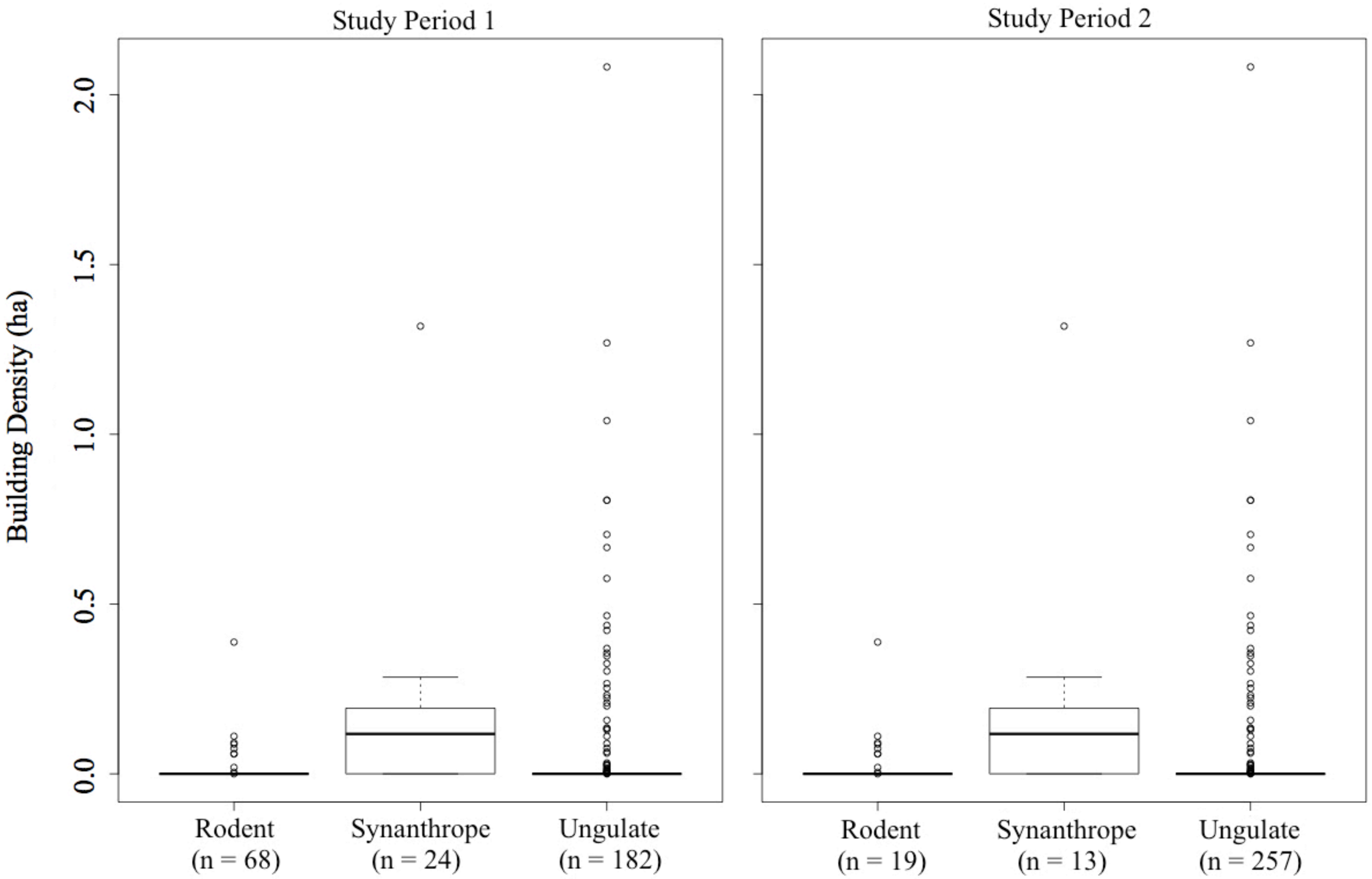

Figure 5. Average building density at cougar kill site locations according to prey type. Plots are separated according to study period, with synanthropes consistently being killed in areas with greater building density than ungulates and rodents. Boxplots represent the lower (25%) and upper (75%) quartiles with the middle band representing the median (50th percentile). Error bars provide a 95% confidence interval for the difference in group means (McGill et al. 1978, Chambers et al. 1983). Open circles represent building density values for individual kills in each prey group.

Table 4. Total kills by prey type made by cougars across study periods.

Study Period	Ungulate	Rodent	Synanthrope	Total
1	182	68	24	274
2	257	19	13	289

Table 5. Total kills made by cougars across the two study periods at three levels of building density. The mean for building density across all kills was 0.05; hence, the three categories of building density were crested to correspond with wildland areas, residential densities below the mean, and residential densities above the mean. Sampling effort was consistent between study periods across the wildland-urban gradient.

Building Density (ha)	**Study Period 1**	**Study Period 2**	**Total**
0	199	213	412
0 – 0.05	23	29	52
> 0.05	52	47	99

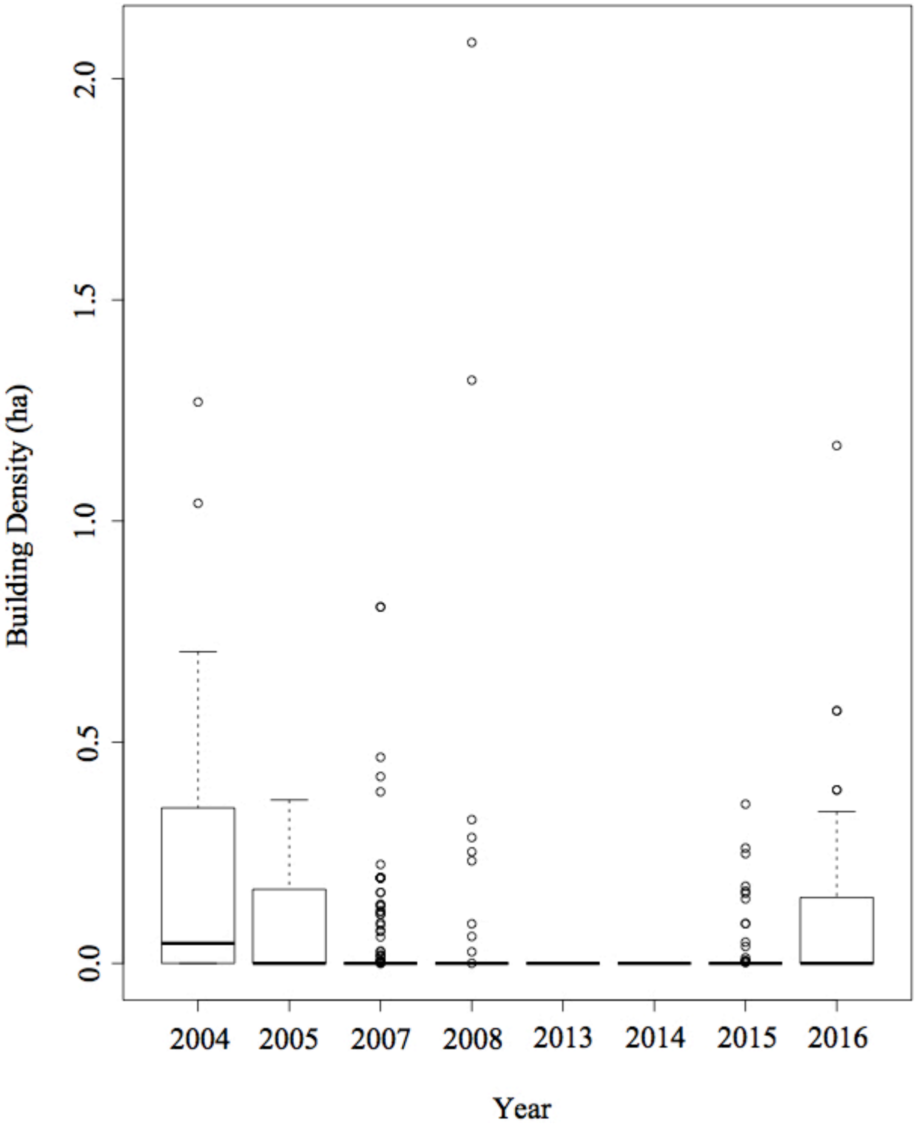

Figure 6. Average building density at all cougar kill locations during every study year since 2004. Despite a few outlying kills occurring in high-density areas in 2004, 2008, and 2016, kills across years occurred on average in areas with < 0.5 built parcels per hectare.

Table 6. Multiplicative change in the odds of predation by cougars on synanthropes, ungulates, and rodents as building density increases by one building per hectare. Odds 95% confidence bounds are included for each prey group.

Prey Group	Multiplicative change in relative odds	Confidence interval (lower bounds)	Confidence interval (upper bounds)
Synanthropes	4.77	1.06	21.53
Ungulates	1.48	0.38	5.75
Rodents	0.00	0.00	0.23

The 95% confidence interval for this variable's coefficient did not overlap zero (β = 1.56, CI = 0.06, 3.07), indicating that its effect was significant. By contrast, the cougar random effect in this model accounted for a considerable amount of variability in synanthrope usage, where the estimated standard deviation of the random effects was $\hat{\sigma} = 1.23$ (95% CI = 0.66, 2.21). Random effect estimates for individual cougars in the top synanthrope model varied considerably (Table 7), with three individuals (F30, M324, and F325) differing significantly from the cougar population average in their predation on synanthropic species (Fig. 7). The multiplicative odds of F30, M324, and F325 preying upon synanthropes were estimated to be 6.78 (95% CI: 2.09, 22.04), 7.07 (95% CI: 3.62, 13.84), and 6.79 (95% CI: 1.71, 26.10) times greater than the average odds among cougars, respectively (Table 8).

Individual cougar identity was also the dominant driver of cougar predation on ungulates. Specifically, the top ungulate model included fixed effects for sex and study period with no interaction effects (Table 9), but the 95% confidence intervals for the coefficients for sex (β = -0.75, CI = -1.61, 0.10) and study period (β = 0.81, CI = -0.01, 1.65) overlapped zero by a small amount and thereby indicated that their effects were marginally non-significant. The estimated standard deviation of the cougar random effects, on the other hand, had a 95% confidence interval not overlapping zero ($\hat{\sigma} = 0.64$, CI = 0.23, 1.11), indicating significant differences in the use of ungulates among individuals in this study. Specifically, two cougars (M323 and M324) had significantly lower estimates than the population average, regardless of study period (Table 10, Fig. 8). The odds of either of these cougars preying upon ungulate species were less than 1, whereas the odds of ungulate predation were relatively consistent across the remaining cougars (Table 11). One cougar in particular, M131, had an especially strong propensity to kill ungulate species, with odds of predation on ungulates by this cat being 2.49 (95% CI = 1.10, 5.63) times

Table 7. Generalized linear mixed model (GLMM) estimates for each cougar random effect in the top synanthrope model with upper and lower 95% confidence bounds. Cougars with 95% CI that do not overlap 0 are highlighted in bold.

Cougar ID	Beta (β)	Confidence interval (low)	Confidence Interval (high)
4	-0.83	-2.62	0.96
5	-0.41	-2.45	1.63
6	-0.86	-2.63	0.92
8	-0.84	-2.62	0.94
12	0.98	-0.20	2.17
14	-0.93	-2.67	0.82
17	-0.39	-1.81	1.04
30	**1.91**	**0.74**	**3.09**
34	0.57	-0.78	1.92
35	0.53	-0.80	1.85
37	0.21	-1.43	1.84
131	0.03	-1.53	1.58
136	-0.14	-1.33	1.06
137	-0.83	-2.63	0.96
309	0.53	-1.21	2.28
323	0.24	-0.70	1.19
324	**1.96**	**1.29**	**2.63**
325	**1.92**	**0.53**	**3.30**
326	0.06	-1.67	1.78
327	-0.58	-2.50	1.35
331	-0.30	-2.42	1.83

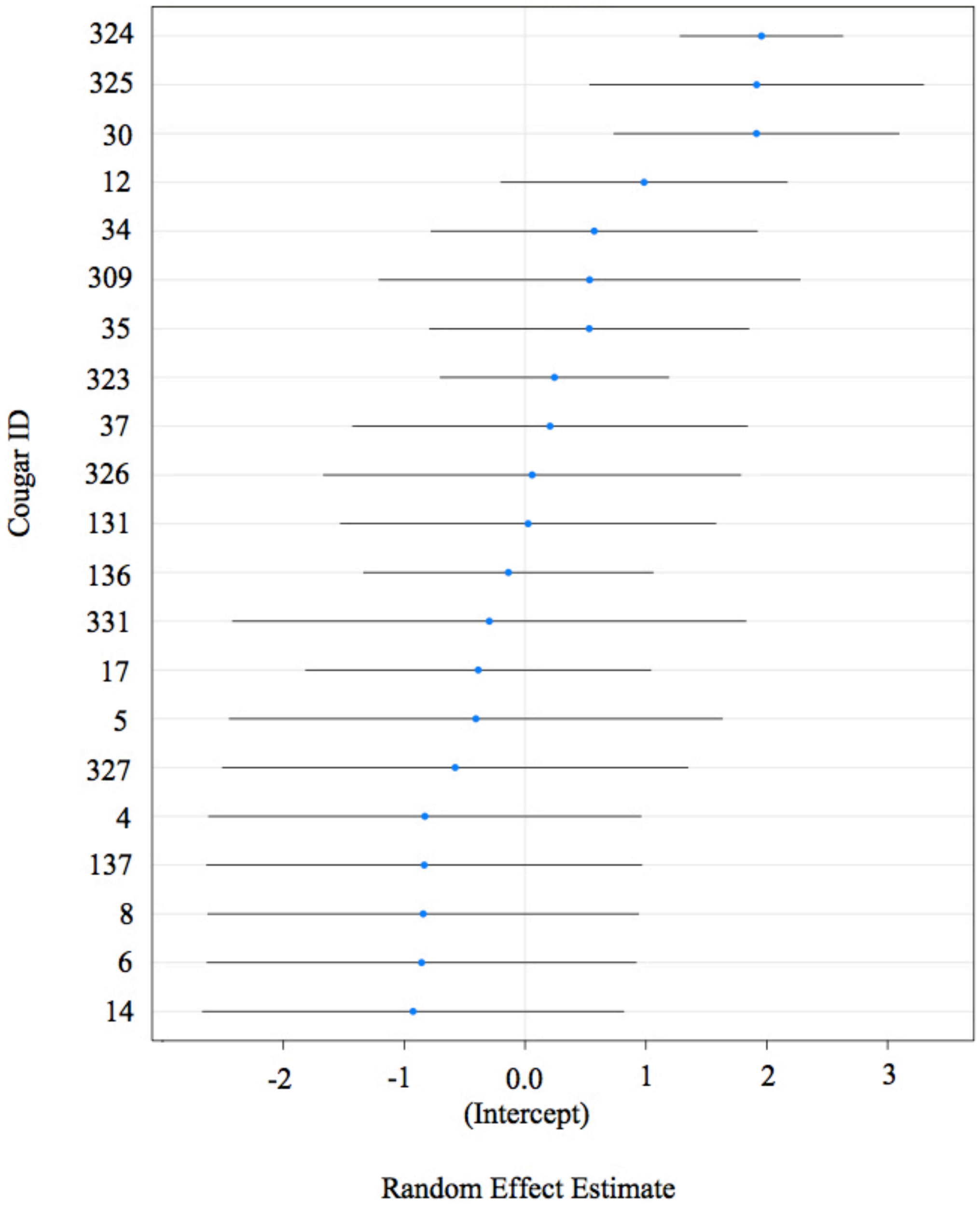

Figure 7. GLMM estimates for each individual cougar random effect in the top synanthrope model. Each cougar represents a deviation from the fixed intercept value, which is the mean intercept among all cougars in the study. Cougars M324, F325, and F30 all differed significantly from the average cougar in their foraging behavior on synanthropes (i.e., their associated 95% confidence intervals did not overlap 0).

Table 8. Multiplicative factors on the odds of synanthrope predation by individual cougars relative to the average cat (odds of synanthrope predation by the average cougar equal 1). 95% confidence intervals for the odds ratios are included and cougars with significant odds (e.g. odds 95% confidence interval does not overlap 1) of synanthrope predation are highlighted in bold.

Cougar ID	Odds of synanthrope predation	Confidence interval (low)	Confidence interval (high)
F4	0.44	0.07	2.61
M5	0.67	0.09	5.11
F6	0.42	0.07	2.50
F8	0.43	0.07	2.55
F12	2.68	0.82	8.74
F14	0.40	0.07	2.26
F17	0.68	0.16	2.83
F30	**6.78**	**2.09**	**22.04**
F34	1.77	0.46	6.82
F35	1.70	0.45	6.36
M37	1.23	0.24	6.29
M131	1.03	0.22	4.84
F136	0.87	0.26	2.88
F137	0.43	0.07	2.62
M309	1.71	0.30	9.73
M323	1.28	0.50	3.28
M324	**7.07**	**3.62**	**13.84**
F325	**6.79**	**1.71**	**27.00**
M326	1.06	0.19	5.95
F327	0.56	0.08	3.84
F331	0.74	0.09	6.21

Table 9. All candidate GLMM models with a Δ $\mathrm{AIC_c} \leq 2$ when compared to the top model for each prey group. Null models and models only including random effects (fixed intercept = 1). Model likelihood and $\mathrm{AIC_c}$ weight calculations are included for more robust model interpretation. Model likelihoods quantify the plausibility that each model is the actual best model, and $\mathrm{AIC_c}$ weights express the weight of evidence that model *i* is actually the best model among the candidate set for a given response variable (Burnham and Anderson 2002).

Response Variable	**Predictor Variables**	**$\mathrm{AIC_c}$**	**$\Delta\mathrm{AIC_c}$**	**Model likelihood**	**$\mathrm{AIC_c}$ Weight**
Synanthrope	Building density, random effect	252.20	0	1	0.51
Synanthrope	Study period, building density, random effect	253.50	1.30	0.52	0.27
Synanthrope	Random effect only	253.90	1.70	0.43	0.22
Synanthrope	None (null model)	274.97	22.8	0.00	0.00
Ungulate	Sex, study period, random effect	537.0	0	1	0.33
Ungulate	Study period, random effect	537.50	0.50	0.78	0.26
Ungulate	Sex, random effect	538.20	1.20	0.55	0.18
Ungulate	Sex, study period, building density, random effect	538.60	1.60	0.45	0.15
Ungulate	Random effect only	540.80	2.80	0.25	0.08
Ungulate	None (null model)	595.65	58.65	0.00	0.00
Rodent	Sex, study period, building density, random effect	426.80	0	1	0.32
Rodent	Sex, study period, building density, no random effect	428.22	1.42	0.49	0.15
Rodent	Sex, study period, building density, sex – study period interaction, random effect	428.30	1.50	0.47	0.15
Rodent	Study period, building density, random effect	428.40	1.60	0.45	0.14
Rodent	Sex, study period, building density, study period – building density interaction, random effect	428.70	1.90	0.39	0.12
Rodent	Sex, study period, building density, sex – building density interaction, random effect	428.80	2.0	0.37	0.12
Rodent	Random effect only	441.70	14.9	0.00	0.00
Rodent	None (null model)	486.73	59.93	0.00	0.00

Table 10. GLMM estimates for each cougar random effect in the top ungulate model with upper and lower 95% confidence bounds. Cougars with 95% CI that do not overlap 0 are indicated in bold.

Cougar ID	**Beta (β)**	**Confidence interval (low)**	**Confidence Interval (high)**
4	-0.14	-0.94	0.66
5	0.45	-0.54	1.45
6	0.45	-0.44	1.34
8	0.24	-0.62	1.09
12	-0.40	-1.25	0.45
14	0.50	-0.38	1.38
17	-0.30	-0.98	0.39
30	-0.69	-1.61	0.24
34	-0.11	-1.05	0.84
35	-0.28	-1.11	0.55
37	-0.08	-0.96	0.79
131	**0.92**	**0.10**	**1.74**
136	-0.27	-0.78	0.25
137	0.28	-0.59	1.15
309	-0.32	-1.18	0.54
323	**-0.59**	**-1.01**	**-0.18**
324	**-0.57**	**-1.11**	**-0.04**
325	-0.35	-1.30	0.60
326	0.08	-0.86	1.03
327	0.28	-0.59	1.15
331	0.36	-0.67	1.39

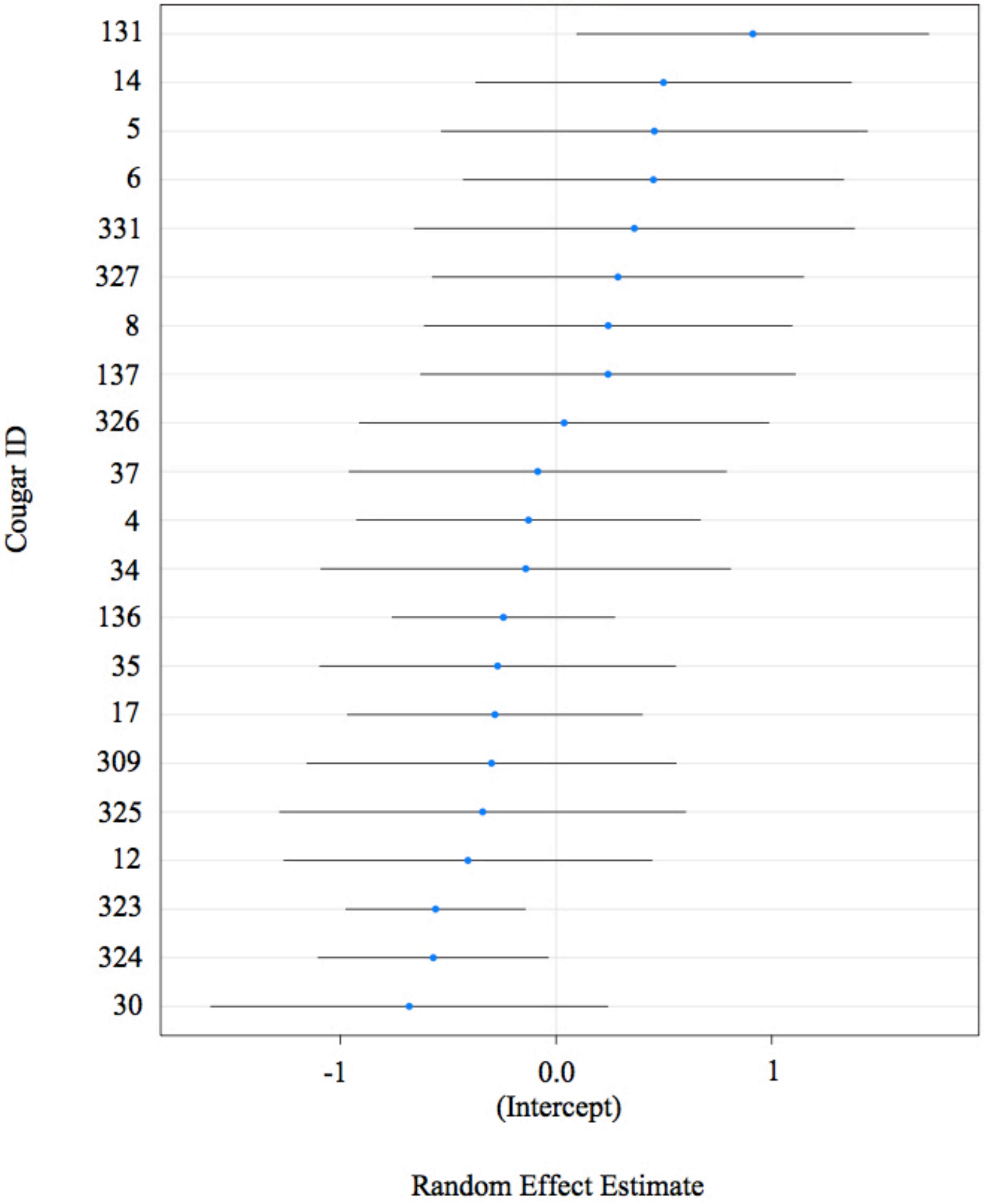

Figure 8. GLMM estimates for each individual cougar random effect for the top ungulate model. Each cougar represents a deviation from the fixed intercept value, which is the mean intercept among all cougars in the study. Cougars M131, M323, and M324 all differed significantly from the average cougar in their reliance on ungulates (i.e., their associated 95% confidence intervals did not overlap 0).

Table 11. Multiplicative factors on the odds of ungulate predation by individual cougars relative to the average cat (odds of ungulate predation by the average cougar equal 1). 95% confidence intervals for odds ratios are included and cougars with significant positive or negative odds of ungulate predation are indicated in bold.

Cougar ID	Odds of Ungulate predation	Confidence interval (low)	Confidence Interval (high)
4	0.88	0.40	1.95
5	1.58	0.59	4.23
6	1.57	0.65	3.79
8	1.27	0.54	2.99
12	0.66	0.28	1.56
14	1.65	0.69	3.93
17	0.75	0.38	1.49
30	0.51	0.20	1.27
34	0.87	0.34	2.24
35	0.76	0.33	1.74
37	0.92	0.38	2.20
131	**2.49**	**1.10**	**5.63**
136	0.78	0.47	1.31
137	1.27	0.53	3.03
309	0.74	0.32	1.74
323	**0.57**	**0.38**	**0.87**
324	**0.57**	**0.33**	**0.96**
325	0.71	0.28	1.82
326	1.04	0.40	2.68
327	1.33	0.56	3.15
331	1.44	0.52	3.99

greater than the average cougar in this study. Odds of ungulate predation were relatively consistent across the wildland-urban gradient, staying near 1 as building density increased (Table 6).

The intensity of urbanization and individual identity were each important drivers of cougar predation on rodents. Namely, the top rodent model included the fixed effects of sex, study period, and building density, along with the random effect for individual cougars, with no interactions among predictors (Table 9). All three fixed effects proved significant in the top model, with the confidence intervals for sex ($\beta = 0.88$, 95% CI = 0.06, 1.70), study period ($\beta = -1.00$, 95% CI = -1.82, -0.18), and building density ($\beta = -6.59$, 95% CI = -11.71, -1.47) not overlapping zero. The occurrence of rodent prey items decreased from study period 1 to study period 2, and the odds of rodent predation decreased as building density increased across the wildland-urban gradient (Table 6). The estimated standard deviation of the cougar random effects was also significant in the top rodent model ($\hat{\sigma} = 0.46$, 95% CI = 0.00, 1.01), with the majority of cougars in the study subsisting on fewer rodents than the average cat (Fig. 9). While the lower bound for the confidence interval of the cougar random effect equals 0, there is a $\Delta AIC_c = 45$ when comparing the null model versus a the model with only the cougar random effect, indicating that the effects of individual cougars are significant. Only one cougar (M323) had a significant, positive association with rodents ($\beta = 0.62$, 95% CI = 0.21, 1.03), with its odds of rodent predation being 1.86 (95% CI = 1.24, 2.80) times greater than the average cougar in this study (Tables 12 and 13).

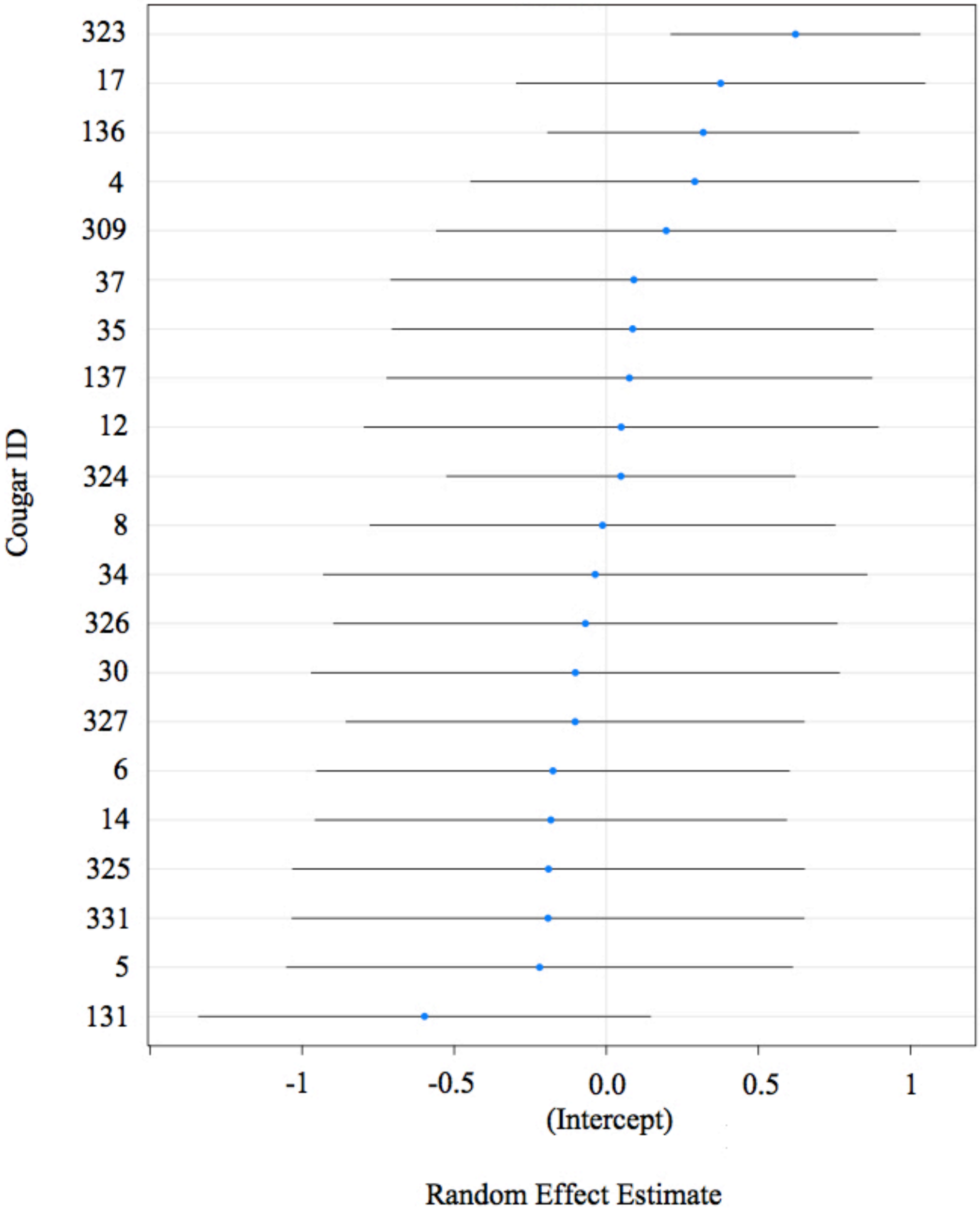

Figure 9. GLMM estimates for each individual cougar random effect in the top rodent model. Each cougar represents a deviation from the fixed intercept value, which is the mean intercept among all cougars in the study. Cougar M323 differed significantly from the average cougar in its foraging behavior on rodents (i.e., its associated confidence interval did not overlap 0).

Table 12. GLMM estimates for each cougar random effect in the top rodent model with upper and lower 95% confidence bounds. Cougars with 95% CI not overlapping 0 indicated in bold.

Cougar ID	**Beta (β)**	**Confidence interval (low)**	**Confidence Interval (high)**
4	0.29	-0.45	1.03
5	-0.22	-1.05	0.61
6	-0.16	-0.95	0.60
8	-0.01	-0.78	0.75
12	0.05	-0.80	0.89
14	-0.18	-0.96	0.59
17	0.38	-0.30	1.05
30	-0.10	-0.97	0.77
34	-0.04	-0.93	0.86
35	0.09	-0.70	0.88
37	0.09	-0.71	0.89
131	-0.60	-1.34	0.14
136	0.32	-0.19	0.83
137	0.08	-0.72	0.87
309	0.20	-0.56	0.95
323	**0.62**	**0.21**	**1.03**
324	0.05	-0.52	0.62
325	-0.19	-1.03	0.65
326	-0.07	-0.90	0.76
327	-0.10	-0.85	0.65
331	-0.19	-1.03	0.65

Table 13. Multiplicative factors on the odds of rodent predation by individual cougars relative to the average cat (odds of rodent predation by the average cougar equal 1). 95% confidence intervals for the odds ratios are included and cougars with significant odds of rodent predation are indicated in bold.

Cougar ID	Odds of Rodent predation	Confidence interval (low)	Confidence Interval (high)
4	1.34	0.64	2.79
5	0.80	0.35	1.84
6	0.84	0.39	1.82
8	0.99	0.46	2.12
12	1.05	0.45	2.44
14	0.83	0.38	1.81
17	1.46	0.74	2.85
30	0.90	0.38	2.15
34	0.96	0.39	2.35
35	1.09	0.49	2.40
37	1.09	0.49	2.43
131	0.55	0.26	1.16
136	1.38	0.83	2.29
137	1.08	0.49	2.39
309	1.22	0.57	2.59
323	**1.86**	**1.23**	**2.80**
324	1.05	0.59	1.86
325	0.83	0.36	1.92
326	0.93	0.41	2.13
327	0.90	0.43	1.91
331	0.83	0.36	1.91

4. DISCUSSION

Prompted by the findings of Kertson et al. (2011a), Smith et al. (2016), and Moss et al. (2016a), I predicted that cougars foraging along a wildland-urban gradient in western Washington would increase their reliance on synanthropic prey species as a positive function of building density both during and between two study periods. Concurrent with my first prediction, building density was a significant predictor of synanthrope predation, although individuals differed markedly in their use of this prey group. My second prediction was repudiated, however, as the occurrence of synanthropic species in cougar diets actually decreased between study period 1 and study period 2; by contrast, ungulates were consistently the top prey item over the course of the study and were used more heavily in study period 2 despite the spread of urbanization. In general, these results suggest that understanding patterns of individual variability may be key to predicting cougar population responses to urbanization, and that under certain conditions cougars may be able to continually rely on ungulate prey even as their environment continues to experience increases in development. Furthermore, my results suggest that an adequate ungulate prey base is a key factor in maintaining cougar persistence in wildland-urban landscapes.

The odds of synanthrope predation by cougars increased with building density, suggesting that urban areas may alter local prey assemblages for individual cougars, and possibly cougar predation risk for certain prey species (Faeth et al. 2005, Lapiedra et al. 2017). While the effect of building density was significant, overall reliance on synanthropic species dropped even as residential density rose between the two study periods. Instead, differences between individuals explained most of the observed variation in usage of synanthropes by cougars. It is possible that these differences among cougars owe to home range arrangement on the landscape, suggesting individual cougar diets may have differed simply because of variation in the diversity of available prey items within their respective home ranges (i.e., because of differences in "ecological opportunity"; Araújo et al. 2011). The distribution of kill site locations for cougars in this study does not provide support for this idea, however. Specifically, M324 and F325, the dominant killers of synanthropic species during study period 1, had overlapping kill site locations with M131, the dominant ungulate killer, and M323, the dominant rodent killer, respectively. M323 was the dominant male in the study site during study period 1, and it is possible that differences in the diets of M323, M324, and F325 reflect spatial avoidance of M323. This may be particularly true for subordinate males, but this possibility remains to be explored. Additionally, F30 significantly differed from all cougars in study period 2 in her reliance on synanthropic species despite her kill locations being similar to those of F12 and F34. Collectively, these results suggest that focal cougars in this study exhibited differences in diet and responded differently to residential development despite having overlapping home ranges. A recent review of predator selectivity indicated that many generalist predator populations consist of individual dietary specialists, with part of the specialization associated with their phenotype (Packer et al. 1990, Pierce et al. 2000, Saulitis et al. 2000, Gaydos et al. 2005, Rutz et al. 2006, Field et al. 2007, Cooper et al. 2007, Maniscalco et al. 2007, Pettorelli et al. 2011). Accordingly, individual specialization is an alternative explanation for the observed variability in synanthrope usage as a function of urbanization, with responses of particular cougars depending on divergent prey preferences stemming from inheritance, learning, and/or competition (Araújo et al. 2011).

The odds of ungulate predation by cougars remained relatively consistent across the wildland-urban gradient, suggesting that cougars were able to maintain similar reliance on ungulates, particularly black-tailed deer, across the wildland-urban gradient despite potential differences in ungulate availability. Individual cougars varied markedly in their use of this prey group, however, despite ungulate usage being greater among cougars in study period 2. Interestingly, cougars that exhibited high reliance on rodent (M323) and synanthropic prey species (F30, M324) differed in their usage of ungulate prey, with F30 relying on ungulates to a degree similar to the population average, while M323 and M324 both relied on ungulate species significantly less than the average cougar. By implication, predicting patterns in individual foraging behavior may not only depend on cougar ID, but prey type as well. The availability of black-tailed deer throughout the wildland-urban gradient might be tied to urbanization, but contrary to our expectation of an inverse relationship, low-density development may actually augment ungulate use of residential landscapes. Hesse (2010) observed that white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*) across British Columbia thrive in edge habitats created by human activity and the establishment of greenways, parks, and planted gardens and trees. Similarly, Duarte et al. (2015) suggest that edge habitats in residential areas can be favorable for red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) in southern Spain. Indeed, species richness across a range of taxa tends to be higher in areas with low to moderate levels of development than in urban centers and preserves (McKinney 2002). This suburban peak is evident in mammals (Racey and Euler 1982), birds and butterflies (Blair 2001), lizards (Germaine and Wakeling 2001), and plants (Kowarik 1995), and is often explained using the intermediate disturbance hypothesis (IDH) whereby moderate disturbance regimes yield a mix of early- and late-successional assemblages (McKinney 2002). By inference, moderate levels of disturbance in western Washington may create landscapes in which black-tailed deer are able to access a diversity of high quality browse while avoiding areas with high amounts of human activity. In accord with this hypothesis, residential development outside of city limits in western

Washington often occurs at low densities and is widely dispersed, and it is common for such areas to contain unique and exotic plants due to cultivation preferences based on individual choices of homeowners (Henderson et al 1998, McKinney 2002). Moreover, the arrangement of rural, low-density housing in western Washington has changed little over time, and such neighborhoods have been shown to reduce the threat of sport hunting toward deer, creating a low risk and high reward landscape for deer throughout wildland-urban gradients (Storm et al. 2007). Previous research on ungulate responses to urbanization in Gallatin Valley, Montana also reported increased nocturnal behavior in both mule deer and white-tailed deer near subdivision (Vogel 1989, Polfus and Krausman 2012). Behavior changes in ungulate species near dwellings, coupled with high quality foraging opportunities and safety from hunting offer a plausible explanation for consistent deer presence in residential areas, and by extension why cougar use of ungulate prey has not decreased over time.

The odds of rodent predation decreased significantly as building density intensified across the wildland-urban gradient, and reliance on rodents decreased significantly between the two study periods. Previous cougar research in western Washington revealed that the majority of beaver and mountain beaver kills occurred within 100m of water, and that cougars frequently foraged along strong habitat edges (Kertson et al. 2011). Accordingly, our results suggest that these areas where cougars target beavers and mountain beavers tend to disappear with urban development, and are therefore consistent with the idea that increasing urbanization in western Washington reduces the quality and availability of riparian habitats for cougars near residences. Interestingly, Kertson et al. (2011a) found that cougars concentrated the majority of their beaver kills during late winter and early spring (February – May). Beavers in western Washington provide a relatively low-risk, high reward prey item for cougars because they are abundant in riparian ecosystems, lack effective anti-predatory adaptations toward stalking predators, and provide substantial biomass with weights that often exceed 20 kg (Kertson et al. 2011a). Thus, if rodents are becoming scarce in residential areas, it is likely cougars will alter their foraging behavior by prey switching to more available species (potentially ungulates or domestics), especially between the months of February-May. Individual cougars differed in their use of rodents, with males exhibiting significantly greater use of rodents than females. M323 was responsible for a substantial portion of rodent kills during this investigation, and may be the primary reason for demographic differences in rodent predation. These results suggest that putative dietary changes are likely to manifest unequally across the population in the study area. Moreover, M323 was the only cougar in the study area that relied on rodent species more than the average cat in this investigation. The greater usage of ungulate and synanthropic prey by cougars when using residential areas implies that any dietary shift at the population level induced by diminishing rodent habitat through urbanization is likely to be modest.

Changes to cougar diets in response to urbanization have been reported previously. For example, housing density influenced cougar consumption of small prey (< 20 kg) in central California (Smith et al. 2016), differential prey use by cougars in western Washington (Kertson et al. 2011a), and prey switching behavior among cougars in northern Colorado (Moss et al. 2016b). Although Kertson et al. (2011a) noted individual patterns in foraging behavior among cougars, to our knowledge no study to date has modeled individual differences in the use of particular prey types along a wildland-urban gradient. In the present study, individual differences among cougars were a significant predictor of predation on all three prey groups, and the dominant driver of cougar use of synanthrope and ungulate prey (which were primarily black-tailed deer). This pattern of individual variation in cougar diets mirrors the individual differences in space use documented by Kertson et al. (2013) in the same system. Although cougars are usually viewed as generalists, the aforementioned spatial overlap of kill site locations for cougars with markedly different diets suggests that these individual differences are unlikely to be a product of unique home range characteristics, and instead appear to be a reflection of individual dietary specialization (Cryan et al. 2012). The generality and causes of this putative pattern of specialization remain to be determined, but it could allow cougars to partition resources in wildland, exurban, and suburban landscapes where the occurrence and abundance of native and non-native prey species is widespread and spatially heterogeneous compared to more homogenized urban centers (Marzluff 2001, Chase and Walsh 2006, McKinney 2006, Shochat et al. 2010). It also suggests that cougar population responses to urbanization, and other forms of human disturbance, are unlikely to be uniform, and therefore, understanding the drivers that cause individuals to specialize on certain prey types is a key to predicting how cougar populations will be shaped by anthropogenic landscape modification.

Investigation of cougar predation patterns in western Washington using cluster methodology allowed for the detection of non-ungulate prey items, but was not without its limitations (Kertson et al. 2011a). For example, kill site examination through GPS cluster analysis has been shown to skew detection rates of predation events toward larger-bodied prey in other large carnivores (e.g., gray wolves, Webb et al. 2008). Additionally, despite similar fix rates among GPS collars in study period 1 and study period 2 (80-95%), data transmission rates differed between collar types. The Televilt Simplex GPS collars used during study period 1 achieved 100% data acquisition through the download on demand capability. Full data acquisition during study period 1 provided adequate opportunities for the detection of predation events spanning <24 hours (Kertson et al. 2011a). The GPS Plus GlobalStar collars used during study period 2, however, frequently had data transmission rates of 60-70%, providing only a subset of the GPS location data (B. Kertson, personal communication) and potentially weakening detection of clusters spanning < 24 hours. It is therefore possible, owing to lower detection probability for small prey, that differences in data transmission between the study periods contributed to a greater proportion of black-tailed deer predation events in study period 2. The individual variation in cougar diets revealed here occurred both during and across the two study periods, however, indicating that the results of this investigation were not simply a function of methodological variation.

4.1. Management and Conservation

The residential landscapes used by cougars in western Washington often fall outside city limits, and these areas have undergone limited development as a consequence of Washington state's approach to managing urban growth. Specifically, in 1990, the Washington state legislature passed the Growth Management Act (GMA; Chapter 36.70A RCW), which largely restricted urban-growth to incorporated townships and cities with the aim of protecting wildlife habitat. By preserving resource production lands within the study site (Robinson et al. 2005), the GMA has apparently maintained enough wildland-like habitat characteristics and corridors for cougars to successfully navigate and forage along the wildland-urban gradient of western Washington. Indeed, similar political will has apparently benefited large carnivore populations in Europe. Namely, in 1992 the European Union (EU) adopted the Habitats Directive, a legislative act that required its state members to make provisions to preserve, protect, and improve the quality of the environment, including the conservation of wild flora and fauna (Council Directive 92/43/EEC 1992). Today, the Habitats Directive covers all 20 EU states with a large carnivore population of at least one species. Accordingly, the average residential density in parts of Europe with permanent large carnivore presence is 19 ± 69.9 inhabitants/km^2, a density similar to that used by cougars along western Washington's wildland-urban gradient (5.251 ± 16.974 buildings/km^2; Chapron et al. 2014). Clearly, proximity to and connectivity with large blocks of wildland habitat remain critical for large carnivores occupying wildland-urban gradients in both the western USA and Europe. Nevertheless, this study and results from Europe indicate that at least some large predator species are capable of maintaining permanent populations near human settlement provided that they are safeguarded by environmental policy and public support (Chapron et al. 2003, Chapron et al. 2014).

Cougars, and large carnivores generally, are controversial species whose management and conservation are complicated by broader emotional, political, and socioeconomic issues (Treves et al. 2003, Chapron and López-Bao 2014, Chapron et al. 2014, Ripple et al. 2014). For example, and much like many other large carnivores (Ripple et al. 2014), cougars are periodically involved in conflicts with livestock producers, ranchers, and rural residents (Gilbert et al. 2016). Modeling individual differences in cougar behavior, as I have done with cougar diets in this study, could aid in mitigating these conflicts by helping to identify individual cougars that may require closer monitoring in residential areas. By distinguishing individual dietary tendencies of this species, for example, wildlife managers could not only determine which animals more frequently use urban areas, but also which animals have greater odds of perpetrating livestock and pet depredations. Targeted predator management has proven useful in minimizing livestock depredations by wolves in Montana, Idaho, and Wyoming (Poudyal et al. 2016). Consideration of individual dietary preferences could facilitate a similar approach to managing cougars that limits lethal removals and other control actions to particular individuals that chronically depredate domestic species.

Finally, cougars in Washington, as well as other predators globally, have been, and to a lesser extent continue to be viewed as troublesome due to safety concerns and predation on livestock (Campbell and Lancaster 2010, Campbell 2013). Yet, my results indicate that, despite individual dietary differences, wild ungulates were the dominant source of prey for cougars across the wildland-urban gradient and in both study periods. This result has two implications for human-cougar coexistence. One, global livestock production continues to encroach on land needed by large carnivores, and human-wildlife conflict over livestock depredations is often exacerbated by the depletion of wild prey (Ripple et al. 2014). In western Washington, cougars rely heavily on black-tailed deer, so promoting the availability of this prey species to cougars in urbanizing areas may be a feasible approach to minimizing the depredation of livestock and other domesticated species. By the same token, minimizing anthropogenic subsidies for deer and habitat quality near homes could be an effective approach for keeping foraging cougars away from residences (Kertson et al. 2011a). Two, the frequency of human conflicts with proliferating large herbivore populations continues to rise in the eastern United States, where cougars are largely absent (Gilbert et al. 2016). Hence, the recovery of cougar populations in these areas, including along wildland-urban gradients, could provide socioeconomic benefits to residents by reducing herbivore abundance and preventing deer-vehicle collisions (Gilbert et al. 2016), possibly neutralizing the economic costs of co-existing with large predators. The results of this study suggest that access to native ungulates, particularly black-tailed deer, could be instrumental in directing cougar foraging toward natural prey, and away from domestic species, along western Washington's wildland-urban gradient. Improving tolerance for large carnivores may depend on demonstrating, as I do in this study, that individual animals may not only differ in their responses to anthropogenic disturbance, but that large carnivores may be able to continue to rely on wild prey in the wake of urban expansion.

LITERATURE CITED

Alberti, M. 2015. Eco-evolutionary dynamics in an urbanizing planet. *Trends in Ecology and Evolution* 30: 114 – 126.

Alberti, M., J. Marzluff, V.M. Hunt. 2017. Urban driven phenotypic changes: empirical observations and theoretical implications for eco-evolutionary feedback. *Philosophical Transactions. The Royal Society Publishing* 372: 20160029. http://dx.doi.org/10.1098/rstb.2016.0229.

Alberti, Marina, Derek Booth, Kristina Hill, Bekkah Coburn, Christina Avolio, Stefan Coe, and Daniele Spirandelli. 2007. The impact of urban patterns on aquatic ecosystems: An empirical analysis in Puget lowland sub-basins. *Landscape and Urban Planning* 80: 345 – 361.

Anderson, Charles R., Frederick G. Lindzey. 2003. Estimating Cougar Predation Rates from GPS Location Clusters. *The Journal of Wildlife Management* 67(2): 307-316.

Araújo, Márcio S., Daniel I. Bolnick, and Craig A. Layman. 2011. The ecological causes of individual specialization. *Ecology Letters* 14: 948 – 958.

Ballard, Warren B. 1995. Bone marrow fat as an indicator of ungulate condition – How good is it? *Alces* 31: 105 – 109.

Bates, Douglas, Martin Maechler, Ben Bolker, Steven Walker, Rune Haubo Bojesen Christensen, Henrik Singmann, Bin Dai, Gabor Grothendieck, and Peter Green. 2016. Package ‘lme4’: Linear Mixed-Effects Models using ‘Eigen’ and S4. R package version 1.1-12.

Beier, P., D. Choate, and R.H. Barrett. 1995. Movement patterns of mountain lions during different behaviors. *Journal of Mammalogy* 76: 1056 – 1070.

Beier, P., P.D. Riley, and R.M. Sauvajot. 2010. Mountain lions (*Puma concolor*). Pages 177 – 189. In: Gehrt, S.D., S.P.D. Riley, and B. Cypher, editors. *Urban carnivores: ecology conflict, and conservation*. John Hopkins University Press, Baltimore, Maryland.

Blair, R.B. 2001. Birds and butterflies along urban gradients in two ecoregions of the U.S. Pgs. 33 – 56 in Lockwood, J.L., and M.L. McKinney, eds. *Biotic Homogenization*. Norwell, MA, USA. Kluwer Academic Publishers.

Burnham, Kenneth P., and David R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. 2nd Ed. New York: *Springer*.

Cain, J.W., P.R. Krausman, B.D. Jansen, and J.R. Morgart. 2005. Influence of topography and GPS fix interval on GPS collar performance. *Wildlife Society Bulletin* 33: 926 – 934.

Campbell, Michael. 2013. The Relevance of Age and Gender for Public Attitudes to Brown Bears (*Ursus arctos*), Black Bears (*Ursus americanus*), and Cougars (*Puma concolor*) in Kamloops, British Columbia. *Society and Animals* 21: 341 – 359.

Campbell, Michael, and Betty-Lou Lancaster. 2010. Public Attitudes toward Black Bears (*Ursus americanus*) and Cougars (*Puma concolor*) on Vancouver Island. *Society and Animals* 18: 40 – 57.

Carbon, C., G.M. Mace, S.C. Roberts, and D.W. Macdonald. 1999. Energetic constraints on the diet of terrestrial carnivores. *Nature* 402: 286 – 288.

Cardillo, Marcel, Andy Purvis, Wes Sechrest, John L. Gittleman, Jon Bielby, and Georgina M. Mace. Human Population Density and Extinction Risk in the World's Carnivores. *PLOS Biology* 2: e197.

Cardillo, Marcel, Georgina M. Mace, Kate E. Jones, Jon Bielby, Olaf R.P. Bininda-Edmonds, Wes Sechrest, C. David L. Orme, and Andy Purvis. 2005. Multiple Causes of High Extinction Risk in Large Mammal Species. *Science* 309: 1239 – 1241.

Chapron, G., J.V. López-Bao. 2014. Conserving carnivores: politics at play. *Science* 343: 234 – 242.

Chapron, G., P. Kaczensky, J.D. Linnell, M.V. Arx, D. Huber, H. Andrén, J.V. López-Bao, M. Adamec, F. Àlvares, O. Anders, L. Balciauskas, V. Balys, P. Bedó, F. Bego, J.C. Blanco, U. Breitenmoser, H. Brøseth, L. Bufka, R. Bunikyte, P. Ciucci, A. Dutsov, T. Engleder, C. Fuxjäger, C. Groff, K. Holmala, B. Hoxha, Y. Iliopoulos, O. Ionescu, J. Jeremic, K. Jerina, G. Kluth, F. Knauer, I. Kojola, I. Kos, M. Krofel, J. Kubala, S. Kunovac, J. Kusak, M. Kutal, O.. Liberg, A. Majic, P. Männil, R. Manz, E. Marboutin, F. Marucco, D. Melovski, K. Mersini, Y. Mertzanis, R. Myslajek, S. Nowak, J. Odden, J. Ozolins, G. Palomero, M. Paunovic, J. Persson, H. Potocnik, P-Y. Quenette, G. Rauer, I. Reinhardt, R. Rigg, A. Ryser, V. Salvatori, T. Skrbinsek, A. Stojanov, J.E. Swenson, L. Szemethy, A. Trajçe, E. Tsingarska-Sedefcheva, M. Váňa, F. Zimmermann, D. Zlatanova, and L. Boitani. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346(6216): 1517 – 1519.

Chapron, G., S. Legendre, R. Ferrière, J. Clobert, and R.G. Haight. 2003. Conservation and control strategies for the wolf (*Canis lupus*) in western Europe based on demographic models. *C.R. Biologies* 326: 575 – 587.

Chase, J.F., and J.J. Walsh. 2006. Urban effects on native avifauna: A review. *Landscape and Urban Planning* 74: 46 – 69.

Cheatum, E.L. 1949. Bone marrow as an index for malnutrition in deer – N.Y. *Conservationist* 3: 19 – 22.

Cooper, A., N. Pettorelli, and S.M. Durant. 2007. Large carnivore menus: factors affecting hunting decisions by cheetahs in the Serengeti. *Animal Behaviour* 73: 651 – 659.

Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora. 2002. No L 206/7.

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

Cryan, Paul M., Craig A. Stricker, and Michael B. Wunder. 2012. Evidence of cryptic individual specialization in an opportunistic insectivorous bat. *Journal of Mammalogy* 93(2): 381 – 389.

Davis, J.L., and D.J. Reed. 1987. Correlations and depletion patterns of marrow fat in caribou bones. *The Journal of Wildlife Management* 51: 365 – 371.

Diamond, Jared. 2002. Evolution, consequences and future of plant and animal domestication. *Nature* 418: 700 – 707.

Dickson, Brett G., and Paul Beier. 2002. Home range and Habitat Selection by Adult Cougars in Southern California. *The Journal of Wildlife Management* 66(4): 1235 – 1245.

Dickson, Brett G., Jeffrey S. Jenness, and Paul Beier. 2005. Influence of Vegetation, Topography, and Roads on Cougar Movement in Southern California. *The Journal of Wildlife Management* 69(1): 264 – 276.

Donihue, C.M., M.R. Lambert. 2015. Adaptive evolution in urban environments. *Ambio* 44: 194 – 203.

Duarte, Jesús, Miguel A. Farfán, John E. Fa, and J. Mario Vargas. 2015. Deer populations inhabiting urban areas in the south of Spain: habitat and conflicts. *European Journal of Wildlife Research* 61: 365 – 377.

Ellis, E.C., K. Klein Goldewijk, S. Siebert, D. Lightman, N. Ramankutty. 2010. Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography* 19: 589-606.

Environmental Systems Research Institute, Inc. (Esri). 2016. ArcGIS for Desktop: How Kernel Density Works. ArcMap 10.3. http://desktop.arcgis.com/en/arcmap/10.3/tools/spatial-analyst-toolbox/how-kernel-density-works.htm

Faeth, Stanley H., Paige S. Warren, Eyal Shochat, and Wendy A. Marussich. 2005. Trophic Dynamics in Urban Communities. *BioScience* 55(5): 399 – 407.

Field, I., C. Bradshaw, J. van den Hoff, H. Burton, M. Hindell. 2007. Age-related shifts in the diet composition of southern elephant seals expand overall foraging niche. *Marine Biology* 150: 1441 – 1452.

Franklin, Jerry F., and C.T. Dyrness. 1973. Natural Vegetation of Oregon and Washington. General Technical Report PNW-8. Pacific Northwest Forest and Range Experimental Station, *USDA Forest Service*. Portland, Oregon, USA.

Gaydos, J.K., S. Raverty, R.W. Baird, and R.W. Osborne. 2005. Suspected surplus killing of harbor seal pups (*Phoca vitulina*) by killer whales (*Orcinus orca*). *Northwest Naturalist* 86: 150 – 154.

Germaine, S.S., and B.F. Wakeling. 2001. Lizard species distributors and habitat occupation along an urban gradient in Tucson, Arizona, USA. *Biological Conservation* 97: 229 – 237.

Gilbert, Sophie L., Kelly J. Sivy, Casey B. Pozzanghera, Adam DuBour, Kelly Overduijn, Matthew M. Smith, Jiake Zhou, Joseph M. Little, and Laura R. Prugh. 2016. Socioeconomic Benefits of Large Carnivore Recolonization Through Reduced Wildlife-Vehicle Collisions. *Conservation Letters* 0: 1 – 9.

Gray, Morgan, Christopher C. Wilmers, Sarah E. Reed, Adina M. Merenlender. 2016. Landscape feature-based permeability models relate to puma occurrence. *Landscape and Urban Planning* 147: 50 – 58.

Henderson, S.P.B., N.H. Perkins, and M. Nelischer. 1998. Residential lawn alternatives: A study of their distribution, form and structure. *Landscape and Urban Planning* 42: 135 – 145.

Hendry, A.P., T.J. Farrugia, and M.T. Kinnison. 2008. Human influences on rates of phenotypic change in wild animal populations. *Molecular Ecology* 17: 20 – 29.

Hesse, Gayle. 2010. British Columbia Urban Ungulate Conflict Analysis. *British Columbia Ministry of Environment*: 1 – 237.

Kertson, Brian N., and John M. Marzluff. 2010. Improving studies of resource selection by understanding resource use. *Environmental Conservation* 38(1): 18 – 27.

Kertson, Brian N., Rocky D. Spencer, Christian E. Grue. 2013. Demographic influences on cougar residential use and interactions with people in western Washington. *Journal of Mammalogy* 94(2): 269-281.

Kertson, Brian N., Rocky D. Spencer, and Christian E. Grue. 2011a. Cougar prey use in a wildland-urban environment in western Washington. *Northwestern Naturalist* 92: 175 – 185.

Kertson, Brian N., Rocky D. Spencer, John M. Marzluff, Jeff Hepinstall-Cymerman, Christian E. Grue. 2011b. Cougar space use and movements in the wildland-urban landscape of western Washington. *Ecological Applications* 21(8): 2866-2881.

Kunkel, K.E. 2003. Ecology, conservation, and restoration of large carnivores in western North America. In: Zabel, C.J., and R.G. Anthony. *Mammal Community Dynamics: Management and Conservation in the Coniferous Forests of Western North America*. Cambridge University Press. Cambridge, UK.

Knopff, Aliah Adams, Kyle H. Knopff, Mark S. Boyce, and Colleen Cassady St. Clair. 2014. Flexible habitat selection by cougars in response to anthropogenic development. *Biological Conservation* 178: 136 – 145.

Knopff, Kyle H., Aliah Adams Knopff, Andrea Kortello, and Mark S. Boyce. 2010. Cougar kill rate and prey Composition in a multiprey system. *The Journal of Wildlife Management* 74(7): 1435 – 1447.

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

Kowarik, I. 1995. On the role of alien species in urban flora and vegetation. Pgs. 85 – 103 in Pysek, P., K. Prach, M. Rejmánek, and P.M. Wade, eds. *Pant Invasions—General Aspects and Special Problems*. Amsterdam, Netherlands: SPB Academic.

Laliberte, A.S., and W.J. Ripple. 2004. Range contractions of North American carnivores and ungulates. *BioScience* 54: 123 – 138.

Lapiedra, Oriol, Zachary Chejanovski, and Jazon J. Kolbe. 2017. Urbanization and biological invasion shape animal personalities. *Global Change Biology* 23: 592 – 603.

Lewis, Jesse S., Kenneth A. Logan, Mat W. Alldredge, Larissa L. Bailey, Sue VandeWoude, and Kevin R. Crooks. 2015. The effects of urbanization on population density, occupancy, and detection probability of wild felids. *Ecological Applications* 25(7): 11880 – 1895.

López-Bao, J.V., P. Kaczensky, J.D.C. Linnell, L. Biotani, G. Chapron. 2015b. Carnivore coexistence: wilderness not required. *Science* 348: 871 – 872.

Maniscalco, J.M., C.O. Matkin, D. Maldini, D. Calkins, and S. Atkinson. 2007. Assessing killer whale predation on Steller sea lions from field observations in Kenai fjords, Alaska. *Marine Mammal Science* 23: 306 – 321.

Markovchick-Nicholls, Lisa, Helen M. Regan, Douglar H. Deutschman, Astrid Widyanata, Barry Martin, Lani Noreke, and Timothy Ann Hunt. 2008. Relationships between Human Disturbance and Wildlife Land Use in Urban Habitat Fragments. *Conservation Biology* 22(1): 99 – 109.

Marzluff, John M., Jack H. DeLap, M. David Oleyar, Kara A. Whittaker, and Beth Gardner. 2016a. Breeding Dispersal of Birds in a Dynamic Urban Ecosystem. *PloSONE* 11(12): e0167829.

Marzluff, John, Barbara Clucas, M. David Oleyar, and Jack DeLap. 2016b. The casual response of avian communities to suburban development: a quasi-experimental longitudinal study. *Urban Ecosystems* 19: 1597 – 1621.

Marzluff, John. 2001. Worldwide urbanization and its effects on birds. Pgs. 19 – 38 in Marzluff, J., R. Bowman, and R. Donnelly, eds. *Avian Ecology and Conservation in an Urbanizing World*. Kluwer Academic Publishers.

Maxwell, Sean, Richard A. Fuller, Thomas M. Brooks, et al. 2016. The ravages of guns, nets and bulldozers. *Nature* 536(7615): 143 – 145.

McDonnell, M.J., A.K. Hahs. 2015. Adaptation and adaptedness of organisms to urban environments. *Annual review of ecology, evolution, and systematics* 46: 261 – 280.

McKinney, Michael L. 2002. Urbanization, Biodiversity, and Conservation: The impacts of urbanization on native species are poorly studied, but education a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *BioScience* 52(10): 883 – 890.

McKinney, Michael L. 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation* 127: 247 – 260.

Moss, Wynne E., Mathew W. Alldredge, Kenneth A. Logan, and Jonathan N. Pauli. 2016b. Human expansion precipitates niche expansion for an opportunistic apex predator (*Puma concolor*). *Scientific Reports* 6:39639. DOI: 10.1038/srep39639.

Moss, Wynne E., Mathew W. Alldredge, Jonathan N. Pauli. 2016a. Quantifying risk and resource use for a large carnivore in an expanding urban-wildland interface. *Journal of Applied Ecology* 53: 371-378.

Musiani, Marco, and Paul C. Paquet. 2004. The Practices of Wolf Persecution, Protection, and Restoration in Canada and the United States. *BioScience* 54(1): 50 – 60.

Newsome, Seth D., Heidi M. Garbe, Evan C. Wilson, and Stanley D. Gehrt. 2015a. Individual variation in anthropogenic resource use in an urban carnivore. *Oecologia* 178: 115 – 128.

Newsome, Thomas M., Justin A. Dellinger, Chris R. Pavey, William J. Ripple, Carolyn R. Shores, Aaron J. Wirsing, and Christopher R. Dickman. 2015b. The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography* 24: 1 – 11.

Newsome, Thomas M., Luigi Boitani, Guillaume Chapron, Paolo Ciucci, Christopher R. Dickman, Justin A. Dellinger, José V. López-Bao, Rolf O. Peterson, Carolyn R. Shores, Aaron J. Wirsing, William J. Ripple. 2016. Food habits of the world's grey wolves. *Mammal Review*. Doi: 10.1111/mam.12067.

Ordeñana, Miguel A., Kevin R. Crooks, Erin E Boydston, Robert N. Fisher, Lisa M. Lyren, Shalene Suidyla, Christopher D. Haas, Sierra Harris, Stacie A. Hathaway, Greta M. Turschak, A. Keith Miles, and Dirk H. Van Vuren. 2010. Effects of urbanization on carnivore species distribution and richness. *Journal of Mammalogy* 91(6): 1322 – 1331.

Packer, C. A. Loveridge, S. Canney, T. Caro, S.T. Garnett, M. Pfeifer, K.K. Zander, A. Swanson, D. MacNulty, G. Balme, H. Bauer, C.M. Begg, K.S. Begg, S. Bhalla, C. Bissett, T. Bodasing, H. Brink, A.C. Burton, B. Clegg, S. Dell, A. Delsink, T. Dickerson, S.M. Dloniak, D. Druce, L. Frank, P. Funston, N. Gichohi, R. Groom, C. Hanekom, B. Heath, L. Hunter, H.H. Delongh, C.J. Joubert, S.M. Kasiki, B. Kissui, W. Knocker, B. Leathem, P.A. Lindsey, S.D. Maclennan, J.W. McNutt, S.M. Miller, S. Naylor, P. Nel, C. Ng'weno, K. Nicholls, J.O. Ogutu, E. Okot-Omoya, B.D. Patterson, A. Plumptre, J. Salerno, K. Skinner, R. Slotow, E.A. Sogbohossou, K.J. Stratford, C. Winterbach, H. Winterbach, and S. Polasky. 2013. Conserving large carnivores: dollars and fence. *Ecological Letters* 16(5): 635 – 641.

Packer, C., D. Scheel, and A.E. Pusey. 1990. Why lions form groups: food is not enough. *American Naturalist* 136: 1- 19.

Palkovacs, E.P., A.P. Hendry. 2010. Eco-evolutionary processes in contemporary time. *F1000 Biology Reports* 2: 1. DOI: 10.3410/B2-1.

Palkovacs, E.P., M.T. Kinnison, C. Cornea, C.M. Dalton, and A.P. Hendry. 2012. Fates beyond traits: ecological consequences of human-induced trait change. *Evolutionary Applications* 5: 183 – 191.

Pettorelli, Nathalie, Tim Coulson, Sarah M. Durant, and Jean-Michel Gaillard. 2011. Predation, individual variability and vertebrate population dynamics. *Oecologia* 167(2): 305 – 314.

Pierce, B.M., V.C. Bleich, and R.T. Bowyer. 2000. Selection of mule deer by mountain lions and coyotes: effects of hunting style, body size, and reproductive status. *Journal of Mammalogy* 81: 462 – 472.

Pimm, Stuart L., Peter Raven. 2000. Extinction by numbers. *Nature* 403: 843-845.

Polfus, Jean L., and Paul R. Krausman. 2012. Impacts of Residential Development on Ungulates in the Rocky Mountain West. *Wildlife Society Bulletin* 36(4): 647 – 657.

Poudyal, Niraj, Nabin Baral, and Stanley T. Asah. 2016. Wolf Lethal Control and Livestock Depredations: Counter-Evidence from Respecified Models. *PloSONE* 11(12): e0148743.

Price, Douglas T., and Ofer Bar-Yosef. 2011. The Origins of Agriculture: New Data, New Ideas An Introduction to Supplement 4. *Current Anthropology* 52(S4): S163 – S174.

Racey, G.D., and D.L. Euler. 1982. Small mammal and habitat response to shoreline cottage development in central Ontario, Canada. *Canadian Journal of Zoology* 60: 865 – 880.

Revilla, Eloy. 2003. What Does the Resource Dispersion Hypothesis Explain, if Anything? *Oikos* 101(2): 428 – 432.

Riley, S.P.D., L.E.K. Serieys, J.P. Pollinger, J.A. Sikich, L. Dalbeck, R.K. Wayne, and H.B. Ernest. 2014. Individual behaviors dominate the dynamics of an urban mountain lion population isolated by roads. *Current Biology* 24: 1- 6.

Ripple, William J., Robert L. Beschta, Jennifer K. Fortin, and Charles T. Robbins. 2013. Trophic cascades from wolves to grizzly bears in Yellowstone. *Journal of Animal Ecology* 83: 223 – 233.

Ripple, William J., James A. Estes, Robert L. Beschta, Christopher C Wilmers, Euan G. Ritchie, Mark Hebblewhite, Joel Berger, Bodil Elmhagen, Mike Letnic, Michael P. Nelson, Oswald J. Schmitz, Douglas W. Smith, Arian D. Wallach, Aaron J. Wirsing. 2014. Status and Ecological Effects of the World's Largest Carnivores. *Science* 343: DOI: 10.1126/science. 1241484.

Robinson, Lin, Joshua P. Newell, and John M. Marzluff. 2005. Twenty-five years of sprawl in the Seattle region: growth management responses and implications for conservation. *Landscape and Urban Planning* 71: 51 – 72.

Rutz, C., M.J. Whittingham, and I. Newton. 2006. Age-dependent diet choice in an avian top predator. *Proceedings of the Royal Society B: Biological Sciences* 273: 579 – 586.

Sandom, C., S. Faurby, B. Sandel, and J.C. Svenning. 2014. Global late Quaternary megafauna extinctions linked to humans, not climate change. *Proceedings of the Royal Society B: Biological Sciences* 281: 20133254.

Saulitis, E., C. Matkin, L. Barrett-Lennard, K. Heise, and G. Ellis. 2000. Foraging strategies of sympatric killer whale populations in Prince Williams Sound, Alaska. *Marine Mammal Science* 16: 94 – 109.

Schielzeth, H., E. Bolund, B. Kempenaers, and W. Forstmeier. 2011. Quantitative genetics and fitness consequences of neophilia in zebra finches. *Behavioral Ecology* 22: 126 – 134.

Severinghaus, C.W. 1949. Tooth Development and Wear as Criteria of Age in White-Tailed Deer. *The Journal of Wildlife Management* 13(2): 195 – 216.

Schochat, E., S. Lerman, J.M. Anderies, P.S. Warren, S.H. Faeth, and C.H. Nilon. 2010. Invasion, Competition, and Biodiversity Loss in Urban Ecosystems. *BioScience* 60(3): 199 – 208.

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

Smith, J. A., Y. Wang, and C.C. Wilmers. 2016. Spatial Characteristics of Residential Development Shift Large Carnivore Prey Habits. *The Journal of Wildlife Management* 80(6): 1040 – 1048.

Storm, Daniel J., Clayton K. Nielsen, Eric M. Schauber, and Alan Woolf. 2007. Space Use and Survival of White-Tailed Deer in an Exurban Landscape. *The Journal of Wildlife Management* 71(4): 1170 – 1176.

Sunquist, Mel, and Fiona Sunquist. 2002. *Wild Cats of the World*. University of Chicago Press, Chicago, USA: 1-452.

Theobald, David M. 2010. Estimating natural landscape changes from 1992 to 2030 in the conterminous US. *Landscape Ecology* 25: 999 – 1011.

Theobald, David M. 2005. Landscape Patterns of Exurban Growth in the USA from 1980 to 2020. *Ecology and Society* 10(1): 32.

Tigas, Lourraine A., Dirk H. Van Vuren, and Raymond M. Souvajot. 2002. Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. *Biological Conservation* 108: 299 – 306.

Torres, S.G., T.M. Mansfield, J.E. Foley, T. Lupo, and A. Brinkhaus. 1996. Mountain lion and human activity in California: testing speculations. *Wildlife Society Bulletin* 24: 451 – 460.

Treves, Adrian, and K. Ullas Karnath. 2003. Human-Carnivore Conflict and Perspectives on Carnivore Management Worldwide. *Conservation Biology* 17(6): 11491 – 1499.

United States Census Bureau. 2015. “Quick Facts.” census.gov. March 31, 2017. < https://www.census.gov/quickfacts/table/PST045216/00 >

Van Oers, K., P.J. Drent, P. de Goede, and A.J. van Noordwijk. 2004. Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. *Proceedings of the Royal Society B: Biological Sciences* 271: 65 – 73.

Vogel, W.O. 1989. Response of deer to density and distribution of housing in Montana. *Wildlife Society Bulletin* 17: 406 – 413.

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

Weaver, John L., Paul C Paquet, Leonard F. Ruggiero. 1996. Resilience and Conservation of Large Carnivores in the Rocky Mountains. *Conservation Biology* 10(4): 964-976.

White, KR, GM Koehler, BT Maletzke, and RB Wielgus. 2011. Differential prey use by male and female Cougars in Washington. *Journal of Wildlife Management* 75: 1115 – 1120.

Wilckens, David T., Joshua B. Smith, Stephanie A. Tucker, Daniel J. Thompson, and Jonathan A. Jenks. 2016. Mountain lion (*Puma concolor*) feeding behavior in the Little Missouri Badlands of North Dakota. *Journal of Mammalogy* 97(2): 373 – 385.

Williams, Terrie M., Lisa Wolfe, Tracy Davis, Traci Kendall, Beau Richter, Yiwei Wang, Caleb Bryce, Gabriel Hugh Elkaim, and Christopher C. Wilmers. 2014. Instantaneous energetics of puma kills reveal advantage of felid sneak attacks. *Science* 346(6205): 81 – 85.

Wilmers, Christopher C., Yiwei Wang, Barry Nickel, Paul Houghtaling, Yasaman Shakeri, Maximilian L. Allen, Joe Kermish-Wells, Veronica Yovovich, and Terrie Williams. 2013. Scale Dependent Behavioral Responses to Human Development by a Large Predator, the Puma. *PloSONE* 8(4): e60590.

Wolf, M., G.S. van Doorn, and F.J. Weissing. 2008. Evolutionary emergence of responsive and unresponsive personalities. *Proceedings of the National Academy of Sciences of the United States of America* 105: 15825 – 15830.