Effects of urbanization on cougar foraging ecology along the wildland–urban gradient of western Washington

CLINT W. ROBINS,[1],† BRIAN N. KERTSON,[2] JAMES R. FAULKNER,[3,4] AND AARON J. WIRSING[1]

[1]School of Environmental and Forest Sciences, University of Washington, Box 352100, Seattle, Washington 98195 USA
[2]Washington Department of Fish and Wildlife, 1775 12th Avenue NW, Suite 201, Issaquah, Washington 98027 USA
[3]Quantitative Ecology and Resource Management, University of Washington, Box 357941, Seattle 98195 USA
[4]National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, Washington 98112 USA

Abstract. Humans have dramatically altered ecosystem structure through landscape manipulation, often leaving refuge patches of suitable habitat for wildlife amidst inhospitable terrain. Large carnivores are especially vulnerable to such habitat modification because they tend to have low population densities and wide-ranging movements necessitated by their food requirements. Cougars (*Puma concolor*), unlike many other large carnivores, have demonstrated an ability to exploit resources in fragmented and managed landscapes. The influence of increasing landscape development on cougar foraging behavior, however, has yet to be fully elucidated. Accordingly, we investigated variation in cougar use of three prey types (synanthropes, ungulates, and rodents) along a wildland–urban gradient in western Washington to determine how urbanization affects the foraging ecology of this apex predator. We predicted that cougar diets would comprise more synanthropic prey (e.g., prolific urban species) and fewer deer as a function of increasing residential development. Generalized linear mixed model results showed that the odds of cougar predation on synanthropic prey did increase with urbanization. The odds of ungulate predation, however, remained relatively consistent across the wildland–urban gradient despite cougar use of black-tailed deer (*Odocoileus hemionus columbianus*) and elk (*Cervus canadensis*) increasing over time. These results suggest that cougar–ungulate predator–prey systems can persist in landscapes with substantial human presence. The odds of forest-associated rodent (*Castor* sp., *Aplodontia* sp.) predation decreased with increasing development, suggesting that urbanization may coincide with more intensive beaver management near residences and thereby reduce beaver and mountain beaver presence in exurban landscapes in western Washington. Most cougars exhibited similar diets, but certain individuals deviated significantly from the population averages characterizing use of all three major prey categories. This variation suggests that cougar population responses to urbanization are unlikely to be uniform and that cases of human–cougar conflict may be linked to individual cats, rather than the population as a whole.

† E-mail: crobins4@uw.edu

INTRODUCTION

Since the onset of plant and animal domestication ~12,000 yr 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 (Palkovacs et al. 2012, McDonnell and Hahs 2015, Alberti et al. 2017). There remains a need, however, for a better understanding of 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). In northeastern Illinois, USA, for example, urbanization has translated into changes to mesopredator community structure, as certain species, like raccoons (*Procyon lotor*), continue to increase in abundance, limiting resources for Virginia opossums (*Didelphis virginiana*) and striped skunks (*Mephitis mephitis*; Prange and Gehrt 2004). Large mammalian carnivores are especially vulnerable to human development as these species tend to have low reproductive rates, must roam widely in search of prey, and often come into conflict with humans over livestock depredation and personal safety (Cardillo et al. 2005, 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, 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). In Luxembourg, for example, the socio-spatial organization of stone marten (*Martes foina*) populations is largely unaffected by urbanization (Herr et al. 2009). In urban Chicago, USA, Newsome et al.

(2015a) showed that individual variation in movement and diet facilitated the successful establishment of coyotes (*Canis latrans*) throughout the Chicago metropolitan area. 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 (Lowry et al. 2013, Moss et al. 2016a).

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). Historically, cougars were associated with wildland environments, but recent studies have revealed that cougars are capable of utilizing areas with an extensive human presence (Beier et al. 2010, 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 (Kertson et al. 2011b, Lewis et al. 2015a, 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, Blecha et al. 2018). Cougars in urbanized ecosystems have also been found to increase their consumption of non-ungulate prey, which is presumably a by-product of increased availability due to landscape development (Smith et al. 2015, Moss et al. 2016a, b). As urbanization intensifies, overlap between cougar and human populations will increase, especially in areas where residential development extends into cougar activity spaces and wild landscapes. Thus far, however, only two studies from the same ecosystem in northern Colorado have addressed changes in cougar foraging behavior over time along a wildland–urban gradient (Moss et al. 2016a, b). No study has yet considered changes in the probability of particular prey species being killed by cougars as they exploit increasingly urbanized portions of the landscape. Additional longitudinal studies of this nature are crucial to broadening our understanding of how the intensity of urbanization functionally changes cougar ecology and for

predicting how cougar populations will fare as urbanization continues to increase. Accordingly, we examined changes to cougar foraging behavior over time along an 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. 2013). Examination of cougar space use along this gradient revealed that resident cougars exhibited similar movement patterns in wildland and residential environments (Kertson et al. 2011*b*) but varied markedly in their space use. 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/1000 radio days; Kertson et al. 2013). Moreover, Kertson et al. (2011*a*) documented differential prey use across the gradient, suggesting that urbanization and corresponding residential development have shaped cougar diets in western Washington. The spatiotemporal relationship between building density and cougar diets in this system has not been investigated, however. Accordingly, we evaluated changes to cougar diets spatially across a wildland–urban gradient using kill site data collected during two study periods, the years 2004–2008 (termed hereafter as "study period 1") and 2013–2016 (termed "study period 2" hereafter), in a region where we were also able to quantify building density (per ha). Under the hypothesis that cougars adjust their foraging behavior to take advantage of widely available prey (Kertson et al. 2011*a*, Moss et al. 2016*a*), we predicted that increasing building density would be associated with an elevated presence of synanthropic species (e.g., prolific urban species; McKinney 2006, 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. 2011*a*). We also included a study period variable in our analysis to determine if any temporal changes to

cougar diets occurred between the two data collection phases. Lastly, we hypothesized that while cougars would forage opportunistically, individuals would be likely to vary in their foraging responses to urbanization, mirroring the individual variation exhibited in their space use (Kertson et al. 2013).

METHODS

Study site

We examined cougar kill site locations in a 4450-km^2 study site encompassing portions of King, Snohomish, and Pierce counties in Washington, USA (590,000 E, 5,260,000 N; Fig. 1). Landownership 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 (7674), and North Bend (6679; US Census Bureau 2015).

The study site is topographically complex and 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. 2011*b*). 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 ecoregion (Franklin and Dyrness 1973). The topographic, physiographic, and developmental characteristics of the study site are described at greater length in Kertson et al. (2011*b*, 2013).

Radio-tagging and GPS cluster analysis

We 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
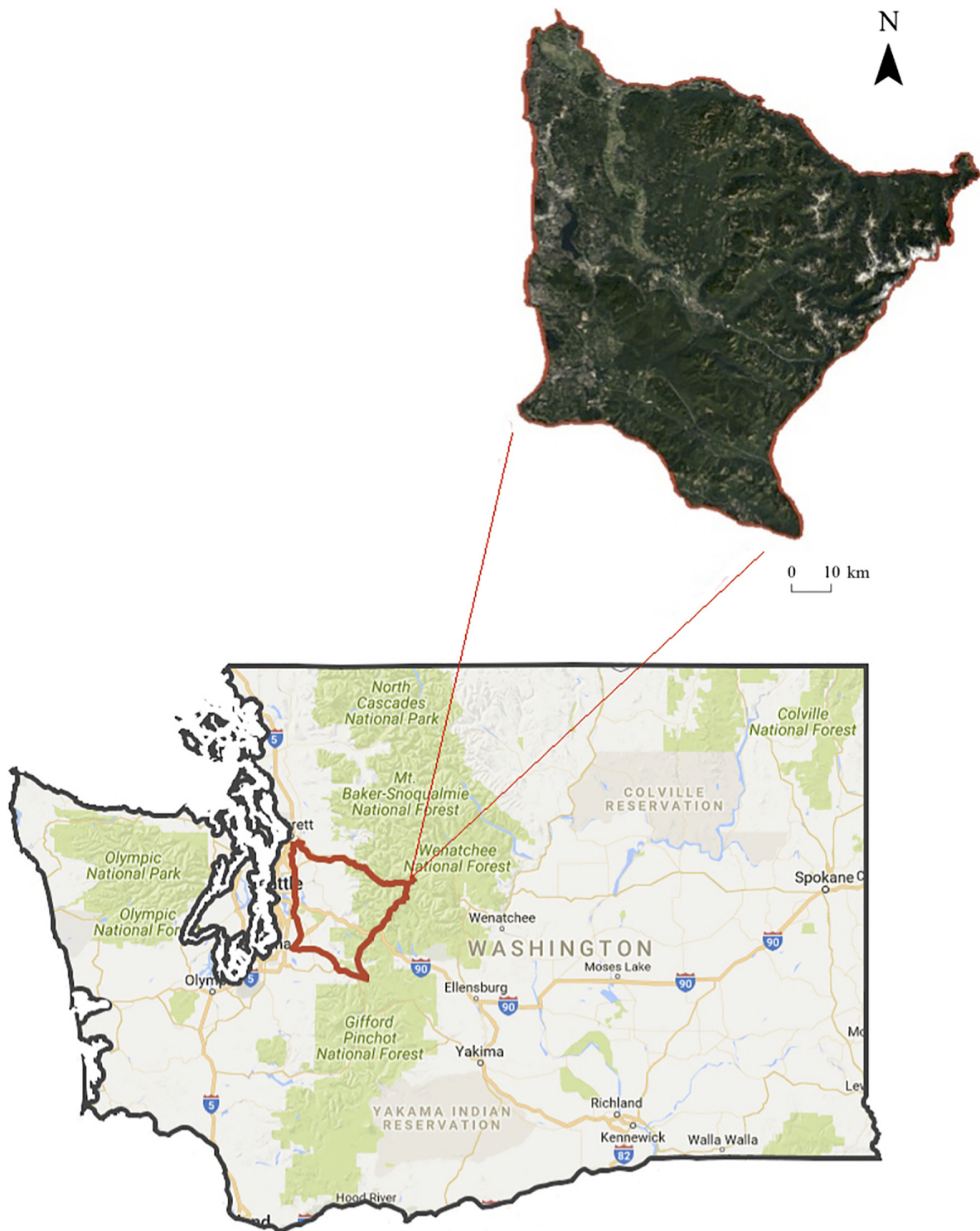
Fig. 1. Location of the 4450-km^2 cougar (*Puma concolor*) study site encompassing portions of King County, Snohomish County, and a small section of wildland in Pierce County (<75 km^2). The study site used by Washington's

(Fig. 1. *Continued*)
Department of Fish and Wildlife during period 1 was smaller (3500 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.

a global positioning system (GPS) radio collar equipped with Vhf/Uhf download or Globalstar satellite uplinks (Models GPS-Simplex; Televilt, Lindesberg, Sweden, and GPS Plus-2; 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 accordance with University of Washington Institutional Animal Care and Use Committee (IACUC) protocol No. 3077-07. All capture methods have been vetted previously and described in detail elsewhere (Kertson and Marzluff 2010, Kertson et al. 2011*a*, *b*, 2013).

We programmed GPS radio collars to attempt a satellite fix for 180 s every four hours at 2:00, 6:00, 10:00, 14:00, 18:00, and 22:00 hours. The 4-h fix interval was chosen to maximize data acquisition and battery life (Cain et al. 2005, Kertson et al. 2011*b*). We identified potential kill site locations during study period 2 in accordance with the methodology used by Kertson et al. (2011*a*) during study period 1. Namely, we first plotted cougar relocations in ArcMap 10.3 and 10.4 (Environmental Systems Research Institute 2016) and Google Earth (Google, Mountain View, California, USA) and then defined location clusters as ≥3 GPS fixes occurring within an area ≤100 m^2 (methods by Anderson and Lindzey 2003 adapted to account for small prey items). We used a handheld GPS receiver (Model Etrex 20; Garmin, Schaffhausen, Switzerland) to navigate to the geometric center of the cluster, and we searched in concentric circles varying between 5 and 10 m apart (depending on visibility) out to the extent of the cluster radius (up to 100 m) or until prey remains were discovered. We 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 we 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, Kertson et al. 2011*a*, Wilckens et al. 2016).

Kill site assessment

Kill site assessment followed the same methodology during study period 2 as in study period 1. Namely, after confirming each kill site location, we adjusted kill site coordinates on-site to correspond to the location of the rumen. Cougars may cache a carcass 0–80 m from the initial kill location during subsequent feeding bouts (Beier et al. 1995), so designating the position of the rumen as the kill location allowed for more consistent assessment of kill site features. Whenever possible, we documented prey species, sex, age, condition, and relative carcass consumption (Kertson et al. 2011*a*). We 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).

Statistical analysis

We used generalized linear mixed models (GLMMs) to test whether building density, a proxy for urbanization intensity (Theobald 2005, 2010), had an effect on the occurrence of certain prey items at cougar kill sites across the wildland–urban gradient. To create a building density predictor variable, we quantified urbanization within the study site using ArcMap 10.4 (Silverman 1986) and GIS parcel data from King and Snohomish counties, Washington, USA. We acquired parcel data for years 2007 and 2015 (King County) and 2004 and 2016 (Snohomish County) through the University of Washington Libraries media archive, along with the associated assessor's tables containing parcel attribute data, and created landscape categories based on Robinson et al. (2005) and Alberti et al. (2007), and urbanization was quantified as the density of built structures per hectare. We used the 2004 and 2007 shapefiles to approximate the extent of landscape development at kill site locations in both Snohomish and King counties during study period 1, whereas the 2015 and 2016 shapefiles

were used to approximate landscape development at kill sites during study period 2. Parcels with forms of development such as parking lots, residences, office spaces, shopping centers, major roads, schools, hospitals, and government institutions were used to generate building density raster layers. In other words, the measure of urbanization in this study can be considered the density of actual physical obstructions to cougar movement across the landscape. 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 land cover composition and configuration.

To quantify building density at each cougar kill location throughout the study site, we 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, we extracted raster cell values for all kill site locations. The resulting values represented a continuous building density variable per hectare. Average building density at kill site locations was 0.05 structures/ha. All kills that occurred in the Pierce County portion of the study area occurred in wildland areas, obviating 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 in cougar diets, we modeled the type of species killed using logistic regressions with building density, cougar sex, and study period as independent variables, and cougar ID included as a random effect. To achieve sample sizes necessary for modeling of cougar diets, we grouped prey species into three ecologically relevant categories: ungulates, synanthropes, and rodents. These prey categories closely mirror those used by Moss et al. (2016*b*), who grouped prey into meaningful categories based on isotopic signatures. The ungulate group in this study consisted of species heavily preyed upon by cougars in western Washington: namely, black-tailed deer (*Odocoileus hemionus columbianus*), elk (*Cervus canadensis*), and mountain goat (*Oreamnos americanus*). Rodents (i.e., beaver,

Castor canadensis; mountain beaver, *Aplodontia rufa*) are largely wildland obligates in our system. Synanthropic species included coyotes, raccoons, opossums, and domestic species. Whereas coyotes are capable of occupying all land cover types in the study area, coyote predation by cougars often occurred along the urban fringe in western Washington, supporting the inclusion of this species in the synanthrope group. Null models contained only a single fixed intercept. We considered all possible interaction effects among fixed predictor variables in candidate models for each response.

We built candidate model sets (i.e., various predictor variable combinations) for each of the three prey categories, with a binary response of either 1 for the prey type of interest (e.g., synanthropes) or 0 for the other two prey categories combined (e.g., ungulates, rodents). We then ranked candidate models based on differences in the Akaike information criterion (AIC) in accordance with Burnham and Anderson (2002). Differences in AIC (ΔAIC) were calculated relative to the best model, and we only considered models with ΔAIC ≤2 relative to the best model to be competitive (Burnham and Anderson 2002). We considered fixed and random effects significant if 95% confidence intervals (CIs) for their respective coefficient estimates did not overlap 0. Profile CIs were used to evaluate the standard deviation of the cougar ID random effect in each top model, and standard Wald CIs were used to quantify the uncertainty of fixed effect estimates. Odds ratios and their associated 95% CIs were used to evaluate the effect magnitude of the fixed and random effects in each of the top models and were considered significant if they did not overlap 1.0. We built all models using the glmer and glm functions in the lme4 package (Bates et al. 2016) in the R statistical package (R Core Team 2016).

Results

Cougar foraging behavior

We evaluated diets from 20 individual cougars to determine whether cougar diets varied spatially (i.e., across the urban gradient), and whether cougar diets changed over time (i.e., between study periods). Overall, cougar diets included 15 different prey species (Fig. 2), with

black-tailed deer (n = 407 kills) and American beaver (n = 70 kills) accounting for the majority of cougar kills based on investigation of GPS clusters (Table 1). Spatially, synanthropic species tended to occur in areas with greater building density than areas associated with rodent and ungulate kills (Appendix S1: Fig. S1). The study period fixed effect was only included in the ungulate and rodent top models (Table 2), indicating little temporal change in cougar predation on synanthropes. The distributions of kill site locations from study period 1 and study period 2 were roughly equivalent across the wildland–urban gradient, minimizing the likelihood that differences in cougar diets between study periods were a function of differences in sampling effort in residential areas (Fig. 3; Appendix S1: Table S1). Despite synanthropic species occurring in areas with greater building density, building density changed little among prey groups across time, and the average residential density at which kill site locations occurred did not vary markedly across all years of the investigation (Fig. 4).

The occurrence of synanthropic species in cougar diets was strongly tied to individual cougar identity, as well as the extent of urbanization (Fig. 5). Namely, the top synanthrope model included building density as the sole fixed effect (Table 2) and indicated that there was a multiplicative increase of 4.92 (95% CI: 1.09, 22.23) in the odds of cougar predation on synanthropic species with each additional building per hectare. 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 $\hat{\sigma}$ = 1.26 (95% CI: 0.68, 2.26). Predicted probabilities of synanthrope kills calculated at average building density were similar across the majority of cougars in this study (Fig. 6). Three individuals (F30, M324, and F325), however, differed significantly from the study average in their predicted probability of predation on synanthropic prey.

There was a high probability of ungulate predation across the wildland–urban gradient (Fig. 5), and 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 and the random cougar effect with no interaction
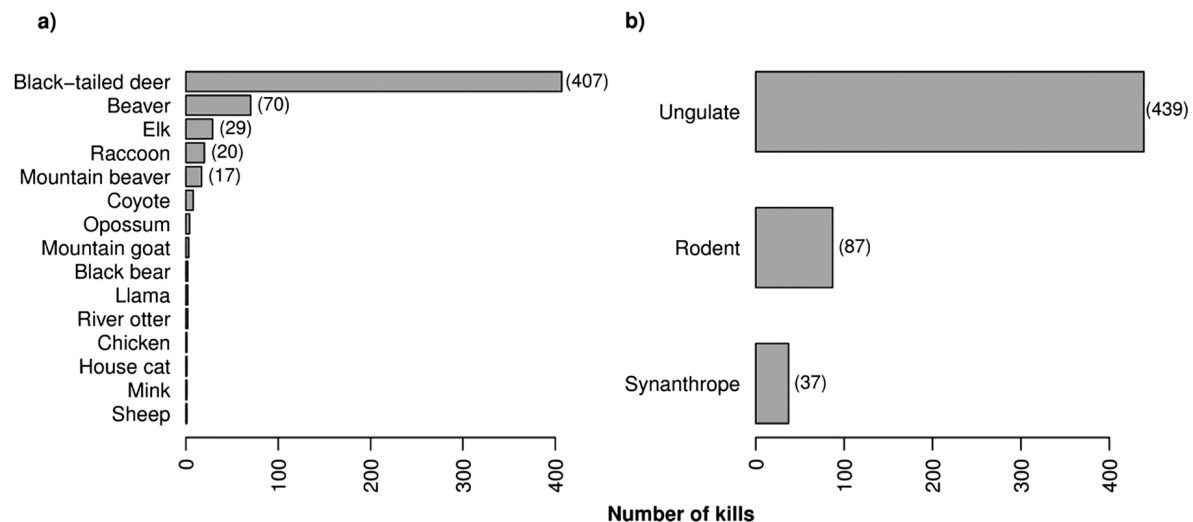

Fig. 2. (a) Numbers of prey individuals killed by cougars (n = 568) across all study years, grouped by species; and (b) the numbers of cougar kills included in each of the three prey categories: ungulates (black-tailed deer, elk, mountain goat); rodents (beaver, mountain beaver); and synanthropes (raccoon, coyote, opossum). Two black bear kills, two river otter kills, and one mink kill were removed when grouping prey because these species, though considered wildland mammals, are not rodents or ungulates. Kill numbers for species and prey groups with ≥20 kills are indicated in parentheses.

Table 1. Percentage of kills by prey type (ungulate, rodent, or synanthrope) for each individual cougar.

Cat ID	Sex	Period	Kills	Building density			Percentage of kills		
				Mean	Min.	Max.	Ung.	Rod.	Syn.
136	F	1	64	0.0	0.0	0.1	75	22	3
137	F	1	18	27.7	0.0	126.9	89	11	0
325	F	1	8	3.0	0.0	13.2	62	0	38
327	F	1	18	0.0	0.0	0.0	89	11	0
331	F	1	7	0.0	0.0	0.0	100	0	0
131	M	1	21	11.1	0.0	70.5	95	0	5
309	M	1	10	2.7	0.0	13.4	50	40	10
323	M	1	78	2.5	0.0	38.8	50	45	5
324	M	1	43	10.9	0.0	80.6	49	23	28
326	M	1	7	49.9	0.0	208.2	71	14	14
6	F	2	35	0.0	0.0	0.0	97	3	0
8	F	2	34	0.0	0.0	0.0	94	6	0
12	F	2	21	11.7	0.0	32.5	81	5	14
14	F	2	39	2.2	0.0	26.1	97	3	0
17	F	2	49	0.0	0.0	0.0	86	12	2
30	F	2	12	7.1	0.0	21.5	67	0	33
34	F	2	16	30.7	11.9	57.1	88	0	12
35	F	2	26	1.6	0.0	14.6	85	8	8
137	F	2	33	0.0	0.0	0.2	88	12	0
5	M	2	10	3.6	0.0	36.0	100	0	0
37	M	2	14	12.4	0.0	117.1	79	14	7

Notes: Also shown are sex, study period, number of kills, and building density (mean, minimum, and maximum) across all kill sites for each cougar. Building density is expressed as number of buildings per 100 ha for visualization purposes.

Table 2. All candidate models with a ΔAIC ≤ 2 when compared to the top model for each prey type.

Response variable	Predictor variables	AIC	ΔAIC	Model likelihood	AIC weight
Synanthrope	Building density, r. effect	251.0	0.0	1.00	0.24
	Sex, building density, r. effect	252.4	1.4	0.50	0.12
	Study period, building density, r. effect	252.4	1.4	0.50	0.12
	R. effect only	252.9	1.9	0.40	0.09
	None (null model)	275.0	24.0	0.00	0.00
Ungulate	Sex, study period, r. effect	537.0	0.0	1.00	0.16
	Sex, study period, sex–study period interaction, r. effect	537.6	0.6	0.76	0.12
	Study period, r. effect	537.6	0.6	0.74	0.12
	Sex, r. effect	537.7	0.7	0.71	0.12
	Sex, study period, building density, r. effect	538.6	1.6	0.45	0.07
	R. effect only	539.7	2.7	0.26	0.04
	None (null model)	595.7	58.7	0.00	0.00
Rodent	Sex, study period, building density, r. effect	426.6	0.0	1.00	0.26
	Sex, study period, building density, sex–study period interaction, r. effect	428.1	1.5	0.48	0.12
	Study period, building density, r. effect	428.5	1.8	0.40	0.10
	Sex, study period, building density, study period–building density interaction, r. effect	428.5	1.9	0.39	0.10
	Sex, study period, building density, sex–building density interaction, r. effect	428.6	2.0	0.37	0.09
	R. effect only	440.9	14.3	0.00	0.00
	None (null model)	486.7	60.1	0.00	0.00

Notes: Null models (intercept only) and models only including random cougar effects are shown for reference. Random effect indicated with r. effect. AIC, Akaike information criterion.
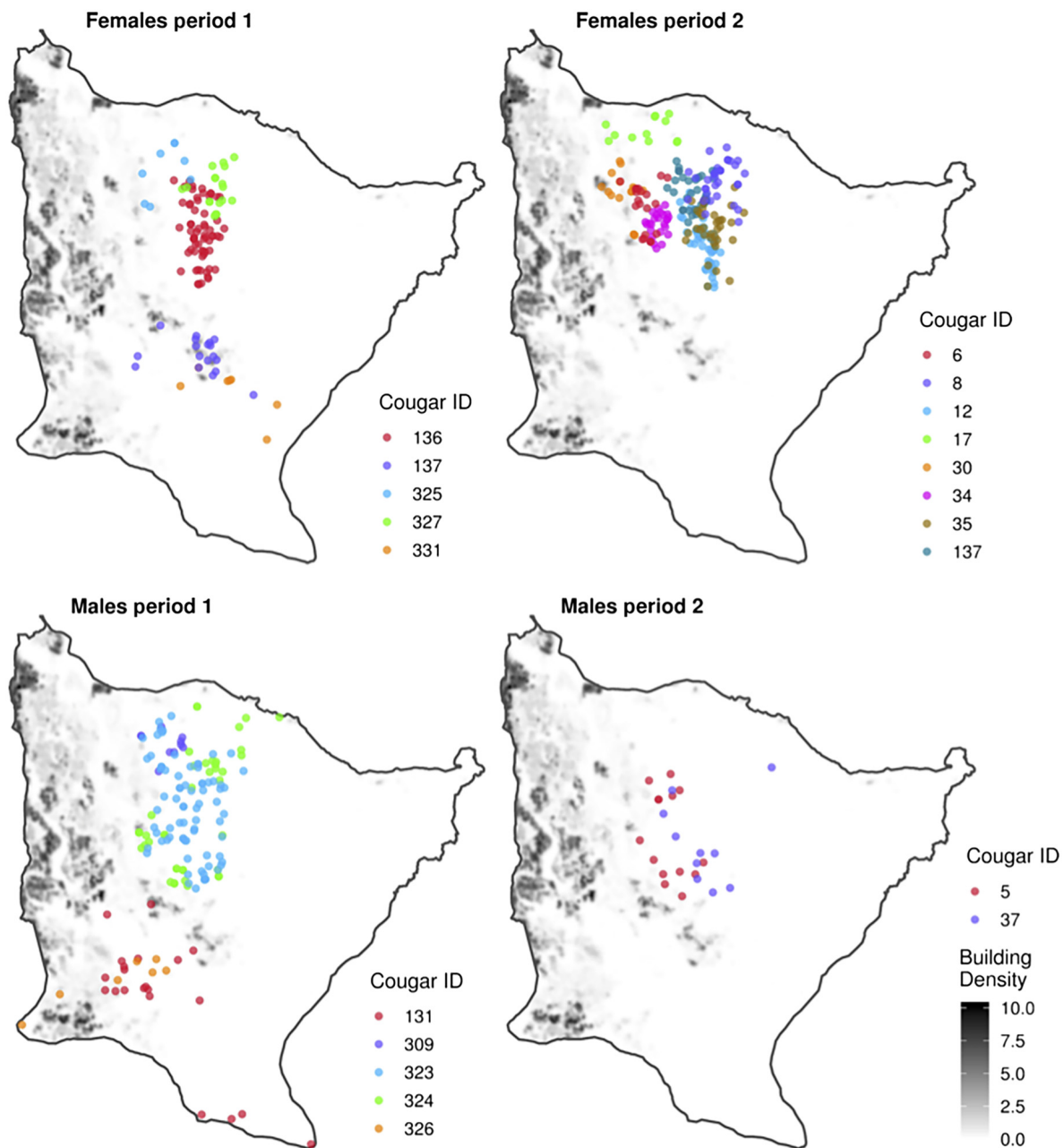
Fig. 3. Cougar kill site distribution across the study area, with panels distinguished by sex and study period (cougar ID indicated). Urbanization across the study area is indicated by the gray scale of 0–10 buildings per hectare.

effects (Table 2). This model suggested that the odds of preying on an ungulate were 2.16 times greater for females compared to males (95% CI: 0.91, 5.15) and were 2.06 times greater in period 2 compared to period 1 (95% CI: 0.92, 4.57), but

the 95% CIs for these odds ratios both included 1.0. The estimated standard deviation of the cougar random effect, on the other hand, had a 95% CI that did not overlap zero ($\hat{\sigma} = 0.62$, CI = 0.23, 1.17) indicating significant differences in the use
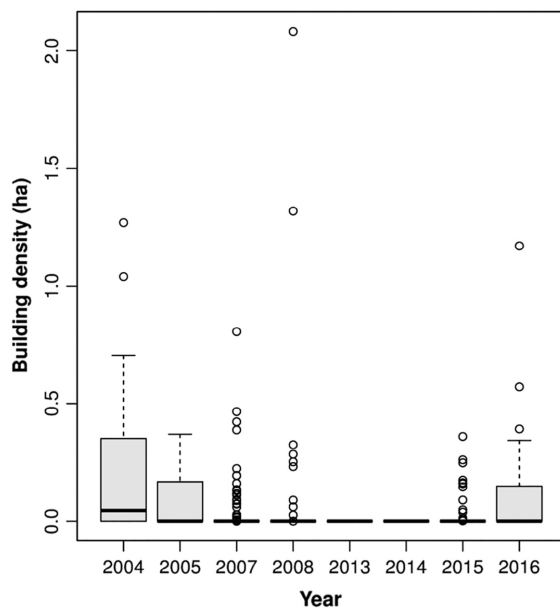
Fig. 4. Average building density at all cougar kill locations during every study year since 2004. Despite a few outlying kills occurring in high-density areas in 2004, 2008, and 2016, kills across years occurred on average in areas with <0.5 built parcels per hectare.

of ungulates among individuals in this study. Specifically, the predicted probabilities of ungulate kills were similar for the majority of cougars; however, three individuals (M309, M323, and M324) exhibited ungulate predation probabilities that were significantly lower than the average study animal (Fig. 6).

The intensity of urbanization (Fig. 5) and individual cougar identity were both 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 2). Additionally, the odds of a rodent kill were estimated to decrease by a multiplicative factor of 1.94 (95% CI: 1.16–3.23) for every increase of just 0.1 buildings per hectare. The odds of a rodent kill for males were 2.49 times greater than those for females (95% CI: 1.07–5.77), and 2.61 times greater in study period 1 than in study period 2 (95% CI: 1.15–5.96). The random effect for cougars had a marginal contribution to the top rodent model after accounting for the other variables ($\hat{\sigma} = 0.49$, 95% CI: 0.00, 1.08). When the
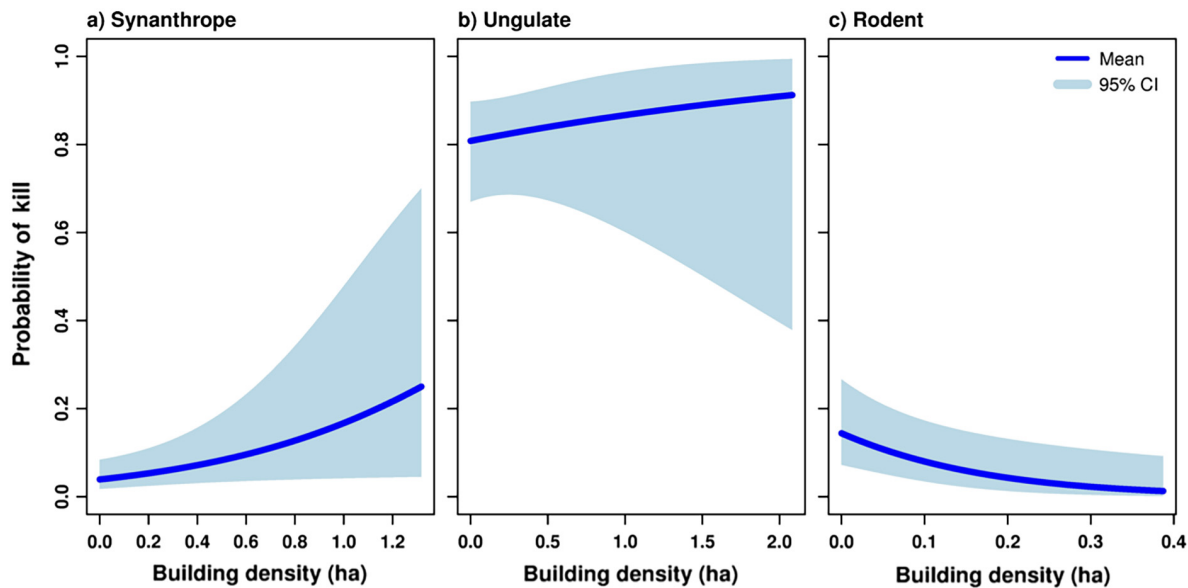

Fig. 5. The probabilities of a cougar kill by prey type (synanthrope (a), ungulate (b), rodent (c)) as a function of increasing building density. Dark blue lines indicate probability estimates and shaded regions indicate 95% confidence intervals. Both ungulate and rodent plots are based on females from study period 1 as probability estimates under both models differed by sex and study period.
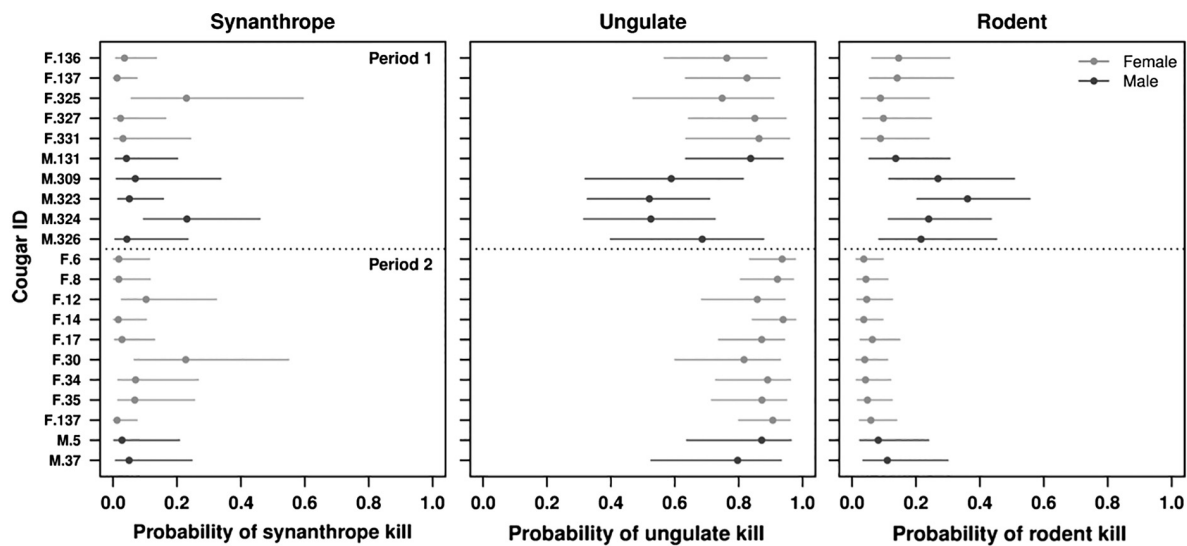
Fig. 6. Predicted probabilities of kills by prey type with associated 95% confidence intervals for each individual cougar. Predictions are from top models, and predictions for the synanthrope and rodent models are calculated at the average building density across all kill sites.

random effect was dropped from the top model, the change in AIC was only 1.57, indicating that the other variables accounted for much of the variability among individual cougars. However, one cougar (M323) had a significantly higher predicted probability of rodent kills at average housing density when compared to the average cougar in this study (Fig. 6).

Discussion

Conflicts with humans remain the key threat to carnivore persistence globally (Chapron et al. 2003, Ripple et al. 2014), and as human populations increase, it is likely that a growing number of species will come into contact with people and anthropogenically altered landscapes (Bateman and Fleming 2012). Urbanization, ranging from low- to high-density residential development, continues to be a principal cause of broad-scale landscape change and can alter animal behavior (Lewis et al. 2015b) as well as ecological processes and community structure (Shochat et al. 2006, McKinney 2008, Ordeñana et al. 2010). Based on the findings of Kertson et al. (2011a), Smith et al. (2016), Moss et al. (2016a), and Blecha et al. (2018), we 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. Consistent with this prediction, building density was a significant predictor of synanthrope predation. The study period variable was not a significant predictor of predation on synanthropic species, suggesting that the study period 1 cougar cohort was similar to the cohort from study period 2 in their predation on synanthropes. As predicted, rodent predation was negatively associated with building density, and rodent predation significantly decreased between the study periods. The change in rodent predation between the study periods may simply be a function of differences in cougar cohorts, as male M323 (study period 1) accounted for 50% of rodent predation during this investigation. Ungulates were consistently the top prey item over the course of the study, and the degree of urban development was not a significant predictor of the use of these prey species, suggesting that under certain conditions, cougars may be able to continually rely on their primary prey even when their environment is subject to anthropogenic changes. Notably, individual differences accounted for a significant amount of variation in the use of all three prey groups. By implication, understanding patterns

of individual variability may be key to predicting how adaptable large carnivores respond to urbanization.

The odds of synanthrope predation by cougars increased as a function of building density, confirming our expectation that individuals exposed to increased opportunity to exploit urban prey would do so. Hence, our findings build on several previous studies (Kertson et al. 2011a, Moss et al. 2016a, Smith et al. 2016, Blecha et al. 2018) that underscore the dietary flexibility of cougars and suggest that individuals in urbanized environments may be able to persist and perhaps mitigate intra-specific competition for traditional prey by exploiting human-associated food. We also observed significant individual variation in synanthrope usage. It is possible that these differences among cougars owed to home range arrangement on the landscape, whereby individual cougar diets differed simply because of variation in the availability of prey items within their respective home ranges (i.e., because of differences in ecological opportunity; Araújo et al. 2011). The kill site locations for cougars in this study overlapped, however, and therefore do not strongly support this idea. We nevertheless acknowledge that the differences in predation on any of the prey types we documented could have stemmed at least in part from intra-specific variation in access to prey but were unable to address this possibility because no prey data were available in our study system. Individual specialization is an alternative explanation for the observed variability in the use of synanthropes, with a recent review of predator selectivity indicating that many generalist predator populations consist of individual dietary specialists, with part of the specialization associated with their phenotype (Pettorelli et al. 2011). Accordingly, the responses of particular cougars to varying degrees of urbanization may depend on divergent prey preferences possibly stemming from inheritance, learning, and/or competition (Araújo et al. 2011).

Contrary to our expectation, the odds of ungulate predation by cougars remained relatively stable across the wildland–urban gradient, suggesting that cougars were able to consistently rely on wild ungulates, particularly black-tailed deer, despite potential differences in ungulate availability as a function of urbanization. Indeed,

the three cougars (M309, M323, M324) that deviated significantly from other study animals in their predation on ungulate prey had the majority of their kill site locations in wildland portions of the study area. The availability of black-tailed deer throughout the wildland–urban gradient might be tied to urbanization (Bender et al. 2004a, b), but contrary to our expectation of an inverse relationship, low-density development may actually augment ungulate use of residential landscapes and these individuals may be particularly susceptible to predation by cougars (Blecha et al. 2018). More importantly, our observations of the continued reliance on black-tailed deer and limited use of livestock by cougars suggest that some predator–prey systems can be maintained at the wildland–urban interface over an extended period of human population growth.

In accordance with our expectation, the odds of rodent predation decreased significantly as building density increased across the wildland–urban gradient. 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 hard habitat edges (Kertson et al. 2011a). Accordingly, our results suggest that these areas where cougars target beavers and mountain beavers may 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. 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 beaver kills during this investigation and may be the primary reason for this demographic disparity in rodent predation. By inference, any dietary shift at the population level induced by diminishing rodent habitat through urbanization is likely to be modest relative to those produced by changes to synanthrope and ungulate availability.

The changes to cougar diets in response to urbanization reported in this study are similar to previous studies elsewhere and suggest widespread applicability of our findings. For example, housing density influenced cougar consumption of small prey (<20 kg) in central California (Smith et al. 2016) 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. This pattern of individual variation in cougar diets mirrors the individual differences in space use documented by Kertson et al. (2011b) in the same system. It also suggests that cougar population responses to urbanization, and other forms of human disturbance, are unlikely to be uniform, and therefore that understanding the drivers that cause individuals to specialize on certain prey types is 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, *Canis lupus*; 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 Vectronic GPS Plus GPS collars used during study period 1 achieved 100% data retrieval through the download on demand capability. Full data retrieval during study period 1 provided adequate opportunities for the detection of predation events spanning <24 h (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 and potentially weakening detection of clusters spanning <24 h. 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, suggesting that the results of this investigation were not simply a function of methodological variation.

Large carnivores are controversial species whose management and conservation are complicated by broader psychological, political, and socioeconomic issues (Treves and Karnath 2003, Chapron et al. 2014, Ripple et al. 2014). Like many other large carnivores, cougars are periodically involved in conflicts with livestock producers and rural residents (Gilbert et al. 2016). Wildlife professionals also frequently feel considerable pressure to reduce large carnivore populations in an effort to bolster ungulate populations (Todd 2002, Hurley et al. 2011). Experimental efforts to reduce depredations and change ungulate demography through broad-scale predator removal have proven to have minimal effect on prey populations (Hurley et al. 2011), with studies on coyote (Austin et al. 1977, Trainer et al. 1981) and cougar (Robinette et al. 1977, Logan and Sweanor 2001) removal exhibiting variable results on mule deer survival. Alternatively, targeted predator management has proven useful in minimizing livestock depredations by wolves in Montana, Idaho, and Wyoming (Poudyal et al. 2016). Though we focused on a relatively small sample of cougars, our results reveal that certain individuals deviated markedly from the average usage of three prey categories. Thus, they provide additional evidence that management actions targeting individual animals are likely to be more effective in reducing human conflict with cougars, and potentially other large predators, than indiscriminate population reduction.

Cougars in Washington, as well as other predators globally, present unique conservation challenges because of human safety concerns and predation on domestic species (Campbell and Lancaster 2010, Campbell 2013). Yet, our results indicate that despite individual dietary differences, most cougars exhibited similar diets that were dominated by wild ungulates across the wildland–urban gradient and in both study periods. This pattern has implications for wildlife management and human–cougar coexistence. First, cougars in our system relied heavily on black-tailed deer, so promoting healthy native ungulate populations in wildland–urban areas may be a feasible approach to minimizing cougar

use of domestic species along urban gradients. By the same token, minimizing anthropogenic subsidies for deer and other food resources for deer near homes could be an effective approach for keeping both deer and foraging cougars away from residences.

LITERATURE CITED

Alberti, M., C. Avolio, D. Booth, B. Coburn, S. Coe, K. Hill, and D. 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.

Alberti, M., V. M. Hunt, and J. Marzluff. 2017. Urban driven phenotypic changes: empirical observations and theoretical implications for eco-evolutionary feedback. Philosophical Transactions. The Royal Society Publishing 372:20160029.

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

Araújo, M. S., D. I. Bolnick, and C. A. Layman. 2011. The ecological causes of individual specialization. Ecology Letters 14:948–958.

Austin, D. D., P. J. Urness, and M. L. Wolfe. 1977. The influence of predator control on two adjacent wintering deer herds. Great Basin Naturalist 37: 101–102.

Bateman, P. W., and P. A. Fleming. 2012. Big city life: carnivores in urban environments. Journal of Zoology 287:1–23.

Bates, D., B. Bolker, R. H. B. Christensen, B. Dai, P. Green, G. Grothendieck, M. Maechler, H. Singmann and S. Walker. 2016. Package 'lme4': linear mixed-effects models using 'Eigen' and S4. R package version 1.1-12. https://cran.r-project.org/web/packages/lme4/index.html

Beier, P., R. H. Barrett, and D. Choate. 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* S. D. Gehrt, S. P. D. Riley, and B. Cypher, editors. Urban carnivores: ecology conflict, and conservation. John Hopkins University Press, Baltimore, Maryland, USA.

Bender, L. C., D. P. Anderson, and J. C. Lewis. 2004*a*. Population ecology of Columbian black-tailed deer in urban Vancouver, Washington. Northwestern Naturalist 85:53–59.

Bender, L. C., D. P. Anderson, and J. C. Lewis. 2004*b*. Annual and seasonal habitat use of Columbian black-tailed deer in urban Vancouver, Washington. Urban Ecosystems 7:41–53.

Blecha, K. A., M. W. Alldredge, and R. B. Boone. 2018. Hunger mediates apex predator's avoidance response in wildland-urban interface. Journal of Animal Ecology 87:609–622.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

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

Campbell, M. 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, M., and B. L. Lancaster. 2010. Public attitudes toward black bears (*Ursus americanus*) and cougars (*Puma concolor*) on Vancouver Island. Society and Animals 18:40–57.

Cardillo, M., J. Bielby, O. R. P. Bininda-Edmonds, K. E. Jones, G. M. Mace, C. D. L. Orme, A. Purvis, and W. Sechrest. 2005. Multiple causes of high extinction risk in large mammal species. Science 309:1239–1241.

Chapron, G., J. Clobert, R. Ferrière, R. G. Haight, and S. Legendre. 2003. Conservation and control

strategies for the wolf (*Canis lupus*) in western Europe based on demographic models. Comptes Rendus Biologies 326:575–587.

Chapron, G., et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346:1517–1519.

Conedera, M., M. Leuenberger, L. Oleggini, C. V. Orozco, G. B. Pezzatti, and M. Tonini. 2015. Geospatial approach for defining the wildland-urban interface in the alpine environment. Computers, Environment and Urban Systems 52:10–20.

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

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

Environmental Systems Research Institute (ESRI). 2016. ArcGIS for desktop: how kernel density works. ArcMap 10.3 and 10.4. http://desktop.arcgis.com/en/arcmap/10.3/tools/spatial-analyst-toolbox/how-kernel-density-works.htm

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

Gilbert, S. L., K. J. Sivy, C. B. Pozzanghera, A. DuBour, K. Overduijn, M. M. Smith, J. Zhou, J. M. Little, and L. R. Prugh. 2016. Socioeconomic Benefits of large carnivore recolonization through reduced wildlife-vehicle collisions. Conservation Letters 10:431–439.

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

Herr, J., T. J. Roper, and L. Schley. 2009. Socio-spatial organization of urban stone martens. Journal of Zoology 277:54–62.

Hurley, M. A., E. O. Garton, M. Hebblewhite, C. L. Maycock, D. M. Montgomery, J. R. Skalski, J. W. Unsworth, and P. Zager. 2011. Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. Wildlife Monographs 178:1–33.

Kertson, B. N., C. E. Grue, J. Hepinstall-Cymerman, J. M. Marzluff, and R. D. Spencer. 2011*b*. Cougar space use and movements in the wildland-urban landscape of western Washington. Ecological Applications 21:2866–2881.

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

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

Kertson, B. N., and J. M. Marzluff. 2010. Improving studies of resource selection by understanding resource use. Environmental Conservation 38:18–27.

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

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

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

Lewis, J. S., M. W. Alldredge, L. L. Bailey, K. R. Crooks, K. A. Logan, and S. VandeWoude. 2015*a*. The effects of urbanization on population density, occupancy, and detection probability of wild felids. Ecological Applications 25:11880–1895.

Lewis, J. S., L. L. Bailey, K. R. Crooks, and S. VandeWoude. 2015*b*. Interspecific interactions between wild felids vary across scales and levels of urbanization. Ecology and Evolution 5:5946–5961.

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

Lowry, H., A. Lill, and B. Wong. 2013. Behavioural responses of wildlife to urban environments. Biological Reviews 88:537–549.

Markovchick-Nicholls, L., D. H. Deutschman, T. A. Hunt, B. Martin, L. Noreke, H. M. Regan, and A. Widyanata. 2008. Relationships between human disturbance and wildlife land use in urban habitat fragments. Conservation Biology 22:99–109.

Maxwell, S., T. M. Brooks, R. A. Fuller, and J. E. M. Watson. 2016. The ravages of guns, nets and bulldozers. Nature 536:143–145.

McDonnell, M. J., and A. K. Hahs. 2015. Adaptation and adaptedness of organisms to urban environments. Annual Review of Ecology, Evolution, and Systematics 46:261–280.

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

McKinney, M. L. 2008. Effects of urbanization on species richness: a review of plants and animals. Urban Ecosystems 11:161–176.

Moss, W. E., M. W. Alldredge, and J. N. Pauli. 2016*a*. Quantifying risk and resource use for a large

carnivore in an expanding urban-wildland interface. Journal of Applied Ecology 53:371–378.

Moss, W. E., M. W. Alldredge, K. A. Logan, and J. N. Pauli. 2016b. Human expansion precipitates niche expansion for an opportunistic apex predator (*Puma concolor*). Scientific Reports 6:39639.

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

Newsome, S. D., H. M. Garbe, S. D. Gehrt, and E. C. Wilson. 2015a. Individual variation in anthropogenic resource use in an urban carnivore. Oecologia 178:115–128.

Newsome, T. M., et al. 2016. Food habits of the world's grey wolves. Mammal Review 46:255–269.

Ordeñana, M. A., et al. 2010. Effects of urbanization on carnivore species distribution and richness. Journal of Mammalogy 91:1322–1331.

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

Pettorelli, N., T. Coulson, S. M. Durant, and J. M. Gaillard. 2011. Predation, individual variability and vertebrate population dynamics. Oecologia 167:305–314.

Pimm, S. L., and P. Raven. 2000. Extinction by numbers. Nature 403:843–845.

Poudyal, N., S. T. Asah, and N. Baral. 2016. Wolf lethal control and livestock depredations: counter-evidence from respecified models. PLoS ONE 11:e0148743.

Prange, S., and S. D. Gehrt. 2004. Changes in mesopredator-community structure in response to urbanization. Canadian Journal of Zoology 82:1804–1817.

Price, D. T., and O. Bar-Yosef. 2011. The origins of agriculture: new data, new ideas: an introduction to supplement 4. Current Anthropology 52:S163–S174.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Radeloff, V. C., J. S. Fried, R. B. Hammer, S. S. Holcomb, J. F. McKeefry, and S. I. Steward. 2005. The wildland-urban interface in the United States. Ecological Applications 15:799–805.

Ripple, W. J., et al. 2014. Status and ecological effects of the world's largest carnivores. Science 343:1241484.

Robinette, W. L., C. H. Hancock, and D. A. Jones. 1977. The Oak Creek mule deer herd in Utah. Publication no. 77-15. Utah Division of Wildlife Resources, Salt Lake City, Utah, USA.

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

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

Severinghaus, C. W. 1949. Tooth developments and wear as criteria of age in white-tailed deer. Journal of Wildlife Management 13:195–216.

Silverman, B. W. 1986. Density estimation for statistics and data analysis. Chapman and Hall, New York, New York, USA.

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. Journal of Wildlife Management 80:1040–1048.

Sunquist, M., and F. Sunquist. 2002. Wild cats of the world. University of Chicago Press, Chicago, Illinois, USA.

Theobald, D. M. 2005. Landscape patterns of exurban growth in the USA from 1980 to 2020. Ecology and Society 10:32.

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

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

Todd, S. 2002. Building consensus on divisive issues: a case study of the Yukon wolf management team. Environmental Impact Assessment Review 22:655–684.

Trainer, C. E., T. P. Kistner, J. C. Lemos, W. C. Lightfoot, and D. E. Toweill. 1981. Mortality of mule deer fawns in southeastern Oregon, 1968–1979. Wildlife Research Report no. 10. Oregon Department of Fish and Wildlife, Portland, Oregon, USA.

Treves, A., and K. U. Karnath. 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. Conservation Biology 17:11491–1499.

United States Census Bureau, Department of Commerce. 2015. Quick facts database. https://www.census.gov/quickfacts/

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

Weaver, J. L., P. C. Paquet, and L. F. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. Conservation Biology 10:964–976.

Webb, N. F., M. Hebblewhite, and E. H. Merrill. 2008. Statistical methods for identifying wolf kill sites using global positioning system locations. Journal of Wildlife Management 72:798–807.

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

Wilmers, C. C., M. L. Allen, P. Houghtaling, J. Kermish-Wells, B. Nickel, Y. Shakeri, Y. Wang, T. Williams, and V. Yovovich. 2013. Scale dependent behavioral responses to human development by a large predator, the puma. PLoS ONE 8:e60590.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2605/full