

Quantifying risk and resource use for a large carnivore in an expanding urban–wildland interface

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Summary

1. Large carnivores, though globally threatened, are increasingly using developed landscapes. However, most of our knowledge of their ecology is derived from studies in wildland systems; thus, for effective conservation and management, there is a need to understand their behavioural plasticity and risk of mortality in more developed landscapes.
2. We examined cougar *Puma concolor* foraging ecology and survival in an expanding urban–wildland system in Colorado from 2007 to 2013. For GPS-collared individuals, we related diet ($n = 41$; isotopic analysis) to age–sex class and fine-scale space use, with regard to levels of habitat development. We also examined how habitat development impacted risk of mortality ($n = 49$), using hazards models and records of cougar–human conflict.
3. Cougars obtained 63–82% of assimilated biomass from native herbivores, and adult females consistently showed higher use of native herbivores than other age–sex classes. Individuals using the most highly developed areas obtained approximately 20% more of their diet from alternative prey (synanthropic wildlife and domestic species) than those in the least developed areas.
4. Overall, survival of adult females was higher than adult males. Yet, use of developed areas substantially increased cougar risk of mortality; for every 10% increase in housing density, risk of mortality increased by 6·5%, regardless of sex.
5. *Synthesis and applications.* Cougars showed flexibility in diet, taking advantage of human-associated prey items, but had high rates of mortality, suggesting that human tolerance, rather than adaptability, may be the limiting factor for range expansion by cougar and other large carnivores. Thus, large carnivore conservation will not only depend upon adequate prey resources, but also limiting potential conflict resulting from depredation of synanthropic wildlife and domestic animals.

Key-words: conflict, cougar, diet composition, foraging, habitat use, mortality risk, mountain lion, *Puma concolor*, stable isotope analysis, urbanization

Introduction

Human-modified habitats are now a dominant global land-cover type (Ellis *et al.* 2010). Highly developed landscapes and their surrounding areas (i.e. urban ecosystems) are rapidly expanding, with urban land cover expected to triple from 2010 to 2030 (Seto, Güneralp & Hutyra 2012). These systems can possess novel community assemblages (Angold *et al.* 2006), reduced biodiversity (McKinney 2006), altered community regulation (Fischer, Cleton & Miller 2012) and even disrupted ecosystem-wide nutrient cycling (Kaye *et al.* 2006). Thus, the behaviour and

resource use of species inhabiting these systems is likely to shift, with resulting implications for species persistence and ecosystem functioning.

Land development generally reduces biodiversity through changes in habitat quantity and quality; however, there is much variance in species resiliency to this process. Prolific urban species (i.e. synanthropes) persist in developed landscapes in part due to their ability to capitalize on differential food availability and novel diet items (McKinney 2006). In contrast, some species, particularly those with expansive home ranges, low population densities and high trophic positions, appear sensitive to human development. Large carnivores generally possess these traits and are also at a high risk of conflict with humans,

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making them the first to be lost from developed landscapes (Crooks 2002; Bateman & Fleming 2012). Consequently, land-use change, coupled with increased mortality from encounters with humans, has caused a wide-scale decline of carnivores over the last century (Ripple *et al.* 2014) – a key driver of biodiversity loss (Estes *et al.* 2011). However, the extirpation of large carnivores like cougars *Puma concolor* (Linnaeus 1771), black bears *Ursus americanus* (Pallas 1780) and wolves *Canis lupus* (Linnaeus 1758) in North America was followed by protection and, in many places, population recoveries (Mech 1995; Hristienko & McDonald 2007; Anderson *et al.* 2010). The repatriation of these species to their native range, including now developed areas, has led to high contemporary rates of mortality from conflict with humans and controversy over their protection and management (Treves & Karanth 2003).

Thus, although there is increasing interest in the recovery of large carnivores, in many cases we may not be adequately prepared for the ecological and social consequences of their return. Our understanding of large carnivore ecology is almost entirely derived from wildland populations, with little research investigating their ecology or functional role in developed areas. In particular, it is unclear how behavioural plasticity might mediate both recovery and conflict. Food resources in developed areas may have higher nutritional quality and be more readily available, which may attract and benefit carnivores (Bateman & Fleming 2012). However, use of anthropogenic food resources likely increases risk of conflict with humans (Beckmann & Lackey 2008), which could pose ecological traps and threaten population persistence. Understanding this trade-off in human-dominated landscapes is needed to better anticipate and manage large carnivore recovery.

In North America, cougars were persecuted until the latter half of the 20th century, leading to wide-scale declines in distribution and abundance. Since then, populations in the western United States have recovered (Anderson *et al.* 2010) and cougars are increasingly observed in developed landscapes (Beier, Riley & Sauvajot 2010). Anthropogenic causes (e.g. vehicle collisions, hunting and direct removal) are the principal sources of mortality for many populations (Orlando 2008; Thompson, Jenks & Fecské 2014). The primary prey of cougars are species of large ungulates (Murphy & Ruth 2010); however, where scarce, like in parts of South America (Murphy & Ruth 2010), or developed areas of North America (Kertson, Spencer & Grue 2011), cougars rely more heavily on smaller-bodied prey. Small-bodied prey, like synanthropic wildlife or domestic pets, are abundant in developed landscapes, which may draw cougars into these areas. Use of small prey by cougars has likely been underestimated by studies of diet based on kill-site investigations (Kertson, Spencer & Grue 2011) or prey remains in faeces. As a result, the relative use of smaller prey and its implication for cougars in developed landscapes remains in question.

The Colorado Front Range of the Rocky Mountains is one of the major urban–wildland interfaces in North America (Radeloff *et al.* 2005). Developed land cover has more than tripled since 1960 (Theobald 1997) and abuts large expanses of protected public lands. Cougars in this region therefore encounter a wide gradient of habitat types, degree of human influence and associated risk factors. We quantified diet composition, space use and survival for the Front Range cougar population. We hypothesized that, like other behaviourally plastic foragers, cougars would exploit developed areas and synanthropic resources, and as a result, would incur higher mortality compared to cougars using less developed landscapes. We also predicted that this use of developed areas would be a more important determinant of diet than the age or sex of the animal.

Materials and methods

STUDY AREA

Our work was conducted as part of a larger, long-term study, in Colorado's northern Front Range, in a 2900-km² study area located in Boulder, Jefferson, Gilpin and Clear Creek counties (Fig. 1), which spans a gradient from wildland to urban. Over one quarter (28%) of the total land area is developed (i.e. urban, exurban or suburban), as classified by Theobald (2005), primarily concentrated along the eastern portion of the study area. About half (49%) of the study area is publicly owned and undeveloped (i.e. wildland). Cougars within our study area generally forage on a diversity of prey species. Native ungulates, primarily elk *Cervus elaphus* (Linnaeus 1758) and mule deer *Odocoileus hemionus* (Rafinesque 1817) as well as smaller-bodied herbivores, like cottontail rabbits *Sylvilagus nuttallii* (Bachman 1837) are abundant in both wildland and developed landscapes. Species of synan-

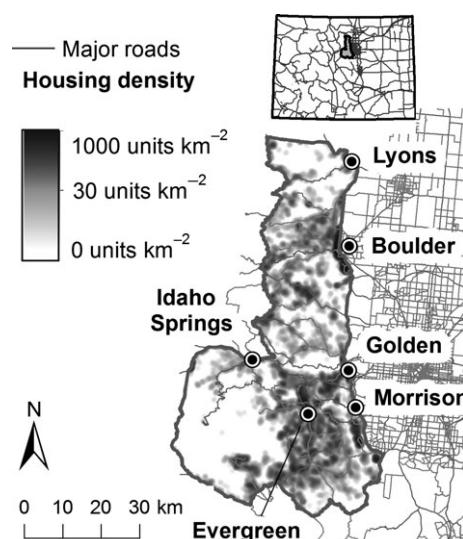


Fig. 1. Front Range study area in Colorado, where we captured and collared cougars *Puma concolor*, 2007–2013. Housing density varies throughout, including developed areas along the eastern edge and undeveloped wilderness area in the south-western portion.

thropic mammals, including foxes *Vulpes* sp., coyotes *Canis latrans* (Say 1823), raccoons *Procyon lotor* (Linnaeus 1758), squirrels (*Sciurus spp.*) and skunks *Mephitis mephitis* (Schreber 1776), occur at relatively high densities in developed areas (Prange & Gehrt 2004). Domestic species, both large-bodied [sheep *Ovis aries* (Linnaeus 1758), goat *Capra aegagrus hircus* (Linnaeus 1758), llama *Lama glama* (Linnaeus 1758), and alpaca *Vicugna pacos* (Linnaeus 1758)] and small-bodied [cats *Felis catus* (Linnaeus 1758), dogs *Canis familiaris* (Linnaeus 1758) and chickens *Gallus domesticus* (Linnaeus 1758)], occur in developed areas but are generally not present in wildland habitat.

CAPTURES AND MONITORING

Cougars were captured from 2007 to 2013 using hounds, cage traps, or foothold snares and immobilized with a mixture of ketamine hydrochloride and medetomidine. Upon capture, we fitted each individual with a GPS PLUS collar (Vectronics Aerospace, Berlin, Germany) that collected 7–8 GPS locations per day, which were remotely downloaded. At each capture, we assessed body condition (Beier 1991) and estimated age using gum-line recession or birth date when mothers were known (Laundré *et al.* 2000). We also sampled hair for stable isotope analysis at captures or at necropsies. We grouped individuals into subadult or adult age classes, based on Logan & Sweeney's (2001) criteria: adults were any individuals older than 24 months who had established a home range, whereas subadults were independent individuals <24 months old. Transient subadults or individuals <6 months old were not included in analyses. All methods were in accordance with ACUC 16-2008 approved by Colorado Parks & Wildlife, Fort Collins, CO, USA.

STABLE ISOTOPE ANALYSIS

We used stable isotope analysis to quantify cougar diet, by comparing the isotopic signature (in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of cougar hair to the isotopic signatures of potential prey items. Hair samples of wild prey species were collected from cougar kill sites or road kills within the study area; we sampled domestic species using shed hairs from farms in the study area. Analysis of hair samples reflects the diet over the entire period of hair growth. Based on the moult chronology of other felids (Parrng, Crumpacker & Kurle 2014), estimates from hair are likely to underestimate winter diet, since growth is slowest during the winter months. Hair samples were prepared using standard methods (Pauli *et al.* 2009) and analysed with a Carlo Erba 1100 Elemental Analyzer (Carlo Erba, Lakewood, NJ, USA) coupled to a Thermo Delta Plus XP IRMS. Results are reported as parts per thousand [‰] ratios relative to international standards of PeeDee Belemnite ($\delta^{13}\text{C}$) and atmospheric nitrogen ($\delta^{15}\text{N}$). We adjusted prey isotopic signatures using isotopic correction factors for carnivores ($\delta^{13}\text{C} = 2.6 \pm 0.1\text{‰}$; $\delta^{15}\text{N} = 3.4 \pm 0.1\text{‰}$) in order to directly compare consumer and prey signatures (Roth & Hobson 2000).

We grouped prey into biologically relevant and isotopically distinct source groups by applying K nearest-neighbour randomization tests (Rosing, Ben-David & Barry 1998). Species that were isotopically indistinct ($P > 0.05$) were grouped, and an unweighted group average was calculated over all samples (see Table S1, Supporting information). We used Bayesian mixing models in the software package MixSIAR (Stock & Semmens 2013) to quantify a population-wide estimate of diet in terms of biomass assimilated. Bayesian mixing models provide estimates of

diet as posterior distributions of likely solutions; we report the 95% credibility interval of these distributions. We grouped all domestic species *a posteriori* because the model could not accurately distinguish between large and small domestic species.

INFLUENCE OF SPACE USE AND AGE-SEX CLASS ON DIET

To quantify housing density, we used a digitized layer of man-made structures within our study area, created using 0.6-m orthoimagery (Blecha, Boone & Alldredge 2013). We generated a rasterized kernel density layer using a 1000-km search radius to describe housing density in units km^{-2} over our study area. Because peak activity, including foraging and feeding, occurs between dusk and dawn, we quantified the median housing density over all night-time GPS locations (between 17:00 and 06:00 h) over the entire period the individual was monitored. We did not restrict our space-use analysis to the period of hair growth, because use of developed areas did not differ by season (Wilcoxon signed rank test; $V = 634$, $P = 0.47$). We removed GPS points occurring during dispersals of individuals outside of our study area. Housing density was log-transformed in linear models to meet assumptions of normality.

We examined whether a series of *a priori* covariates influenced isotopic signature. Covariates examined were housing density, age, sex and interactions between age and sex (age-sex class) and housing density and age. We used linear mixing models and selected the best models to predict carbon and nitrogen signature, using Akaike's information criterion, corrected for small sample sizes (AIC_c). Carbon signature indicates the degree of anthropogenic food in diet (Newsome *et al.* 2010), while nitrogen signature indicates the trophic position of an individual (Kelly 2000); therefore, we examined these as separate response variables. Finally, to illustrate how these isotopic changes related to dietary inputs, we used MixSIAR to estimate the diets of the 10 individuals using the most urban areas (those in the upper quartile of housing density) compared to the 10 individuals using the least urban areas (those in the lower quartile of housing density).

SOURCES AND RISKS OF MORTALITY

We calculated sources of mortality and estimated annual survival for adult resident cougars using the Kaplan–Meier procedure for staggered entry (Pollock *et al.* 1989). Survival estimates were calculated for males and females separately, for each year of the study period (2007–2013), and average annual survival and variance were determined using the delta method (Powell 2007). We tested how sex and housing density at night-time locations affected an individual's risk of mortality, using proportional hazards models (Cox 1972) in the statistical package survival for R (Therneau 2013). Finally, we analysed incident reports collected by Colorado Parks & Wildlife from our study area from 2011 to 2014 to explore cougar–human interactions leading to mortality events.

Results

CAPTURES AND MONITORING

For survival and space-use analyses, we utilized data from 49 GPS-collared, adult cougars (30 females; 19 males).

Twenty-eight of these individuals (21 adult females; seven adult males) along with an additional 13 subadults (seven females; six males) were also sampled for estimates of diet. Of the 62 total individuals included in the study, the average duration of monitoring was 517 days (range: 4–1952), over which we collected an average of 1570 night-time GPS locations per individual. All individuals used in analysis of space use had >50 GPS locations within the study area. All adults weighed 37–68 kg and were considered in good condition.

STABLE ISOTOPE ANALYSIS

We obtained isotope signatures of 141 hair samples of potential prey items, comprising at least 16 species (Table S1). Prey species clustered into four isotopically distinct groups, which represented biologically meaningful classes of prey (see Table S1; K nearest-neighbour; $P < 0.01$). Isotopic signatures of cougars fell within the mixing space of the potential diet items; however, there was considerable individual-level variation in isotopic signature (Fig. 2). Because prey associated with developed landscapes (synanthropic wildlife and domestic species) were enriched in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Fig. 2), cougars with higher isotope signatures relied more heavily on these prey items; thus, raw isotope values of both carbon and nitrogen were a useful proxy for use of alternative prey.

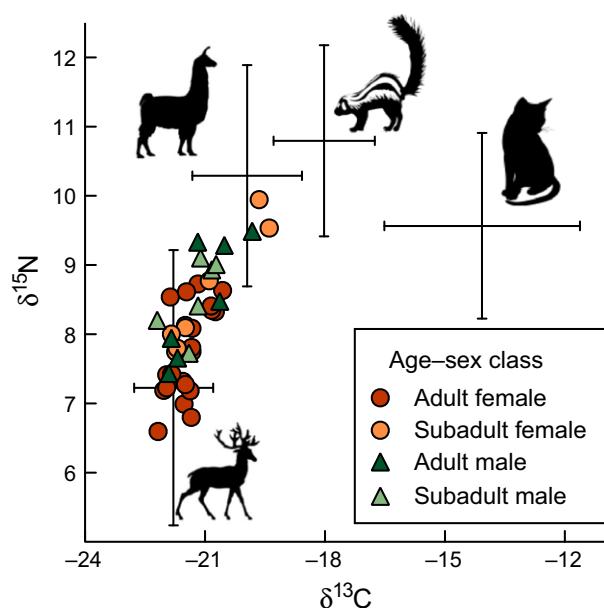


Fig. 2. Isotope signatures of cougars *Puma concolor* ($n = 41$) and their potential prey in the Colorado Front Range study area, 2007–2013. Prey are plotted as mean \pm SD of groups, from left to right: native herbivores, large domestic species, synanthropic wildlife and small domestic species. Prey associated with developed areas (i.e. synanthropic wildlife and domestic species) are isotopically enriched; therefore, cougars with higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values rely more heavily upon these prey items.

Native herbivores were the most important diet source for the population, comprising 63–82% of diet. This source group contained elk, deer and rabbits; but, because elk and deer have body masses an order of magnitude larger, the use of this prey group is likely to reflect mostly consumption of ungulate biomass, rather than of rabbit. Domestic species (small pets and livestock) were also important sources of biomass (5–36%), followed by synanthropic wildlife (0–15%).

INFLUENCE OF SPACE USE AND AGE-SEX CLASS ON DIET

The median housing density at night-time locations differed widely between individuals (median: 6 units km^{-2} ; range: 0–65 units km^{-2}). Use of developed areas did not differ between age-sex classes ($F_{3,32} = 0.59$; $P = 0.62$).

The $\delta^{15}\text{N}$ signature of cougars was best predicted by housing density and sex, whereas housing density alone predicted $\delta^{13}\text{C}$. All competitive models for both isotopes (Table 1) included housing density as a covariate. Log-housing density showed a significant positive relationship with nitrogen ($\beta = 0.35$; $P < 0.001$) and carbon ($\beta = 0.20$; $P = 0.01$; Fig. 3). Variation in isotopic signature translated to substantial differences in diet. Individuals in the lower quartile of housing density (i.e. the least urban foragers) obtained roughly 82% of diet (95% BCI: 67–93%) from native herbivores, compared to 63% (43–81%) for those in the upper quartile of housing density.

Age, sex or age-sex class were also included in several of the top models, suggesting that demographic classes differed in foraging strategy. Adult female cougars had lower isotopic signatures ($\bar{x} \pm \text{SE}$; $\delta^{13}\text{C} = -21.43\text{‰} \pm 0.10$; $\delta^{15}\text{N} = 7.75\text{‰} \pm 0.14$) than the other three age-sex classes (MANOVA, Wilk's $\lambda = 0.69$; $P = 0.03$) indicating the highest reliance on native herbivores. Subadult females, adult males and subadult males did not differ from one another ($\lambda = 0.90$, $P = 0.81$) in isotopic signature ($\delta^{13}\text{C} = -21.08\text{‰} \pm 0.18$; $\delta^{15}\text{N} = 8.55\text{‰} \pm 0.17$).

SOURCES AND RISKS OF MORTALITY

A total of 62% (16 of 26) of mortalities in adult cougars were human associated. Of the human-associated mortalities, over half ($n = 10$) were caused by lethal removal, either by a management agency or by private landowners. Other human-associated mortalities were hunting ($n = 3$) and vehicular trauma ($n = 3$). Natural deaths ($n = 5$) were those caused by intraspecific conflict ($n = 3$) or injury ($n = 2$). The cause of death was undetermined for five individuals.

Annual survivorship of adult male cougars was lower (0.63 ± 0.09 SE) than females (0.77 ± 0.08 SE). Housing density and sex both significantly impacted risk of mortality (Fig. 4). Males had a fourfold increase in hazard ($e^\beta = 3.79$, $P = 0.005$), and for every 10% increase in

Table 1. Results of model selection to predict isotope signatures (i.e. diet) of cougars *Puma concolor* in the Colorado Front Range, 2007–2013

	AIC	AIC _C	ΔAIC _C	k*	L†	w _{i‡}
$\delta^{15}\text{N}$ model						
Log (HD) + sex	-35.86	-34.57	-	4	1.00	0.38
Log (HD) + age-sex class	-36.68	-33.78	0.79	6	0.67	0.26
Log (HD) + sex + age (months)	-35.12	-33.12	1.45	5	0.48	0.18
Log (HD) + sex + age-sex class	-36.68	-32.68	1.89	7	0.39	0.15
Log (HD)	-30.48	-29.73	4.84	3	0.09	0.03
Sex	-21.66	-20.91	13.66	3	0.00	0.00
Age (months)	-20.47	-19.72	14.85	3	0.00	0.00
Null	-19.51	-19.15	15.42	2	0.00	0.00
Age-sex class	-21.07	-19.07	15.50	5	0.00	0.00
$\delta^{13}\text{C}$ model						
Log (HD)	-39.80	-39.05	-	3	1.00	0.37
Log (HD) + sex	-39.85	-38.56	0.49	4	0.78	0.29
Log (HD) + age (months)	-39.12	-37.83	1.22	4	0.54	0.20
Null	-35.28	-34.92	4.13	2	0.13	0.05
Age (months)	-34.92	-34.17	4.88	3	0.09	0.03
Log (HD) + age-sex class	-36.80	-33.91	5.14	6	0.08	0.03
Sex	-34.65	-33.90	5.15	3	0.08	0.03
Age-sex class	-31.82	-29.82	9.23	5	0.01	0.00

Covariates tested were selected *a priori* and included housing density (HD) at night-time locations, sex, age-sex class, age in months and interactions between housing density and age-sex class. The corrected AIC_C was used to select top-ranking models. All top-ranking models include HD, indicating that the degree of human development at cougar foraging sites influenced diet composition.

*k = number model parameters.

†L = relative likelihood.

‡w_i = AIC_C weight.

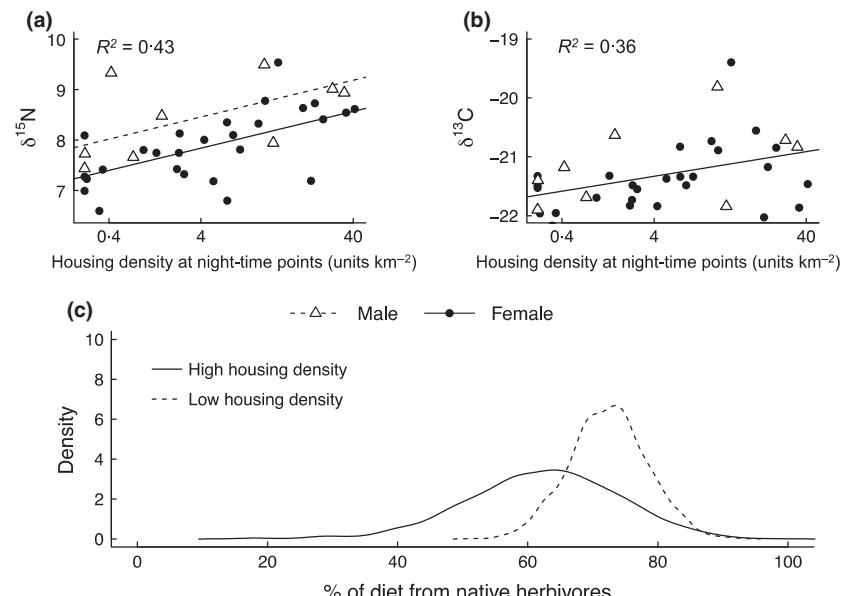


Fig. 3. Comparison between housing density (HD) at night-time GPS locations and diet for individual cougars *Puma concolor* in the Colorado Front Range study area, 2007–2013. The best predictors of (a) $\delta^{15}\text{N}$ were HD and sex, with adult females having the lowest $\delta^{15}\text{N}$ signatures. The best predictor of (b) $\delta^{13}\text{C}$ was HD alone, with no effect of age or sex. Enrichment in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ translated to a lowered reliance on native herbivore species (c). Wildland individuals or those in the lower quartile of housing density obtained about 20% more of their diet from native herbivores than those in the upper quartile of housing density. Lines represent the distribution of possible solutions from Bayesian mixing models in MixSIAR.

housing density, hazard increased by 6.5% ($e^\beta = 1.86$, $P = 0.005$). Using these parameter estimates, a male in the upper quartile of housing density (i.e. an urban forager) would have an annual survival probability of 0.57 ± 0.09 , compared to 0.75 ± 0.07 for a male in the lower quartile. Females in the upper and lower quartiles would have annual survival rates of 0.72 ± 0.04 and 0.90 ± 0.04 , respectively.

Out of 182 incident reports during the course of our study, 11% ended in lethal removal, either by landowners or government. The probability of lethal removal was lowest (2%) in cases where cougars were sighted without prey ($n = 87$), either travelling or resting. When cougars were reported in association with prey (either with a kill or interacting with another species; $n = 85$), 18% resulted in lethal removal. Of all lethal removals that occurred, the

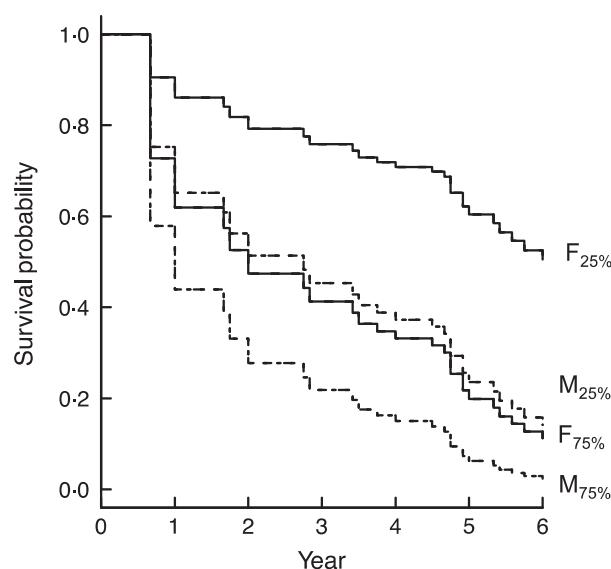


Fig. 4. Survival functions estimated by Cox proportional hazards models, for both adult male (M) and female (F) cougars *Puma concolor* in the Colorado Front Range study area, 2007–2013. Survival is shown at two levels of housing density: the upper (75%) and lower (25%) quartiles for each sex ($M_{25\%} = 1.37$ units km^{-2} , $F_{25\%} = 2.7$ units km^{-2} , $M_{75\%} = 5.72$ units km^{-2} , $F_{75\%} = 23$ units km^{-2}). Survival is lower for males and for individuals that forage in developed areas.

majority (75%) were associated with conflict with domestic species.

Discussion

Cougars in the urban–wildland interface displayed a high degree of intrapopulation variability in diet, primarily associated with housing density. Native ungulates remained the dominant prey across the population, although the magnitude of use varied by age–sex class and level of landscape development. In particular, adult females consumed more native herbivores than adult males and subadults, a pattern observed previously (Anderson & Lindzey 2003) and one that remained consistent across all levels of housing density. Although subadults exploit maternal kills, they also typically rely more on smaller-bodied prey, likely due to foraging inexperience (Knopff 2010). Mule deer were prevalent across the study area, including the developed parts where hunting pressure was low (Huwer & Kraft 2012). Yet, despite the abundance of deer, cougars of all age–sex classes increased consumption of non-ungulate prey in developed areas, utilizing both domestic and synanthropic species. This pattern was consistent with previous findings (Kertson, Spencer & Grue 2011).

Our estimate of native herbivore consumption from stable isotope analysis is lower than previously estimated by kill-site investigations in our study area (Blecha, Boone & Alldredge 2013). Unlike kill-site investigations or faecal analysis, isotopic analysis quantifies the assimilated diet of an individual and is not biased towards larger-bodied

prey. It is possible, then, that kill sites overestimate consumption of large-bodied prey, especially given that cougars do not always fully ingest their prey and that incomplete consumption of ungulate kills can be high in urban and exurban areas (Smith, Wang & Wilmers 2015). Alternatively, our isotopic analysis may have overestimated the importance of alternative prey. Mixing models are sensitive to the choice of discrimination factor (Parng, Crumpacker & Kurle 2014). The correction we used, developed in foxes, could have introduced bias into our model and underestimated cougar reliance on primary prey. Further, if we did not sample all important diet sources and failed to capture the isotopic mixing space completely, estimates of diet could be inaccurate. Nevertheless, even if our estimate of diet composition was influenced by these factors, we are confident in the relationship between diet and space. Indeed, raw isotopic values correlated strongly with space use. Thus, we emphasize the utility of isotopic analysis, which can be applied to non-invasively collected samples, as an estimator of diet as well as space use and likelihood of conflict.

There are several potential explanations for higher use of alternative prey in developed areas. Domestic species and a number of synanthropic wildlife often reach higher densities in developed relative to wildland habitat (Batemann & Fleming 2012). It is possible, then, that a dietary shift is proportionate to prey abundance. However, cougars exhibit prey switching (Knopff 2010), and there may be advantages in handling or search time when consuming smaller-bodied prey. Cougars in some developed areas spend less time at kill sites and abandon prey at a higher rate because of perceived risk (Smith, Wang & Wilmers 2015). Selecting small-bodied prey could therefore reduce time spent at kills. However, this pattern has not been observed elsewhere (Kertson, Spencer & Grue 2011), and our data suggest that, even though they are consuming small prey, cougars remain in developed areas long enough to be captured by GPS fixes at 3-h intervals. Without quantifying the relative abundance of prey species throughout our study area, we cannot identify whether use of small prey is a response to their abundance or a risk-avoidance strategy.

While cougars generally select against developed areas (Beier, Riley & Sauvajot 2010; Kertson *et al.* 2011), this avoidance is not complete. Indeed, cougars show a functional response, becoming more prone to use developed areas as they become more common (Knopff *et al.* 2014). Yet, this strategy increases risk of mortality. Why cougars utilize developed areas despite heightened risk is unclear. Cougars in our study were all within a healthy weight range and displayed no evidence of starvation, suggesting that use of developed areas is not a response to nutritional stress. Cougars tend to hunt more efficiently in edge habitat (Holmes & Laundré 2006), and patchiness associated with development might facilitate stalking of prey (Knopff *et al.* 2014). Alternatively, cougars could be forced into risky, suboptimal habitat when territories in

wildland areas become saturated; in this case, we would expect transients or subadults to be the most likely users of urban areas (Logan & Sweeney 2001). We found use of developed areas did not differ by age–sex class, though small sample sizes could reduce our power to detect such differences. Finally, the abundance of prey could attract cougars to developed areas, acting as an ecological trap (Merkle *et al.* 2013). Likely it is a combination of factors that attract cougars into developed landscapes; though generally avoided, the presence of prey, adequate cover and proximity to wildland habitat indicate suitable locations to forage (Kertson *et al.* 2011).

It is not simply presence in developed areas that increases risk of mortality for cougars; use of prey played a role in mortality risk, with lethal removal most likely when cougars were sighted with domestic species. Thus, we expect that foraging behaviour in developed areas could play a role in cougar population viability. Adult female survival, the most elastic vital rate (Lambert *et al.* 2006) was reduced by about 16% in highly developed areas. Cougars do not typically exhibit a high degree of plasticity in maternity rate, nor do we expect that juvenile recruitment could increase enough to compensate for reduced adult female survivorship. Thus, though cougars are highly plastic and able to utilize developed areas and prey, this strategy ultimately bears a cost, with likely implications for population growth. Unlike in other behaviourally plastic species, dietary flexibility does not appear to be sufficient for success in developed areas. In fact, these behavioural shifts, especially use of domestic species, could exacerbate, rather than mitigate risk.

Cougars, like many other large-bodied carnivores, are often portrayed as extremely sensitive, wildland obligates, requiring large tracts of undisturbed habitat for dispersal and sufficient prey (Crooks 2002; Beier, Riley & Sauvajot 2010; Riley *et al.* 2014). Yet, though the maintenance of intact habitat is certainly important for long-term viability, we found that cougars in a rapidly developing landscape were remarkably adaptable in their ability to forage in these habitats. Our study adds to the growing appreciation of large carnivores' resilience to habitat change (e.g. Bouyer *et al.* 2015; Odden *et al.* 2014). As developed landscapes are ecologically similar (McKinney 2006), we expect the pattern observed here to be replicated geographically. As the distribution of developed landscapes grows, conservation of large carnivores will have to include conservation within less-pristine landscapes. Consequently, it is not sufficient to predict carnivore behaviour or inform management plans based solely on observations of a species' ecology in wildland landscapes.

There has been a recent, and successful, push towards restoring natural habitat characteristics within developed landscapes (Angold *et al.* 2006). Such habitat enhancement also carries with it the return of biotic interactions – including those between large predators and their prey. Because of the foraging flexibility of large carnivores, predation events are likely to occur near humans and may

spill over to include domestic species. Often, these conflicts are met with carnivore removal. Rather than a management response after conflict, a more viable approach would be to manage those features that draw predators to unwanted areas in developed landscapes. For instance, improving waste management and limiting domestic pets or abundant synanthropes would reduce alternative prey availability. Similarly, habitat alterations such as buffers between natural and residential areas could be used to reduce the movement of both predators and prey into areas featuring high human densities. Ultimately, however, there will be ecological interactions in human-dominated environments, regardless of management strategies, including some that will be concerning to the public. Consequently, this necessitates a dialogue about what developed ecosystems should feature and whether public tolerance can adapt along with wildlife.

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Data accessibility

Cougar and prey isotopic signatures and cougar survival data are available from the Dryad data repository: doi:10.5061/dryad.23qp6 (Moss, Alldredge & Pauli 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Isotopic signatures of prey species.