



## Research Article

# Spatial Characteristics of Residential Development Shift Large Carnivore Prey Habits

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**ABSTRACT** Understanding how anthropogenic development affects food webs is essential to implementing sustainable growth measures, yet little is known about how the spatial configuration of residential development affects the foraging behavior and prey habits of top predators. We examined the influence of the spatial characteristics of residential development on prey composition in the puma (*Puma concolor*). We located the prey remains of kills from 32 pumas fitted with global positioning system (GPS) satellite collars to determine the housing characteristics most influencing prey size and species composition. We examined how differences in housing density, proximity, and clustering influenced puma prey size and diversity. We found that at both local (150 m) and regional (1 km) spatial scales surrounding puma kill sites, housing density (but not the clustering of housing) was the greatest contributor to puma consumption of small prey (<20 kg), which primarily comprised human commensals or pets. The species-specific relationships between housing density and prey occupancy and detection rates assessed using camera traps were not always similar to those between housing density and proportions of diet, suggesting that pumas may exercise some diet selectivity. The influence of development on puma diet may affect puma disease risk, energetics, and demographics because of altered species interactions and prey-specific profiles of energetic gain and cost. Our results can help guide future land-use planners seeking to minimize the impacts of development on wild species interactions and community dynamics. © 2016 The Wildlife Society.

**KEY WORDS** coexistence landscape, habitat fragmentation, hunting behavior, mountain lion, prey selection, puma, *Puma concolor*, residential development.

Habitat loss, conversion, and modification are the largest global influences on species extinction and declines globally (Pimm and Raven 2000), a trend which is expected to continue throughout the 21st century (Sala et al. 2000). In addition, residential development growth rates in the United States outpace population growth by 25%, further increasing the human footprint (Theobald 2005). These patterns are influenced by extensive development that occurs at low densities adjacent to or embedded within wildland areas. Altogether, exurban developments encompass >7 times the land area of urban development.

As development continues to transform wild areas, attention has been drawn to the spatial characteristics of new developments and how smart growth can assuage environmental impacts (Theobald et al. 2005, Baldwin et al. 2007). The spatial attributes of housing developments can be more

important than the overall density of structures on the landscape in regard to providing habitat for sensitive species (Theobald et al. 1997), yet housing density is regularly provided as the only measure of development in ecological studies through use of the urban–rural gradient framework (Hansen et al. 2005). Not all patterns of anthropogenic development are expected to affect biotic communities equally, and the behavior and ecology of species persisting in modified habitats are likely influenced by the spatial configuration of development. Although a preserve abutting an urban interface might support many native animal populations, landscapes comprising low-density development have been reported to decrease species diversity because of the widespread and diffuse nature of human disturbances (Merenlender et al. 2009). Adding nuance to urban–rural gradient research by incorporating animal responses to spatial characteristics of development enhances the ability to predict and understand the ecological ramifications of different development types and guide future land-use planning.

Habitat loss and fragmentation disproportionately affect large carnivores because they have large home ranges and a

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history of conflict with humans (Ripple et al. 2014); on average, individual carnivore species have lost approximately 50% of high-quality habitat globally (Crooks et al. 2011). Anthropogenic disturbances change the composition of animal communities by extirpating sensitive species and promoting generalists (McKinney 2006), which subsequently affects animal resource use and diet in modified habitats globally (Newsome et al. 2015). Carnivores may be expected to alter their prey habits in these sub-optimal, human-modified habitats in response to changes in prey availability. Large carnivores sometimes take advantage of human-associated prey; there are numerous accounts of carnivores consuming livestock and other anthropogenic food (Bateman and Fleming 2012). Leopards (*Panthera pardus*; Athreya et al. 2016) and hyenas (*Crocuta crocuta*; Abay et al. 2011) have been documented to consume synanthropic prey almost exclusively in developed areas. Changes in prey size and composition affect carnivores because consuming larger sized prey is often more energetically efficient and can increase survival probability (Bartoń and Hovestadt 2013). Although many large carnivores, particularly felids, are obligate carnivores and, therefore, unlikely to directly consume anthropogenic subsidies (e.g., garbage, pet food, bird seed), they can hunt species that do directly exploit these subsidies. These synanthropic prey species alter spatial patterns of prey availability and subsequently the profitability and catchability of the prey available within a carnivore's territory or home range in relation to existing human developments.

Pumas (*Puma concolor*) behaviorally respond to anthropogenic disturbances, primarily in regard to temporal activity patterns and space use (Kertson et al. 2011, Wilmers et al. 2013, Lewis et al. 2015, Smith et al. 2015, Wang et al. 2015). Although pumas in North America primarily consume large ungulate prey (Villepique et al. 2011), they are generalist predators and also consume a diversity of other species (Knopff et al. 2010, Moss et al. 2015). In exurban habitats, alternative and synanthropic prey species of pumas are often much smaller than the dominant prey species, consisting largely of mesopredators (Moss et al. 2015). A reduction in average prey size in residential areas is likely to influence puma handling time and hunting strategies, ultimately altering puma energetics, movement, and space use. We examined the patterns of use of alternative prey for pumas in the Central Coast region of California. In California, exurban (or low-density) development is projected to be the greatest contributor to habitat loss through 2050, amounting to 52,000 km<sup>2</sup> (12.9 million acres) of land in the state (Mann et al. 2014); therefore, understanding changes in puma resource use in this state is essential for their management.

We investigated the magnitude and nature of the relationship between anthropogenic development and puma prey habits. We examined patterns of prey composition across an urban–rural gradient at 2 spatial scales representing the local and regional conditions surrounding a kill site. We predicted that increased hunting of small prey (<20 kg) would increase overall prey diversity and increase use of synanthropic prey species, but that this relationship

would be strongest at the smaller scale representing the immediate environment. We then explored if the spatial characteristics of development (i.e., housing density, clustering, proximity) corresponded with changes in prey composition and size. We anticipated that the density, configuration, and proximity of houses would all affect consumption of small prey species. We also examined if females and males had different diets and relationships to housing parameters. We anticipated that because females have higher housing density in their home ranges on average (Smith et al. 2015), they would kill in more developed areas and have higher composition of small prey in their diet than males. Finally, we assessed if diet patterns mirrored prey occupancy and detection rates along a housing density gradient.

## STUDY AREA

We conducted research in the Santa Cruz Mountains in the Central Coast region of California, USA. The Santa Cruz Mountains are bordered by the Bay Area to the north, the Pacific Ocean to the west, Monterey Bay to the south, and a high-speed freeway to the east (Highway 101). Our 1,700-km<sup>2</sup> study area was composed of a mosaic of land-use types, including small towns, low-density residential development, resource extraction lands for logging and mining, and a diversity of public and private parks and preserves. One major 4-lane highway, Highway 17, and 1 2-lane highway, Highway 9, divided the study area north-to-south. The habitat largely comprised oak (*Quercus* spp.) woodland forest, redwood (*Sequoia sempervirens*) forest, mixed hardwood forest, chaparral, and grassland. The climate in this region is Mediterranean and is characterized by a summer dry season and winter wet season. The elevation ranges from 0 m to 1,154 m and topography is steep and mountainous. Pumas are the last large carnivore in the region, and black-tailed deer (*Odocoileus hemionus columbianus*) are the only remaining abundant ungulate (with the exception of a few pockets where non-native wild boar [*Sus scrofa*] are present). Other available prey species are largely meso- and small carnivores, pets, and livestock.

## METHODS

### Puma Locations and Cluster Analysis

We captured and collared 32 adult (>2 year old) pumas from 2008 to 2014 comprising 15 females and 17 males. We captured pumas with the use of trailing hound dogs, cage traps, or leg-hold snares. We used Telazol (Fort Dodge Laboratories, Fort Dodge, IA, USA) to anesthetize pumas. We followed animal care and use protocols authorized by the University of California, Santa Cruz, California, USA (no. WILMC1011). We fitted each puma with a combined global positioning (GPS) radio-collar (Model GPS Plus 1 or 2 D, Vectronics Aerospace, Berlin, Germany), programmed to take a GPS fix every 4 hours. We had 2 methods of obtaining location data: we remotely downloaded location data from active GPS collars with an ultra high frequency (UHF) terminal every 4 weeks, or we received locations

transmitted via cell phone towers every 1–3 days. We attempted to remove and replace collars on pumas near the end of the collar's battery life to get continuous long-term data on collared pumas.

We developed a custom program integrated in the geographical information systems program ArcGIS (v.10; ESRI, Redlands, CA, USA) using the programming languages R (v.3.1.3; R Development Core Team 2013) and Python (v. 2.6; Python Software Foundation, Wilmington, DE, USA) to identify clusters of GPS locations that were potential kill sites (i.e., where a kill was consumed; Wilmers et al. 2013). We defined clusters as groups of  $\geq 2$  locations in which each location was within 100 m of the cluster centroid and 6 days of another GPS location of the same individual puma. We generated clusters immediately after remotely downloading GPS locations.

We investigated puma GPS clusters in the field for the presence of a kill from March 2009 to July 2014. To avoid bias in visitation across human use zones, we investigated clusters in reverse chronological order, regardless of accessibility or cluster size, with the exception that we visited clusters near other clusters in groups to optimize field time. We did not investigate some clusters because of the inaccessibility of terrain or because we were not able to get permission from the property owner. We visited clusters within 30 days of the first location in the cluster. We investigated each cluster by navigating to the centroid of the cluster and searching the area by spiraling outward from the center for 30 minutes. If we found a prey item (or multiple prey items), we documented the species, age class, and sex of the prey when possible. We excluded prey weighing  $< 1$  kg from analyses because we lacked definitive evidence of puma predation.

### Housing Descriptors

To calculate descriptors of housing impact at kill sites, we manually digitized every building in the Santa Cruz Mountains from high-resolution satellite imagery (source: ESRI World Imagery). We calculated proximity as the distance from a kill to the nearest house using the Near tool in ArcMap (v10.1, ESRI). We determined housing density at each kill at 2 scales to investigate the spatial extent of influence of housing on prey composition. Specifically, we constructed buffers around kill sites with radii of 150 m and 1 km, and calculated the number of houses/km<sup>2</sup> within each buffer using the Spatial Join tool in ArcMap. We chose the smaller buffer size to represent the local scale because the scale of human influence most likely to impact puma movements has been reported to be 150 m in this study area (Wilmers et al. 2013). We selected the 1-km buffer size to represent the regional scale to account for the estimated upper home range sizes of most small, synanthropic prey species (e.g., raccoons [*Procyon lotor*]; Beasley et al. 2007). We estimated the spatial clustering of houses at each kill site by measuring the average distance to the nearest neighbor among houses within the buffer zones of 150 m and 1 km of a kill using the Generate Near Table tool in ArcMap. Lower values represent greater clustering.

We categorized kills into housing density levels to classify differential prey diversity and size by housing type. We binned the housing densities at both scales into 4 housing density levels as described by Theobald (2005): no housing, rural ( $> 0.0$ – $0.06$  houses/ha), exurban ( $> 0.06$ – $1.24$  houses/ha), and suburban ( $> 1.24$ – $9.88$  houses/ha). No kills were present at urban densities ( $> 9.88$  houses/ha).

### Prey Diversity and Small Prey Use

We calculated the proportion of diet contributed by each prey species with regard to both frequency of kills and edible biomass (Table 1). We assessed dietary diversity by calculating a prey diversity index using the Shannon–Wiener diversity index (Yip et al. 2014) for each housing density level at the 150-m and 1-km scales. We also calculated prey diversity for males and females and used Mann–Whitney  $U$  non-parametric tests to examine sex differences in housing metrics (i.e., proximity, density, clustering) and proportion of small prey consumed. We binned prey into large ( $> 20$  kg) and small ( $< 20$  kg) categories for subsequent analyses of housing covariates on prey size. We constructed a mixed effects binomial logistic regression model with individual puma as a random effect and prey size class as a binary response variable to determine which spatial housing characteristics at a kill site best predicted prey size. We used a random effect of puma to control for differences in sample sizes among individuals for the scale representing the pumas' local environment (150-m scale) and the scale representing the regional area characteristics (1-km scale). We excluded clusters associated with den sites (confirmed from field investigations) from this analysis. We normalized the housing covariates for the analysis so we would not bias coefficients of variables. For this portion of our analysis, we used only kill sites that had  $\geq 1$  house present in the scale of analysis (i.e., local or regional) to assess which spatial characteristics of development most influenced prey size given the presence of development. We constructed 7 models that represented every permutation of the 3 variables (i.e., housing density, proximity, clustering): 3 univariate models, 3 bivariate models, and a full model. We investigated correlations between each pair of the 3 descriptors, and found that no pair of descriptors was correlated at the 1-km scale ( $r < 0.5$  for all pairs), but that housing density and proximity to a house were correlated at the 150-m scale ( $r = 0.61$ ). Therefore, we excluded the 2 models containing both variables at the 150-m scale, leaving 5 candidate models. We compared Akaike's Information Criterion (AIC) values for the suite of models for each scale to identify which model best fit the data (Burnham and Anderson 2002).

We ran Mann–Whitney  $U$  non-parametric tests to compare prey size class in relation to the housing covariates in the best-fit model using all kill sites, including those where no housing was present. This analysis allowed us to quantify the magnitude of differences in housing covariates at kill sites of large and small prey at both scales examined.

### Prey Species Occupancy and Detection

To gain insight on prey availability, we distributed 50 motion-sensor cameras on animal and human trails across a

**Table 1.** Frequency and proportion of prey killed by puma in each of 4 housing density categories in the Santa Cruz Mountains, California, USA, 2009–2014 at the local (150-m buffer) and regional scale (1-km buffer) for all prey species over 1 kg. For prey size, S refers to small prey (1–20 kg) and L refers to large prey (>20 kg). Edible biomass estimates are included in the total column. Percentages in each housing column represent the proportion of the diet made up by the individual species within the given housing density. Species are listed in order of % of diet (frequency).

| Species               | Prey size (S, L) | Local scale    |           |             |              | Regional scale |           |             |              | Total (% frequency/<br>% edible biomass) |
|-----------------------|------------------|----------------|-----------|-------------|--------------|----------------|-----------|-------------|--------------|--|
|                       |                  | No housing (%) | Rural (%) | Exurban (%) | Suburban (%) | No housing (%) | Rural (%) | Exurban (%) | Suburban (%) |  |
| Black-tailed deer     | L                | 253 (84.3)     | 28 (84.8) | 51 (68.0)   | 16 (51.6)    | 46 (93.9)      | 80 (83.3) | 195 (78.6)  | 27 (58.7)    | 348 (79.3/90.0 <sup>ab</sup> )           |
| Raccoon               | S                | 14 (4.7)       | 4 (12.1)  | 8 (10.7)    | 5 (16.1)     | 3 (6.1)        | 4 (4.2)   | 18 (7.3)    | 6 (13.0)     | 31 (7.0/2.0 <sup>cd</sup> )              |
| Domestic cat          | S                | 4 (1.3)        | 0 (0)     | 8 (10.7)    | 6 (19.4)     | 0 (0)          | 1 (1.0)   | 8 (3.2)     | 9 (19.6)     | 18 (4.1/0.9 <sup>cd</sup> )              |
| Virginia opossum      | S                | 5 (1.7)        | 0 (0)     | 3 (4.0)     | 2 (6.5)      | 0 (0)          | 0 (0)     | 9 (3.6)     | 1 (2.2)      | 10 (2.3/0.2 <sup>cd</sup> )              |
| Wild boar             | L                | 8 (2.7)        | 0 (0)     | 1 (1.3)     | 0 (0)        | 0 (0)          | 3 (3.1)   | 6 (2.4)     | 0 (0)        | 9 (2.1/1.9 <sup>bc</sup> )               |
| Domestic goat         | L                | 1 (0.3)        | 0 (0)     | 4 (5.3)     | 2 (6.5)      | 0 (0)          | 1 (1.0)   | 4 (1.6)     | 2 (4.3)      | 7 (1.6/1.6 <sup>bf</sup> )               |
| Domestic cow          | L                | 4 (1.3)        | 0 (0)     | 0 (0)       | 0 (0)        | 0 (0)          | 4 (4.2)   | 0 (0)       | 0 (0)        | 4 (0.9/2.1 <sup>bg</sup> )               |
| Coyote                | S                | 3 (1.0)        | 0 (0)     | 0 (0)       | 0 (0)        | 0 (0)          | 1 (1.0)   | 1 (0.4)     | 1 (2.2)      | 3 (0.7/0.4 <sup>cd</sup> )               |
| Domestic pig          | L                | 2 (0.7)        | 0 (0)     | 0 (0)       | 0 (0)        | 0 (0)          | 0 (0)     | 2 (0.8)     | 0 (0)        | 2 (0.5/0.4 <sup>bc</sup> )               |
| Striped skunk         | S                | 2 (0.7)        | 0 (0)     | 0 (0)       | 0 (0)        | 0 (0)          | 1 (1.0)   | 1 (0.4)     | 0 (0)        | 2 (0.5/0.0 <sup>cd</sup> )               |
| North American beaver | S                | 1 (0.3)        | 0 (0)     | 0 (0)       | 0 (0)        | 0 (0)          | 0 (0)     | 1 (0.4)     | 0 (0)        | 1 (0.2/0.2 <sup>cd</sup> )               |
| Bobcat                | S                | 1 (0.3)        | 0 (0)     | 0 (0)       | 0 (0)        | 0 (0)          | 1 (1.0)   | 0 (0)       | 0 (0)        | 1 (0.2/0.1 <sup>cd</sup> )               |
| Wild turkey           | L                | 1 (0.3)        | 0 (0)     | 0 (0)       | 0 (0)        | 0 (0)          | 0 (0)     | 1 (0.4)     | 0 (0)        | 1 (0.2/0.1 <sup>dh</sup> )               |
| Domestic chicken      | S                | 1 (0.3)        | 0 (0)     | 0 (0)       | 0 (0)        | 0 (0)          | 0 (0)     | 1 (0.4)     | 0 (0)        | 1 (0.2/0.0 <sup>di</sup> )               |
| Gray fox              | S                | 0 (0)          | 1 (3.0)   | 0 (0)       | 0 (0)        | 0 (0)          | 0 (0)     | 1 (0.4)     | 0 (0)        | 1 (0.2/0.0 <sup>cd</sup> )               |

<sup>a</sup> Black-tailed deer mass (Rue 2004).

<sup>b</sup> Ungulate proportion edible (Wilmers et al. 2003).

<sup>c</sup> Mass of non-ungulate mammals (Jameson and Peeters 2004).

<sup>d</sup> Small prey proportion edible (Prange et al. 1979).

<sup>e</sup> Mass of pig and boar (Saunders and McLeod 1999).

<sup>f</sup> Mass of domestic goat (Gambaryan 1974).

<sup>g</sup> Mass of domestic cow (Beal et al. 1990).

<sup>h</sup> Mass of wild turkey (Sibley 2003).

<sup>i</sup> Mass of domestic chicken (Latshaw and Bishop 2001).

housing density gradient from no housing to suburban housing. We chose to use animal and human trails for camera placement because of the presence of extensive trail networks in our study area and the known use of trails for hunting by pumas in other regions (Harmson et al. 2010). Camera placement on trails is appropriate for many of the primary prey species in our study area, including cats (Kays et al. 2015), deer, Virginia opossums (*Didelphis virginiana*), and raccoons (Erb et al. 2012). At each camera, we calculated housing density within 150-m and 1-km buffers and classified cameras into the same housing density levels used above (no housing, rural, exurban, and suburban). We set cameras to take 3 photos at 1-second increments following a trigger with a 60-second break before the camera could be triggered again. We recorded every animal occurrence as 1 detection per set of 3 photos. For our target prey species, we then constructed a dataset comprising weekly detection histories from consolidated detections in weekly intervals from October 2011 to October 2012.

To determine if prey occupancy or detection was a function of housing density, we developed occupancy models for each prey species making up  $\geq 2\%$  of puma diet using the weekly detection history dataset. Occupancy models estimate the probability of species site occupancy ( $\psi$ ) and detection ( $p$ ) and can incorporate the effects of covariates on these probabilities. We qualitatively associate prey activity with detection probability and prey presence with occupancy. We used 1-week detection intervals, where species were present

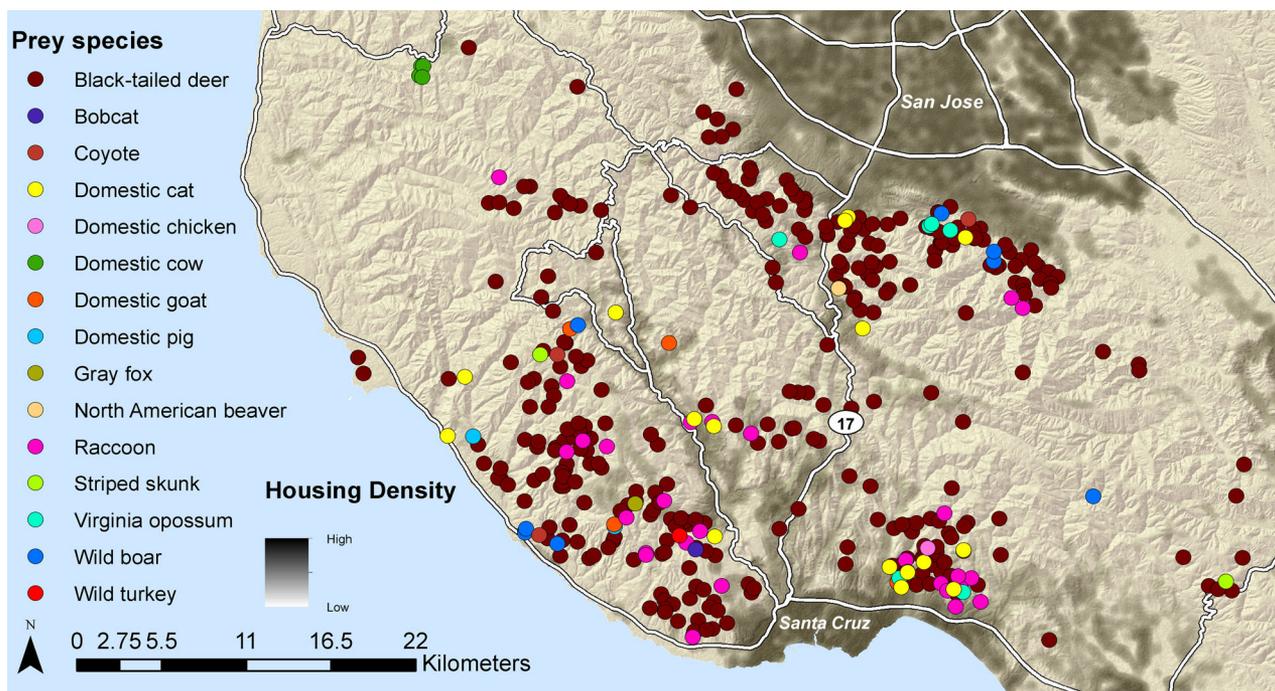
or absent over each monitored weeklong period. This method allows us to model if each prey species was ever detected at a camera ( $\psi$ ) and the probability of detecting each species at a camera ( $p$ ), providing measures of presence and relative use (Royle and Nichols 2003, Royle et al. 2005). Because some species in our study area are rare and distributed heterogeneously, whereas others are common but vary spatially in their abundance, occupancy modeling is the best approach to capture the variation in space use for a diversity of prey species across a housing density gradient.

Using the program Presence (v.5.9, Hines 2006), we tested 4 models: 1) occupancy and detection are constant across all sites (null model); 2) occupancy varies with housing density but detection is constant; 3) occupancy is constant but detection varies with housing density; and 4) both occupancy and detection vary with housing density. We used AIC to compare the 4 models to evaluate if housing density informed the probabilities of occurrence and detection of primary prey species.

## RESULTS

### Kill Sites and Diet Composition

We visited 1,476 clusters from 32 pumas, 439 of which had evidence of prey remains (Fig. 1). We visited on average 13.7 ( $\pm 2.3$  SE) kills/puma, with a median of 10 kills. Small prey between 1 kg and 20 kg were visited by pumas for 6.2 ( $\pm 0.8$  SE) GPS locations on average; therefore, we



**Figure 1.** Study area in the Santa Cruz Mountains, California, USA with all confirmed kill sites of pumas color-coded by species, 2009–2014.

believe we reliably found a large proportion of kills of this size. We found that 68% of kills had no housing within 150 m of the kill. However, within 1 km of a kill site, the majority of kills occurred at exurban housing densities (56%).

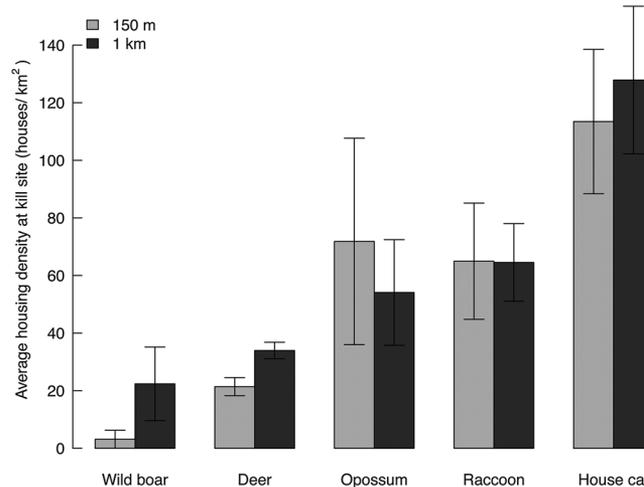
Black-tailed deer were the most common prey item, making up 79% of kills and 90% of edible prey biomass (Table 1). Other prey items included bobcat (*Lynx rufus*), coyote (*Canis latrans*), domestic cat, domestic chicken, domestic cow, domestic goat, gray fox (*Urocyon cinereoargenteus*), North American beaver (*Castor canadensis*), raccoon, striped skunk (*Mephitis mephitis*), turkey (*Meleagris gallopavo*), Virginia opossum, and wild boar (Table 1). Domestic animals made up 7% of kills, and other synanthropic species (raccoons, opossums, and skunks) comprised 10% of kills. Of alternative (non-deer) prey, the 4 other species making up  $\geq 2\%$  of puma kills were raccoons (7%), domestic cats (4%), opossums (2%), and wild boar (2%). Of these species, domestic cat kill sites were present in the highest housing density areas on average at both housing density scales, followed by raccoons, opossums, deer, and finally wild boar (Fig. 2). Of the primary prey species, domestic cats were killed closest to housing on average ( $97 \pm 18$  SE m), followed by opossums ( $169 \pm 30$  SE m), raccoons ( $382 \pm 90$  SE m), deer ( $454 \pm 22$  SE m), and wild boar ( $484 \pm 73$  SE m). The diversity of prey species killed and the proportion of small ( $< 20$  kg) prey at puma kill clusters increased with housing density at both examined scales (Table 2). Notably, diversity was lowest when no houses were present within 1 km of a kill site.

### Spatial Patterns of Development and Use of Small Prey

Our best-fit models predicting prey size class for the local and regional scales both contained only the housing density

covariate (Tables 3 and 4), and all models containing the housing density covariate performed better than models without. Although 2 alternative models at the regional scale and 1 alternative model at the local scale fell within  $2 \Delta AIC$ , they each contained additional variables. This implies that although some models with additional housing variables were indistinguishable in terms of their fit of the data, these variables did not improve the fit of a density-only model.

Small prey were consumed at kill sites closer to a house ( $W = 17,068$ ,  $P < 0.001$ ), in more clustered housing ( $W = 2,528$ ,  $P = 0.002$  for local scale;  $W = 13,864$ ,  $P < 0.001$  for regional scale), and with higher housing densities ( $W = 8,920$ ,



**Figure 2.** Average housing density ( $\pm$ SE) of kill sites for species comprising  $\geq 2\%$  of puma diet in the Santa Cruz Mountains, California, USA, 2009–2014. Housing density within 150 m (local scale) and 1 km (regional scale) of a kill site are shown.

**Table 2.** Species diversity (Shannon–Wiener  $H'$ ) of prey killed by pumas and percentage of kills that were small prey (1–20 kg) at 4 housing density levels in the Santa Cruz Mountains, California, USA, 2009–2014 for 2 scales of influence (local: 150-m buffer, regional: 1-km buffer) around confirmed puma kill sites.

| Housing density class | $H'$ diversity index |          | Small prey consumed (%) |          |
|-----------------------|----------------------|----------|-------------------------|----------|
|                       | Local                | Regional | Local                   | Regional |
| No housing            | 0.775                | 0.230    | 10.7                    | 6.2      |
| Rural                 | 0.501                | 0.763    | 15.2                    | 8.3      |
| Exurban               | 1.082                | 0.939    | 25.3                    | 16.5     |
| Suburban              | 1.307                | 1.200    | 41.9                    | 37.0     |

$P \leq 0.001$  for local scale;  $W = 8,334$ ,  $P \leq 0.001$  for regional scale; Fig. 3). The average ( $\pm$ SE) distance away from a house where a small kill was made was  $290 \pm 46$  m, in contrast to  $449 \pm 21$  m for large kills. At small kills, the average nearest neighbor distance for houses at the local scale was  $44 \pm 6$  m, whereas it was  $86 \pm 10$  m at kill sites of large prey. This pattern held at the regional scale, but the magnitude of the difference was less pronounced ( $72 \pm 30$  m for small prey,  $84 \pm 9$  m for large prey). Average housing density at the local scale was  $70 \pm 13$  houses/km<sup>2</sup> for small prey and  $22 \pm 3$  houses/km<sup>2</sup> for large prey. Similarly, at the regional scale, average housing density was  $75 \pm 10$  houses/km<sup>2</sup> for small prey and  $35 \pm 3$  houses/km<sup>2</sup> for large prey.

### Sex-Specific Responses to Housing at Kill Sites

Males made kills at lower housing densities than females at the local ( $W = 16,935$ ,  $P \leq 0.001$ ) and regional ( $W = 16,972$ ,  $P = 0.003$ ) scales. Males also killed farther away from the nearest house on average ( $W = 24,139$ ,  $P = 0.004$ ), with a

**Table 3.** Results of mixed effects binomial logistic regression model predicting puma prey size class from 3 housing descriptors within 1 km of a kill site: housing density (density), average nearest neighbor distance (clustering), and distance to the nearest house (proximity) for kill sites in the Santa Cruz Mountains, California, USA, 2009–2014. Each housing density covariate has been normalized for comparison of coefficients, where positive coefficients indicate that larger values of the variable are associated with large prey. All models shown have a random intercept for individual puma and are listed in order of Akaike's Information Criterion (AIC).

| Model rank | AIC    | $\Delta$ AIC | Covariates | Coefficient | SE   |
|------------|--------|--------------|------------|-------------|------|
| 1          | 337.56 | 0.00         | Density    | -0.47       | 0.13 |
|            |        |              | Intercept  | 1.92        | 0.22 |
| 2          | 337.81 | 0.26         | Density    | -0.38       | 0.14 |
|            |        |              | Proximity  | 0.24        | 0.19 |
|            |        |              | Intercept  | 1.92        | 0.22 |
| 3          | 339.50 | 1.94         | Density    | -0.48       | 0.13 |
|            |        |              | Clustering | -0.04       | 0.15 |
|            |        |              | Intercept  | 1.91        | 0.21 |
| 4          | 339.57 | 2.01         | Density    | -0.39       | 0.14 |
|            |        |              | Clustering | -0.08       | 0.15 |
|            |        |              | Proximity  | 0.26        | 0.19 |
|            |        |              | Intercept  | 1.92        | 0.22 |
| 5          | 342.91 | 5.35         | Proximity  | 0.44        | 0.17 |
|            |        |              | Intercept  | 1.90        | 0.22 |
| 6          | 344.84 | 7.28         | Clustering | -0.04       | 0.17 |
|            |        |              | Proximity  | 0.45        | 0.18 |
|            |        |              | Intercept  | 1.90        | 0.22 |
| 7          | 350.30 | 12.74        | Clustering | 0.06        | 0.17 |
|            |        |              | Intercept  | 1.87        | 0.21 |

**Table 4.** Results of mixed effects binomial logistic regression model predicting puma prey size class from 3 housing descriptors within 150 m of a kill site: housing density (density), average nearest neighbor distance (clustering), and distance to the nearest house (proximity) for kill sites in the Santa Cruz Mountains, California, USA, 2009–2014. Each housing density covariate has been normalized for comparison of coefficients, where positive coefficients indicate that larger values of the variable are associated with large prey. All models shown have a random intercept for individual puma and are listed in order of Akaike's Information Criterion (AIC).

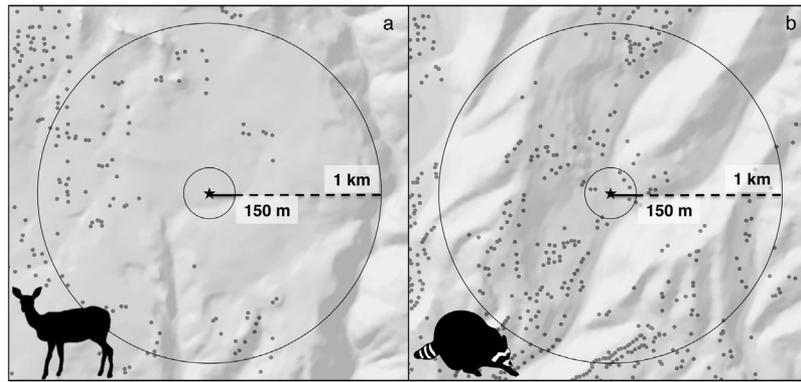
| Model rank | AIC    | $\Delta$ AIC | Covariates | Coefficient | SE   |
|------------|--------|--------------|------------|-------------|------|
| 1          | 146.91 | 0.00         | Density    | -0.64       | 0.23 |
|            |        |              | Intercept  | 1.96        | 0.52 |
| 2          | 147.28 | 0.37         | Density    | -0.49       | 0.25 |
|            |        |              | Clustering | 0.47        | 0.44 |
|            |        |              | Intercept  | 1.93        | 0.51 |
| 3          | 148.80 | 1.89         | Clustering | 0.82        | 0.47 |
|            |        |              | Intercept  | 1.85        | 0.46 |
| 4          | 150.38 | 3.47         | Clustering | 0.72        | 0.48 |
|            |        |              | Proximity  | 0.17        | 0.26 |
|            |        |              | Intercept  | 1.85        | 0.47 |
| 5          | 151.97 | 5.06         | Proximity  | 0.37        | 0.24 |
|            |        |              | Intercept  | 1.82        | 0.48 |

mean ( $\pm$ SE) of  $479 \pm 35$  m away in contrast to  $400 \pm 23$  m for females. Clustering between houses did not differ among male and female kill sites at the local ( $W = 2,111$ ,  $P = 0.54$ ) or regional scales ( $W = 14,567$ ,  $P = 0.71$ ).

Despite differences in housing density at kill sites, males and females did not appear to differ in their use of small, alternative prey species. There was no significant difference in average use of small prey between sexes ( $Z = 1.81$ ,  $P = 0.07$ ), and diversity indices were similar ( $H'_{\text{female}} = 0.885$ ,  $H'_{\text{male}} = 0.905$ ).

### Prey Species Occupancy and Detection

At the local scale, only occupancy of domestic cats was positively associated with housing density, whereas cat and raccoon occupancy was positively associated with housing density at the regional scale (Appendix A, available in Supporting Information online). However, the null model for each of the 3 above analyses was among the top models within 2  $\Delta$ AIC; therefore, it is possible that the housing parameter is uninformative (Arnold 2010). Deer occupancy was ubiquitous across the study area; deer were photographed at every camera station, but deer detection was positively associated with housing density at the local and regional scales. Wild boar occupancy and detection were negatively associated with housing density at the local scale, whereas only boar occupancy was negatively associated with housing density at the regional scale. The null models for detection and occupancy of opossums performed best at both scales; however, the models including housing as a covariate to inform occupancy were within 2  $\Delta$ AIC of the null and cannot be ruled out as possible explanations of the data. Relationships between housing and occupancy of cats, raccoons, and wild boar (at the local and regional scale) indicated that the presence of these species were affected by development, whereas housing relationships to detection probabilities of deer and wild boar (at the local scale) indicated that although these species are present across housing density levels at these



**Figure 3.** Representative examples of (a) deer (large) and (b) raccoon (small) kill sites (puma predation) in relation to housing in the Santa Cruz Mountains, California, USA, 2009–2014. Circles represent 150-m and 1-km buffers around kill sites, gray dots are houses and black stars are the kill sites. In comparison to small kills, large kills are characterized by little to no housing within 150 m, lower housing density within 1 km, less clustered housing, and greater distance to the nearest house.

scales, they are likely to vary in frequency or activity in response to development.

## DISCUSSION

We found strong evidence for diet shifts in pumas associated with the density of nearby residential development. Pumas killed a higher diversity of prey and a higher proportion of small (<20 kg) prey in areas more greatly affected by development. Although we were regularly able to find small prey between 1 kg and 20 kg, we acknowledge possible undersampling of small prey due to the likelihood of fewer remains present at the kill site, and we anticipate that our estimates of small prey use are likely conservative. Patterns of higher diversity and small prey use in developed areas held at local and regional spatial scales examined for housing density, indicating that landscape-level changes affect puma prey composition similarly to immediate disturbances. In considering 1-km buffer zones around each kill, the majority of kills occurred at an exurban housing density, although most kills had no housing present within a 150-m buffer zone. Pumas, therefore, are able to use a modified landscape for making kills but generally do so in lower housing density zones than the surrounding habitat.

Puma prey composition shifted primarily with regard to the number of houses present on the landscape at the local and regional scales. This result supports the notion that changes in prey habits are likely to be more greatly affected by the magnitude of development rather than the spatial features associated with development. However, housing clustering and proximity to housing did significantly differ by prey size, indicating that although the amount of housing development appeared to be the most important housing covariate, more clustered configuration of housing may also contribute to the hunting of smaller prey species. The Santa Cruz Mountains are predicted to experience continual development in the 21st century (U.S. Environmental Protection Agency 2010). If these projections are realized, pumas in this region will be increasingly exposed to habitat modifications, one of which is an altered prey community and disturbance landscape.

Unlike other western puma populations, pumas in the Santa Cruz Mountains have access to only 1 large, valuable

prey item, the black-tailed deer. Deer are the only abundant ungulate that has persisted in the Santa Cruz Mountains (wild boar are not abundant and are patchily distributed), yet were rarely preyed upon when housing was at exurban or suburban densities within 150 m of the kill, despite having higher detection probabilities with increasing development. Our previous work shows that risk avoidance behaviors increase at kill sites near residential areas and that pumas kill more often to compensate for the energetic costs of these behavioral adaptations (Smith et al. 2015). This result may explain why deer are not killed as regularly in the highest housing density areas and are replaced by small prey. Despite showing surprisingly weak evidence for positive associations with development, the proportion of small prey kills increased strongly with housing density. The discrepancy between species-specific patterns of occupancy and proportion of kills may be indicative of some selection by pumas for smaller prey in developed areas, possibly because they are more quickly consumed than deer and require less time investment in risky habitats. More work is needed to explore optimal decision making regarding prey choice in risky, human-dominated landscapes.

Although deer currently remain the primary prey species for pumas in the Santa Cruz Mountains, a development-mediated diet shift toward prey that are 5–10 times smaller than their primary prey likely affects puma movement because of reduced handling time. In addition, movement increases at kill sites near residential development because of behavioral avoidance of human disturbances (Smith et al. 2015). Previous work in our study area has found that pumas increase movement, with corresponding higher caloric demands, in more developed areas (Y. Wang, San Francisco Bay Bird Observatory, unpublished data). Changes in movement patterns related to prey habits and behavioral disturbances may interact to alter energetic costs in disturbed habitats. Future research should examine the relationship between prey densities, energetic value, handling time, and search time to understand the long-term energetic effects of differential prey use on carnivore movement and energetics in developing landscapes.

Higher consumption of synanthropic species can also contribute to human–wildlife conflict. Domestic cats were

the third most common prey item for pumas in our study area, representing a direct conflict between homeowners and pumas. However, the use of non-domestic human-associated species (e.g., raccoons) may also be a source of conflict if pumas hunt for these prey items near residential areas. Biocentric development planning can work to minimize this conflict by considering the impacts of different thresholds of development on puma hunting behavior and more effectively minimizing overlap between areas of human and puma use.

Disease transmission is another serious risk encountered by large carnivores predating upon synanthropic species. Although pumas are resistant to some diseases that afflict ungulates (Krumm et al. 2009), they are likely to be vulnerable to diseases carried by other carnivores. Pumas who regularly kill domestic cats may be at elevated risk of acquiring diseases that rely upon horizontal methods of transmission (e.g., direct contact between individuals), such as feline immunodeficiency virus (FIV; Bevins et al. 2012). Endangered Florida panthers (*P. c. coryi*), the only population of pumas living on the east coast, have already contracted FIV from domestic cats (Barr et al. 1989). Even between pumas and raccoons, despite their disparate lineages, there is evidence supporting regular cross-species transmissions of parvoviruses (Allison et al. 2013). For small, vulnerable populations of pumas surrounded by urban habitats, low genetic diversity can exacerbate prevalence of disease (Ernest et al. 2003).

The most biologically significant changes in behavior are those that influence the long-term trajectory of an animal population by affecting the reproductive success of individuals. In pumas, females often make kills and bring their weaned but dependent kittens to the carcass to feed (Hornocker and Negri 2009). Kittens are then able to feed, while their mother leaves the kill area to search for another prey item. A transition to feeding on small prey would disrupt this pattern of moving kittens around to large food patches, possibly with negative energetic impacts for both kittens and their mother. Females tend to avoid human development when denning in our study area (Wilmers et al. 2013), which might be in part related to the suitability of a prey community to support the rearing of kittens. Further examination of the bioenergetic consequences of human-induced prey switching on kitten rearing is needed to understand the demographic ramifications of pervasive development.

## MANAGEMENT IMPLICATIONS

Ultimately, we recommend that land use planners minimize development in puma habitat to promote the maintenance of behavior and species interactions. We observed diet shifts in even low levels of development, and these shifts were observable at the regional scale. Although our results suggest that puma hunting behaviors are altered with increasing development, high-density developments may actually serve to preserve species interactions if they offset extensive low-density development and are paired with the establishment of ample protected areas and corridors in which pumas can continue exercising their evolved behaviors. Elimination

of widespread low-density development will best preserve animal community dynamics by minimizing exposure to human disturbances and subsidies to wildlife.

Residents living on the urban fringe may perceive our results positively because pumas play an important role in preying on urban mesopredator pest species. However, if reduction of puma activity near residential development is a goal of local wildlife management, we encourage reduction of wildlife subsidies to puma prey species. In particular, containment of pets (particularly house cats) and garbage resources used by urban raccoon and opossum populations would reduce small prey available to pumas in developed areas. Detection rates of deer increased with housing density and may serve as an attractant for pumas. Increased use of deer fencing around lawns and gardens is likely to reduce deer activity and, therefore, available prey in residential areas. Actions to limit anthropogenic food subsidies to pumas and their prey may serve to reduce human-puma conflict in rural and exurban areas.

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