Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California

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A B S T R A C T

Human-driven declines of apex predators can trigger widespread impacts throughout ecological communities. Reduced apex predator occupancy or activity can release mesopredators from intraguild competition, with unknown repercussions on the ecological community. As exurban development continues to expand worldwide, it is important to document how mesopredators are impacted by the combined influences of apex predators and humans. We used motion-detecting camera traps to examine spatial and temporal patterns of meso- and apex predator occupancy and activity in a fragmented landscape in California. We hypothesized that both spatial and temporal partitioning among the carnivore guild would be affected by varied levels of human influence. We found that higher residential development reduced puma occupancy but was not related to the occupancy of mesopredators. Bobcats, grey foxes, and Virginia opossums were detected more often at sites occupied by pumas, whereas coyotes and raccoons were detected less often. The detection probabilities of smaller mesopredators were related to coyotes, a dominant mesopredator, but the magnitude and direction of these correlations differed depending upon puma occupancy. We also found that species altered their activities temporally in locations with higher human use, with pumas, bobcats and coyotes reducing diurnal activities and increasing nocturnal ones. These activity shifts were reflected in reduced temporal partitioning between intraguild competitors, with unknown effects on species interactions and repercussions to the prey community. Our results suggest that human development and activity alters predator community structure through both direct and indirect pathways. Therefore effective carnivore conservation requires an understanding of how mesopredators respond to varying levels of apex predator and anthropogenic influences.

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1. Introduction

Anthropogenic-driven extirpation of apex predators from ecosystems across the globe has had led to large changes in community structure and dynamics in diverse ecosystems (Estes et al., 2011). Such changes to the predator guild can greatly alter ecological networks by releasing mesopredators from intraguild predation and competition, thus initiating trophic cascades that propagate throughout food webs (Levi and Wilmers, 2012; Noss et al., 1996; Pace et al., 1999; Polis and Holt, 1992). The combined extirpation of apex predators and release of mesopredators has been identified as a possible cause for the decline or extinction of songbirds and small mammals, because they are disproportionately preyed upon by mesopredators (Crooks and Soulé, 1999; Johnson et al., 2007; Ritchie and Johnson, 2009).

Habitat fragmentation due to human development can lead to the extirpation of top predators (Gehrt et al., 2010; Šálek et al., 2014) and irreversibly alter ecosystem stability (Hansen et al., 2005). Exurban development (0.06–2.5 houses/hectare) is the fastest growing form of land use change in the United States, and building low-density developments adjacent to wildlands results in habitat fragmentation, increased human wildlife contact and conflict, and homogenization of ecological communities (Hansen et al., 2005; McKinney, 2006). The spread of human development or activity into nearby open space disrupts both sensitive species (e.g. apex predators) and entire communities by altering predator interactions and their traditional ecological roles. These changes do not always progress linearly with increasing levels of development; instead abrupt shifts in community composition may occur with gradual increases in exurban development (Hansen et al., 2005). Because exurban development now encompass more than five times as much land as do suburban and urban development, it is crucial that we understand how low-density human pressures alter the composition and interactions of nearby predator

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communities in order to balance conservation and development needs (Bateman and Fleming, 2012).

While apex predators limit mesopredators through competition and predation, they also affect mesopredator survival and reproduction through indirect, trait-mediated effects (Ritchie and Johnson, 2009). Natural selection favors adaptations such as behavioral avoidance through spatiotemporal partitioning, which reduce costly interactions between mesopredators and dominant competitors (Gehrt and Clark, 2003; Wang and Fisher, 2012; Wilson et al., 2010). Within the predator guild, however, apex predators can also benefit smaller predators by suppressing larger-bodied mesopredators (Berger and Conner, 2008; Elmhagen et al., 2010). Levi and Wilmers (2012) demonstrated an "intraguild cascade" in which the apex predator, gray wolves (*Canis lupus*), suppressed the mesopredator, coyotes (*Canis latrans*), and thereby released the smaller red foxes (*Vulpes vulpes*). In addition, carrion provided by apex predators can serve as an important food source for smaller predators (Allen et al., 2015a; Ruth and Murphy, 2009; Selva et al., 2005; Wilmers and Getz, 2005). Therefore, the relationship between dominant and smaller predators may reflect a complex balance of risk-avoidance and energetic needs, all of which may be influenced by anthropogenic subsidies and disturbances and direct predation.

We used camera traps to simultaneously examine how the combined influences of bottom-up exurban development and top-down apex predator pressures affected mammalian mesopredator communities in the Santa Cruz Mountains of California. Native carnivores in the region include pumas (*Puma concolor*, an apex predator), coyotes (a dominant mesopredator and an emerging apex predator in many urbanizing regions), bobcats (*Lynx rufus*; a dominant mesopredator), and subordinate mammalian mesopredators (e.g., grey foxes, *Urocyon cinereoargentus,* striped skunks, *Mephitis mephitis*, Virginia opossum, *Didelphus virginianus*, and raccoons, *Procyon lotor*). We placed motion-detecting digital cameras along a gradient of human development to test whether spatial and temporal niche partitioning of the local predator community shifted across disparate levels of human influence.

Based on results from previous studies of human impacts on predators, we expected the predator community to respond to the combined influences of higher ordered predators and development and formulated the following hypotheses. (1) Predator responses to anthropogenic pressures would vary by species: Puma occupancy would decline as human development and activity increased due to their particular sensitivity to anthropogenic influences (Crooks, 2002; Wilmers et al., 2013). Exurban development would not reduce the occupancy probabilities of bobcats, coyotes and grey foxes because we expected these versatile predators to adapt to low levels of development, especially when access to nearby open spaces are available (Goad et al., 2014; Riley, 2006). However, we expected detection levels of bobcats to decline with higher development, because this species is less likely to use developed areas (Riley, 2006). In contrast, we expected occupancy probabilities for synanthropic species, such as raccoons and striped skunks, and domestic species (e.g., domestic cats, *Felis catus*) to increase with development (Bateman and Fleming, 2012; McKinney, 2006). (2) Predator interactions would be altered with increasing anthropogenic development: Dominant mesopredators (i.e. coyotes and bobcats), which have greater niche overlap with pumas, would be deterred by higher puma occupancy and activity whereas subordinate mesopredators would be released by this suppression of their competitors (Levi and Wilmers, 2012). In areas where puma occupancies declined, we expected coyotes would act as an emergent apex predator and negatively affect the occupancy and detection of smaller mesopredators (Gehrt and Prange, 2007; Levi and Wilmers, 2012; Pace et al., 1999). (3) Subordinate predators would exhibit temporal avoidance of dominant ones to reduce

risk of intraguild predation and competition (Palomares and Caro, 1999; Polis and Holt, 1992). However, we expected areas with higher human activity would reduce temporal niche partitioning by restricting wildlife activities during diurnal hours (George and Crooks, 2006; Reed and Merenlender, 2008).

2. Methods

2.1. Study Site

Our study occurred in the southern Santa Cruz Mountains in west-central California, an area encompassed within Santa Cruz, Santa Clara and San Mateo counties (Fig. 1). This region has a legacy of preserving large tracts of open space, with 24% of the surrounding San Francisco Bay Area held in some form of public land trust or conservation easement (Rissman and Merenlender, 2008). The Santa Cruz Mountains includes diverse habitats ranging from intact wildlands to urban regions, providing a gradient of environmental conditions to study the impacts of development on interspecific interactions. Significant portions of public land are available for a wide variety of recreational activities, including biking, hiking, and dog walking. There are also many large private landholdings, some of which are managed for resource extraction activities, but are not open to the public for recreation. Our study area abuts the urban municipalities of Santa Cruz and the South Bay Area and contains several small suburban and exurban mountain communities. A major highway bisects our study region, and numerous arterial (>35 mph), neighborhood (<35 mpg) and unpaved roads also mark the landscape.

The Santa Cruz Mountains experiences a dry season from May to October and a wet season from November to April. Small to large-sized mammalian carnivores that occur in the Santa Cruz Mountains include: pumas, bobcats, coyotes, grey foxes, red foxes, raccoons, striped skunks, Virginia opossums (hereafter opossums), western spotted skunks (*Spilogale gracilis*), American badgers (*Taxidea taxus*), and two domestic species, cats and dogs (*Canis lupus familiaris*).

2.2. Camera trap survey

Between May 2011 and June 2013 we placed cameras (Bushnell Trophy Cam; Bushnell Corp., Overland Park, KS, USA) at 50 locations throughout the study site (Fig. 1) to monitor animal activity across a gradient of human development from undeveloped to exurban neighborhoods. We measured human development from building structures identified from high-resolution satellite imagery. We digitized structures manually in exurban landscapes and used address points to locate houses in suburban and urban areas to create a development layer in ArcGIS (v. 10.0, ESRI 2010, Redlands, CA). We used ArcGIS to randomly select 50 camera locations across a stratified development gradient of approximately 0–2 houses per hectare. We further restricted potential camera locations to within 100 meters from a road or trail for access purposes and at least 1 km away from the next closest camera.

We traveled to each randomly generated location and placed a camera along the closest trail or road to maximize native carnivore detection (Gompper et al., 2006). Most trails we selected were used by vehicles on an infrequent to regular basis. When recreational trails were not available, we placed the camera on a well-defined game trail wide enough for people to walk on. We programmed the cameras to take three photographs when triggered with a one-minute delay between successive image sets. We excluded data collected by cameras when they were heavily obscured by fallen or growing vegetation or when interference by humans or animals significantly altered the camera angle or field of visibility. We
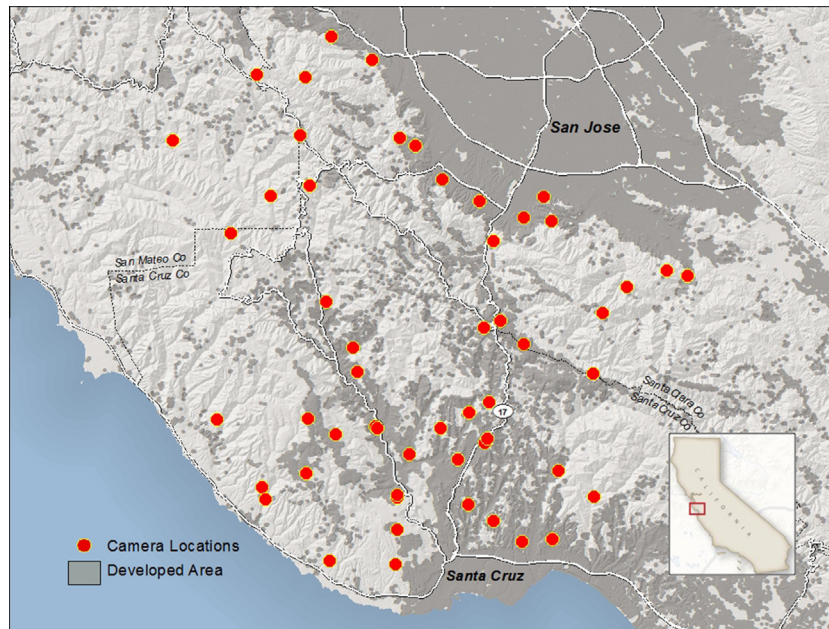
Fig. 1. Map of study area with camera locations marked with red dots and housing development areas represented by grey. Inset marks location of the Santa Cruz Mountains in California. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

visited all cameras for maintenance either every one or two months, depending on the amount of activity at the site.

2.3. Spatial activity analyses

We used single-season, two-species occupancy models to explore how apex predators and humans development influenced mesopredator occupancy and detection. Occupancy models improve upon traditional methods of examining spatial patterns of species occurrence by providing unbiased estimates of species occupancy and explicitly accounting for imperfect detection (MacKenzie et al., 2004, 2002). Habitat and survey covariates can also be incorporated when estimating both occupancy and detection through a logit link (MacKenzie et al., 2004, 2002). We used two-species occupancy models to test whether the occupancy and detection of subordinate species were influenced by the occupancy of more dominant species. We also tested whether the subordinate predators responded to habitat and anthropogenic factors conditional upon occupancy by pumas. Lastly, we incorporated coyote activity as covariates to test whether they influenced the occupancy and detection of subordinate mesopredators.

We compiled a detection history for all carnivore species during a truncated study period lasting from October 2011 to October 2012. We demarcated each survey period as a full week beginning Monday at 10AM PST for a total of 53 surveys. We assumed that our cameras were closed to occupancy changes over the one-year period because the species we targeted for monitoring live several years in the wild and maintain generally stable home ranges (Riley, 2006). For each survey period, we recorded whether a species was present or absent based on whether it was captured by the camera trap. Upon completion of our camera-trapping study, we had enough data to model occupancy for 8 predators: pumas, coyotes, bobcats, grey foxes, raccoons, striped skunks, opossums, and domestic cats.

We used the program PRESENCE 5.9 (United States Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland; MacKenzie et al. 2006), which utilizes a maximum-likelihood-estimation modeling approach to compare all models. We used the conditional parameterization of the two-species occupancy

model (Richmond et al., 2010) to examine interactions between pairs of dominant and subordinate carnivores. Under this model structure, we had *a priori* categorizations of dominant (A) and subordinate (B) species, and the conditional model parameterization allowed us to explicitly test whether species B occupancy (ψ_B) and detection (p^B, r^B) estimates were conditional upon those of species A. We did not test whether the detection of species B was influenced by the detection of species A (i.e., we set $r^{BA} = r^{Ba}$) because of limited data due to the infrequent detection of pumas. The full set of parameters and covariates utilized by the models and their descriptions is listed in Table 1.

Our occupancy covariates for native predators were human development and percent forest habitat, which we included because many native carnivores are positively associated with natural vegetation (Šálek et al., 2014). We derived our development covariate using the kernel density tool in ArcGIS to calculate housing density from the GIS housing layer at radii (h) of 100 m, 300 m, and 500 m. We selected these values to reflect the range of scales

Table 1
List of parameters and covariates and their definitions used in occupancy models.

Parameter or covariate	Description
ψ^A	Probability of site occupancy for species A
ψ^{BA}	Probability species B occupies site given species A occupies the site
ψ^{Ba}	Probability species B occupies site given species A does not occupy the site
p^A	Probability of detection for species A, independent of presence of species B
p^B	Probability of detection for species B, given species A is absent
r^B	Probability of detection for species B, given species A and B are present
Development (D)	Kernel housing density estimates with a radius of 500 m
Forest (F)	Percent forested habitat in the surrounding area with 500 m radius
Coyote activity (C)	Average coyote activity per 100 days

at which pumas responded to housing densities (Wilmers et al., 2013). We found that a radius of 500 m minimized model Akaike Information Criterion (AIC; Anderson and Burnham, 2002; Arnold, 2010) and therefore used that scale for our development covariates. We classified forest habitat by placing a circular buffers with radii 100 m, 300 m, and 500 m above the camera location to match the scales of the development covariate. We then extracted vegetation data from the California GAP Analysis Project (Lennartz et al., 2008) and calculated percentage forest cover by dividing the area classified as forest or woodland by the total area of the circular buffer. We again found that a scale of 500 m minimized model AIC and used that scale for subsequent analyses. We also used human development, as defined above, for our detection covariate. For mesopredators subordinate to coyotes, we included coyote activity as occupancy and detection covariates. Coyote activity was defined as the average number of coyote photos taken at each site per 100 days. We z-transformed all forest cover, development, and coyote activity covariates.

The candidate model set for the conditional two-species parameterization is very large due to all the potential combinations of model parameters. To simplify the *a priori* size of the candidate model set, we carried out a multi-step modeling approach following Richmond et al. (2010). First, we identified the best occupancy and detection model for species A by fitting 8 single-species, single-season models to the puma data with all combinations of occupancy, detection and site-specific covariate parameters (Appendix A (Richmond et al., 2010)). We used AIC rankings to identify the best single species occupancy models for pumas and used the resulting top model in all subsequent two-species co-occurrence occupancy analyses.

Using the best occupancy and detection covariates for pumas, we then modeled co-occurrence between pumas and all subordinate species (coyotes, grey foxes, bobcats, raccoons, domestic cats, striped skunks and opossums). For each species pair, we first held ψ^B constant and compared the conditional and unconditional detection models for species B (i.e., $p^B \neq r^B$ vs. $p^B = r^B$). For all puma-mesopredator pairs, the conditional model was the better model, so we used it to evaluate candidate covariates (i.e., development, coyote detection). We compared 25 candidate models to evaluate the influence of coyote activity and development on mesopredator detection probabilities and to test whether covariates affected detection differently conditional upon puma site occupancy. We discarded models from further inference if they contained uninformative parameters as identified by Arnold (2010) and were not within 2 ΔAIC of the top ranked model. We then used AIC rankings to determine the best model.

Once we identified the top detection model, we held that portion of the model constant and compared different models to test whether species B occupancy was affected by covariates and species A occupancy. Bobcats, coyotes, raccoons and striped skunks were prevalent across the landscape (occupancy rates >83%), and in preliminary one-species occupancy analyses, we found including occupancy covariates did not improvement models. Therefore, we did not model the effects of puma occupancy or any covariates on their probability of occupancy for these common species. For domestic cats, we only compared models with and without human development as an occupancy covariate since we did not expect puma occupancy or percent forest cover to affect cat occupancy. Because cats are almost always pets, we expected that their presence or occupancy on the landscape would be primarily associated with human development. For all other species pairs, we compared conditional occupancy models ($\psi^{BA} = \psi^{Ba}$) to unconditional ones ($\psi^{BA} \neq \psi^{Ba}$) with all combinations of occupancy covariates. We followed the previous protocol and discarded any models including uninformative parameters from comparison

(Arnold, 2010), and we used AIC to rank all models for comparison.

2.4. Temporal activity analyses

For each photograph captured during our study period, we recorded the date, time, camera site ID, and species. To reduce pseudoreplication, we did not record photos of animals of the same species if they occurred within 30 min of a previous photo (Brook et al., 2012; Lucherini et al., 2009; Monterroso et al., 2013). Furthermore, if the camera captured two or more individuals of the same species in one photograph we treated the event as one time data point.

We examined whether species activity patterns differed between sites with disparate levels of human activity by separating our data into photographs that were captured at sites with high human use ($n = 19$; 2.05–120 people/day) and those with low human use ($n = 31$; 0.03–1.39 people/day). We identified the threshold by visually examining the distribution of human activity data (George and Crooks, 2006) and identifying a natural break at about 2 photos day. We therefore defined high human use sites as all those in which the cameras captured a mean of $\geqslant 14$ or more humans/week and low-use sites as those with <14 humans/week.

We used the non-parametric kernel density estimation procedure described in Ridout and Linkie (2009) and Linkie and Ridout (2011) to compare whether 10 species (pumas, bobcats, coyotes, grey foxes, opossums, striped skunks, raccoons, domestic cats, domestic dogs, and humans) offset their temporal activities at the two different human activity levels. We first converted all times to radians and used kernel density estimation to generate a probability density distribution of each species' activity pattern at each human activity level (Ridout and Linkie, 2009). Next, we calculated the overlap term $\hat{\Delta}$, a value ranging from 0 to 1, which is defined as the area under the curve formed by taking the smaller of two density functions at each time point (Ridout and Linkie, 2009). We expected a higher $\hat{\Delta}$ value if species did not change their temporal activity patterns at high human use sites and a $\hat{\Delta}$ value closer to 0 if they altered their activity greatly. Ridout and Linkie (2009) outlined three methods for estimating $\hat{\Delta}$ and suggested using $\hat{\Delta}_1$ for small sample sizes ($n < 50$) and $\hat{\Delta}_4$ for larger sample sizes, which we follow. We also compared $\hat{\Delta}_4$ at high versus low use sites for 15 species pairs to test whether temporal overlap between species pairs increased in areas of higher human use. Finally, we obtained 95% confidence intervals for these estimates from 1000 bootstrap samples. All statistics were analyzed using the *overlap* package (Meredith and Ridout, 2014) in R (R Development Core Team, 2013).

To compare how human activity and development might impact temporal overlap between mesopredator species pairs on a continuous scale, we used the same method outlined above to calculate $\hat{\Delta}_1$ between species pairs at each camera station. For these analyses we focused on temporal partitioning among three mesopredators pairs for which we had the most data: coyotes, grey foxes and bobcats. We then used multiple regression to determine how forest cover, development, and human activity affected the amount of temporal overlap between species. Our covariates for forest cover and development are described previously, and we calculated human activity by log-transforming the average number of humans photographed per day at each camera location. We started with the full model:

$$\hat{\Delta}_1 = \beta_0 + \beta_1(Human\ Activity) + \beta_2(Development) + \beta_3(Forest\ Cover).$$

and used likelihood-ratio tests to compare nested models to identify the best model (Johnson and Omland, 2004).

3. Results

Our cameras operated for 21,950 cumulative trap nights at the 50 sites (mean = 439 nights; SD = 100), and we identified at least 68 species of animals from 193,815 photo sets. All carnivores, except for domestic dogs (8.2% nocturnal activity), were primarily active at night, with some species, such as grey foxes (94.6%), opossums (96.6%) and striped skunks (94.0%), almost exclusively so (Table 2).

3.1. Puma response to human development

The top model for pumas identified development as both an influential negative occupancy covariate ($\beta = -1.52$, SE = 0.47) and detection covariate ($\beta = -0.52$, SE = 0.19), which aligned with our predictions. All 8 single-species, single-season occupancy models for pumas are listed in Appendix A. The best models (ΔAIC < 2) included development as an occupancy variable and all models including development as an occupancy covariate had a cumulative AIC weight of greater than 0.99. The cumulative AIC weight for all models including development as a detection covariate was greater than 0.98.

3.2. Mesopredator responses to human and top predator influences

We modeled interactions between pumas (the dominant predator) and 7 subordinate predators for a one-year period, with the top models (ΔAIC < 2) for each species pair summarized in Appendix B. Contrary to our expectations, no mesopredators occupancy probabilities were clearly related to puma occupancy. However, opossum and grey fox conditional and unconditional occupancy models had almost equal weight (ΔAIC < 0.2), which means that it was inconclusive whether puma presence was correlated with the occupancy of either species. Opossums occupancy was positively correlated with coyote activity ($\beta = 1.05$, SE = 0.69) and higher forest cover ($\beta = 0.58$, SE = 0.38). Domestic cat occupancy was positively correlated with development ($\beta = 0.60$, se = 0.32), which is in line with what we expected since they are close human associates.

All subordinate species' detection probabilities (as opposed to occupancy rates) were related to the presence of pumas, although not necessarily in the directions we predicted. In general, bobcats, grey foxes, opossums and striped skunks were more likely to be detected at sites with pumas whereas raccoons and coyotes were less likely to be detected (Fig. 2). Striped skunk and raccoon detection probabilities increased with development whereas bobcat and
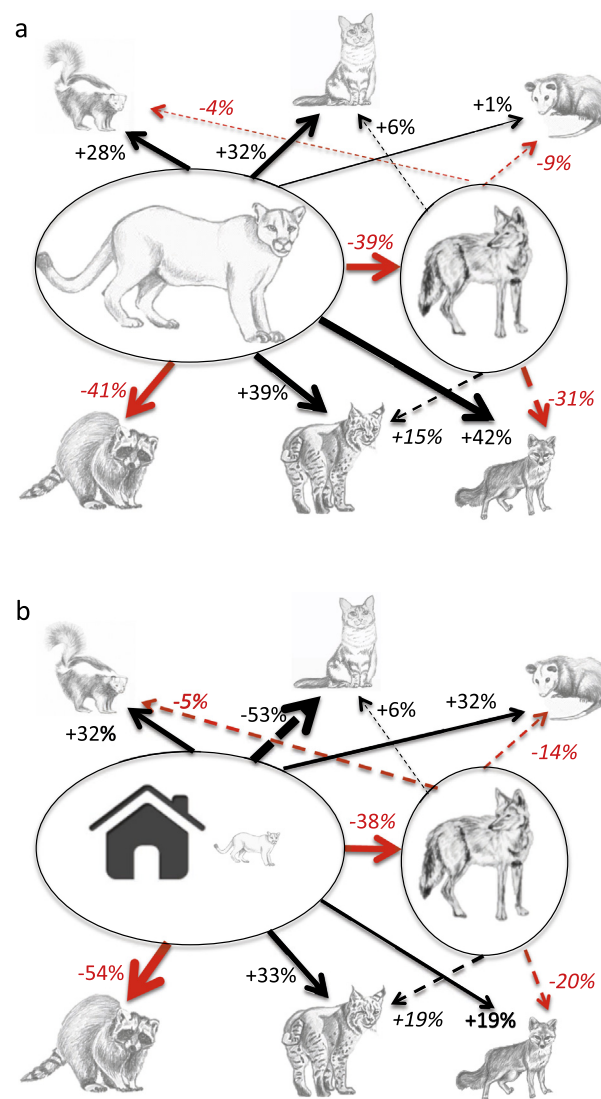
Table 2
Summary statistics for the top 11 species captured by the camera traps.

Species	Number of photographs	Cameras captured (out of 50 cameras)	Percentage of nighttime captures (%)
Bobcat	4223	49	70.4
Domestic cat	1429	25	75.4
Coyote	2241	47	58.3
Deer	16,354	50	46.6
Dog	9650	44	8.2
Grey fox	2464	34	94.6
Human	142,616	50	8.8
Opossum	986	34	96.6
Puma	217	33	80.7
Raccoon	1065	47	90.7
Striped skunk	3024	49	94.0

Fig. 2. A conceptual diagram detailing the average percent differences in mesopredator detection probabilities with puma occupancy and coyote activity in low (a) and high (b) development sites. Low development is represented by a development *z*-score of −1 and high development by 1. Solid arrows originating from pumas represent the differences in mesopredator detection probabilities at sites occupied by pumas compared to sites unoccupied by pumas. A positive value means the species is more likely to be detected when pumas are present and a negative value means the species is less likely to be detected. Dashed arrows originating from coyotes represent the differences in mesopredator detection probabilities at sites occupied by pumas with low coyote activity (*z*-score = −0.5) and with high coyote activity (*z*-score = 1). Coyote activity did not influence raccoon detection at sites occupied by pumas. The widths of the arrows are relative to the percent differences in detection probabilities. The size of the puma in each panel represents how its occupancy changes from low to high development.

coyote detections showed the opposite pattern (Fig. 3). Opossums, domestic cats and grey foxes responses to development were conditional upon puma occupancy (Fig. 3). Opossum detection was positively correlated with human development at puma-occupied sites and negatively correlated with development at sites without pumas. At sites occupied by pumas, grey fox detection was negatively correlated with higher development whereas domestic cat detection increased with development at sites where pumas were absent. Domestic cat detection responded very strongly to increasing development, which likely explains the contrasting pattern between puma occupancy and cat detection in areas of low versus high development (Fig. 2).
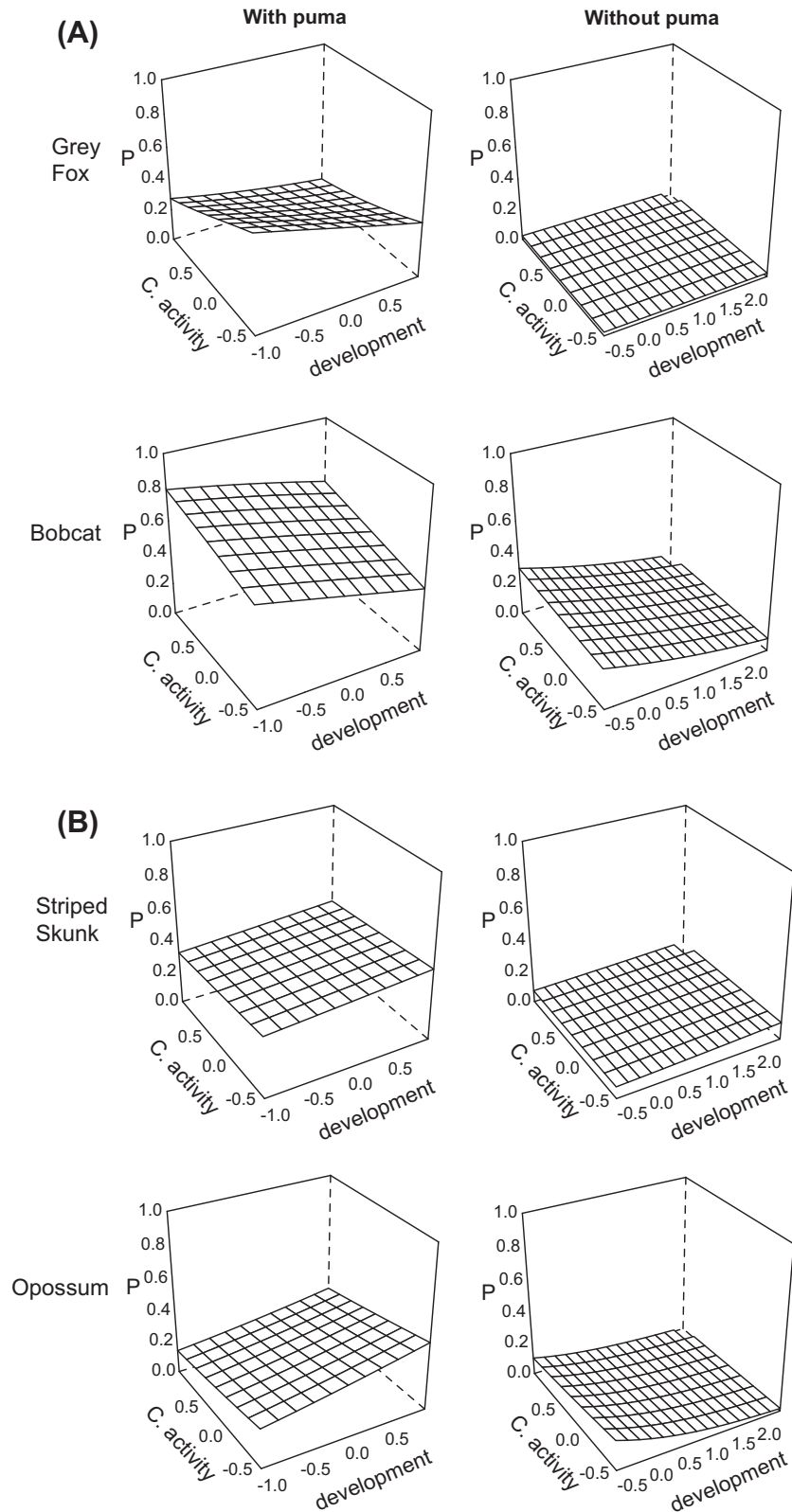
Fig. 3. Estimated detection probabilities (P) for 6 mesopredator species as a function of puma occupancy, coyote activity (C. activity), and human development. Development and coyote activity values have been z-transformed. Negative z values represent lower development or coyote activities and larger values represent higher development or coyote activities.

3.3. Mesopredator responses to coyote influence

As we predicted, many subordinate species detections were lower with increased coyote activity, although some species responded to coyotes differently depending upon puma occupancy status (Fig. 2). Bobcats were more likely to be detected and opossums less likely to be detected at sites with higher coyote activity (Fig. 3). Grey fox detection exhibited the most negative
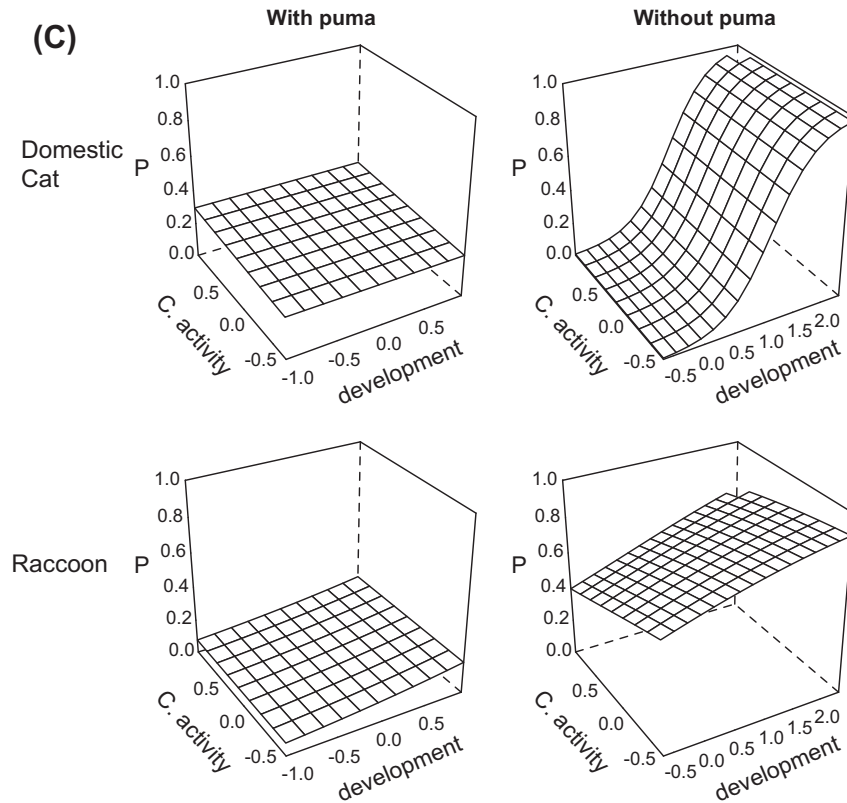
Fig. 3 (continued)

relationship to coyote activity, but only at sites occupied by pumas (Fig. 3). At sites without pumas, grey fox detection was near zero and showed no relationships with any covariates (Fig. 3). Striped skunk and cat detections were also correlated with coyote activity, but these associations were weak (Fig. 3). Finally, raccoon detections decreased with coyote activity at sites not occupied by pumas (Fig. 3).

3.4. Temporal responses to human influences

In accordance with our predictions, predator species reduced their diurnal activities in areas more regularly used by people. Pumas and coyotes increased nighttime activity and reduced daytime activity, particularly during the morning hours, in sites with high human activity (Fig. 4). Bobcats exhibited similar activity peaks and valleys at both levels of human use, but with overall lower daytime and higher nighttime activity levels. Grey fox, opossum, striped skunk and raccoon activity patterns did not change at high human use sites, most likely because these species were almost exclusively active nocturnally. Humans and dogs in high human use sites were more active in mornings and less active in afternoons, possibly reflecting a bias toward morning recreation in parks.

Coyotes and smaller mesopredator species (grey fox, opossum, raccoon, and striped skunk) showed the highest temporal segregation of all species pairs in both low (45.4–54.5% overlap) and high (65.3–73.9%) human use areas (Table 3). All $\hat{\Delta}_4$ (overlap) values between coyotes and smaller mesopredators increased by more than 15% in higher human use sites with non-overlapping confidence intervals. Coyote and domestic cat temporal overlap also increased by 19.9% from 70.4% to 90.3%. Pumas exhibited the lowest temporal overlap with opossums and coyotes. However, overlap increased somewhat between pumas and opossums and

coyotes at high human use locations. At a finer spatial scale, we found that overlap between all three mesopredator species pairs (bobcat and grey fox, coyote and grey fox, and bobcat and coyote) significantly increased with human activity and overlap between bobcats and coyotes significantly increased with both human activity and development (Table 4).

4. Discussion

Our study explored how the combined influences of top predators and humans affect the activity and composition of the carnivore community. As we expected, pumas and native mesopredators exhibited differential sensitivity to human development and activity. Exurban habitats and open space areas with high levels of human activity were still occupied and used by pumas, while bobcats and coyotes were ubiquitous across the landscape. Puma presence and coyote activity were associated with changes in mesopredator activity (Fig. 3), while human activity increased temporal overlap among predators in areas of higher human use (Table 3). Because our results are correlational in nature, we discuss our findings in the context of the broader literature and explore some alternate variables that may have affected our observations.

4.1. Anthropogenic influences on apex predator occupancy and activity

As we predicted, puma occupancy and activity declined with increasing exurban development and human activity. Despite the negative association with development, pumas continued to utilize sites with moderate to high levels of exurban development, particularly if these locations bordered open spaces. This finding supports the conclusions drawn by Wilmers et al. (2013) that pumas regularly travel and hunt throughout human-dominated landscapes in spite of their preference for undeveloped habitats. Our
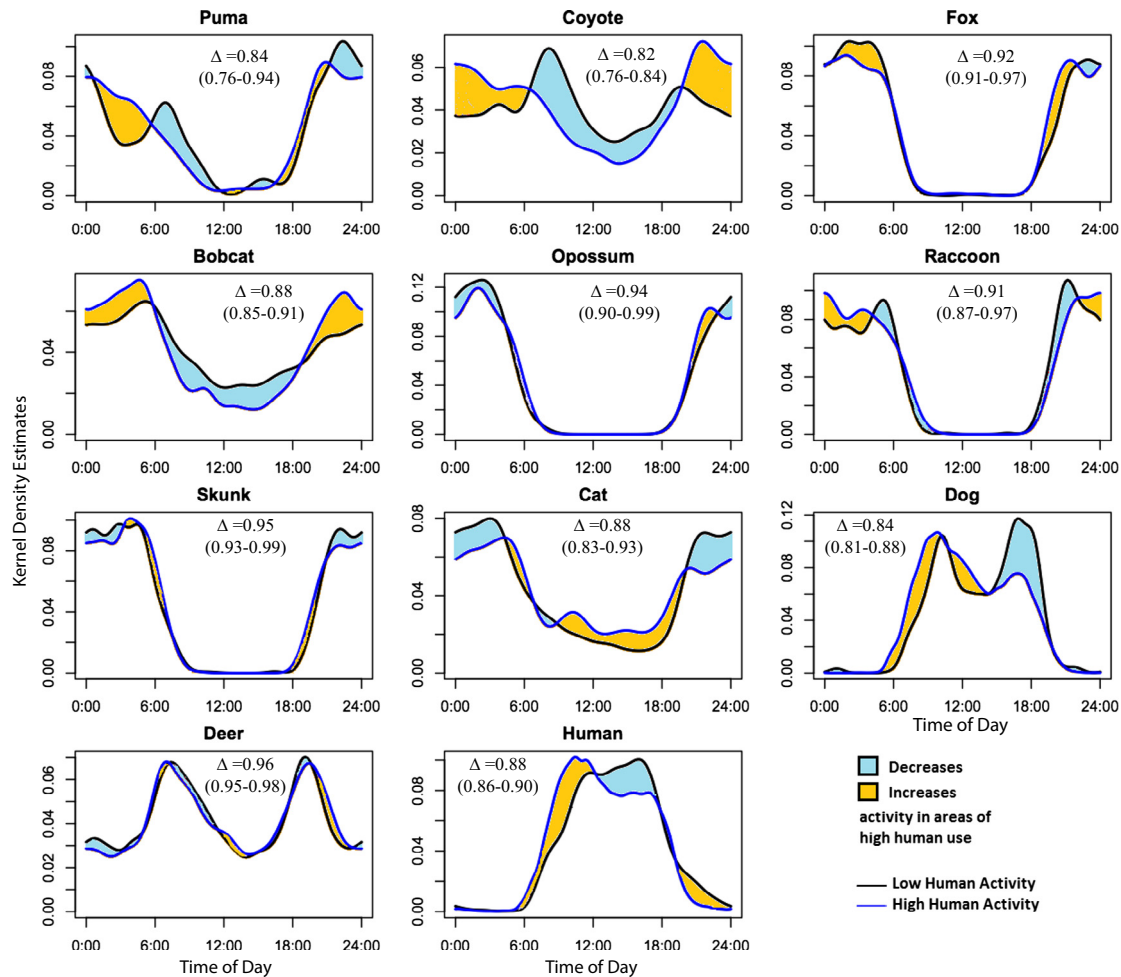
Fig. 4. Kernel density estimates of daily activity patterns of 10 animal species and humans in areas of high (blue lines) and low (black lines) human use in the Santa Cruz Mountains. Temporal activity shifts for species are represented by $\hat{\Delta}$, with $\hat{\Delta} = 1$ representing no temporal shifts between low and high human use areas and $\hat{\Delta} = 0$ representing complete activity shift. Light blue colors indicate a decrease in activity and yellow colors represent an increase in activity in areas of higher human use.

findings also suggest that pumas, like other predators (Carter et al., 2012; Riley et al., 2003; Schuette et al., 2013), may utilize temporal partitioning to avoid humans by reducing their morning activity and increasing their nighttime activity between midnight and 6AM at sites of higher human use (Fig. 4).

4.2. Puma influences on mesopredators

Our research revealed that mesopredator species displayed disparate responses to pumas (Fig. 3). Coyote and raccoon detection probabilities were the most negatively associated with puma occupancy. Coyotes and raccoons may have reduced their activity in sites occupied by pumas to avoid encountering a dominant competitor (Ritchie and Johnson, 2009) and intraguild predator (Logan and Sweanor, 2001). In contrast, bobcats, grey foxes and striped skunks were all detected more often at sites with pumas, suggesting that these three mesopredators can either successfully avoid confrontations with pumas or benefit from suppressed activity of coyotes and raccoons. Although we expected bobcats to avoid pumas due to their similarities as felids and because pumas sometimes kill and consume bobcats, a previous study also found no evidence that bobcats avoided pumas (Hass, 2009). Opossum detection probabilities were positively associated with higher development sites occupied by pumas. While this is surprising because pumas prey on opossums, opossums may be benefitting from reduced activity of raccoons due to puma occupancy of these sites (Ginger et al., 2003).

4.3. Development influences on mesopredator activity

Bobcats and coyotes were present throughout all levels of exurban development, although their detection probabilities declined with increased development. Coyote detections decreased to a lesser degree with higher development than bobcat detections, indicating that bobcats are perhaps more sensitive to development. Our results partially support previous studies that show bobcat detection declining with development (Goad et al., 2014; Ordenana et al., 2010; Riley, 2006). In contrast to those studies however, we did not observe declining bobcat occupancy across our development gradient, possibly because we capped our development gradient at exurban levels. We found no impact by development on coyote occupancy and only a weak negative influence on detection. This corroborates previous research highlighting the coyote's ability to thrive in anthropogenic ecosystems (Bateman and Fleming, 2012; Prange and Gehrt, 2004), which provides further confirmation that they may be an emergent apex predator in developed areas.

Confirming our expectations, detections of synanthropic species, such as raccoons and striped skunks, were positively correlated with higher human development, but their occupancies were consistent across all development levels. In contrast, grey fox detections decreased with higher development. While Bidlack (2007) and Riley (2006) concluded that grey foxes were capable of persisting in small urban patches, our results aligned more with the meta-analysis of camera-trap studies from southern California,

Table 3
Overlap values ($\hat{\Delta}_4$) between species pairs in areas of low and high human use. Bolded rows indicate differences between low and high overlap are statistically significant at $p < 0.05$.

Species pair	Low use $\hat{\Delta}_4$ (95% CI)	High use $\hat{\Delta}_4$ (95% CI)	Difference (High–Low)
Puma, Domestic cat	0.800 (0.706–0.869)	0.817 (0.745–0.896)	−0.017
Puma, Raccoon	0.793 (0.774–0.937)	0.844 (0.725–0.866)	0.051
Puma, Grey fox	0.775 (0.697–0.852)	0.806 (0.733–0.891)	0.031
Puma, Striped skunk	0.749 (0.674–0.825)	0.836 (0.776–0.930)	0.087
Puma, Bobcat	0.748 (0.649–0.813)	0.851 (0.777–0.921)	0.103
Puma, Coyote	0.708 (0.621–0.782)	0.837 (0.764–0.908)	0.129
Puma, Opossum	0.659 (0.554–0.730)	0.771 (0.680–0.850)	0.112
Coyote, Bobcat	**0.851 (0.799–0.875)**	**0.915 (0.889–0.945)**	**0.064**
Coyote, Domestic cat	**0.704 (0.641–0.726)**	**0.903 (0.858–0.944)**	**0.199**
Coyote, Raccoon	**0.545 (0.485–0.557)**	**0.739 (0.681–0.781)**	**0.194**
Coyote, Grey fox	**0.543 (0.479–0.555)**	**0.701 (0.665–0.727)**	**0.158**
Coyote, Striped skunk	**0.52 (0.465–0.530)**	**0.732 (0.695–0.764)**	**0.212**
Coyote, Opossum	**0.454 (0.389–0.464)**	**0.653 (0.594–0.672)**	**0.199**
Bobcat, Grey fox	**0.675 (0.630–0.699)**	**0.771 (0.745–0.788)**	**0.114**

Table 4
Top models describing the influence of covariates on species temporal overlap between foxes and coyotes, bobcats and foxes, and bobcats and coyotes.

Species Pair	Intercept estimates (Standard errors)	Variable	Coefficient estimates (Standard errors)	p-value	Adj. R^2
Fox, coyote	**0.487 (0.059)**	Human activity	**0.139 (0.049)**	<0.019	0.417
Bobcat, fox	**0.689 (0.026)**	Human activity	**0.065 (0.023)**	<0.013	0.269
Bobcat, coyote	**0.701 (0.018)**	Development	**0.073 (0.024)**	<0.001	0.323
		Human activity	**0.074 (0.020)**		

which found grey foxes to be sensitive to urban development (Ordenana et al., 2010). It is also possible that grey foxes, like red foxes (Gosselink et al., 2003), may use urban patches as refugia from coyotes (Riley, 2006), but we did not monitor any urban site. Taken together, this suggests the carnivore community in our study area was generally adaptable to varying levels of anthropogenic disturbances, although some species were more sensitive to humans than others.

4.4. Combined influences of coyotes and pumas on mesopredator activity

The relationship between mesopredator detection probabilities and coyotes did not always match our predictions (Fig. 3). Contrary to our expectations, bobcats were more likely to be detected with increased coyote activity. Although coyotes are intraguild predators of bobcats, previous studies have shown that the two will coexist in close spatiotemporal proximity (Fedriani et al., 2000). This co-occurrence may also be due to their similar adaptability to disparate habitats and prey species and relative tolerance of human disturbances. Opossum and grey fox detection probabilities declined with higher coyote activity, as we expected based on previous research (Crooks and Soulé, 1999). Raccoon detections only exhibited a negative relationship with coyote activity at sites without pumas. While both pumas and coyotes will kill raccoons, raccoons are a frequent prey species of pumas in California (Allen et al., 2015b; Smith et al., 2015) and may consequently respond more strongly to pumas than coyotes.

Changes in apex predator membership (Levi and Wilmers, 2012) and human development can influence foodwebs by altering relationships between predator guild members. For example, our results suggest a potential among-predator cascade involving pumas, coyotes and grey foxes. We found evidence that grey foxes were detected less where coyote activity was high and rarely at sites not occupied by pumas, whereas coyotes were detected less frequently at sites occupied by pumas. Because coyotes were present at most sites, it appears that they do coexist with pumas and

grey foxes on a coarse spatial scale. However, coyotes and grey foxes may practice more fine-scale avoidance to circumvent their more dominant competitors. In cases where puma occupancy is reduced in more developed areas, coyote activity may increase, with unknown impacts on grey foxes and the prey community.

Domestic cat occupancy increased with development, as we expected, but their detection probabilities exhibited complex relationships with apex predator occupancy. Cat detection was positively correlated with development at sites without pumas (Fig. 3), and also exhibited a weak positive relationship with increased coyote activity at sites with pumas. This result is difficult to interpret and contradictory to what we expected since both coyotes and pumas are known predators of domestic cats (Crooks and Soulé, 1999; Gehrt et al., 2013). At sites without pumas, cat owners may be more willing to let their pets out whereas at sites with pumas, they may restrict cat activities out of fear of predation. Alternatively, since there is relatively little selective pressure for domestic cats to exhibit behavioral avoidance of predators, native predator activity and occupancy may not be appropriate determinants of domestic cat detection rates. Instead, because most domestic cats are pets, they might not have properly modulated fear responses to predators and their responses to wild predators may be based on their individual experiences and thus any correlational patterns may be spurious. To tease out these complex patterns between domestic cats and wild carnivores, more targeted research on cat activities and owner preferences is necessary.

4.5. Anthropogenic influences on temporal partitioning

Consistent with our predictions, we found that higher human activity was associated with increased temporal overlap between bobcat, coyote, and grey fox species pairs on a site-by-site basis, and higher development was also significantly correlated with greater bobcat and coyote overlap (Table 4). While shifts toward increased nocturnal activity in response to humans are well documented (Riley et al., 2003), previous studies have not considered the potential ramifications of these shifts on species interactions.

Temporal partitioning between predators species is a potential evolutionary strategy employed by subordinate species to avoid encountering and being killed by a dominant competitor (Gehrt and Prange, 2007; Hayward and Slotow, 2009; Palomares and Caro, 1999; Schuette et al., 2013). However, higher levels of human activity intensified temporal overlap between grey foxes and the more dominant bobcats and coyotes, potentially augmenting interspecific conflict between competing predators. The consequences of reduced temporal niche partitioning on species interactions and exploitation of prey species are unknown and require further exploration. For example, if coyotes increase nighttime activity, they may disproportionately target nocturnal prey species and release diurnal species from predation.

5. Conclusion

Our study results add to the global body of evidence that documents both the ability of carnivores to coexist in close proximity with humans and the diverse repercussions that such intimate cohabitation has on the carnivore community (Goad et al., 2014; Recio et al. in press; Schuette et al., 2013; Šálek et al., 2014). Unlike previous studies, we simultaneously investigated how the predator community was affected by the combined influences of increasing human development and activity and declining apex predator occupancy and activity. Occupancy models can be powerful tools for studying species interactions and, combined with non-invasive monitoring methods, can provide a useful framework for assessing species responses to new developments or mitigation actions.

Human-occupied landscapes that encompass or border large areas of open space are capable of supporting diverse predator communities, but increasing development pressures may threaten the carnivore community. This highlights the need for preserved areas, both for human recreation and to mitigate the influence of development on wildlife. Parks, in particular, serve the dual purposes of protecting the land from development and creating opportunities for nature recreation and education for people (Zaradic et al., 2009). Management regulations (e.g., by limiting human activities temporally or spatially) should balance the benefits of human recreation and access to nature with the negative impacts on native wildlife communities. As anthropogenic influences increase, studies like ours can help elucidate the context-dependent spatiotemporal responses of mesopredators to the combined influences of humans and apex predators to better inform management options, environmental outreach needs, and future research directions. This is particularly relevant, as expanding exurban development will directly impact apex predator behavior and occupancy, with cascading influences on mesopredators and the rest of the ecological community.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2015.05.007.

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