OIKOS

Research

Human activity reduces niche partitioning among three widespread mesocarnivores

Justine A. Smith, Austen C. Thomas, Taal Levi, Yiwei Wang and Christopher C. Wilmers

J. A. Smith (http://orcid.org/0000-0001-8753-4061) (jsmith5@ucsc.edu), Dept of Environmental Sciences, Policy and Management, Univ. of California, Berkeley, CA 94720, USA. JAS and C. C. Wilmers, Center for Integrated Spatial Research, Environmental Studies Dept, Univ. of California, Santa Cruz, Santa Cruz, CA, USA. – A. C. Thomas, Washington Dept of Fish and Wildlife, Olympia, WA, USA. – T. Levi, Dept of Fisheries and Wildlife, Oregon State Univ., Corvallis, OR, USA. – Y. Wang, San Francisco Bay Bird Observatory, Milpitas, CA, USA.

Anthropogenic disturbances can constrain the realized niche space of wildlife by inducing avoidance behaviors and altering community dynamics. Human activity might contribute to reduced partitioning of niche space by carnivores that consume similar resources, both by promoting tolerant species while also altering behavior of species (e.g. activity patterns). We investigated the influence of anthropogenic disturbance on habitat and dietary niche breadth and overlap among competing carnivores, and explored if altered resource partitioning could be explained by human-induced activity shifts. To describe the diets of coyotes, bobcat, and gray foxes, we designed a citizen science program to collect carnivore scat samples in low- ('wildland') and high- ('interface') human-use open space preserves, and obtained diet estimates using a DNA metabarcoding approach. Habitat use was determined at scat locations. We found that coyotes expanded habitat and dietary niche breadth in interface preserves, whereas bobcats and foxes narrowed both niche breadth measures. High human use was related to increased dietary niche overlap among all mesocarnivore pairs, increased coyote habitat overlap with bobcats and foxes, and a small reduction in habitat overlap between bobcats and foxes. The strongest increase in diet overlap was among coyotes and foxes, which was smaller in magnitude than their habitat overlap increase. Finally, coyote scats were more likely to contain nocturnal prey in interface preserves, whereas foxes appeared to reduce consumption of nocturnal prey. Our results suggest that dominant and generalist mesocarnivores may encroach on the niche space of subordinate mesocarnivores in areas with high human activity, and that patterns in resource use may be related to human-induced activity shifts.

Keywords: anthropogenic disturbance, niche overlap, nonconsumptive effects

Introduction

As human activity amplifies in many regions across the globe, wildlife are increasingly exposed to novel cues and threats associated with anthropogenic development. Terrestrial carnivores display a large diversity of responses to this proliferation of

---

human activity; some carnivores are particularly sensitive to risk from humans and respond by altering their space use (Wilmers et al. 2013), activity patterns (Barrueto et al. 2014, Wang et al. 2015), and feeding behavior (Smith et al. 2015), whereas others benefit from human development due to high tolerance of humans (McKinney 2006), exploitation of anthropogenic resource subsidies (Newsome et al. 2014), and reduced risk of predation or competition (Crooks and Soulé 1999). Although behavioral plasticity allows some carnivores to persist in human-dominated systems by mitigating exposure to anthropogenic stressors and risks (Bateman and Fleming 2012, Oriol-Cotterill et al. 2015, Carter and Linnell 2016), increases in more adaptable species can have unexpected direct and indirect effects on subordinate carnivores or prey (Ritchie and Johnson 2009, Ripple et al. 2013). Thus human activity, by differentially impacting individual carnivore populations, has the potential to alter the niche space of all carnivore species in a community.

The realized niche of a wildlife population is often redefined in human-dominated landscapes, particularly because anthropogenic disturbance hinders some species while benefitting others and therefore alters species interactions indirectly (Alberti et al. 2003). Indirect effects of human activity may be especially prevalent in carnivores, which often partition their use of space and time in order to access shared prey resources (Vanak et al. 2013). Because carnivores frequently share similar geographic ranges and habitat requirements, they form hierarchies among species that force inferior competitors into altered niche spaces defined by fine scale selection of microhabitats or temporal activity patterns (Cozzi et al. 2012, Kamler et al. 2012, Remonti et al. 2012). In some instances, interspecific competition is the most impactful driver of temporal partitioning (Hayward and Slotow 2009), allowing for coexistence when carnivores exploit the same prey communities.

Human-induced carnivore behavior change, particularly in dominant and adaptable species, are likely to exacerbate anthropogenic impacts on carnivore community dynamics. Human activity can instigate temporal shifts among multiple carnivore species towards increased nocturnal and reduced diurnal activity in response to human activity on trails (Riley et al. 2003, Wang et al. 2015). Mesocarnivores in areas with high human activity may also benefit from reduced large carnivore presence (Wang et al. 2015), making nocturnal hours potentially less risky than they are in undisturbed environments. Human impacts on temporal niche space may therefore contribute to altered competitive dynamics among carnivores by increasing temporal overlap while hunting.

Modern coexistence theory suggests that the niche of species is inherently a function of species interactions, and the capacity for species to coexist relies on both their niche overlap and their difference in fitness (Chesson 2000, Letten et al. 2017). Human activity may therefore constrain the potential for coexistence by broadening differences in fitness (through benefiting tolerant species) and narrowing overlap (through behavioral adaptation). In this study, we seek to understand the relationship between human disturbance (activity and development) and differential resource partitioning in a carnivore community as it relates to behavioral adjustments by a dominant mesocarnivore. Specifically, we test the differences in habitat and diet niche partitioning among three widespread mesocarnivores in open space preserves that are characterized by high and low levels of human activity. We hypothesized that in open space preserves more heavily impacted by human use, habitat and dietary niche expansion of dominant and adaptable mesocarnivores would be related to increased niche overlap among mesocarnivore species. We also hypothesized that these changes would be related to human-induced activity shifts toward increased nocturnal and reduced diurnal activity, resulting in temporally-driven changes in diet.

Methods

Study system

We conducted this study in the Santa Cruz Mountains in the Central Coast region of California. The region has a Mediterranean climate with a wet season in the winter and dry season in the summer. Elevation ranges from sea level to 1155 m, and annual rainfall varies from 58–121 cm across the mountain range. The Santa Cruz Mountain region supports or contains many different land uses, including privately protected land, state and county parks, open space preserves, cities, exurban communities, and extractive industries. The extensive wildland–urban interface in the Santa Cruz Mountains is known to impact carnivore feeding behavior (more nocturnal feeding, reduced feeding time and avoidance of housing; Wilmers et al. 2013, Smith et al. 2015) and utilization of prey species (more synanthropic prey species; Smith et al. 2016).

The northern region of the Santa Cruz Mountains abuts high-density suburban and urban development, yet much of its land is preserved as open space by the Midpenisula Regional Open Space District. Many preserves are located directly adjacent to development, whereas others are buffered by protected areas. Preserves at the wildland-urban interface (hereafter referred to as 'interface') experience disturbance from houses as well as greater human foot traffic due to their higher accessibility in comparison to more distant preserves surrounded by native habitat (hereafter referred to as 'wildland'). Our work was conducted on three interface preserves (within two miles of an urban area) and four wildland preserves (greater than five miles from an urban area; Fig. 1). Visitation data from 2007–2010 estimate that the three interface preserves studied experienced a total of 739 125 visitors year^{-1}, whereas the four wildland preserves saw 156 950 visitors year^{-1} (Midpeninsula Regional Open Space District 2011). All seven preserves in this study contained grassland (herbaceous), chaparral (shrubland), and forest (hardwood or mixed evergreen) habitat.

We chose coyotes *Canis latrans*, bobcats *Lynx rufus* and gray foxes *Urocyon cinereoargenteus* as our focal species due to their shared prey base (Fedriani et al. 2000, Larson et al. 2015), pro-
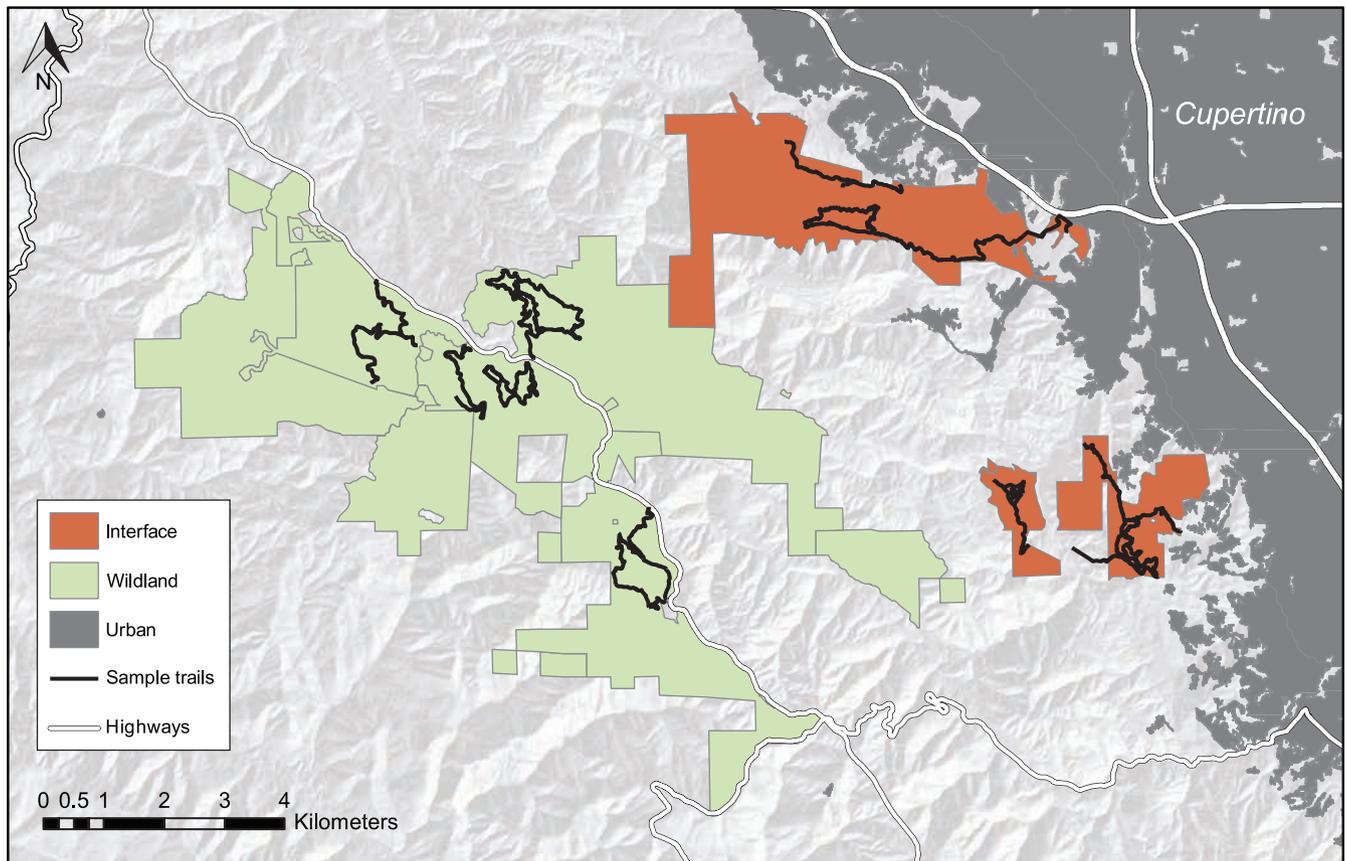
Figure 1. Midpeninsula Regional Open Space District wildland and interface preserves and trails sampled for mesocarnivore scats in the Santa Cruz Mountains, California.

pensity to eat prey with distinct diel activity patterns (Neale and Sacks 2001), well-documented intraguild hierarchy (Fedriani et al. 2000, Chamberlain and Leopold 2005), differential tolerance of human development (Ordeñana et al. 2010), and observed temporal responses to anthropogenic disturbances (Riley et al. 2003, Wang et al. 2015). Coyotes are known to be highly adaptable to human activity (Gehrt et al. 2009), often selecting for developed habitats (Ordeñana er al. 2010), and have dramatically expanded their range due to human expansion and extirpation of large carnivores (Prugh et al. 2009, Ripple et al. 2013). Conversely, bobcats and gray foxes can be more sensitive to human activity and often avoid developed areas (Ordeñana et al. 2010), although foxes may be relatively more adaptable than bobcats (Riley 2006).

In coastal California, coyotes and bobcats have become more nocturnal in areas of increased human activity and development (Riley et al. 2003, Wang et al. 2015). In contrast, gray foxes, the subordinate of the three species, are highly nocturnal regardless of human activity but become slightly more active during morning hours when disturbed (Wang et al. 2015). Activity of mesocarnivore primary prey in the region is closely tied to diel patterns; deer mice (*Peromyscus*), voles (*Microtus*), woodrats (*Neotoma*), and rabbits (*Sylvilagus*) are more nocturnal, whereas tree squirrels (*Sciurus*), ground squirrels (*Spermophilus*), and most songbirds are primarily diurnal

(Jones et al. 2009, Myers et al. 2017). The flexibility in coyote and bobcat activity patterns and their generalist diets facilitate the exploitation of both diurnal and nocturnal prey species and the ability to switch prey given declines in preferred prey (Prugh 2005). Therefore, these species are well-suited to explore the influence of human activity on niche breadth and partitioning among carnivores.

Scat collection

We developed a citizen science program called Conservation Scats to collect scat samples and train community members in animal tracking. Although dry scats can be comparable to fresh scats in dietary DNA amplification success and proportion of total scat DNA, dry scats can have a lower proportion of food DNA (McInnes et al. 2017). We chose to minimize fecal DNA degradation by only collecting scat samples up to one week old to retain sufficient DNA product for analysis (Fernando et al. 2000), with the acknowledgement that drier samples likely experienced some degradation. Each scat collection period consisted of two field days: on the first day we removed all scats from our study trails; on the second day (seven days later) we collected all fresh coyote, bobcat and gray fox scats from cleared trails. We collected all scats that were potentially from our target carnivore species, with the

3

exception of those from domestic dogs, which could be identified by the composition and consistency of the scat. We conducted four scat collection periods in May 2014, June 2014, January 2015 and March 2015. Approximately 37 miles of trails were sampled during each collection day (Fig. 1), and the same trails were sampled during each collection period. We froze all collected samples at –20C for 3–13 months prior to DNA extraction.

Molecular scat analysis

We used a DNA metabarcoding diet analysis approach that allows for the identification of multiple species in complex mixed samples. Traditional dietary analyses based on fecal dissection and microscopic examination of prey remains is often biased due to different digestibility of individual prey species and the identification skill of the observer (Pompanon et al. 2012), and many prey species, particularly of small mammals and birds, are difficult to distinguish morphologically. In contrast, DNA metabarcoding allows for the identification of individual species from complex environmental DNA (eDNA) samples based on high-throughput sequencing of marker genes (Yoccoz 2012). DNA metabarcoding has recently been used to detail carnivore diets from fecal samples for individual species (Shehzad et al. 2012, De Barba et al. 2014).

Scat processing
For molecular diet analysis from scats, DNA can be extracted from the prey remains that survive digestion (e.g. bones, fur) or from the scat matrix material (i.e. the part of the scat not made up of identifiable remains of bone, hair, or vegetation). Given that not all prey structures survive the digestive process equally, we chose to use the scat matrix material assuming that it is most representative of relative prey biomass and would best capture the diversity of species (Hibert et al. 2013).

Scats were removed from the freezer and thawed in sterile plastic containers lined with a nylon mesh paint strainer bag. Each container was filled with a sufficient quantity of 95% ethanol to cover the scat, and the scat was manually homogenized using a wooden tongue depressor. Once thoroughly broken apart, the paint strainer containing undigested structures was removed leaving behind ethanol preserved scat matrix in the container. DNA was extracted from the samples using the QIAamp Fast DNA Stool Mini Kit as per the manufacturer's instructions.

PCR amplification and sequencing
For this study, we focused on vertebrate prey species due to their association with diel activity patterns and high utilization by mesocarnivores. Vertebrates, and mammals in particular, comprise the majority of the diet in all three of our study mesocarnivores (Larson et al. 2015). We amplified a ~100 bp region of the mitochondrial 12S gene using the pan-vertebrate primers identified in (Riaz et al. 2011) that were designed using the program ecoPrimers in the Obitools package (De Barba et al. 2014, Boyer et al. 2016):

F (5′- ACTGGGATTAGATACCCC -3′) R (5′- TAGAACAGGCTCCTCTAG -3′). A two-stage labelling scheme was used to multiplex many individual scats on a single sequencing flow cell. For each scat, the initial PCR amplification was done with one of 16 labelled (10 bp tag) forward primers following the thermocycling protocol described in Riaz et al. (2011). We used previously-developed primer tags created with EDITTAG software (Thomas et al. 2016). Amplicons from 16 uniquely labelled samples were then normalized, pooled and given a unique TruSeq Illumina adapter sequence via post-PCR ligation using a KAPA LTP library preparation kit. Lastly, samples were pooled for 150 bp SE sequencing on the Illumina MiSeq. To achieve our desired sequencing depth (> 2000 prey DNA sequences per sample post-filtering), scat amplicons were sequenced on two separate MiSeq runs, each with an independent pool of separate amplicons.

Bioinformatics pipeline
The overall bioinformatics approach we employed was as follows: 1) generation of a local reference database containing 12S sequences for all potential prey and predator taxa in the study region, 2) Clustering of MiSeq sequence data and selection of representative (most abundant) sequences to ensure that species are appropriately represented in the local reference database, 3) taxonomic assignment of each individual sequence via BLAST search to the local database, 4) a confirmation process using GenBank to identify any taxonomic ambiguities in species or genera assignments.

Sequences were automatically sorted (MiSeq post processing) by amplicon pool using the indexed TruSeq adapter sequences. FASTQ sequence files for each library were imported into QIIME for demultiplexing and sequence assignment to species (Caporaso et al. 2010). For a sequence to be assigned to a sample it had to match the full forward and reverse primer sequences, and match the 10 bp primer tag for that sample (allowing for up to twomismatches in either primers or tag sequence).

We created a local reference library of all extant terrestrial vertebrates in the Santa Cruz Mountains using available 12S sequences in GenBank. For species for which there were no 12S gene sequences in GenBank, we instead used one congener or one confamilial sequence. In total, 66 species-specific sequences, 33 genus-specific sequences, and 3 family-specific sequences were used to represent potential diet species in our local database. Two BLAST reference libraries were created, with one containing only predator species and the other containing identified potential prey species.

DNA sequences that were assigned to scat samples were clustered with USEARCH (similarity threshold = 0.99; minimum cluster size = 3; de novo chimera detection), and a representative sequence from each cluster (based on abundance) was entered into a GenBank nucleotide BLAST search (Altschul et al. 1990, Edgar 2010). If the top matching species for any cluster was not included in the existing database (or the sequence differed indicating allelic variation), the top matching entry was put in the reference database.

This procedure minimized the potential for incorrect species assignment or prey species exclusion.

For taxonomic assignment, a local BLAST search was done against our custom 12S reference databases with each sequence that was assigned to a sample. Two passes were performed with the dataset, first using the reference database containing only predator 12S sequences, and then a second pass using the 12S prey sequence database. A species was assigned to a sequence based on the best match in the database (threshold BLASTN e-value $< 1 \times 10^{-20}$ and a minimum identity of 0.9), and the proportions of each species' sequences were quantified by sample after excluding predator sequences or any identified environmental contaminants (i.e. human DNA), and excluding species representing fewer than 1% of the reads in each sample (Caporaso et al. 2010).

To confirm the quality of our species assignments, we entered a subset of assigned sequences into a full GenBank BLASTN search. For each species with fewer than five sequence reads per scat sample, we did a BLASTN search for each individual. If the top species assignment did not match the assignment from our reference library, we eliminated the sequence. For all other species, we ran a minimum of three sequence reads in a BLASTN search. If the BLASTN output for each of the three sequences matched the species assigned from the reference library with a maximum e-value of 1×10^{-50} (Hiiesalu et al. 2012), the remainder of assignments for that prey species were kept. For species with variability in assignment accuracy (i.e. some sequence assignments matched the BLASTN results while others did not), we ran one sequence assigned as the species from each scat in which the species occurred and excluded incorrect matches from further analyses. For outputs in which multiple species had equal similarity matches, the lowest parsimonious taxonomic level was used.

The predator species for each scat sample was inferred based on the relative proportions of predator sequences in each scat. The predator species with the largest proportion of sequences was assigned as the depositing predator. This could be easily determined because the depositing predator was responsible for 95.4 ± 0.6 SE percent of predator sequences per scat.

Habitat composition

Habitat utilization for each mesocarnivore species was determined from habitat composition at scat locations. To compare mesocarnivore habitat use to available habitat, we also simulated a hypothetical carnivore using habitat types randomly by measuring habitat composition at 300 random locations on sampled trails. We extracted the proportion of habitat classifications within 50 m of each scat or random location from the CALVEG Zone 6 Existing Vegetation map (USDA Forest Service 2014). The seven habitat classes present in our study area include conifer forest, hardwood forest, mixed forest, shrubland, herbaceous (grassland), agricultural and urban. We assessed mesocarnivore habitat selection by calculating selection ratios of proportion of used locations to proportion of random locations in each habitat class (Manly et al. 2002).

Diet assessment

We determined relative proportion of a prey species in the diet of each carnivore species using two methods: 1) frequency of occurrence (FOO) in scats; and 2) the proportion of DNA reads in each scat measured as relative read abundance (RRA; Kartzinel et al. 2015). RRA theoretically better represents diet because it allows for dietary contributions to reflect biomass if DNA is conserved and amplified equally for all prey species. However, RRA can be biased if the primer used does not match equally for all target prey species, if prey have different DNA densities, or if prey DNA experiences differential degradation during digestion (Deagle et al. 2013). Our primer region had 1–3 base pair mismatches in the majority of herpetofauna species, therefore we may have underestimated contribution of reptile and amphibian taxa (Pawluczyk et al. 2015, Piñol et al. 2015). In the case of uneven primer mismatches between species, FOO data also may be less biased against contribution of particular prey species to carnivore diets. We calculated all diet measures using both RRA and FOO data to compare the qualitative differences between the two approaches. RRA was measured as the proportion of sequence reads in a sample divided by the total number of sequences in that sample (Kartzinel et al. 2015).

Habitat and diet niche differentiation

We ran permutational MANOVA tests to assess differences in diet composition for each carnivore species and among carnivore species between interface and wildland preserves. In order to examine the strength of association between carnivores and their prey, we also conducted a correspondence analysis (CA), which uses a contingency table of prey count data by carnivore to examine the statistical difference in partitioning of prey species (Bendixen 1995). We calculated the correlation coefficient of the CA for wildland and interface preserves using both RRA and FOO diet estimates, where a larger correlation coefficient represents greater differentiation between the diets of carnivore species.

Habitat and diet niche breadth

We measured both dietary and habitat niche breadth in wildland and interface preserves separately for gray foxes, bobcats, and coyotes using Hurlbert's standardized niche breadth (B_A), a measure of Levins' formula that can be interpreted on a [0,1] scale (Hurlbert 1978):

$$B_{Ajk} = \frac{\left(1 / \sum p_{ijk}{}^2\right) - 1}{n_k - 1}$$

where p_{ijk} is the relative proportion of each sampled item $i =$ [habitat types or prey species] of carnivore $j =$ [bobcat, coyote, gray fox] in preserve type $k =$ [wildland, interface]

and n is the number of total available outcomes in preserve type k. B_{Ajk} ranges from 0 (highly specialized) to 1 (highly generalized). To compare habitat niche breadth at random locations on trails to that of carnivore scat locations, we also calculated wildland and interface habitat niche breadth at previously described random locations (Peers et al. 2012). We used a bootstrapping approach to correct for differences in sample sizes (Reynolds and Aebischer 1991), whereby we took the average of niche breadth measures calculated by subsampling 15 scats or locations with replacement for 10 000 iterations for each carnivore by preserve type.

Habitat and diet niche overlap

We used Pianka's adaptation of the niche overlap (O_{jk}) metric to determine habitat and diet overlap among all pairs of target carnivores in both preserve types (Pianka 1973):

$$\hat{O}_{jmk} = \sum_i^n \hat{p}_{ijk}\, \hat{p}_{imk} \Big/ \sqrt{\sum_i^n \hat{p}_{ijk}^{\,2}\, \hat{p}_{imk}^{\,2}}$$

where p_{ijk} is the proportion of habitat type or prey species i in carnivore j in preserve type k, p_{imk} is the proportion of habitat type or prey species i in carnivore m in preserve type k, and n is the total number of available habitat types or prey species. A value of $O_{jmk} = 0$ represents no overlap, whereas a value of $O_{jmk} = 1$ represents complete overlap.

Nocturnal prey consumption

To assess the role of human-induced activity shifts on carnivore diet, we compared the proportion of nocturnal prey consumed and the number of scats containing nocturnal and diurnal prey in interface and wildland preserves for each carnivore species using one-tailed two-proportion z-tests.

Data deposition

Data available from the Dryad Digital Repository: < http://dx.doi.org/10.5061/dryad.54h24 > (Smith et al. 2018).

Results

Habitat composition, niche breadth and overlap

We collected 302 carnivore scats, 284 of which could be identified to predator species (Supplementary material Appendix 1). Habitat composition at mesocarnivore scat locations was influenced by preserve type (F = 48.62, p = 0.001), mesocarnivore species (F = 7.79, p = 0.001), and an interaction between preserve type and mesocarnivore (F = 2.71, p = 0.022), indicating that mesocarnivores differentially alter habitat use in response to preserve type. Foxes (F = 15.61, p = 0.001), bobcats (F = 22.73, p = 0.001) and coyotes (F = 8.01, p = 0.004) all differed in their habitat use between wildland and interface preserves. Coyotes expanded their habitat niche breath in interface preserves, whereas bobcats and foxes contracted their habitat niche breadth (Table 1). Niche breadth of random locations on sample trails were essentially identical in wildland and interface preserves (Table 1). Habitat overlap between coyotes and both bobcats and foxes was higher in interface preserves by 10.4% and 7.9%, respectively, but was lower between bobcats and foxes (–3.8%; Fig. 2c).

Diet composition, niche breadth and overlap

Scat samples contained 36 total prey species or taxonomic units (Table 2), averaging 7613 ± 594 SE prey DNA sequences per sample (Supplementary material Appendix 2). Diet composition measured by RRA and FOO was influenced by preserve type (pseudo-F_{RRA} = 4.49, df_{RRA} = 1, p_{RRA} = 0.001, R^2_{RRA} = 0.01; pseudo-F_{FOO} = 12.00, df_{FOO} = 1, p_{FOO} = 0.001, R^2_{FOO} = 0.04), mesocarnivore species (pseudo-F_{RRA} = 7.41, df_{RRA} = 2, P_{RRA} = 0.001, R^2_{RRA} = 0.05; pseudo-F_{FOO} = 11.13, df_{FOO} = 2, p_{FOO} = 0.001, R^2_{FOO} = 0.07), and an interaction between preserve type and mesocarnivore (pseudo-F_{RRA} = 2.15, df_{RRA} = 2, p_{RRA} = 0.021, R^2_{RRA} = 0.01; pseudo-F_{FOO} = 2.40, df_{FOO} = 2, p_{FOO} = 0.014, R^2_{FOO} = 0.02). Both RRA and FOO diet data suggested that foxes (pseudo-F_{RRA} = 3.12, df_{RRA} = 1, p_{RRA} = 0.014, R^2_{RRA} = 0.02; pseudo-F_{FOO} = 7.12, df_{FOO} = 1, p_{FOO} = 0.001, R^2_{FOO} = 0.05) and bobcats (pseudo-F_{RRA} = 3.82, df_{RRA} = 1, p_{RRA} = 0.002, R^2_{RRA} = 0.04; pseudo-F_{FOO} = 5.97, df_{FOO} = 1, p_{FOO} = 0.001, R^2_{FOO} = 0.06) significantly altered their diet between wildland and interface preserves, whereas

Table 1. Percent habitat composition within 50 m of mesocarnivore scat locations and 300 random locations on sampled trails in wildland and interface preserves. Selection ratios (SR) are in parentheses, where values >1 indicate selection and values <1 indicate avoidance. SRs are reported as NA if the habitat did not appear in random locations on sampled trails for that preserve type.

|	Coyote		Bobcat		Gray fox		Trails	
	Wildland	Interface	Wildland	Interface	Wildland	Interface	Wildland	Interface
Forest	14.3 (0.25)	25.5 (0.63)	56.4 (1.00)	32.3 (0.79)	51.1 (0.91)	36.5 (0.89)	56.2	40.8
conifer	0.0 (0.00)	0.0 (NA)	0.0 (0.00)	0.0 (NA)	0.0 (0.00)	0.0 (NA)	1.8	0.0
hardwood	1.1 (0.12)	25.5 (0.63)	19.0 (2.04)	32.3 (0.79)	17.9 (1.92)	36.5 (0.89)	9.3	40.8
mixed	13.2 (0.29)	0.0 (NA)	37.4 (0.83)	0.0 (NA)	33.2 (0.74)	0.0 (NA)	45.1	0.0
Herbaceous	66.3 (1.83)	34.2 (2.33)	26.3 (0.73)	6.2 (0.42)	19.1 (0.53)	10.5 (0.71)	36.2	14.7
Shrubland	19.4 (2.55)	33.0 (0.90)	17.3 (2.28)	61.5 (1.68)	29.8 (3.92)	51.7 (1.42)	7.6	36.5
Agriculture	0.0 (NA)	0.0 (0.00)	0.0 (NA)	0.1 (0.01)	0.0 (NA)	1.4 (0.21)	0.0	6.7
Urban	0.0 (NA)	7.4 (5.29)	0.0 (NA)	0.0 (0.00)	0.0 (NA)	0.0 (0.00)	0.0	1.4
Habitat niche breadth	0.197	0.382	0.406	0.156	0.416	0.226	0.337	0.340
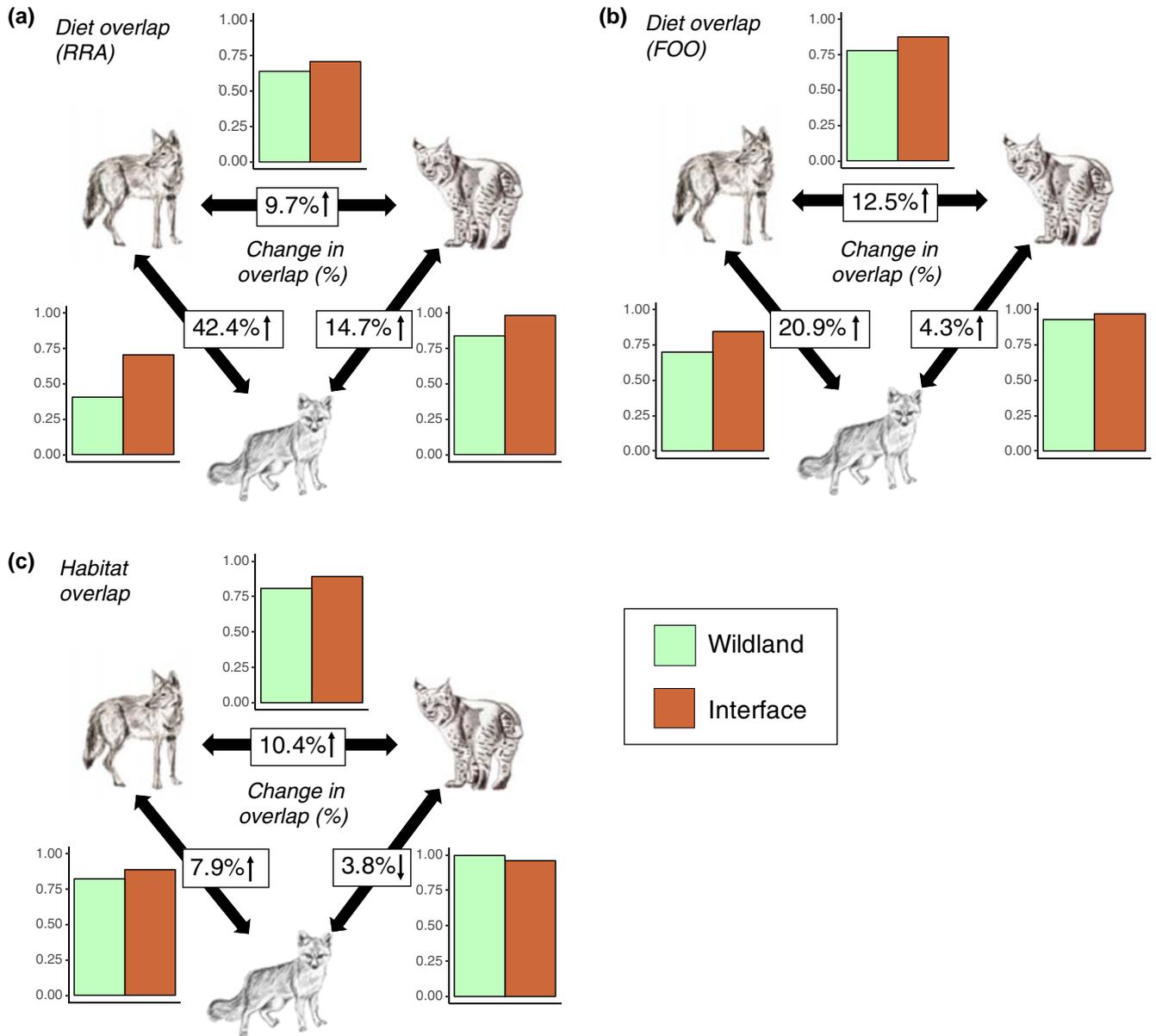
Figure 2. Niche overlap and percentage change in overlap among three mesocarnivore species for (a) RAA diet, (b) FOO diet, and (c) habitat in wildland and interface open space preserves in the Santa Cruz Mountains.

coyotes differed only in FOO diet estimates in scat samples (pseudo-$F_{RRA} = 1.44$, $df_{RRA} = 1$, $p_{RRA} = 0.127$, $R^2_{RRA} = 0.03$; pseudo-$F_{FOO} = 2.37$, $df_{FOO} = 1$, $p_{FOO} = 0.046$, $R^2_{FOO} = 0.04$). CAs indicated that differentiation between carnivore diets was higher in wildland ($R = 0.70$) than interface ($R = 0.63$) preserves (Fig. 3a–b). CAs conducted with FOO data show similar patterns, but with smaller correlation coefficients ($R_{wildland} = 0.52$, $R_{interface} = 0.46$; Fig. 3c–d). In comparison to wildland preserves, dietary niche breadth (B_A) in interface preserves was higher for coyotes and lower for foxes for both RRA and FOO measures (Table 3). Bobcat dietary niche breadth estimated by RRA and FOO approaches resulted in qualitative differences between interface and wildland preserves, whereby dietary niche breadth was lower in interface preserves using RRA diet estimates and higher using FOO diet estimates.

Diet overlap between all pairs of carnivore species increased with human activity (Fig. 2a, b). The largest increase in overlap was observed between coyotes and gray foxes, whereby RRA overlap was 42% higher in interface preserves in comparison to wildland preserves. Bobcats and gray foxes had the most similar diets of any three pairs of carnivores with almost complete diet overlap in interface preserves, reaching an RRA overlap value of 0.984 (Fig. 2a). Diet overlap values using FOO data were qualitatively similar, but ubiquitously larger in magnitude (Fig. 2b).

Nocturnal prey consumption

In coyotes, proportion of scats containing nocturnal prey increased from 82% in wildland preserves to 100% in interface preserves ($p = 0.02$) and proportion of scats containing diurnal

Table 2. Prey species detected in coyote, bobcat, and gray fox scats in wildland and interface open space preserves in the Santa Cruz Mountains, California. Proportions are listed as the mean relative read abundance (RRA), with frequency of occurrence (FOO) in parentheses. Activity patterns are simplified as nocturnal (N) and diurnal (D).

	Activity Pattern[a]	Coyote		Bobcat		Gray fox	
		Wildland	Interface	Wildland	Interface	Wildland	Interface
Mammals							
Chaetodipus californicus	N	–	–	1.1 (2.0)	–	0.2 (2.4)	0.5 (1.4)
Didelphis virginiana	N	–	2.6 (1.6)	<0.1 (0.5)	–	–	–
Felis catus[b]	N	1.0 (1.3)	8.9 (5.4)	0.8 (1.0)	0.1 (2.3)	–	0.2 (1.4)
Lepus californicus	N	1.3 (8.9)	4.2 (9.3)	–	0.1 (1.1)	–	<0.1 (0.9)
Microtus californicus	N	9.3 (6.3)	5.5 (5.4)	17.3 (20.8)	0.5 (5.7)	12.0 (15.5)	1.2 (9.0)
Neotoma fuscipes	N	9.3 (13.9)	16.7 (18.6)	25.7 (21.3)	49.3 (28.4)	45.4 (24.4)	46.1 (30.3)
Odocoileus hemionus	D[c]	18.0 (12.7)	1.2 (2.3)	1.6 (3.0)	4.2 (6.8)	0.6 (2.4)	0.8 (1.4)
Peromyscus spp.	N	1.0 (5.1)	0.7 (3.1)	5.9 (9.9)	2.6 (6.8)	16.5 (19.6)	8.6 (10.4)
Rattus spp.	N	–	–	–	2.4 (3.4)	–	–
Scapanus latimanus	D	–	<0.1 (1.6)	0.9 (0.5)	<0.1 (1.1)	0.1 (0.6)	1.1 (1.8)
Sciurus spp.	D	0.2 (1.3)	6.9 (3.1)	8.2 (4.0)	1.5 (2.3)	0.4 (1.8)	2.3 (3.6)
Spermophilus beecheyi	D	0.5 (2.5)	3.0 (4.7)	0.2 (2.5)	0.1 (2.3)	–	0.1 (1.4)
Sylvilagus spp.	N[d]	18.8 (15.2)	21.7 (17.1)	23.3 (15.8)	22.4 (17.0)	10.9 (10.1)	23.6 (19.0)
Thomomys bottae	N	30.6 (17.7)	20.6 (15.5)	7.5 (8.9)	5.2 (6.8)	3.7 (6.5)	3.1 (4.5)
Birds							
Callipepla californica	D	0.1 (1.3)	2.0 (0.8)	–	2.8 (1.1)	–	0.1 (0.9)
Cardinalidae	D	0.1 (1.3)	–	<0.1 (1.0)	–	1.2 (0.6)	–
Cathartes aura	D	2.8 (1.3)	–	–	–	–	–
Columbidae	D	–	1.8 (1.6)	–	–	–	1.9 (1.8)
Gallus gallus[b]	D	–	0.5 (1.6)	–	0.5 (2.3)	0.1 (0.6)	2.2 (2.7)
Emberizidae	D	–	–	0.4 (1.0)	–	–	–
Meleagris gallopavo	D	5.3 (3.8)	0.8 (3.9)	3.7 (4.5)	5.7 (4.5)	1.4 (3.0)	2.4 (2.7)
Mimus polyglottos	D	–	–	–	–	0.6 (1.8)	0.2 (0.5)
Passeriformes (other)	D	0.9 (3.8)	0.7 (1.6)	3.3 (2.5)	0.1 (3.4)	1.5 (3.0)	0.1 (0.9)
Pavo cristatus[b]	D	–	–	–	–	–	1.4 (0.5)
Pelicaniformes	D	<0.1 (1.3)	–	–	–	–	–
Picidae	D	–	–	–	–	0.1 (0.6)	–
Strigidae	N	–	–	–	–	0.3 (0.6)	–
Sylvioidea	D	–	–	–	<0.1 (1.1)	–	0.6 (0.5)
Troglodytidae	D	–	–	–	–	<0.1 (0.6)	–
Turdidae	D	0.5 (1.3)	1.0 (0.8)	<0.1 (0.5)	–	2.4 (2.4)	–
Tyto alba	N	–	<0.1 (0.8)	–	–	–	0.4 (0.9)
Amphibians							
Anaxyrus boreas	N	–	–	–	–	–	0.6 (0.5)
Aneides flavipunctatus	N	–	–	–	–	<0.1 (0.6)	–
Batrachoseps attenuatus	N	–	0.1 (0.8)	–	–	–	<0.1 (0.5)
Pseudacris sierra	N	–	–	–	–	<0.1 (0.6)	–
Rana spp.	D[e]	0.4 (1.3)	1.2 (0.8)	<0.1 (0.5)	1.4 (3.4)	1.5 (2.4)	2.1 (2.7)

[a]Activity pattern data from PanTHERIA (Jones et al. 2009) and Animal Diversity Web (Myers et al. 2017) unless otherwise specified
[b]Domestic and/or feral species
[c]Derived from camera trap data collected from 17 cameras in the study area, March–November 2015 (Wilmers unpubl.)
[d]Based on *Sylvilagus bachmani*
[e]Based on *Rana boylii*

prey exhibited a marginally significant decrease from 68% to 47% (p=0.06; Table 3). A marginally significant increase in RRA nocturnal prey consumption (p=0.053) was observed in coyotes in interface preserves, where coyote diet comprised approximately 10% more nocturnal prey (Table 3). Gray foxes appeared to reduce their RRA proportion of nocturnal prey consumed in interface preserves, although the difference in proportions was only marginally significant (p=0.055). Bobcats did not vary the RRA proportion of nocturnal prey consumed by preserve type (p=0.40), and neither fox nor bobcat scats in interface and wildland preserves differed in

the number of scats containing nocturnal prey (p=0.28 and p=0.57, respectively) or diurnal prey (p=0.20 and p=0.37, respectively; Table 3). No mesocarnivore altered their FOO proportion of nocturnal prey consumed (p=0.14, p=0.12, p=0.71 for coyotes, bobcats and foxes, respectively).

Discussion

We provide evidence that differential responses by mesocarnivore species to human activity may influence the way in which mesocarnivores partition resources. Coyotes
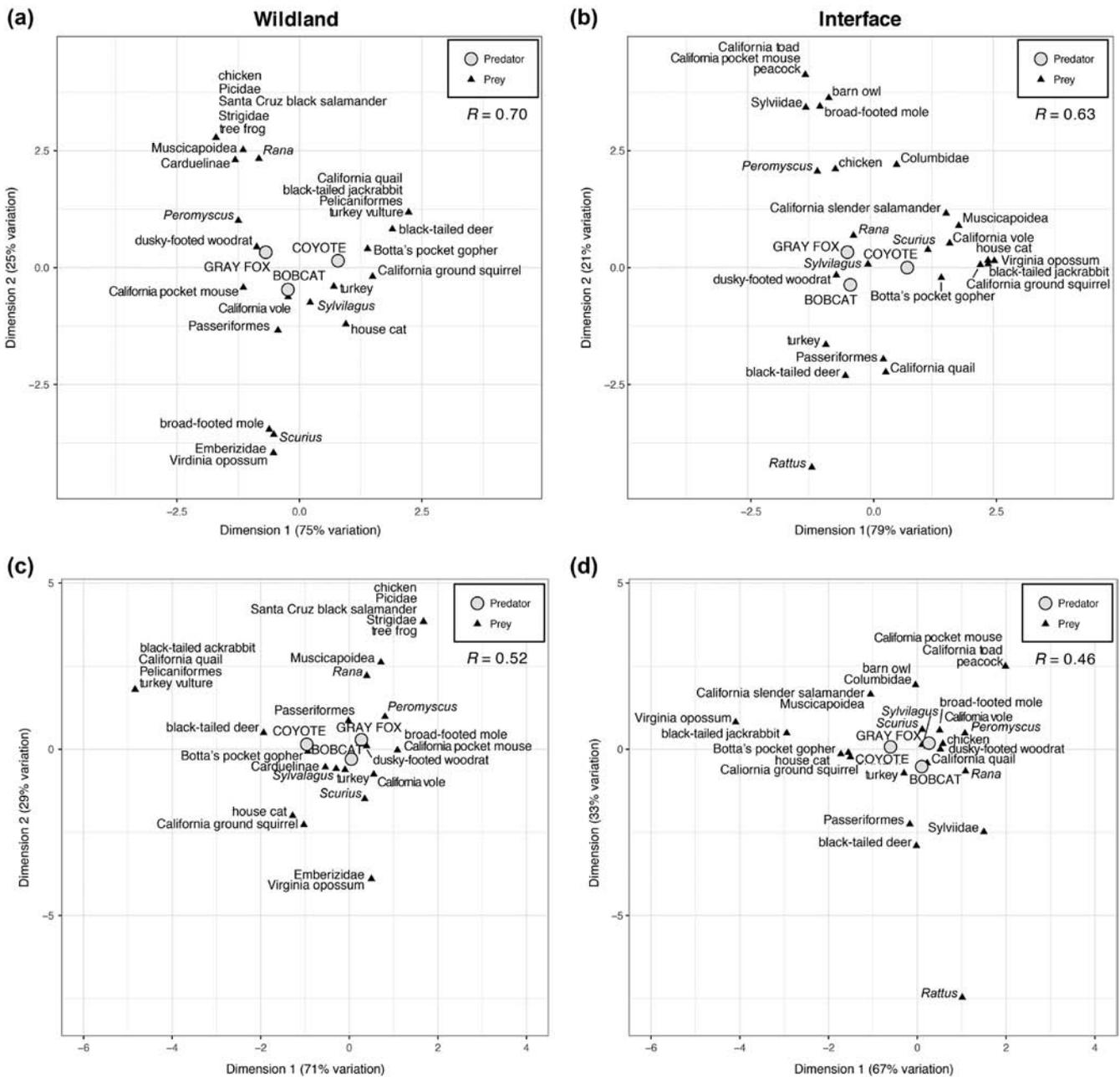
Figure 3. Correspondence analysis of mesocarnivore diet associations in using RRA diet estimates in (a) wildland and (b) interface preserves and using FOO diet estimates in (c) wildland and (d) interface preserves. Shorter distances between mesocarnivores represents increased similarity in their diets. Prey that appear close together are more similar in their proportional contribution to the diets of the mesocarnivore species. Greater association between mesocarnivores and their prey were observed in wildland preserves than in interface preserves.

broadened their habitat niche breadth in interface preserves, while bobcats and foxes contracted their niche breadth. Habitat niche breadth at random locations on sampled trails did not differ between interface and wildland preserves, indicating that shifts in habitat niche breadth in mesocarnivores were likely behavioral. However, there were some compositional differences, as interface preserves were characterized by more shrubland and less grassland habitat than wildland preserves overall. Coyotes, which strongly preferred grassland habitat in both interface and wildland preserves, appeared able to adapt to changes in habitat availability by increasing

utilization of shrubland and forest, in addition to selecting urban areas. Bobcats and foxes appeared to prefer shrubland habitats, avoid grasslands, and use forests approximately equal to their availability in both interface and wildland preserves. Therefore, the movement of coyotes into habitat types generally preferred by bobcats and foxes may contribute to increased habitat overlap among mesocarnivores in interface preserves and is likely facilitated by human activity. Coyotes were the only species found to use urban habitats in this study, and a larger number of coyote scats were found in interface preserves, despite the lower availability of preferred

Table 3. Summary statistics from coyote, bobcat, and gray fox diet analyses in wildland and interface open space preserves in the Santa Cruz Mountains, California. For measures of niche breadth and % nocturnal diet, we report estimates from both RRA data and FOO data (in parentheses). Significant differences between interface and wildland preserves are noted for measures of nocturnal prey consumption, scats containing nocturnal prey, and scats containing diurnal prey.

	Coyote		Bobcat		Gray fox	
	Wildland	Interface	Wildland	Interface	Wildland	Interface
No. of scat samples	22	34	75	28	49	76
Mean prey items/scat	3.59	3.82	2.71	3.26	3.45	2.92
Total prey species richness	18	22	18	19	22	24
Dietary niche breadth	0.109 (0.209)	0.142 (0.213)	0.114 (0.160)	0.062 (0.167)	0.076 (0.159)	0.068 (0.143)
Nocturnal prey composition (%)	71.2˙ (67.1)	81.0˙ (77.5)	81.5 (80.2)	82.7 (71.6)	90.0˙ (80.3)	84.6˙ (78.7)
Scats containing nocturnal prey (%)	81.8*	100*	94.7	100	100	96.1
Scats containing diurnal prey (%)	68.2˙	47.1˙	42.9	39.5	38.7	48.1

Significance levels: *p < 0.05; ˙p < 0.10.

grasslands. This result corroborates previous finding that coyotes respond positively to human activity, perhaps because of their tolerance of people and reduced risk of puma predation (Gehrt et al. 2009, Ordeñana er al. 2010, Ripple et al. 2013, Wang et al. 2015).

Differences in dietary niche breadth estimated in RRA and FOO data showed the same qualitative patterns as habitat niche breadth for coyotes and foxes. Bobcats, however exhibited niche contractions in interface preserves for habitat and RRA diet estimates, but a dietary niche expansion using FOO data. This inconsistency could be explained by the characteristics of the data used; in interface preserves, bobcats might become more specialized from a biomass perspective, but consume a greater number of species. Incongruities in our analyses using both data types highlight the importance of considering the appropriate unit of analysis for any diet analysis using DNA metabarcoding techniques.

We found that all pairs of mesocarnivores increase diet overlap in interface preserves and coyotes increase habitat overlap with bobcats and foxes, indicating that niche partitioning is degraded in areas with higher human activity. One possible explanation for shifts in diet overlap is increased utilization of nocturnal prey species by coyotes, and subsequent attempts by foxes to mitigate increased coyote nocturnal hunting activity by hunting more diurnally-active prey. The proportion of coyote scats containing nocturnal prey increased from 82% in wildland preserves to 100% in interface preserves while scats containing diurnal prey declined from 68% to 47%, supporting observed activity shifts for coyotes in our study area from a previous study where coyotes exhibited the greatest decrease in diurnal activity with increasing disturbance of our three study species (Wang et al. 2015). The increase in proportion of scats containing nocturnal prey reflects the extent of coyote encroachment on the niche space of highly nocturnal foxes. Although foxes may be able to adapt to some extent by consuming more diurnal prey items, their dependence on hunting at night is evidenced by their high proportion of scats containing nocturnal prey in both preserve classes. Coyote shifts toward increased nocturnal prey utilization could further constrain the realized niche of the less generalist gray fox.

Although an increase in diet overlap cannot provide direct inference on the degree of exploitation competition without knowing the relative abundances of all available prey resources, it offers insight into constraints on fine-scale temporal and spatial niche partitioning, particularly in light of inconsistent differences in patterns of habitat utilization. However, factors beyond habitat use and temporal niche partitioning might contribute to increased diet overlap among carnivores. We cannot discount that the patterns we observed might be influenced by prey responses to human activity, which could alter prey diversity. Although logistical constraints for this study made acquiring density estimates for the large diversity of carnivore prey species infeasible, we attempted to minimize impacts of habitat by sampling in preserves with similar habitat types. The potential for differential prey availability does not alter the interpretation of our results on carnivore diet and overlap in response to anthropogenic disturbance, but could influence inferences made regarding the mechanism for these changes. In addition, although we only analyzed use of vertebrate prey resources in this study, canids hunting in preserves that abut residential areas could also experience some spillover of plant-based anthropogenic food not captured by our analysis. A combination of human-induced behavioral changes among carnivores, altered prey community composition, and influx of non-vertebrate anthropogenic subsidies might all contribute to shifts in carnivore diet composition and overlap.

In addition to habitat, preserve type, and activity patterns, prey use appeared to be tied to size and habitat preferences of the carnivores. Dusky-footed woodrat *Neotoma fuscipes* and brush rabbit *Sylvilagus* spp. were the most utilized diet items among mesocarnivores as a whole, but use of woodrat decreased with increasing carnivore species size. Larger prey species such as black-tailed jackrabbit *Lepus californicus*, house cat *Felis catus*, Virginia opossum *Didelphis virginiana*, and black-tailed deer *Odocoileus hemionus* were primarily consumed by coyotes, whereas small and forest-associated deer mice *Peromyscus* spp. were consumed mostly by gray foxes. The pocket gopher *Thomomys bottae* and ground squirrel *Spermophilus beecheyi*, two grassland species, were consumed in the highest proportions by coyotes. The partitioning of prey species by size and habitat association highlights the importance of habitat heterogeneity and prey diversity in

supporting carnivore coexistence. Conservation of intact carnivore communities likely requires a holistic lens that focuses on the maintenance of diverse habitats, prey species, and access to prey in both day and night.

High diet and habitat overlap in interface preserves indicates that mesocarnivores in areas with high human activity likely hunt in similar habitat types and times of day to access the same resources. Reduced partitioning could therefore result in increased antagonistic interspecific interactions among carnivores or spatial shifts resulting from interspecific avoidance (Remonti et al. 2012). This is of particular relevance in regard to the coyote, which has expanded its range by 40% and is now the top predator in many ecosystems due to a reduction of top carnivores and increased human development (Prugh et al. 2009). Coyotes can suppress the populations of subordinate mesocarnivores, including gray foxes (Riley et al. 2007, Levi and Wilmers 2012, Serieys et al. 2015). Our results support that coyotes are the most adaptable mesocarnivore in this system due to their ability to expand their niche breadth in novel conditions, allowing them to encroach on the niche space of subordinate and less generalist gray foxes. Further work should investigate the degree to which mesocarnivore declines in the presence of coyotes are accentuated or explained by enhanced exploitation competition due to human-imposed restrictions in dietary niches.

Foxes and bobcats were the only mesocarnivore pair to exhibit a slight decrease in habitat overlap and an increase in diet overlap. Differential overlap responses may be a result of a heightened tradeoff that emerges from near-complete habitat overlap and very high diet overlap in wildland preserves. Because foxes and bobcats appear to prefer the same resources in wildland areas, they may struggle to further partition these resources with increased pressure from human activity and altered coyote behavior. Our work indicates that there may be a functional response between the degree of overlap in the fundamental niches of two species and the magnitude of their reduction of niche partitioning in response to novel stressors.

Indirect effects of animal behavioral adaptations to anthropogenic disturbances, through avoidance of both humans and human-adapted species, may contribute to altered composition of animal communities in human-dominated landscapes. Nearly all federally protected lands in the United States are open to recreation of some kind, and pressures on these lands are projected to increase with high rates of housing development near protected areas (Radeloff et al. 2010). Although land preservation is an essential first step to conserving ecosystems, protected lands at the wildland–urban interface may not fully maintain natural ecosystem processes and species interactions due to high levels of human activity. Mitigation of human influences on the behavior of wildlife and its cascading effects should be considered for the preservation of intact animal communities and relationships in the midst of global change.

References

Alberti, M. et al. 2003. Integrating humans into ecology: opportunities and challenges for studying urban ecosystems. – BioScience 53: 1169–1179.

Altschul, S. F. et al. 1990. Basic local alignment search tool. – J. Mol. Biol. 215: 403–410.

Barrueto, M. et al. 2014. Anthropogenic effects on activity patterns of wildlife at crossing structures. – Ecosphere 5: 1–19.

Bateman, P. and Fleming, P. 2012. Big city life: carnivores in urban environments. – J. Zool. 287: 1–23.

Bendixen, M. T. 1995. Compositional perceptual mapping using chi squared trees analysis and correspondence analysis. – J. Marketing Manage. 11: 571–581.

Boyer, F. et al. 2016. obitools: a unix-inspired software package for DNA metabarcoding. – Mol. Ecol. Resour. 16: 176–182.

Caporaso, J. G. et al. 2010. QIIME allows analysis of high-throughput community sequencing data. – Nat. Methods 7: 335–336.

Carter, N. H. and Linnell, J. D. C. 2016. Co-adaptation is key to coexisting with large carnivores. – Trends Ecol. Evol. 31: 575–578.

Chamberlain, M. J. and Leopold, B. D. 2005. Overlap in space use among bobcats (*Lynx rufus*), coyotes (*Canis latrans*) and gray foxes (*Urocyon cinereoargenteus*). – Am. Midl. Nat. 153: 171–179.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. – Annu. Rev. Ecol. Syst. 31: 343–366.

Cozzi, G. et al. 2012. Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. – Ecology 93: 2590–2599.

Crooks, K. R. and Soulé, M. E. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. – Nature 400: 563–566.

Deagle, B. E. et al. 2013. Quantifying sequence proportions in a DNA-based diet study using Ion Torrent amplicon sequencing: which counts count? – Mol. Ecol. Resour. 13: 620–633.

De Barba, M. et al. 2014. DNA metabarcoding multiplexing and validation of data accuracy for diet assessment: application to omnivorous diet. – Mol. Ecol. Resour. 14: 306–323.

Edgar, R. C. 2010. Search and clustering orders of magnitude faster than BLAST. – Bioinformatics 26: 2460–2461.

Fedriani, J. M. et al. 2000. Competition and intraguild predation among three sympatric carnivores. – Oecologia 125: 258–270.

Fernando, P. et al. 2000. Mitochondrial DNA variation, phylogeography and population structure of the Asian elephant. – Heredity 84: 362–372.

Gehrt, S. D. et al. 2009. Home range and landscape use of coyotes in a metropolitan landscape: conflict or coexistence? – J. Mammal. 90: 1045–1057.

Hayward, M. W. and Slotow, R. 2009. Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. – S. Afr. J. Wildl. Res. 44: 109–125.

Hiiesalu, I. et al. 2012. Plant species richness belowground: higher richness and new patterns revealed by next-generation sequencing. – Mol. Ecol. 21: 2004–2016.

Hibert, F. et al. 2013. Unveiling the diet of elusive rainforest herbivores in next generation sequencing era? The tapir as a case study. – PLoS One 8: e60799.

Hurlbert, S. H. 1978. The measurement of niche overlap and some relatives. – Ecology 59: 67–77.

Jones, K. E. et al. 2009. PanTHERIA: a species-level database of life history, ecology and geography of extant and recently extinct mammals. – Ecology 90: 2648.

Kamler, J. F. et al. 2012. Resource partitioning among cape foxes, bat-eared foxes, and black-backed jackals in South Africa. – J. Wildl. Manage. 76: 1241–1253.

Kartzinel, T. R et al. 2015. DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. – Proc. Natl Acad. Sci. USA 112: 8019–8024.

Larson, R. N. et al. 2015. Food habits of coyotes, gray foxes, and bobcats in a coastal southern California urban landscape. – W. N. Am. Nat. 75: 339–347.

Letten, A. D. et al. 2017. Linking modern coexistence theory and contemporary niche theory. – Ecol. Monogr. 87: 161–177.

Levi, T. and Wilmers, C. C. 2012. Wolves-coyotes-foxes: a cascade among carnivores. – Ecology 93: 921–929.

Manly, B. F. J. et al. 2002. Resource selection by animals, 2nd edn. – Kluwer.

McInnes, J. C. et al. 2017. Optimised scat collection protocols for dietary DNA metabarcoding in vertebrates. – Methods Ecol. Evol. 8: 192–202.

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

Midpeninsula Regional Open Space District 2011. – Visitor Estimate Survey Project. 16.

Myers, P. et al. 2017. The animal diversity web (online). – < http://animaldiversity.org >.

Neale, J. C. C. and Sacks, B. N. 2001. Resource utilization and interspecific relations of sympatric bobcats and coyotes. – Oikos 94: 236–249.

Newsome, T. M. et al. 2014. Human-resource subsidies alter the dietary preferences of a mammalian top predator. – Oecologia 175: 139–150.

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

Oriol-Cotterill, A. et al. 2015. Landscapes of coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. – Oikos 124: 1263–1273.

Pawluczyk, M. et al. 2015. Quantitative evaluation of bias in PCR amplification and next-generation sequencing derived from metabarcoding samples. – Anal. Bioanal. Chem. 407: 1841–1848.

Peers, M. J. et al. 2012. Reconsidering the specialist-generalist paradigm in niche breadth dynamics: resource gradient selection by Canada lynx and bobcat. – PLoS One 7: e51488.

Pianka, E. R. 1973. The structure of lizard communities. – Annu. Rev. Ecol. Syst. 4: 53–74.

Piñol, J. et al. 2015. Universal and blocking primer mismatches limit the use of high-throughput DNA sequencing for the quantitative metabarcoding of arthropods. – Mol. Ecol. 15: 819–830.

Pompanon, F. et al. 2012. Who is eating what: diet assessment using next generation sequencing. – Mol. Ecol. 21:1931–1950.

Prugh, L. R. 2005. Coyote prey selection and community stability during a decline in food supply. – Oikos 110: 253–264.

Prugh, L. R. et al. 2009. The rise of the mesopredator. – Bioscience 59: 779–791.

Radeloff, V. C. et al. 2010. Housing growth in and near United States protected areas limits their conservation value. – Proc. Natl Acad. Sci. USA 107: 940–945.

Remonti, L. et al. 2012. Intraguild dietary overlap and its possible relationship to the coexistence of mesocarnivores in intensive agricultural habitats. – Popul. Ecol. 54: 521–532.

Reynolds, J. C. and Aebischer, N. J. 1991. Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the Fox *Vulpes vulpes*. – Mamm. Rev. 21: 97–122.

Riaz, T. et al. 2011. ecoPrimers: inference of new DNA barcode markers from whole genome sequence analysis. – Nucleic Acids Res. 39: e145.

Riley, S. P. et al. 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. – Conserv. Biol. 17: 566–576.

Riley, S. P. D. 2006. Spatial ecology of bobcats and gray foxes in urban and rural zones of a national park. – J. Wildl. Manage. 70: 1425–1435.

Riley, S. P. D. et al. 2007. Anticoagulant exposure and notoedric mange in bobcats and mountain lions in urban southern California. – J. Wildl. Manage. 71: 1874–1884.

Ripple, W. J. et al. 2013. Widespread mesopredator effects after wolf extirpation. – Biol. Conserv. 160: 70–79.

Ritchie, E. G and Johnson, C. N. 2009. Predator interactions, mesopredator release and biodiversity conservation. – Ecol. Lett. 12: 982–998.

Serieys, L. E. K. et al. 2015. Anticoagulant rodenticides in urban bobcats: exposure, risk factors and potential effects based on a 16-year study. – Ecotoxicology 24: 844–862.

Shehzad, W. et al. 2012. Carnivore diet analysis based on next-generation sequencing: application to the leopard cat (*Prionailurus bengalensis*) in Pakistan. – Mol. Ecol. 21: 1951–1965.

Smith, J. A. et al. 2015. Top carnivores increase their kill rates on prey as a response to human-induced fear. – Proc. R. Soc. B 282: 20142711.

Smith, J. A. et al. 2016. Spatial characteristics of residential development shift large carnivore prey habits. – J. Wildl. Manage. 80: 1040–1048.

Smith, J. A. et al. 2018. Data from: uman activity reduces niche partitioning among three widespread mesocarnivores. – Dryad Digital Repository, < http://dx.doi.org/10.5061/dryad.54h24 >.

Thomas, A. C. et al. 2016. Quantitative DNA metabarcoding: improved estimates of species proportional biomass using correction factors derived from control material. – Mol. Ecol. Resour. 16: 714–726.

USDA Forest Service - Pacific Southwest Region - Remote Sensing Lab. 2014. ExistingVegCenCoast1997_2013_v1. – < www.fs.usda.gov/detail/r5/landmanagement/resourcemanagement/?cid=stelprdb5347192 >.

Vanak, A. T. et al. 2013. Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. – Ecology 94: 2619–2631.

Wang, Y. et al. 2015. Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. – Biol. Conserv. 190: 23–33.

Wilmers, C. C. et al. 2013. Scale dependent behavioral responses to human development by a large predator, the puma. – PLoS One 8: e60590.

Yoccoz, N. G. 2012. The future of environmental DNA in ecology. – Mol. Ecol. 21: 2031–2038.

Supplementary material (available online as Appendix oik-04592 at < www.oikosjournal.org/appendix/oik-04592 >). Appendix 1–2.