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Human presence drives bobcat interactions among the U.S. carnivore guild

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Abstract

Mammalian carnivores are elusive and enigmatic species that often play keystone roles in ecosystems through direct and indirect effects. Growing evidence shows that human activity can impact carnivore behavior and community structure by altering predator-prey interactions, shifting diel activity patterns, and altering wildlife movement. Our goal was to investigate the ecological role of bobcats (*Lynx rufus*) across carnivore communities in the continental USA by quantifying variation in spatiotemporal patterns and determining what environmental and human factors influenced carnivore community interactions. Using camera trap data from the inaugural nationwide Snapshot USA project dataset collected from September – October 2019, we constructed diel activity density curves, applied multispecies occupancy models, and calculated attraction-avoidance ratios. Our results suggest that bobcats display the greatest flexibility in their diel activity among the suite of carnivores sampled. Further, bobcats respond differentially at large spatial scales relative to the presence of dominant or subordinate carnivores, with fluctuating impacts mediated by human and environmental factors. Bobcats' co-occurrence with dominant carnivores (i.e., wolves *Canis* sp., pumas *Puma concolor*) was influenced primarily by human-related factors, whereas co-occurrence with subordinate carnivores (i.e., foxes) was more influenced by environmental factors (i.e., precipitation, gross primary production [GPP]). Bobcats appear to interpret humans as the apex predator on the landscape regardless of the presence of dominant or subordinate species. Understanding the influence of humans as "super predators", as well as the importance of environmental factors that impact intraguild carnivore interactions across the USA is critical for establishing successful management practices to promote functioning communities.

Keywords Apex predator · Bobcat · carnivore · Intraguild interactions · Occupancy modeling · Spatiotemporal activity

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Introduction

Large mammalian carnivores often play complex and sometimes keystone roles in structuring terrestrial ecosystems by driving trophic cascades Miller et al. 2018; Suraci et al. 2019; Dröge et al. 2016; Clinchy et al. 2016). Yet, in most cases small to medium-sized carnivores (i.e., < 15 kg, hereafter 'mesocarnivores') make up most predators in local food webs (Roemer et al. 2009). Smaller size and increased adaptability allow mesocarnivores to be far more numerous than larger, apex predators, and to be more diverse in behavior and distributions in nearly all land cover types (Roemer et al. 2009). Consequently, mammalian carnivore guilds have emerged as exciting ecological models for examining the many ways in which intraguild interactions (e.g., resource competition, intraguild predation) reverberate across trophic levels to affect and even mediate ecological processes (Lombardi et al. 2020; Gompper et al. 2016; López-Bao et al. 2016; Green et al. 2018). Intraguild interactions can facilitate or limit species' coexistence by driving carnivore temporal and spatial distributions (Miller et al. 2018), mediating carnivore and prey densities, and influencing species' behavior (Gompper et al. 2016; Grassel et al. 2015). Thus, research focusing on mesocarnivores and their interplay with prey, larger carnivores, and human activity is crucial to understanding drivers of spatial and temporal dynamics as well as species co-occurrence across human-modified landscapes.

Wildlife communities can be strongly influenced by competition between interacting carnivore species, and changes in population density of even a single carnivore species can have significant ecological effects throughout an ecosystem Miller et al. 2018; Suraci et al. 2019; Dröge et al. 2016; Clinchy et al. 2016). In fact, large carnivores have the potential to initiate top-down effects that influence mesocarnivores' behavior, abundance, and distribution through both consumptive and non-consumptive pathways (Shores et al. 2019; Dellinger et al. 2018). For example, following gray wolf (*Canis lupus*) reintroduction on Isle Royale (Michigan, U.S.A.) in 1958, coyotes (*Canis latrans*) were driven to near local extinction (Linnell and Strand 2000). In contrast, coyote populations have grown and range expanded across much of North America following historical wolf extirpation in conjunction with the remarkable adaptability of coyotes to urban environments. This expansion resulted in population changes for several smaller carnivore species such as kit fox (*Vulpes macrotis*), and black-footed ferrets (*Mustela nigripes*) (Linnell and Strand 2000), especially as coyotes began to fulfill the role of a *de facto* apex predator.

Multiple behavioral mechanisms can enable carnivore coexistence: temporal partitioning, habitat segregation (López-Bao et al. 2016; Dröge et al. 2016), and the ability of subordinate species to adopt strategies such as active avoidance (Ruiz-Villar et al. 2021) or prey-switching (Ghoddousi et al. 2017) to avoid or reduce competition with dominant sympatric species. However, carnivore community structure is also mediated by environmental factors that correspond to unique ecoregion characteristics (e.g., climate, vegetation), and varying levels of human disturbance (e.g., urbanization, recreation). Environmental factors play a key role in carnivores' associations with distinct land cover characteristics (Gompper et al. 2016), wherein traits related to resource use are critical for carnivore co-occurrence and moderating intraguild conflict (Davies et al. 2007; Green et al. 2018). Further, carnivores are highly sensitive to human disturbance due to their large home range requirements, high metabolic demands (Ripple et al. 2014), and history of direct persecution (Smith et al. 2015; Kays et al. 2017). Thus, some carnivores perceive humans as "super predators" and consequently respond by modifying their habitat use and behavior (Clinchy et al. 2016; Smith et al. 2017), driving widespread community and ecosystem-level effects that can increase species spatiotemporal overlap (Murphy et al. 2021). Human disturbance and subsequent landscape transformation can also affect carnivores indirectly by impeding species movement, shifting when and where encounters occur (Murphy et al. 2021), and further diverting time and energy to risk avoidance behaviors (e.g., vigilance, fleeing [Breck et al. 2019]).

The bobcat (*Lynx rufus*) is a widespread mesocarnivore that serves as a *de facto* top predator in many ecosystems across North America. Thus, the bobcat can mediate wildlife community structure, and influence ecosystem functions (Roberts and Crimmins 2010). Like many mesocarnivores, bobcat populations across much of the continental United States suffered from landscape transformation associated with human development (Rose et al. 2020) and overexploitation for pelts (Johnson et al. 2010). However, since the early 1990s, many bobcat populations have recovered and are increasing (Roberts and Crimmins 2010). Still, bobcats, and many mesocarnivores, are viewed as harvestable resources or pests that require active management (Roemer et al. 2009). Despite exploitation, bobcat populations have shown remarkable resilience to anthropogenic pressures, as indicated by an expanding geographic range and exploitation of peri-urban spaces (Young et al. 2019; Johnson et al. 2010). Thus, bobcats serve as an excellent ecological model to investigate predators that operate at two functional levels (e.g., apex and subordinate) in the carnivore hierarchy depending on local community structure and habitat characteristics (Roemer et al. 2009). Further, understanding how bobcats coexist with potentially dominant (e.g., puma [*Puma concolor*], gray wolf, red wolf [*Canis rufus*], coyote) and subordinate (e.g., red fox [*Vulpes vulpes*], gray fox [*Urocyon cinereoargenteus*]) carnivores can provide new insights for understanding carnivore guild dynamics and implementing effective carnivore conservation and management strategies (Robert and Crimmins 2010).

To investigate species co-occurrence and drivers of bobcat spatiotemporal activity within the carnivore guild of the United States (U.S.A.), we used 2019 Snapshot USA camera trap dataset (Cove et al. 2021), which is a large collaborative effort to sample mammal populations throughout the 50 US states using standardized methods across stratified habitats and urbanization zones. We explored variation in bobcat spatiotemporal activity and assessed carnivore co-occurrence by constructing diel activity density curves (Lashley et al. 2018), applying multispecies occupancy models (Rota et al. 2016), and calculating attraction-avoidance ratios (Parsons et al. 2016). We tested three hypotheses: **(1)** bobcat spatial and temporal activity varies based on the presence or absence of dominant carnivores among the communities represented across the U.S.A., **(2)** bobcats, as a *de facto* apex predator in the absence of wolves and pumas, would influence subordinate mesocarnivores, and **(3)** environmental variability and human disturbance (i.e., human intensity) would influence bobcat spatiotemporal activity differently depending on which species are present in the carnivore community. We predicted that bobcats would reduce their temporal overlap with dominant carnivores (i.e., pumas, gray and red wolves) and avoid sites previously visited by both dominant and subordinate carnivores. Our research findings provide novel insights into carnivore co-occurrence and community structure across a diverse range of ecosystems that can aid future management of expanding bobcat populations across the U.S.A.

Materials and methods

Study area

This study was conducted across the contiguous lower 48 states of the U.S.A. (Fig. 1), which extend across a vast latitudinal range (25.17° to 46.07°) and consists of varying elevation and climates resulting in a diverse land cover types and vegetation communities that comprise 10 unique ecoregions that highlight the major ecological areas of the U.S.A. (EPA 2016; Cove et al. 2021). The myriad lands of the U.S.A. support abundant medium to large-sized predators and prey (e.g., >500 g) commonly captured on camera traps (Cove et al. 2021). Members of the carnivore guild make up a substantial portion of these species including coyote, bobcat, puma, and several fox species; some exhibit extensive ranges reaching coast to coast and experience considerable variation in environmental conditions, hunting practices, and management strategies.

Data Acquisition

We used the published Snapshot USA 2019 dataset, generated through a collaborative nation-wide camera-trapping initiative that resulted in the beginning of a systematic effort to document annual trends and distributions of mammal communities across the United States (Cove et al. 2021). Snapshot USA used the eMammal platform, a data management system and archive for camera trap research projects (McShea 2016 - https://emammal.si.edu/snapshot-usa). A full description of Snapshot USA 2019 methods and full dataset are available in Cove et al. (2021).

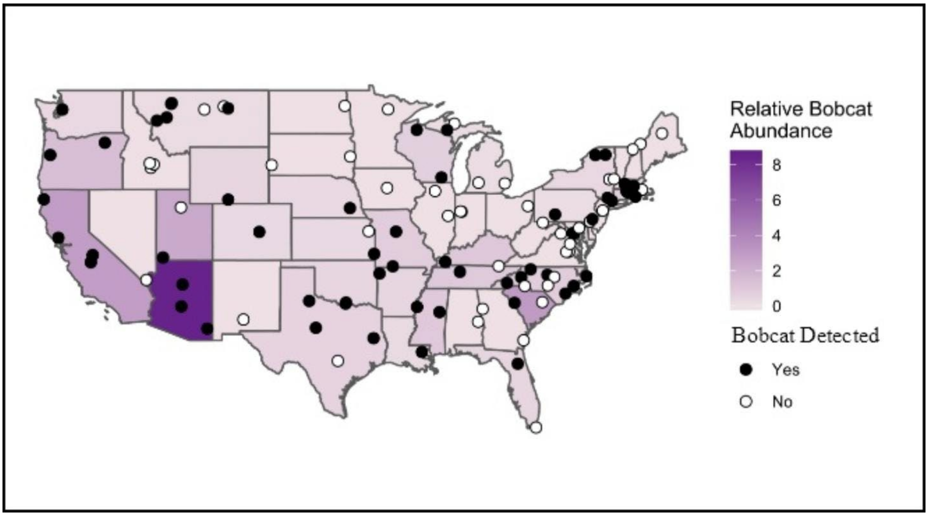

Fig. 1 Map of study area consisting of the 48 contiguous United States with the color of each state representing relative bobcat abundance (RAB = detections$_i$/total trap nights X 100) inferred from camera trap detections across arrays with dots signifying whether bobcats were detected (solid) or not detected (open) at an array

We queried Snapshot USA 2019 data by selecting all detections of nine carnivore species (American badger [*Taxidea taxus*], bobcat, coyote, fisher [*Pekania pennanti*], gray fox, gray wolf, red fox, red wolf, and puma) from the contiguous USA that exhibit primarily carnivorous diets and for which there were at least 30 detections. Previous research demonstrates that 30–50 detections can provide acceptable diel pattern estimates when investigating rare species (Lashley et al. 2018). Puma was included with only 29 detections; this exception was made because pumas are expected to elicit a strong response on bobcat activity (Wang et al. 2015) and thus were of particular interest. Despite the well-documented interactions between bobcat and Canada lynx (*Lynx canadensis*), we had to exclude this species due to the extremely limited number of detections that consisted of only 3 total in the lower 48 states, thus not allowing for viable comparisons. Although lynx share many similar features with the congener bobcat leading to occasional misidentification Gooliaf and Hodges (2018), Thornton et al. (2019) and Kays et al. (2022) provided evidence that this misidentification was not a limitation in our analyses due to the restricted range of lynx and the multiple photo burst requirements of the Snapshot dataset. We defined a detection as a single eMammal aggregated sequence, grouped as (a) consecutive images with individuals of the same or different species at the same site, and (b) images that were taken within one minute of the previous image. Our query resulted in 5,076 detections from 108 camera trap arrays across all 48 contiguous states. We calculated the relative abundance (RAB) of each carnivore species *i* across ecoregions at the individual camera level using the following formula:

$$\mathrm{RAB_i} = \mathrm{detections_i}/\mathrm{total\ trap\ nights\ X\ 100}.$$

Due to the difficulty of estimating true abundance of species at a national scale and for species which individuals are not uniquely identifiable, we used RAB that offers a simple and accurate index of abundance (Parsons et at. 2017), but does not account for potential bias arising from imperfect detection (Palmer et al. 2018).

Statistical analyses

We implemented statistical tests and models for all temporal and spatial analyses in RStudio version 1.3.1073 (R Core Team 2021). Given the amount of data recorded for each species, they were included in different parts of our analyses (Table 1).

Table 1 Breakdown of species included in each portion of the analyses

Analysis	Bobcat	American Badger	Coyote	Fisher	Gray Fox	Gray Wolf	Red Fox	Red Wolf	Puma
Temporal Activity	X	X	X	X	X	X	X	X	X
Single-Species Occupancy	X								
Multispecies Occupancy	X		X*		X	X	X	X	X
Spatiotemporal Avoidance	X		X		X		X		X

*Included in analysis as a covariate

Temporal activity

We determined diel activity patterns using the start of detection times for nine carnivore species across four different U.S.A. time zones. Detection times were anchored to sunrise and sunset events using NOAA calculations in a Microsoft Excel VBA translation (https://peltiertech.com/2021). We converted sunrise and sunset to radians via the 'transtime' function in the package 'activity' (Rowcliffe 2021) to express detection times relative to the two solar events. We constructed 95% kernel density estimation curves and estimated the mean temporal overlap coefficient (Δ; scaled from 0 to 1) using the function overlapEst in package 'overlap' (Meredith and Ridout 2020). The estimator Δ_1 was applied when the species with the smaller sample was less than 50 observations and the estimator Δ_4 was used when the species with the smaller sample was greater than 75 observations, with no species having a value between 50 and 75 (Meredith and Ridout 2020). We then calculated confidence intervals using a bias-corrected logit-scale bootstrap of 10,000 resampled estimates for each species-species pair to determine if the two species have exclusionary ($\Delta = 0$) or complete overlap ($\Delta = 1$; Ridout and Linkie 2009; Schmid and Schmidt 2006; Miller et al. 2018). We then performed a Watson's Two-Sample Test of Homogeneity (Rao and SenGupta 2001) using function 'watson.two.test' in the package 'circular' (Agostinelli and Lund 2017) to determine if times of detection for each species differed significantly from each other, and a Wald Test bootstrapped 1,000 times to compare activity level estimates calculated using the package 'activity' (Rowcliffe 2021) among species. Activity level (act) is an ecological metric that refers to the proportion of time an animal spends active, providing an index for energy expended, foraging effort, and even vulnerability to risk (Rowcliffe et al. 2014). Finally, we repeated this process using only bobcat detections to determine whether bobcat activity patterns showed significant differences across ecoregions, areas of various harvest management (Elbroch 2017) or population status (e.g., furbearer, threatened) (Roberts and Crimmins 2010).

Single-species and multispecies occupancy models

The purpose of using occupancy modeling was to test two independent but not mutually-exclusive hypotheses: **(1)** The Dominant Hypothesis, where both wolves and pumas will have top-down effects on bobcat spatiotemporal behavior, and **(2)** The Subordinate Hypothesis, where bobcats will elicit top-down effects on red and gray fox spatiotemporal behavior. If the dominant hypothesis is supported, we would expect bobcat occupancy to be negatively correlated with wolf and puma presence, and if the subordinate hypothesis holds then fox occupancy would be negatively correlated with bobcat presence.

We created binary detection history matrices (1 = detected, 0 = not detected) using the start and end date for each camera array using the function detectionHistory in the package 'camtrapR' version 2.0.3 (Niedballa et al. 2016), for six of the nine carnivore species. We excluded badgers and fishers from occupancy analyses because these species occupy distinct ranges, as well as coyotes due to the species occurring at >90% of sites. Further, we combined red wolves and gray wolves into a single category, 'wolf', given that we expect similar responses from bobcats to both species. For our analysis, we summarized detection events at the camera array level by aggregating data across all deployments within each array. We accounted for imperfect detection by using weekly sampling occasions that included data from only the first 8 weeks of collection, which provided adequate repeat samples at each camera array while minimizing the amount of "missing" sampling occasions as the number of operational camera sites declined towards the end of the study period (Naidoo and Burton 2020). Although this excluded data from analysis, adding additional weeks had little to no effect on improving our estimates given that few sites collected data longer than eight weeks, and no additional array captured a bobcat that had not been detected in the previous eight weeks.

Before fitting single and multi-species models we centered and scaled all numerical covariates (Table 2) and checked for correlations between all covariate pairs using the function 'cor' available in base R and package corrplot (Wei and Simko 2017) to visualize the values, with a threshold of 0.7 (Dormann et al. 2013) to remove any correlated covariates. The only covariates that were highly correlated were minimum and maximum temperature (Pearson's r=0.87), thus we excluded them from our final models. We first explored the effects of remaining covariates on probability of occupancy and detection of bobcat using single-species occupancy models (Mackenzie et al. 2003). We started by evaluating a set

Table 2 Descriptive statistics of environmental, human, and sampling covariates included in General Linear Mixed Models and Occupancy models for the detections of 9 carnivore species across 108 camera trap arrays. AICc was calculated by running single-species bobcat occupancy models; models in bold ranked above the null model (AICc=643.96)

Model/Covariate	Description	Mean	Max	Min	AICc Value
Human Impact Model					
***Human intensity**	# of individual human detections	169.00	6142.00	0	639.39
***Human population size**	human pop. density (GPW) at 1km sq.	326.60	8084.00	0	641.86
Nearest building	average distance to nearest building (m)	830.71	5289.19	28.32	644.32
Bobcat hunting status	protected, legal, no limits	NA	NA	NA	645.14
Cultivated land	average cultivated land at 1km2.	0.04	0.49	0	645.41
Environmental Impact Model					
*Gross Primary Productivity (GPP)	Ave. cumulative GPP	12534.97	25318.50	1567.99	644.55
[a]Max Temperature	max temp. (C)	20.41	31.16	8.41	644.64
[a]Min Temperature	min temp. (C)	8.07	25.05	-4.47	645.89
*Precipitation	3-hour accumulation of total precipitation	0.19	0.61	0	645.73
Ecoregion	ecoregion based on EPA Level I	NA	NA	NA	656.15
Miscellaneous Covariates					
***Coyote Detection Rate**	coyote detections per array/survey days	0.05	0.44	0	627.82
Survey Days	total # of survey days	488.00	1674.00	94.00	645.13
Bobcat Pop. Status	decreasing, stable, increasing, unknown	NA	NA	NA	649.36

*Inclusion in the final multi-covariate models.

[a] From nearest NOAA station.

of covariates on detection while holding occupancy (ψ) as a constant intercept. Once the best supported parameterization for detection was found, we held it constant and ran several univariate single-species occupancy models to evaluate the effects of various environmental and anthropogenic factors on bobcat occupancy based on AICc values (Burnham and Anderson 2002). After investigating each covariate's effect on bobcat occupancy, we created two additive impact models based on *a priori* hypotheses to determine which factors have greater influence on dominant and subordinate carnivores' relationships with the bobcat: **(1)** Human Impact Model (i.e., human intensity, human population density [Table 2]) and **(2)** Environmental Impact Model (i.e., precipitation, gross primary production [GPP] [Table 2]).

Finally, we implemented multispecies occupancy models to investigate our previously stated hypotheses in which dominant carnivores may have top-down effects on bobcat, and bobcat may have top-down effects on subordinate carnivores (Rota et al. 2016). Each model identified the probability that two or more species would occupy the same site as a function of our selected model covariates (Rota et al. 2016). Additionally, we fit our Human Impact and Environmental Impact models with and without a covariate for coyote detection rate for the dominant carnivores due to the strong association between coyote and bobcat occupancy. We ran all occupancy models using the R-package 'unmarked' (Fiske 2011).

Spatiotemporal avoidance

We used detection data from 5 species with large enough sample sizes (n > 4) across the 108 arrays to test the relative attraction and/or avoidance of a site by bobcat after previous visitation by another carnivore, and relative attraction and/or avoidance of a site by another carnivore after a visitation by a bobcat (Parsons et al. 2016). This approach estimates spatiotemporal avoidance, or to what extent a site visited by species A is influenced by visitations of species B (Niedballa et al. 2019). We carried over our top-down effect hypotheses from our occupancy models, thus we continued to use dominant and subordinate groups of carnivores for our analyses. We used Avoidance Attraction Ratios (Parsons et al. 2016) where odds ratios (i.e., odds of detecting species B in the absence of species A relative to the odds of detecting species B directly after an observation of species A) were calculated holding bobcat as both our species A and species B against the other four species (Niedballa et al. 2019). We created AARs by converting detection times to Julian hours, then comparing the time interval after/before a bobcat and another carnivore visited a site, referred to as the T2/T1 ratio, and then the time interval with/without the visitation of a bobcat or another carnivore, referred to as the T4/T3 ratio (Parsons et al. 2016). The T2/T1 ratio measures the net effects of both attraction and avoidance between bobcat and other carnivores, where a log-transformed value > 1 can indicate either avoidance of the dominant species by the subordinate species or attraction to the subordinate by the dominant species. A high T4/T3 indicates avoidance by the subordinate species, while a low value (log-transformed < 1) indicates the dominant attraction or no relationship. Thus, the two ratios can be used to discern the direction and nature of potential species interactions.

Following AAR calculations, we performed three analyses using log-transformed ratios: **(1)** We used T4/T3 ratios to run two-tailed t-tests to determine whether bobcat avoided or were attracted to a site after visitation from another species, and vice versa. A mean ratio greater than zero indicates species avoidance, whereas a mean less than 0 indicates species attraction (Parsons et al. 2016). **(2)** We also used T4/T3 ratios to run an analysis of variance (ANOVA) to determine (a) if bobcat avoided any carnivore species more than another, and (b) if any species avoided bobcat more than another. If we found significant effects based on an $\alpha = 0.05$, we performed a *post-hoc* Tukey-Pairwise Comparison to determine which pair of carnivores displayed a significant relationship, and the magnitude difference between that pair. And **(3)** using General Linear Mixed Models (GLMMs) we investigated whether human activity or environmental variables (Table 2) altered how bobcats responded to dominant and subordinate carnivores based on the T2/T1 ratios. We ran the Human Impact and Environmental Impact models and a null model for the dominant and subordinate groups and used the R package 'AICcmodavg' (Mazerolle 2020) to compare the strength of the model effects on bobcat avoidance and attraction.

Results

With data from 108 independent camera arrays across the contiguous U.S.A., we recorded 5,076 detections of nine target carnivore species: American badger, bobcat, coyote, fisher, gray fox, gray wolf, red fox, red wolf, puma (Table 3). Bobcats were captured 417 times and occurred at 52 camera arrays (Fig. 1). Seven other carnivore species were captured with greater than 30 detections, with coyotes having the largest sample size (2,405 detections) and making up almost half of the total detections (Table 3).

Coyote had the highest nationwide RAB (4.61 ± 0.58SE detections/100TN; TN = trap night) and were the only carnivore detected in the tropical wet forest ecoregion, followed by red foxes that were also highly prevalent nationwide (3.68 ± 0.58SE detections/100TN). At the ecoregion level, bobcats were most prevalent in the southern semi-arid highlands, but this ecoregion consisted of only one site. Further, the Mediterranean ecoregion consisted of multiple sites and hosted the highest RAB for both coyote and gray fox, along with the

Table 3 Number of aggregated eMammal camera trap image sequences (Sample size), number of arrays out of 108 in which a species was detected, estimates of overlap with bobcat activity (and related 95% confidence intervals), and activity level estimates within the 24-hour cycle for nine carnivore species at the national scale. Percent nocturnal includes all detections occurring outside the approximate bounds of sunrise and sunset throughout the study period

Species	*Sample Size*	*Number of Arrays*	*Overlap Est.*	*Overlap CI*	*Activity Level Est.*	*% Nocturnal*
Bobcat	417	52	------------	-------------------	0.640	65%
Coyote	2405	98	0.905	0.852–0.934	0.632	68%
Fisher	75	18	0.767	0.634–0.850	0.444	48%
Gray Fox	480	33	0.738	0.664–0.774	0.464	85%
Gray Wolf	32	8	0.806	0.683–0.910	0.475	50%
Red Fox	1570	45	0.810	0.693–0.917	0.463	81%
American Badger	37	15	0.839	0.735–0.923	0.508	74%
Red Wolf	31	1	0.694	0.585–0.778	0.340	93%
Puma	29	9	0.758	0.225–0.996	0.431	85%

second highest for bobcat. In addition, we observed a pattern of increasing coyote RAB with increasing bobcat RAB across all ecoregions.

Temporal overlap

Most carnivores showed primarily nocturnal activity patterns (Fig. 2), with the percent of time active between sunset and sunrise being over 50% for eight of the nine species, except for fisher, which exhibited 48% nocturnal activity (Table 3). Bobcat had the third lowest percentage of nocturnal activity at 65%, while red wolf exhibited the highest percentage of nocturnal activity at 93%. Daily activity peaks occurred before sunrise and after sunset for all species except fisher and gray wolf, each with a large peak following sunrise. Temporal overlap among bobcat and each carnivore species varied from 0.69 to 0.90 with coyote exhibiting the highest overlap and red wolf exhibiting the lowest (Table 3).

Activity level estimates revealed that bobcats spent the greatest proportion of the 24-hour cycle active (act = 0.64), followed by coyotes (act = 0.63), both spending > 10% more time of the 24-hours cycle active than the other seven carnivore species. Additionally, bobcats had a significantly higher activity level than fisher, gray fox, red fox, red wolf, and puma (Fig. 3; Table 3). Distribution of bobcat temporal activity was significantly different from the other eight carnivores, with the greatest variation between bobcat and gray fox (U^2 test = 1.717 – Fig. 3). No significant differences for activity distribution were found between harvest status and population status (Table S4), but activity level estimates were significantly different for regions where bobcat populations were increasing (act = 0.616) versus decreasing (act = 0.375; Fig. S1). Decreasing populations' activity plot reveal low activity in the afternoon and strong peaks nearing midnight, while increasing populations' exhibits steadier activity patterns throughout the day (Fig. S1). Two pairs of ecoregions returned

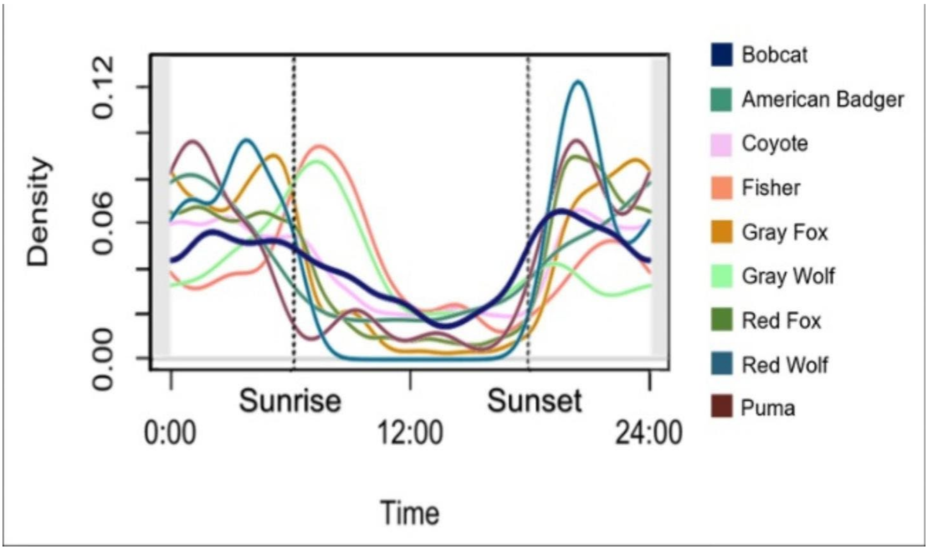

Fig. 2 Kernel density graphs of temporal activity patterns for nine carnivore species anchored on sunrise and sunset using nationwide U.S. detection data

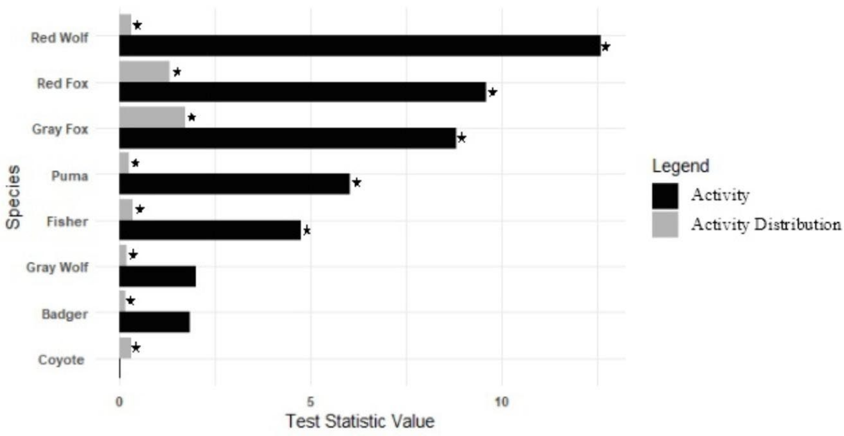

Fig. 3 Results for carnivore activity distributions (i.e., Watson U2 tests) and activity level estimates (i.e., Wald tests comparing bobcat diel activity to eight other carnivores with stars indicating significance

significant differences in activity distributions (Northern Forests-Eastern Temperate Forests [U^2 test = 0.194]; Southern Semiarid Highlands-Eastern Temperate Forests [U^2 test = 0.229]; Table S3 and Table S4). Several ecoregions also showed a significantly different activity level when paired with the Temperate Sierras ecoregion (Fig. S2 and Table S7).

Single-species occupancy modeling

Top-ranked single-species models for bobcat occupancy included human-related covariates and coyote detection rate associated with Ψ, but no environmental covariates. We excluded latitude from single species models because there was no clear biological reason for inclusion and bobcats were detected across the entire north-south range of the study area.

Multispecies occupancy modeling

Dominant Hypothesis| The 'Human Impact' model with the addition of coyote detection rate as a covariate was the top-ranked model for assessing top-down effects of wolves and pumas on bobcats (Table S5). Bobcat occupancy was negatively associated with wolf and puma presence but neither relationship was significant. Further, bobcat occupancy was affected negatively by human intensity (β = -3.60 ± 1.89SE), but positively associated with higher coyote detection rates (β = 1.93 ± 0.52SE; Table S6).

Subordinate Hypothesis| The 'Environmental Impact' model was the top-ranked model for top-down effects between bobcats and red and gray foxes (Table S7). Bobcat occupancy was negatively associated with red fox presence (β = -1.32 ± 0.45SE) and positively but non-significantly associated with gray fox (β = 0.39 ± 0.52SE). The only significant relationship among compared covariates was precipitation, which had a significant negative effect (β = -1.35 ± 0.47SE) on bobcat and gray fox interaction (Table S8).

Spatiotemporal avoidance

T-Tests| Due to low sample sizes (n=4) for multiple carnivores, AARs were only calculated for coyote and fox (i.e., gray and red fox) when performing t-tests. When holding bobcat as species A, bobcats displayed avoidance of coyotes (T-test: meanT4/T3=0.82, t=6.20, p<0.0001) and avoidance of foxes (T-test: meanT4/T3=0.68, t=3.48, p=0.006). When holding bobcat as species B, coyotes (T-test: meanT4/T3 = -0.18, t = -2.81, p=0.007) displayed attraction to bobcats while foxes did not change their behavior when bobcat were present (Table S9).

Analysis of Variance (ANOVA)| In our one-way ANOVAs we included all species that had multiple AAR values, even with low sample sizes (i.e., red fox [n=4], puma [n=4]). Bobcats avoided species differently (F=2.84, df=3, p=0.05; Table S13); specifically, bobcats avoided pumas more than coyotes (Tukey Pairwise Comparison, mean diff = -1.06, CI [-2.03, -0.08]). No carnivore species were found to avoid bobcat significantly more than other species (F=0.69, df=4, p=0.60; Table S10).

General Linear mixed models

Dominant | Dominant models held bobcats as species A and the dominant carnivores as species B. Neither impact model had a greater model weight than the null model (w_i = 0.70; Table S15 and Table S16), indicating the overall patterns observed in previous T-tests – bobcats avoid coyotes and coyotes are attracted to bobcats – did not appear to vary with human impact or environmental factors (Fig. 4).

Subordinate | Subordinate models held subordinate carnivores as species A and bobcat as species B. The Human Impact model ranked highest with the greatest model weight (w_i=0.80, R^2=0.40). Human intensity showed a near-significant positive effect

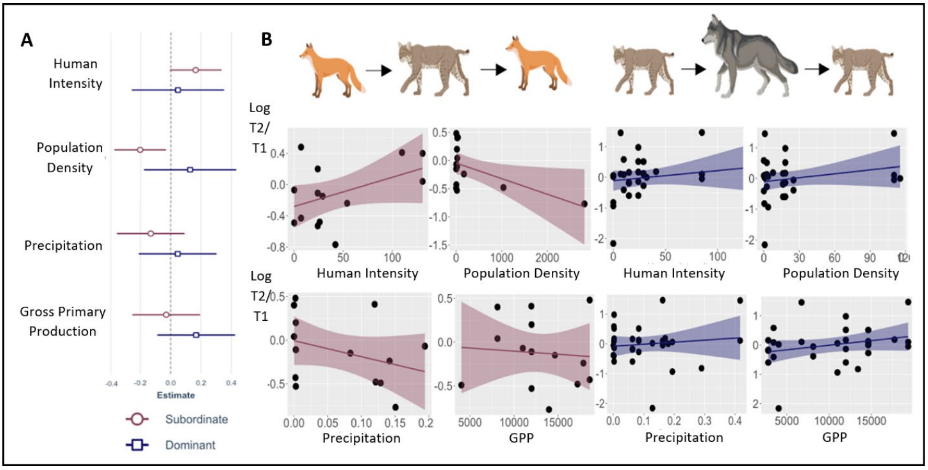

Fig. 4 **(a)** Effect of human intensity, human population density, precipitation, and gross primary production (GPP) for dominant and subordinate carnivores. **(b)** Relationship between each model covariate (i.e., human intensity, human population density, precipitation, and GPP) and logT2/T1 ratio for dominant (blue) and subordinate (red) carnivores. Bands represent 95% confidence intervals

(β = 0.004 ± 0.002SE), whereas human population density had a significant negative effect (β = -0.0003 ± 0.0001SE; Fig. 4, Table S13).

Discussion

Many researchers have investigated the spatiotemporal behavior of carnivores, yet few studies have encompassed a study area as large and diverse in both ecosystem structure and carnivore diversity as the contiguous United States and that covers most of the total distribution of a species. Our large-scale survey of carnivore communities encompassed nine species including our focal species, the bobcat. Bobcats exhibited consistent distribution of temporal activity across the variable U.S.A. landscape. However, the small variation observed in bobcat temporal activity among ecoregions provides evidence that bobcats can persist and locally modify their behaviors to survive across ecosystems. Flexibility in traits such as foraging strategy can allow carnivores to coexist successfully in different communities with varying environmental factors (Monterroso et al. 2014). Indeed, bobcat diel activity curves were significantly different from all eight carnivores in that bobcats were generally more diurnal and utilized a greater proportion of the 24-hour cycle than other carnivores. Furthermore, we provide evidence that bobcats respond differently on a large spatial scale to dominant carnivores (i.e., wolf, puma) and subordinate carnivores (i.e., red and gray fox), with fluctuating impacts mediated by human and environmental factors. Based on our Human Impact model, heightened human intensity resulted in bobcats displaying weaker avoidance responses to dominant carnivores, but stronger avoidance responses to subordinate carnivores (Fig. 4). These data support the concept of the human "super predator" (Clinchy et al. 2016), which suggests that bobcats perceive humans as the greatest threat. Therefore, even when dominant carnivores such as pumas and wolves are present, bobcats tend to prioritize avoiding contact with people. Dominant carnivores were negatively associated with bobcat occupancy and observed to be strongly impacted by human-related factors, while co-occurrence with subordinate carnivores was affected more by environmental factors. Given the Human Impact model (i.e., human intensity, human population density) best explained dominant carnivores' and bobcat landscape use, as well as negatively affecting the probability of the two species occupying the same space, our results suggest that human impacts surpass environmental impacts in structuring carnivore communities.

Throughout this study, we addressed differing effects that dominant and subordinate carnivores had on temporal and spatial activity of bobcats. Our findings indicate that bobcats used the greatest proportion of the day when compared to other species evaluated, suggesting bobcats may mediate competition through behavioral plasticity allowing for flexible temporal activity patterns (Frey et al. 2017). Greater plasticity in temporal behavior allows bobcats to adjust their activity in the presence or absence of potential competitors and avoid prey access constraints by using time periods when common prey species (i.e., diurnal squirrels, chipmunks) are most active (Monterroso et al. 2014). Spatiotemporally, bobcats showed avoidance behavior towards all species tested (Table S9), while no carnivore avoided bobcats more than another. Further, our Human Impact model was the only model to elicit significant effects on either carnivore group. Both human intensity and human population influenced bobcat spatiotemporal behavior, but the strong effect of human population was primarily driven by two outliers (Fig. 4). We chose not to exclude these data from analysis as they reflected real-world data that could reveal an important relationship. Future surveys would benefit from targeting camera trap efforts in highly urban environments (*sensu* Herrera et al. 2021) to help us better capture the gradient of urbanization and understand carnivore-human interactions in an urbanizing planet.

Our multispecies occupancy models revealed differing trends for which factors impacted relationships among carnivore community members. Dominant carnivores and their relationship with bobcats were highly associated with human factors (i.e., human population density, human intensity), but effects varied between wolves and pumas. Human factors negatively affected the probability of bobcat-wolf interactions, which might result from wolves commonly using man-made features such as low-use roads/trails to traverse the landscape (Lesmerises et al. 2013), while bobcats generally select home range sites with low road densities (Poessel et al. 2014). On the other hand, human intensity resulted in a positive effect on the probability of bobcat-puma interactions, as did coyote detection rate. Although these positive interactions were weak, these results provide an example of how humans may act as a 'super predator'' on the landscape (Table S6; Clinchy et al. 2016), and how coyotes may positively mediate the interactions between the two species (Breck et al. 2019; Cove et al. 2012). Interactions between bobcat and gray fox were strongly influenced by precipitation, with heightened average 3-hour precipitation throughout the study period negatively corresponding with their interactions. This negative effect was not observed for red fox; thus, precipitation likely affects the two fox species differently. The differences in how red and gray foxes respond to environmental variables may allow for spatial partitioning to avoid direct competition, but likely requires high resolution tracking data to further elucidate.

The relationship between bobcats and coyotes was unique among carnivores investigated. Specifically, coyotes were recorded at nearly every site where bobcats were captured, coyotes were the only species to show an attraction to bobcats, and coyotes had ~ 90% temporal overlap with bobcats (Table 3). Given the high spatiotemporal similarities between these two species, we expect to find differences across multiple niche dimensions such as diet and landcover preference that allow coyotes and bobcats to coexist at such a high level across multiple niche axes (Hutchinson 1957). For example, bobcats are obligate carnivores, whereas coyotes are highly adaptable and omnivorous allowing them to be ubiquitous across the U.S.A. (Breck et al. 2019; Duncan et al. 2020). Differences in diet may allow these two species to spatiotemporally coexist closely, but coyote attraction to bobcats could potentially be a result of coyote seizing opportunities to usurp bobcat kills (Allen et al. 2015). Coyotes and bobcats are two of the most ubiquitous mesocarnivores in the U.S.A. and our results showcase that these species overlap strongly in space and time. As such, high resolution tracking data for both red foxes and coyotes could enable ecologists to test fundamental ecological theories about the partitioning of multiple niche axes to advance our understanding of species' competitive coexistence.

Snapshot USA data used for these analyses were generated by a collaborative standardized effort among researchers across the country, resulting in a nationwide camera trapping dataset (Cove et al. 2021). Yet for many rare carnivores, subsequent data from ongoing Snapshot USA surveys will be required to produce robust results that would allow us to fully understand the complex carnivore community across the U.S.A. For example, bobcats and lynx share many common morphological and behavioral traits that could result in intense competition. However, the lynx's range has contracted ~ 40%, shifting north into Canada, while the bobcat is reclaiming much of their former habitat throughout North America (Laliberte and Ripple 2004; Marrotte et al. 2020). Further, where these two species co-occur, researchers have found they exhibited habitat partitioning across different land cover types, prey, and snow conditions, with bobcats preferentially using areas that lynx avoided (Marrotte et al. 2020). Additional future camera trap surveys in targeted areas of sympatry for these felids will be required for further inference into the drivers of their niche partitioning.

Our findings revealed that bobcats are adaptable predators that coexist with several dominant and subordinate carnivores with variation in activity and occupancy based on the community structure, and environmental and anthropogenic factors. Bobcats have the potential to function in different capacities within a carnivore guild, driven by the presence of dominant carnivores such as wolves and pumas, and are highly influenced by human factors that can outweigh the environmental effects of their habitat. Furthermore, our results provide evidence that bobcat may help facilitate behavioral cascades among dominant carnivores (i.e., wolf, puma) and subordinate carnivores (i.e., foxes), but more research must be conducted to assess whether these findings hold across their entire range (Shores et al. 2019). Knowledge about intra-guild relationships within diverse carnivore communities such as across the U.S.A. is essential for understanding the role of the human "super predator" and how anthropogenic changes will continue to influence wildlife communities.

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Author contribution TH and DJRL conceived the idea and secured funding; All contributors collected data for Snapshot USA; TH led manuscript writing with technical assistance from MVC and DJRL. MLA and CN assisted with analysis of temporal activity. AMJ assisted with analysis of spatiotemporal avoidance. FI assisted with analysis of single and multispecies occupancy modeling. All authors reviewed and provided constructive feedback on the manuscript.

Data Availability All data from this manuscript has been archived as part of Snapshot USA 2019 available at https://doi.org/10.1002/ecy.3353.

Declarations

Conflict of interest The authors declare they have no conflicts of interest/no competing interests.

References

Agostinelli C, Lund U (2017) Circular Statistics. *Package 'circular*'. https://cran.rproject.org/web/packages/circular/circular.pdf

Allen ML, Elbroch LM, Wilmers CC, Wittmer HU (2015) The Comparative Effects of Large Carnivores on the Acquisition of Carrion by Scavengers. Am Nat 185:822–833. https://doi.org/10.1086/681004

Breck SW, Poessel SA, Mahoney P, Young JK (2019) The intrepid urban coyote: a comparison of bold and exploratory behavior in coyotes from urban and rural environments. Sci Rep 9:2104. https://doi.org/10.1038/s41598-019-38543-5

Burnham KP, Anderson DR (2002) Model Selection and Inference: A Practical Information-Theoretic Approach. 2nd Edition, Springer-Verlag, New York. https://doi.org/10.1007/b97636

Clinchy M, Zanette LY, Roberts D et al (2016) Fear of the human "super predator" far exceeds the fear of large carnivores in a model mesocarnivore. Behav Ecol 27:1826–1832. https://doi.org/10.1093/beheco/arw117

Cove MV, Jones BM, Bossert AJ et al (2012) Use of Camera Traps to Examine the Mesopredator Release Hypothesis in a Fragmented Midwestern Landscape. Am Midl Nat 168:456–465. https://doi.org/10.1674/0003-0031-168.2.456

Cove MV, Kays R, Bontrager H, et al (2021) SNAPSHOT USA 2019: a coordinated national camera trap survey of the United States. Ecol e03353. https://doi.org/10.1002/ecy.3353

Davies TJ, Meiri S, Barraclough TG, Gittleman JL (2007) Species co-existence and character divergence across carnivores. Ecol Lett 10:146–152. https://doi.org/10.1111/j.1461-0248.2006.01005.x

Dellinger JA, Shores CR, Marsh M et al (2018) Impacts of recolonizing gray wolves (Canis lupus) on survival and mortality in two sympatric ungulates. Can J Zool. https://doi.org/10.1139/cjz-2017-0282

Dormann CF, Elith J, Bacher S et al (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Dröge E, Creel S, Becker M, M'soka J (2016) Spatial and temporal avoidance of risk within a large carnivore guild. Ecol and Evol 7:189–199. https://doi.org/10.1002/ece3.2616

Duncan N, Asher O, Weckel M et al (2020) Baseline diet of an urban carnivore on an expanding range front. J of Urban Ecol 6. https://doi.org/10.1093/jue/juaa021

Elbroch LM, Robertson L, Combs K, Fitzgerald J (2017) Contrasting bobcat values. Biodivers and Conserv 26:2987–2992. https://doi.org/10.1007/s10531-017-1397-6

Environmental Protection Agency (2016) Level I Ecoregions Regions of North America. https://www.epa.gov/eco-research/ecoregions-north-america

Excel VBA, Translation (2021) Peltier Tech Blog. https://peltiertech.com/

Fiske I, Chandler R (2011) unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. J of Stat Softw 43:1–23. https://www.jstatsoft.org/v43/i10/

Frey S, Fisher JT, Burton AC, Volpe JP (2017) Investigating animal activity patterns and temporal niche partitioning using camera-trap data: challenges and opportunities. Remote Sens in Ecol and Conserv 3:123–132. https://doi.org/10.1002/rse2.60

Gompper ME, Lesmeister DB, Ray JC et al (2016) Differential Habitat Use or Intraguild Interactions: What Structures a Carnivore Community? PLoS ONE 11:e0146055. https://doi.org/10.1371/journal.pone.0146055

Grassel SM, Rachlow JL, Williams CJ (2015) Spatial interactions between sympatric carnivores: asymmetric avoidance of an intraguild predator. Ecol and Evol 5:2762–2773. https://doi.org/10.1002/ece3.1561

Green DS, Matthews SM, Swiers RC et al (2018) Dynamic occupancy modelling reveals a hierarchy of competition among fishers, grey foxes and ringtails. J of Anim Ecol 87:813–824. https://doi.org/10.1111/1365-2656.12791

Ghoddousi A, Soofi M, Hamidi AK, Lumetsberger T, Egli L, Ashayeri S, Khorozyan IH, Kiabi B, Waltert M (2017) When pork is not on the menu: Assessing trophic competition between large carnivores and poachers. Biol Conserv 209:223–229. https://doi.org/10.1016/j.biocon.2017.02.032

Herrera DJ, Moore SM, Flockhart DT, McShea WJ, Cove MV (2021) Thinking outside the park: recommendations for camera trapping mammal communities in the urban matrix. J Urban Ecol 7. https://doi.org/10.1093/jue/juaa036

Hutchinson GE(1957) Concluding remarks. – Cold Spring Harb. Symp. Quant Biol 22:145– 159

Johnson SA, Walker HD, Hudson CM (2010) Dispersal Characteristics of Juvenile Bobcats in South-Central Indiana. The J of Wildl Management 74:379–385. https://doi.org/10.2193/2008-253

Kays R, Lasky M, Allen ML, Dowler RC, Hawkins MT, Hope AG, Cove MV (2022) Which mammals can be identified from camera traps and crowdsourced photographs? J Mammal. https://doi.org/10.1093/jmammal/gyac021

Kays R, Parsons AW, Baker MC et al (2017) Does hunting or hiking affect wildlife communities in protected areas? J of Appl Ecol 54:242–252. https://doi.org/10.1111/1365-2664.12700

Laliberte AS, Ripple WJ (2004) Range Contractions of North American Carnivores and Ungulates. BioSci 54:123–138. https://doi.org/10.1641/0006-3568(2004)054[0123:RCONAC]2.0.CO;2

Lashley MA, Cove MV, Chitwood MC et al (2018) Estimating wildlife activity curves: comparison of methods and sample size. Sci Rep 8:1–11. https://doi.org/10.1038/s41598-018-22638-6

Lesmerises F, Dussault C, St-Laurent M-H (2013) Major roadwork impacts the space use behaviour of gray wolf. Landsc and Urban Plan 112:18–25. https://doi.org/10.1016/j.landurbplan.2012.12.011

Linnell JDC, Strand O (2000) Interference interactions, co-existence and conservation of mammalian carnivores. Divers Distrib 6:169–176. https://doi.org/10.1046/j.1472-4642.2000.00069.x

Lombardi JV, MacKenzie DI, Tewes ME et al (2020) Co-occurrence of bobcats, coyotes, and ocelots in Texas. Ecol and Evol 10:4903–4917. https://doi.org/10.1002/ece3.6242

López-Bao JV, Mattisson J, Persson J et al (2016) Tracking neighbours promotes the coexistence of large carnivores. Sci Rep 6:23198. https://doi.org/10.1038/srep23198
MacKenzie DI, Nichols JD, Hines JE et al (2003) Estimating Site Occupancy, Colonization, and Local Extinction When a Species Is Detected Imperfectly. Ecol 84:2200–2207. https://doi.org/10.1890/02-3090
Marrotte RR, Bowman J, Morin SJ (2020) Spatial segregation and habitat partitioning of bobcat and Canada lynx. FACETS 5:503–522. https://doi.org/10.1139/facets-2019-0019
Mazerolle MJ(2020) Model selection and multimodel inference based on (Q) AIC(c). *Package 'AICcmodavg'*. https://cran.r-project.org/web/packages/AICcmodavg/AICcmodavg.pdf
McShea WJ, Forrester T, Costello R, He Z, Kays R (2016) Volunteer-run cameras as distributed sensors for macrosystem mammal research. Landsc Ecol 31:55–66. https://doi.org/10.1007/s10980-015-0262-9
Meredith M, Ridout M(2020) Estimates of coefficient of overlapping for animal activity patterns. *Package 'overlap'*. https://cran.r-project.org/web/packages/overlap/overlap.pdf
Miller JRB, Pitman RT, Mann GKH et al (2018) Lions and leopards coexist without spatial, temporal or demographic effects of interspecific competition. J of Anim Ecol 87:1709–1726. https://doi.org/10.1111/1365-2656.12883
Monterroso P, Alves PC, Ferreras P (2014) Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: implications for species coexistence. Behav Ecol Sociobiol 68:1403–1417. https://doi.org/10.1007/s00265-014-1748-1
Murphy A, Diefenbach DR, Ternent M et al (2021) Threading the needle: How humans influence predator-prey spatiotemporal interactions in a multiple-predator system. J of Anim Ecol 90:2377–2390. https://doi.org/10.1111/1365-2656.13548
Naidoo R, Burton AC (2020) Relative effects of recreational activities on a temperate terrestrial wildlife assemblage. Conserv Science and Pract 2:e271. https://doi.org/10.1111/csp2.271
Niedballa J, Sollmann R, Courtiol A, Wilting A (2016) camtrapR: an R package for efficient camera trap data management. Methods in Ecol and Evol 7:1457–1462. https://doi.org/10.1111/2041-210X.12600
Niedballa J, Wilting A, Sollmann R et al (2019) Assessing analytical methods for detecting spatiotemporal interactions between species from camera trapping data. Remote Sens in Ecol and Conserv 5:272–285. https://doi.org/10.1002/rse2.107
Palmer MS, Swanson A, Kosmala M et al (2018) Evaluating relative abundance indices for terrestrial herbivores from large-scale camera trap surveys. Afr J Ecol 56:791–803. https://doi.org/10.1111/aje.12566
Parsons AW, Bland C, Forrester T et al (2016) The ecological impact of humans and dogs on wildlife in protected areas in eastern North America. Biol Conserv 203:75–88. https://doi.org/10.1016/j.biocon.2016.09.001
Parsons AW, Forrester T, McShea WJ et al (2017) Do occupancy or detection rates from camera traps reflect deer density? J of Mammal 98:1547–1557. https://doi.org/10.1093/jmammal/gyx128
Poessel SA, Burdett CL, Boydston EE et al (2014) Roads influence movement and home ranges of a fragmentation- sensitive carnivore, the bobcat, in an urban landscape. Biol Conserv 180:224–232. https://doi.org/10.1016/j.biocon.2014.10.010
Rao JS, SenGupta A (2001) Topics in Circular Statistics, Sect. 7.5. World Scientific Press, Singapore
Ridout MS, Linkie M (2009) Estimating overlap of daily activity patterns from camera trap data. JABES 14:322–337. https://doi.org/10.1198/jabes.2009.08038
Ripple WJ, Estes JA, Beschta RL et al (2014) Status and Ecological Effects of the World's Largest Carnivores. Science 343. https://doi.org/10.1126/science.1241484
Roberts NM, Crimmins SM (2010) Bobcat Population Status and Management in North America: Evidence of Large-Scale Population Increase. J of Fish and Wildl Management 1:169–174. https://doi.org/10.3996/122009-JFWM-026
Roemer GW, Gompper ME, Van Valkenburgh B (2009) The Ecological Role of the Mammalian Mesocarnivore. BioSci 59:165–173. https://doi.org/10.1525/bio.2009.59.2.9
Rose C, Prange IS, Landry SM (2020) Extirpated, immigrated, genetically stratified—first demographic assessment of a recovering bobcat (Lynx rufus) population after a century of extinction. Mamm Res 65:423–434. https://doi.org/10.1007/s13364-019-00462-1
Rota CT, Ferreira MAR, Kays RW et al (2016) A multispecies occupancy model for two or more interacting species. Methods in Ecol and Evol 7:1164–1173. https://doi.org/10.1111/2041-210X.12587
Rowcliffe JM, Kays R, Kranstauber B et al (2014) Quantifying levels of animal activity using camera trap data. Methods in Ecol and Evol 5:1170–1179. https://doi.org/10.1111/2041-210X.12278
Rowcliffe M(2021) Animal activity statistics. *Package 'activity'*.https://cran.r-project.org/web/packages/activity/activity.pdf
R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Ruiz-Villar H, Jubete F, Revilla E et al (2021) Like cat and fox: diurnal interactions between two sympatric carnivores in pastoral landscapes of NW Spain. Eur J Wildl Res 67:16. https://doi.org/10.1007/s10344-021-01469-3
Schmid F, Schmidt A (2006) Nonparametric estimation of the coefficient of overlapping - theory and empirical application. Comput Stat and Data Anal 50:1583–1596. https://doi.org/10.1016/j.csda.2005.01.014
Shores CR, Dellinger JA, Newkirk ES et al (2019) Mesopredators change temporal activity in response to a recolonizing apex predator. Behav Ecol 30:1324–1335. https://doi.org/10.1093/beheco/arz080
Smith JA, Suraci JP, Clinchy M et al (2017) Fear of the human 'super predator' reduces feeding time in large carnivores. Proc of the R Soc B: Biol Sciences 284:20170433. https://doi.org/10.1098/rspb.2017.0433
Smith JA, Wang Y, Wilmers CC (2015) Top carnivores increase their kill rates on prey as a response to human-induced fear. Proc of the R Soc B: Biol Sciences 282:20142711. https://doi.org/10.1098/rspb.2014.2711
Suraci JP, Clinchy M, Zanette LY, Wilmers CC (2019) Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. Ecol Lett 22:1578–1586. https://doi.org/10.1111/ele.13344
Wei T, Simko V(2017) Visualization of a correlation matrix. *Package 'corrplot'*. https://cran.r-project.org/web/packages/corrplot/corrplot.pdf
Wang Y, Allen ML, Wilmers CC (2015) Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. Biol Conserv 190:23–33. https://doi.org/10.1016/j.biocon.2015.05.007
Young JK, Golla J, Draper JP et al (2019) Space Use and Movement of Urban Bobcats. Anim 9:275. https://doi.org/10.3390/ani9050275

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