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NOTE

# Assessing spatiotemporal patterns of mesocarnivores along an urban-to-rural gradient

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## Abstract

Rapid increases in human development and activity are affecting the spatial and temporal dynamics of mammalian mesocarnivore communities. We used 40 motion-sensitive cameras along an urban-to-rural gradient, and single-season occupancy models, to evaluate the habitat use of a local mesocarnivore guild (coyote [*Canis latrans*], bobcat [*Lynx rufus*], red fox [*Vulpes vulpes*], gray fox [*Urocyon cinereoargenteus*], and raccoon [*Procyon lotor*]) near Newburgh, New York, USA, during May–September 2021. Additionally, we fit circular kernel density estimations to assess how mesocarnivores may alter their diel and nocturnal activity patterns in response to human development. Red foxes were positively associated with urban areas and were also significantly more active at night in semiurban areas versus rural and urban locations. Coyotes demonstrated some adaptability to urban areas, being generally more nocturnal as urbanization increased but were also more likely to use higher elevation sites and areas with more natural habitat cover. We did not find support for a spatial shield hypothesis, as red foxes and raccoons were often detected in the same semiurban and urban sites as coyotes. Bobcats generally avoided human-dominated areas, whereas raccoons were ubiquitous throughout the gradient and exhibited similar daily and nocturnal activity levels in all land cover types. Overall, our results document how anthropogenic disturbance may alter mesocarnivore community structure and landscape use, providing information for managing urban carnivore populations and mitigating human–wildlife conflict, particularly at the local scale.

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**KEYWORDS**

*Canis latrans*, motion-sensitive cameras, New York, occupancy modeling, *Procyon lotor*, spatiotemporal dynamics, urbanization, *Vulpes vulpes*

Human-altered landscapes and subsequent habitat fragmentation affect the health and stability of wildlife populations globally (Haddad et al. 2015, Crooks et al. 2017). An estimated 50% of the world's land surface is modified through residential development, agriculture, forestry, and extractive industries (Hooke and Martín-Duque 2013). These landscape changes affect animal behavior, abundance, distribution, diet, genetics, and survival (Frankham 2005, Karelus et al. 2017, Sirami et al. 2017, Magioli et al. 2019, Wilson et al. 2020). Thus, understanding community- and species-level responses to landscape modification is important for promoting successful wildlife management and conservation efforts.

Larger mammalian carnivores (e.g., gray wolves [*Canis lupus*] and cougars [*Puma concolor*]) are particularly sensitive to land use alterations associated with human development because of their low densities and fecundity, large spatial requirements (Ripple et al. 2014), and conflicts with humans (White and Gehrt 2009, Lozano et al. 2019). Larger carnivore responses to human-modified landscapes are species-dependent, but richness of large carnivores often decreases as urbanization intensifies (Ordeñana et al. 2010, Crooks et al. 2011). The absence of large carnivores from fragmented urban areas can facilitate the ecological release of mesocarnivore species (i.e., mammalian carnivores <15 kg; Roemer et al. 2009), where mesocarnivores increase in abundance following freedom from competition (Crooks and Soulé 1999, Prugh et al. 2009, Hody and Kays 2018). Many mesocarnivores have become successful urban dwellers owing to their flexible habitat and dietary needs, and higher reproductive capabilities (Šálek et al. 2015). Mesopredators may also survive close to humans by exploiting abundant anthropogenic resources (McKinney 2002, Newsome et al. 2015). The behavioral, ecological, and trophic plasticity of mesocarnivores make them ideal candidates for evaluating how human land use change may influence their interspecific interactions, habitat use, and community structure.

Compared to their natural habitats, mesocarnivores may spatiotemporally segregate urban landscapes differently to coexist while avoiding humans (Parsons et al. 2019, Seveque et al. 2020). Human-related pressures may directly and indirectly force competing species into different niche spaces characterized by selection of microhabitats or changes in temporal activity patterns (Cozzi et al. 2012, Kamler et al. 2012, Curveira-Santos et al. 2021). For example, larger-bodied, dominant mesocarnivores often select for areas with less human disturbance and greater access to cover-rich habitats (Gosselink et al. 2003, Gehrt et al. 2009, Mueller et al. 2018). Comparatively, smaller, subordinate species are often more tolerant of the heavily developed areas that their dominant competitors avoid (Bateman and Fleming 2012). Some subordinate mesocarnivores use humans as protection against larger competitors at higher levels of development, a hypothesis known as the human shield effect (Berger 2007). Furthermore, greater human activity may incite dominant and subordinate mesopredators to become more nocturnal to reduce human encounters (George and Crooks 2006, Gaynor et al. 2018, Moll et al. 2018). The constraint of activity patterns in response to human disturbance can reduce carnivore temporal niche partitioning, leading to additional antagonistic encounters between species (Wang et al. 2015, Smith et al. 2018). Despite a growing body of research on mesocarnivore responses to urbanization, previous work has primarily focused on a single species (Larson et al. 2016). A better understanding of the spatiotemporal dynamics of diverse mesocarnivore communities in urban systems will be important for implementing effective conservation and land management protocols, and providing insight for mitigating potential human–carnivore conflict.

We investigated whether landscape characteristics and co-occurring species influence mesocarnivore habitat use and activity patterns along an urban–rural gradient in the northeastern United States. The local carnivore guild includes coyote (*Canis latrans*), a dominant mesocarnivore and emerging apex predator in many urbanizing ecosystems in North America, bobcat (*Lynx rufus*), a dominant mesocarnivore, and subordinate mesocarnivores

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(red fox [*Vulpes vulpes*], gray fox [*Urocyon cinereoargenteus*], and raccoon [*Procyon lotor*]). Based on prior research on sympatric mesocarnivore dynamics in urban landscapes, we formulated 3 hypotheses. Dominant mesocarnivore habitat use would be negatively associated with urban landscape factors, whereas subordinate mesocarnivore habitat use would be positively related to urban landscape variables (Randa and Yunger 2006, Riley 2006, Clare et al. 2015, Mitchell et al. 2015, Handler et al. 2020). More specifically, among dominant species, we expected coyotes to use urban areas more frequently than bobcats (Flores-Morales et al. 2019) but still prefer sites with greater access to open, undeveloped landscapes that provide sufficient cover and foraging opportunities (Ellington and Gehrt 2019, Franckowiak et al. 2019, Pluemer et al. 2019). Among subordinate species, we hypothesized that gray fox would demonstrate the lowest use of urban landscapes because of their preference for undeveloped forests in their home range and core areas (Temple et al. 2010, Deuel et al. 2017, Lombardi et al. 2017).

In urban areas with limited natural habitat availability, subordinate mesocarnivores should adjust their temporal behavior to reduce overlap with dominant competitors (Shores et al. 2019, Haswell et al. 2020). Moreover, we expected both red and gray fox would exhibit stronger temporal avoidance of coyotes in more urbanized locations, as coyotes have been documented to suppress and kill foxes (Sargeant et al. 1987, Fedriani et al. 2000, Gosselink et al. 2003, Lesmeister et al. 2015). As seen in other urban landscapes (Gehrt and Prange 2007), we also predicted that raccoon temporal activity would be relatively unaffected by other mesocarnivore presence.

Our third hypothesis was that compared to rural settings, dominant and subordinate mesocarnivores would become more nocturnal in urban areas to avoid human encounters (Wang et al. 2015, Gaynor et al. 2018). We anticipated that dominant competitors would increase their nocturnal activity more than subordinate species because of a greater perceived risk of human persecution (Kitchen et al. 2000, Fox 2006).

## STUDY AREA

Our study took place along an urban-to-rural gradient on the eastern border of Orange County, New York, USA (41.3912°N, −74.3118°W), approximately 96 km north of New York City (Figure 1). The study area covered 250 $km^2$ and was bounded by the Hudson River to the east. Urban camera stations were located within the northernmost region of the survey area, near the City of Newburgh. The City of Newburgh has an estimated population of 28,856 and a population density of 2,855/$km^2$ (U.S. Census Bureau 2020). Semiurban cameras were located outside the denser Newburgh center, largely in New Windsor (316 people/$km^2$) and Cornwall (601 people/$km^2$), New York. Rural sites were primarily in forest preserves and state park lands to the southern and western regions of the study site, including Black Rock Forest (15.86 $km^2$), Stewart State Forest (27.11 $km^2$), Storm King State Park (7.68 $km^2$), and Schunnemunk Mountain State Park (10.92 $km^2$), and several privately owned, undeveloped land parcels. The park areas were managed by Black Rock Forest, New York State Department of Environmental Conservation, and New York State Department of Parks, Recreation and Historic Preservation. All 4 locations were open to public recreation year-round.

As part of the northeastern coastal forests ecoregion (89,691 $km^2$), the landscape was dominated by dry-mesic, mixed-oak forest (*Quercus* spp.), and interspersed with chestnut oak (*Q. prinus*), white ash (*Fraxinus americana*), maple (*Acer* spp.), hickory (*Carya* spp.), and American beech (*Fagus grandifolia*; U.S. Forest Service 1992). Patches of other forest community types, such as pine (*Pinus* spp.), were also present, particularly at high elevations or rocky summits. The valleys were primarily characterized by forested wetlands dominated by red maple (*Acer rubrum*). The annual seasons in the survey region included spring (21 Mar–20 Jun), summer (21 Jun–22 Sep), autumn (23 Sep–20 Dec), and winter (21 Dec–20 Mar). Mean annual precipitation in the study area was 104.42 cm, and the average annual high and low temperature was 15.8°C and 3.8°C, respectively (National Weather Service 2022). Elevations ranged from 0 to 507 m throughout the study site. In addition to the focal mesocarnivores, common mammalian species included American black bear

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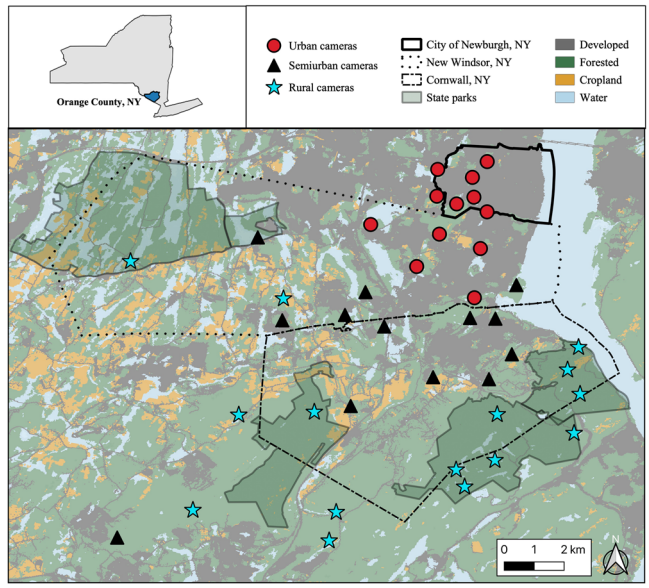


**FIGURE 1** Locations of 40 motion-sensitive cameras categorized by gradient (urban, semiurban, rural) to estimate mesocarnivore occupancy in eastern Orange County, New York, USA, May to September 2021.

(*Ursus americanus*), eastern gray squirrel (*Sciurus carolinensis*), eastern chipmunk (*Tamias striatus*), striped skunk (*Mephitis mephitis*), Virginia opossum (*Didelphis virginiana*), white-tailed deer (*Odocoileus virginianus*), and woodchuck (*Marmota monax*; S. D. LaPoint, Black Rock Forest, unpublished data).

## METHODS

### Motion-sensitive camera surveys

We deployed motion-sensitive infrared cameras at 40 sites across our study area between 19 May and 7 September 2021. We deployed 10 Reconyx HyperFire 2 Professional Covert IR (Reconyx, Holmen, WI, USA) cameras along this gradient on a rotating interval, for 4 deployment periods lasting between 21 and 33 days ($\bar{x}$ = 26.80). To define the 3 levels of the gradient, we leveraged the 2019 National Land Cover Urban Imperviousness dataset and standardized bin levels from Marzluff (2001) to evaluate the mean impervious surface percentage within a 1-km radius of each camera station: urban (21.61–54.03% impervious), semiurban (5.14–20.43% impervious), and rural (0.00–3.08% impervious; Dewitz, J., and U.S. Geological Survey 2021). Given that motion-sensitive camera stations were, on average, >1 km apart, ($\bar{x}$ = 1.68 km), we selected the buffer size to avoid significant overlap in land cover sampled within the gradient. We deployed 12 cameras in urban areas, 13 in semiurban areas, and 15 in rural areas.

At each site, we attached a motion-sensitive camera to a tree roughly 0.6 m above the ground. We aimed cameras facing north, when possible, to reduce false triggers caused by exposure to sunlight. We removed vegetation that was in the field of view and could erroneously activate the motion-sensitive camera. We fastened approximately 3 kg of white-tailed deer carcass 2 m above the ground to an adjacent tree roughly 4 m from the camera. We also applied canid-specific scent lure (around 7.5 mL) to the deer carcass (Caven's Gusto and Caven's Tree Climber; Minnesota Trapline Products, Pennock, MN, USA). We used the lure to maximize the probability of animal detection by retaining individuals within the camera detection radius, thereby improving the application and functioning of our statistical models (MacKenzie et al. 2017), particularly over a shorter study period. This is a

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common practice for motion-sensitive camera studies of carnivores (Gerber et al. 2012, Du Preez et al. 2014) and although the use of attractants may incur modest bias for mesocarnivore habitat use (Holinda et al. 2020), the effect of bait on animal movement is eclipsed by natural landscape heterogeneity (Stewart et al. 2019).

All cameras were set to take 10 images in rapid succession (<1 sec between pictures) for each detection event, re-triggering instantly if the animal was still in view (Kays et al. 2021). Upon camera retrieval, we recorded the detection distance for each camera measured as the maximum distance it would trigger when a person walked back-and-forth in front of the camera. This metric provides an index of the camera's sampling area based on its ability to detect a passing mammal, given site-specific vegetation density and topography that may hinder the camera. Finally, we triggered the camera upon arrival and departure at each site by holding up a digital clock on our smartphone to record the date and time of camera deployment. This information serves as a confirmation of the camera's operational status that can be used to deduce functionality errors (i.e., incorrect timestamps).

We uploaded and managed all camera images via the Smithsonian Institute's eMammal database (eMammal.si.edu, accessed 10 Jan 2022). This system groups consecutive camera images into single sequences (i.e., events) if they were <1 minute apart. We considered sequences of the same species at the same camera station to be temporally independent if they were >30 minutes apart, consistent with other motion-sensitive camera protocols (Lucherini et al. 2009, Alexander et al. 2016, Sollmann 2018). Additionally, if ≥2 individuals of the same species were photographed in 1 sequence, we counted it as a single detection event.

## Site and survey characteristics

We evaluated 11 site-specific environmental covariates that may influence mesocarnivore occupancy ($\psi$; Table 1). We extracted data from a variety of geospatial layers in QGIS (version 3.16.11). We calculated the percentage of land cover within circular buffers surrounding each camera using the 2019 National Land Cover Data. We tested 2 local scales to represent land cover at the camera site (250-m, 500-m radius) and 1 larger scale (5-km radius) to best evaluate the home range size of our target species (Bekoff 1977, Lotze and Anderson 1979, Fritzell and Haroldson 1982, Larivière and Pasitschniak-Arts 1996). We determined that a radius of 500 m minimized model Akaike's Information Criterion (AIC) for all target mesocarnivores (Burnham and Anderson 2002, Arnold 2010) and therefore used that scale for our landscape covariates. Land cover was characterized as percent forest (deciduous, evergreen, mixed forest), percent developed (open space [<20% impervious], low-intensity development [20–49% impervious], medium-intensity development [50–79% impervious], high-intensity development [80–100% impervious]), percent cropland (hay or pasture, cultivated crops), percent grassland (grassland or herbaceous, shrub or scrub), and percent wetland (woody wetland and emergent herbaceous wetland; Dewitz, J., and U.S. Geological Survey 2021). Given that mammalian carnivores may have large home ranges and be able to move between camera sites surveyed, potentially beyond the 500-m land cover buffer, occupancy can be defined as species use of sampled areas (MacKenzie et al. 2004). Additionally, we leveraged the 2010 United States Census Grids from the Socioeconomic Data and Applications Center to extract the mean number of housing units within a 500-m radius of each camera (Socioeconomic Data and Applications Center 2010). We also measured linear distances to several natural and anthropogenic features, including roads, wetlands, and water (U.S. Geological Survey 2019, Orange County New York Geographic Information System Division 2022), and derived elevation and slope at each camera site using 30-m digital elevation models (U.S. Geological Survey 2019).

We modeled detection probability ($\rho$) using 13 covariates (Table 1). We summarized the weekly average temperature, precipitation, wind speed, cloud cover, and moon illumination for each of our 4 camera deployment periods using data collected from the nearest weather station in Montgomery, New York, Orange County (www.weather.gov, accessed 5 Feb 2022). Environmental conditions such as rainfall and air temperature may influence detection probability by altering animal behavior or motion-sensitive camera function, making these factors important to consider in statistical analyses (Kays et al. 2009, Burton et al. 2015). We also considered site-specific

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**TABLE 1** Summary of 11 site covariates influencing occupancy ($\psi$) and 13 survey covariates influencing detection ($p$) included in single-species, single-season occupancy models for mesocarnivores based on data collected from 40 motion-sensitive cameras in eastern Orange County, New York, USA, May to September 2021.

| Variable | Description | Max. | Min. |
|---|---|---|---|
| Site covariates ($\psi$) | | | |
| Elevation | Point elevation (m) at camera site | 434.0 | 23.0 |
| Slope | Gradient of incline (degrees) at camera site | 427.5 | 14.3 |
| Housing density | Number of housing units within a 500-m camera buffer | 264.0 | 0 |
| Distance to water | Distance (m) to nearest water source (streams, creeks, rivers, reservoirs, or lakes) | 1,130.6 | 5.1 |
| Distance to wetland | Distance (m) to nearest wetland | 3,954.1 | 25.6 |
| Distance to roads | Distance (m) to nearest road | 1,193.8 | 33.1 |
| Urban cover | Proportion of urban cover within 500-m camera buffer | 87.1 | 0 |
| Forest cover | Proportion of forest cover within 500-m camera buffer | 100.0 | 0 |
| Crop cover | Proportion of crop cover within 500-m camera buffer | 42.1 | 0 |
| Grassland cover | Proportion of grassland cover within 500-m camera buffer | 7.1 | 0 |
| Wetland cover | Proportion of wetland cover within 500-m camera buffer | 77.9 | 0 |
| Survey covariates ($p$) | | | |
| Temperature | Average temperature (°C) during each weekly survey block taken from nearest National Weather Service Station | 24.2 | 12.7 |
| Rainfall | Average precipitation (cm) during each weekly survey block taken from nearest National Weather Service Station | 2.2 | 0 |
| Wind speed | Average wind speed (km/hr) during each weekly survey block taken from nearest National Weather Service Station | 15.2 | 7.2 |
| Moon illumination | Average moon phase during each weekly survey block taken from nearest National Weather Service Station, ranging from 0 (new moon), 0.5 (full moon), and 1 (next new moon) | 1 | 0 |
| Cloud cover | Average cloud cover (%) during each weekly survey block taken from nearest National Weather Service Station (0 = no cloud cover; 100 = full cloud cover) | 73.4 | 0 |
| Detection distance | The maximum distance (m) each camera trap triggered when a person walked back-and-forth in front of the camera | 23.7 | 4.3 |
| Coyote capture rate | Number of independent coyote detections/survey week at each camera site | 1.4 | 0 |
| Red fox capture rate | Number of independent red fox detections/survey week at each camera site | 1.9 | 0 |
| Raccoon capture rate | Number of independent raccoon detections/survey week at each camera site | 1.1 | 0 |
| Bear capture rate | Number of independent black bear detections/survey week at each camera site | 0.4 | 0 |
| Human capture rate | Number of independent human detections/survey week at each camera site | 0.9 | 0 |

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**TABLE 1** (Continued)

| Variable | Description | Max. | Min. |
|---|---|---|---|
| Dog capture rate | Number of independent domestic dog detections/survey week at each camera site | 0.4 | 0 |
| Cat capture rate | Number of independent domestic and feral cat detections/survey week at each camera site | 0.6 | 0 |

detection distance (m), a measure of how far away the motion-sensitive camera could detect a person, to account for potential variation in camera capture rates across space and time (Kolowski et al. 2021). Additionally, we included the weekly capture rates (number of independent detections per survey week at each camera site) of coyote, raccoon, and red fox during the 4 deployment periods to account for how mesocarnivores may influence each other's detectability. We did not include bobcat and gray fox capture rates as detection covariates because sample sizes were small. We also considered the weekly capture rate of black bears during each deployment timeframe because bears provide potential protection for subordinate mesocarnivores (i.e., foxes) from coyote competition (Moll et al. 2021). Finally, we evaluated the weekly capture rates of humans, dogs, and cats for the 4 deployment periods as additional factors that may influence mesocarnivore detection probability.

## Occupancy models

We generated single-species, single-season occupancy models using package unmarked (version 1.1.1) for Program R (version 4.2.1) to estimate the probability of mesocarnivore detection ($\rho$) and occupancy ($\psi$) among sampled sites and explore the potential site and survey factors influencing species habitat use (Fiske and Chandler 2011, R Core Team 2022). We created binary detection histories (1 = detected; 0 = not detected) for coyote, raccoon, and red fox at each camera site. We developed gray fox models but removed them from our final results given that 14 of 15 detections occurred at a single, semiurban camera (Table S1, available in Supporting Information). We also excluded bobcats from occupancy analyses because low sample size prevented model convergence. To account for imperfect detection, we used weekly sampling occasions to limit the number of observations where the count of detections is 0 (MacKenzie et al. 2003, 2017), resulting in 3–5 repeated surveys/site. We used a shorter 2-week survey period for 2 sites where the camera malfunctioned or was damaged.

To fit and compare the single-species models estimating $\rho$ and $\psi$, we used a maximum likelihood-based modeling framework, explicitly accounting for imperfect detection (MacKenzie 2006, Long et al. 2011). To avoid model over-parameterization that could reduce the accuracy of species detection and occupancy estimates, we assessed only univariate candidate models (i.e., 1 covariate each for $\rho$ and $\psi$) and did not consider models comprising combinations of multiple covariates (Gálvez et al. 2013, Curveira-Santos et al. 2019). For each species, we first estimated $\rho$ (holding $\psi$ constant) to assess which of the 13 survey variables best predicted detection probability. We also considered an intercept-only (null) model, $\rho(.)$, in which $\rho$ and $\psi$ were fixed, to provide a reference for the ability of survey covariates to explain differences in detection probabilities. We compared the candidate detection models using Akaike's Information Criterion corrected for small sample sizes ($AIC_c$). We ranked models according $\Delta AIC_c$, the difference between the lowest $AIC_c$ and the $AIC_c$ of the $i$th models ($\Delta_i$), and Akaike weights ($\omega_i$), which provide the level of support as a percentage for each model considered (Akaike 1973, Burnham and Anderson 2002, Wagenmakers and Farrell 2004). For each species, we chose the most parsimonious detection model as indicated by the lowest $AIC_c$ and highest $\omega_i$ to subsequently model occupancy parameters.

After identifying the most supported $\rho$ model, we fit *a priori* occupancy models that individually tested relationships between $\psi$ and 11 environmental covariates. We also included the null occupancy model, $\psi(.)$, as a

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reference point. For each species, the candidate $\psi$ models were again ranked using $\Delta AIC_c$ values, with the best models as those with the lowest $AIC_c$ and highest $\omega_i$ (Burnham and Anderson 2002). We considered models to be competitive if $\Delta AIC_c < 2$ (Burnham and Anderson 2002, Arnold 2010). Among the top-ranked model(s), we explored the 90% confidence intervals for the $\rho$ and $\psi$ beta coefficients. We used a wider interval because of the smaller sample size of our focal species. If confidence intervals did not overlap with zero, we considered this to be a marginally significant result.

In the package corrplot (version 0.2-0) within Program R, we determined correlations between all numeric covariates for $\rho$ and $\psi$ using a Spearman's rank correlation with an exclusion threshold of $|r_s| > 0.7$ (Dormann et al. 2013, Wei and Simko 2021). Among $\rho$ covariates, significant multicollinearity occurred between precipitation and cloud cover ($r = 0.74$). Among $\psi$ covariates, urban cover and forest cover ($r = -0.90$), elevation and forest cover ($r = 0.72$), elevation and distance to roads ($r = 0.80$), and elevation and urban cover ($r = -0.75$) were correlated. We accounted for correlated covariates in the interpretation of model results for $\rho$ and $\psi$ for each mesocarnivore species. Further, we standardized all numeric covariates prior to model analysis by subtracting the mean and dividing by the standard deviation of each covariate using scale() in the base R package (version 3.6.2; R Core Team 2022).

## Temporal activity

We used detection date and time from the first camera photo of each sequence to evaluate the diel and nocturnal activity patterns of bobcat, coyote, gray fox, raccoon, and red fox across all camera sites. We also further explored whether daily and nocturnal activity patterns varied across the urbanization gradient for 3 mesocarnivore pairs for which we had the most data: coyote, raccoon, and red fox. Given the length and location of our survey, we converted time of day from clock time to solar time in the activity package (version 1.3.1) for all temporal analyses (Rowcliffe et al. 2014, Rowcliffe 2021), in which solar time is anchored to the mean sunrise and sunset across the study area. Solar time bases the passage of time on the sun's position and provides a more accurate scale for daily activity patterns at higher latitudes (>30°) and over longer study timelines (>3 months) where daylight length varies (Nouvellet et al. 2012, Vazquez et al. 2019). Additionally, in alignment with the mean start and end of civil twilight throughout our survey (i.e., dawn and dusk; https://gml.noaa.gov/grad/solcalc/, accessed 25 Mar 2022), we defined nocturnal detections as those occurring 30 minutes after sunset (2041) and 30 minutes before sunrise (0515).

For our first analysis, we evaluated the daily activity levels (percentage of time spent active over the 24-hour day) for all 5 mesocarnivore species by fitting circular kernel density distributions to solar time in the activity package (Rowcliffe 2021). We also fit kernel density distributions to calculate the nocturnal activity levels for each mesocarnivore, which represented the percentage of time spent active between dusk and dawn. Lastly, we used a Wald test with 10,000 bootstrap samples to determine whether there was a statistically significant difference ($P < 0.05$) between 2 mesocarnivores' daily and nocturnal activity levels (Ridout and Linke 2009). We repeated this approach to analyze coyote, raccoon, and red fox nocturnal activity levels across all urban, semiurban, and rural camera sites. Furthermore, we explored the diel and nocturnal activity levels for red fox and coyote, raccoon and coyote, and raccoon and red fox detected at the same urban, semiurban, and rural camera sites.

For our second analysis, we estimated the temporal activity overlap among mesocarnivore pairs using the overlap package (version 1.3.1073; Ridout and Linke 2009). We used the kernel density estimations for each mesocarnivore's activity pattern to calculate the coefficient of overlap ($\hat{\Delta}$) between 2 species (Ridout and Linke 2009). The overlap term, which ranges from 0 (no overlap) to 1 (complete overlap), is represented by the area under the curve that is formed by taking the minimum of the 2 kernel density functions at each time point (Meredith and Ridout 2021). To estimate $\hat{\Delta}$, we selected $\hat{\Delta}_1$ if ≥1 species had a small sample size ($n < 50$) and $\hat{\Delta}_4$ if both species had large sample sizes ($n > 50$; Ridout and Linke 2009). We obtained confidence intervals (95%) of

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each overlap index from 10,000 smoothed bootstrap samples (Meredith and Ridout 2021). We considered coefficients of overlap without overlapping confidence intervals to be significantly different. We also applied the same methodology for evaluations of temporal overlap between red fox and coyote, raccoon and coyote, and raccoon and red fox detected at the same urban, semiurban, and rural sites.

## RESULTS

We deployed motion-sensitive cameras at 40 sites for a survey effort of 4,440 trap nights over a 16-week survey period. Two cameras were not operational for their full deployment timeframe, 1 because of battery failure ($n$ = 14 days) and the other from attempted theft ($n$ = 11 days). A total of 1,897 detections (i.e., sequences) of 22 different vertebrate species were recorded, including 497 unique detections of 6 mesocarnivore species (Table 2; Table S2, available in Supporting Information). Striped skunk was only present in 4 sequences and was not included in subsequent statistical analyses. Red fox was the most frequently detected mesocarnivore with 223 independent detections at 32 of 40 cameras ($\psi$ = 0.83 ± 0.07, $p$ = 0.60 ± 0.04). Unique coyote detections totaled 130 at 29 of 40 sites ($\psi$ = 0.76 ± 0.07, $p$ = 0.54 ± 0.05), followed by 119 raccoon detections across 32 of 40 locations ($\psi$ = 0.87 ± 0.07, $p$ = 0.48 ± 0.05). Gray fox was detected 15 times at only 2 cameras ($\psi$ = 0.05 ± 0.04, $p$ = 0.53 ± 0.18), and bobcat totaled 6 unique detections at 5 sites ($\psi$ = 0.34 ± 0.29, $p$ = 0.10 ± 0.09). We also calculated latency to detection (the average time across all study sites to get the first photograph of an animal) for each species to determine if the deployment length was sufficient for detecting each target mesocarnivore. The lowest latency was recorded for red fox (3.6 days) and the highest latency was for striped skunk (18.8 days; Table 2).

Red fox and raccoon were both detected at 100.0% of urban sites, followed by coyote at 50.0% of sites. Bobcat and gray fox were not detected at any urban locations. Among semiurban sites, red fox was detected at 84.6% of cameras, compared to coyote and raccoon at 76.9% and 69.2% of sites, respectively. Bobcat and gray fox were both present at 5.0% of semiurban stations. In the rural regions of the gradient, coyote was the most frequently detected mesocarnivore (86.7% of sites), whereas raccoon was recorded at 73.3% of cameras and red fox at 60.0%. Bobcat was detected at 10.0% of rural sites and gray fox were not present in any rural settings (Table S2).

**TABLE 2** Summary of 6 mesocarnivore species detected at 40 motion-sensitive cameras in eastern Orange County, New York, USA, May to September 2021.

| Species | Individual detections[a] | Unique detections[b] | Locations detected $n$ = 40 | Latency to detection[c] | Predicted occupancy[d] |
|---|---|---|---|---|---|
| Red fox | 280 | 223 | 32 | 3.6 days | 0.83 |
| Coyote | 176 | 130 | 29 | 5.5 days | 0.76 |
| Raccoon | 182 | 119 | 32 | 5.9 days | 0.87 |
| Gray fox | 19 | 15 | 2 | 8.5 days | 0.05 |
| Bobcat | 7 | 6 | 5 | 10.0 days | 0.34 |
| Striped skunk | 4 | 4 | 4 | 18.8 days | 0.10 |

[a]Total sequences captured of a species across all camera sites, including sequences taken ≤30 minutes apart and those with ≥2 individuals in the same sequence.

[b]Total sequences of the same species at the same motion-sensitive camera that occurred >30 minutes apart.

[c]Average time across all camera sites to detect the first individual of a species.

[d]Estimated occupancy probability of each species across all survey locations.

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## Occupancy modeling results

Detection and occupancy likelihood were influenced by different survey and site covariates for each mesocarnivore species (Figure 2; Table 3). The highest-ranking model for red fox, carrying 33% of the cumulative model weight ($\omega_i$), indicated a positive effect of camera detection distance ($\beta$ = 0.62 ± 0.25, 90% CI = 0.21–1.03) on $\rho$ (Figure 2). Red foxes were also more likely to use areas close to roads (e.g., 0–500 m; $\beta$ = −1.16 ± 0.47, 90% CI = −1.93to−0.39). Urban cover ($\beta$ = 1.94 ± 1.15, 90% CI = 0.05–3.83) and elevation ($\beta$ = −1.16 ± 0.54, 90% CI = −2.05to−0.28) were also included in the competitive model set (i.e., $\Delta AIC_c < 2$) but received 1.64 and 1.84 times less support than the top model, respectively (Table 3). Urban cover and elevation were strongly correlated with distance to roads, suggesting the competitiveness of the 3 models was a consequence of covariates that were similar to the top-ranked model. Thus, we only considered the top model to have a notable effect on red fox habitat use.

The best-fit model for coyote ($\omega_i$ = 0.55) indicated that $\rho$ was best predicted by the weekly capture rate of American black bears ($\beta$ = 0.49 ± 0.23, 90% CI = 0.12–0.87), with coyote having an approximately 25% detection probability at sites with no American black bears but nearly a 75% detection likelihood at sites with 1 bear recorded per week (Figure 2). Additionally, coyote $\psi$ was greater at elevations >200 m ($\beta$ = 2.27 ± 1.35, 90% CI = 0.04–4.50; Figure 2), with no competing models based on $AIC_c$ score (Table 3).

No covariates strongly influenced raccoon $\rho$, so detection was held constant in subsequent models evaluating $\psi$. The highest ranked model ($\omega_i$ = 0.27) indicated that raccoon $\psi$ declined with increasing distance from wetlands ($\beta$ = −1.69 ± 1.38), though this relationship was not significant (90% CI = −3.97–0.58; Figure 2). Forest cover ($\beta$ = −1.13 ± 0.99, 90% CI = −2.76–0.49) and housing density ($\beta$ = 1.46 ± 1.02, 90% CI = −0.90–3.83) were also within 2 $\Delta AIC_c$ of the top model; therefore, there was minimal evidence that any environmental factors strongly affected raccoon habitat use in the study area (Burnham and Anderson 2002; Table 3).

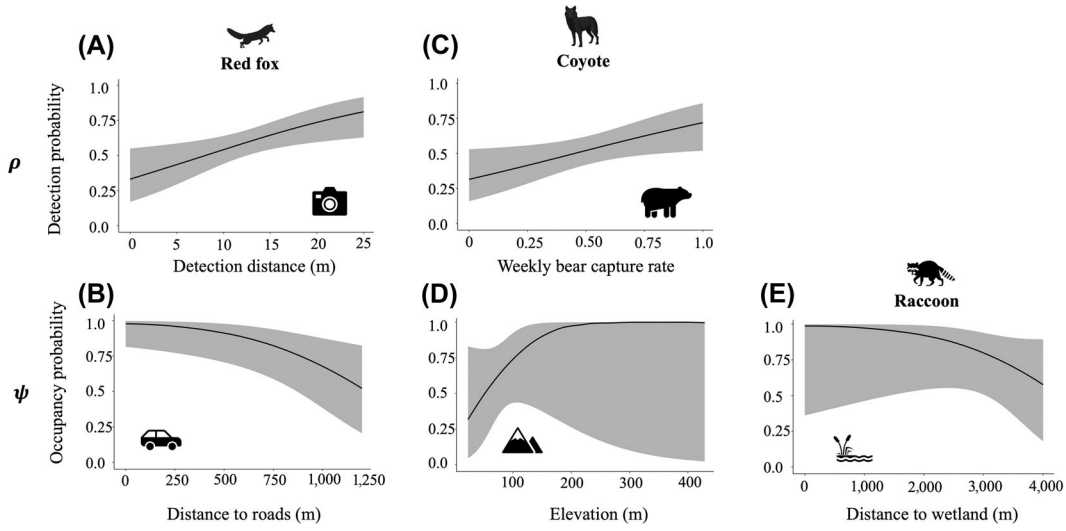


**FIGURE 2** Covariate effect size plots of the top predictors for detection and occupancy for red fox (A, B), coyote (C, D), and raccoon (E) based on data collected from 40 motion-sensitive cameras in eastern Orange County, New York, USA, May to September 2021. The solid black line depicts the probability of use estimates, while the shaded area represents the upper and lower 90% confidence intervals.

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**TABLE 3** Single-species, single-season occupancy model results for detection probability ($\rho$) and occupancy ($\psi$) for red fox, coyote, and raccoon based on data collected from 40 motion-sensitive cameras in eastern Orange County, New York, USA, May to September 2021. Models were ranked based on Akaike's Information Criterion corrected for small sample sizes ($AIC_c$). We present the top 4 models for each species and the intercept-only model.

| Model | $AIC_c$ | $\Delta AIC_c$[a] | $\omega$[b] | $K$[c] | $-2\,L$[d] |
|---|---|---|---|---|---|
| Red fox | | | | | |
| $\rho$(detection distance) + $\psi$(distance to roads) | 210.67 | 0.00 | 0.33 | 4 | 100.76 |
| $\rho$(detection distance) + $\psi$(urban cover) | 211.66 | 0.99 | 0.20 | 4 | 101.26 |
| $\rho$(detection distance) + $\psi$(elevation) | 211.89 | 1.55 | 0.18 | 4 | 101.38 |
| $\rho$(detection distance) + $\psi$(forest cover) | 212.72 | 2.71 | 0.12 | 4 | 101.79 |
| $\rho$(detection distance) + $\psi$(.) | 215.82 | 4.60 | 0.03 | 2 | 102.97 |
| Coyote | | | | | |
| $\rho$(bear) + $\psi$(elevation) | 204.27 | 0.00 | 0.55 | 4 | 97.57 |
| $\rho$(bear) + $\psi$(distance to roads) | 207.31 | 3.04 | 0.12 | 4 | 99.08 |
| $\rho$(bear) + $\psi$(urban cover) | 207.98 | 3.70 | 0.09 | 4 | 99.42 |
| $\rho$(bear) + $\psi$(forest cover) | 208.59 | 4.32 | 0.06 | 4 | 99.73 |
| $\rho$(bear) + $\psi$(.) | 209.75 | 5.11 | 0.04 | 2 | 100.12 |
| Raccoon | | | | | |
| $\rho$(.) + $\psi$(distance to wetland) | 225.94 | 0.00 | 0.27 | 3 | 109.63 |
| $\rho$(.) + $\psi$(forest cover) | 227.59 | 1.65 | 0.12 | 3 | 110.46 |
| $\rho$(.) + $\psi$(housing) | 227.81 | 1.88 | 0.11 | 3 | 110.56 |
| $\rho$(.) + $\psi$(.) | 227.99 | 2.06 | 0.10 | 2 | 111.84 |
| $\rho$(.) + $\psi$(urban) | 228.51 | 2.57 | 0.08 | 3 | 110.92 |

[a]Difference in $AIC_c$ value of given model and top model.
[b]$AIC_c$ model weight.
[c]Total number of model parameters.
[d]Twice the negative log-likelihood value.

## Temporal activity results

All 5 mesocarnivores exhibited similar diel and nocturnal activity patterns across all camera sites (Table 4; Figure S1, available in Supporting Information). Coyotes spent the greatest percentage of the 24-hour day active (44.0%), while bobcats spent the least (24.0%), although the difference was not significant ($W$ = 3.28, $P$ = 0.07; Table S3, available in Supporting Information). Nocturnal activity levels for each mesocarnivore were >60.0%, with raccoon and bobcat displaying the highest percentage of nocturnal activity and gray fox exhibiting the lowest (Table 4). No mesocarnivore pair exhibited a significant difference in nighttime activity throughout the study area (Table S3). Additionally, the coefficients of overlap ($\hat{\Delta}$) for mesocarnivore species 24-hour temporal activity patterns across all camera sites were >50.0% (Figure 3; Figure S2, available in Supporting Information). Overall, red fox and coyote had the highest overlap ($\hat{\Delta}_4$ = 0.87, 95% CI = 0.82–0.95), and bobcat and raccoon had the lowest ($\hat{\Delta}_1$ = 0.53, 95% CI = 0.29–0.82; Figure 3). On average, bobcat had the lowest range of activity overlap with its mesocarnivore counterparts throughout all camera sites ($\hat{\Delta}_1$ = 0.53–0.57), and red fox had the highest ($\hat{\Delta}_4$ = 0.57–0.87; Figure 3).

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**TABLE 4** Summary of 24-hour and nocturnal activity level estimates for red fox, coyote, raccoon, gray fox, and bobcat based on the number of independent detections from 40 motion-sensitive cameras in eastern Orange County, New York, USA, May to September 2021.

| Species | Sample size | Activity estimate | SE | 95% CIs | |
|---|---|---|---|---|---|
| | | | | CI lower | CI upper |
| Diel activity levels[a] | | | | | |
| Red fox | 223 | 0.348 | 0.037 | 0.278 | 0.419 |
| Coyote | 130 | 0.439 | 0.047 | 0.324 | 0.507 |
| Raccoon | 119 | 0.339 | 0.030 | 0.267 | 0.387 |
| Gray fox | 15 | 0.393 | 0.098 | 0.157 | 0.523 |
| Bobcat | 6 | 0.237 | 0.101 | 0.048 | 0.441 |
| Nocturnal activity levels[b] | | | | | |
| Red fox | 223 | 0.681 | 0.076 | 0.537 | 0.830 |
| Coyote | 130 | 0.738 | 0.085 | 0.543 | 0.867 |
| Raccoon | 119 | 0.815 | 0.064 | 0.640 | 0.887 |
| Gray fox | 15 | 0.649 | 0.130 | 0.345 | 0.869 |
| Bobcat | 6 | 0.823 | 0.142 | 0.420 | 0.823 |

[a]The percentage of the 24-hour day that an animal is active.

[b]The percentage of the period between dusk (2041) and dawn (0515) that an animal is active.

Coyotes, raccoons, and red foxes did not significantly change their diel activity levels across all urban, semiurban, and rural sites (Table 5; Appendix A; Figure S2). Coyotes generally increased their daily activity patterns in more urbanized areas, spending nearly half of the day active in urban and semiurban parts of the interface (Table 5). Nocturnal activity analyses in all urban, semiurban, and rural sites indicated that coyotes exhibited the greatest increase in nighttime activity levels across the gradient, being 20.8% more active in urban versus rural areas (Table 5), but the difference was not significant ($W = 2.36$, $P = 0.13$; Appendix A). Red fox had the highest percentage of nocturnal activity in semiurban areas (87.1%), which was significantly greater than their nighttime activity in urban ($W = 4.24$, $P = 0.04$) and rural locations ($W = 7.82$, $P = 0.005$; Appendix A). Raccoons maintained relatively consistent nocturnal activity levels in urban (83.9%), semiurban (70.8%), and rural sites (80.8%; Table 5; Appendix A).

Daily and nocturnal activity analyses for coyote and red fox detected at the same urban, semiurban, and rural sites suggests that red fox and coyote did not have significant differences in activity levels in any part of the interface (Figure 4; Appendix B). Coyotes and red foxes still generally increased their diel and nocturnal activity levels in more urbanized sites even when both canids were detected. Comparatively, raccoon diel activity levels were 23.4% and 21.7% lower than coyote levels, respectively, when both species were detected in urban ($W = 7.72$, $P = 0.005$) and semiurban ($W = 6.19$, $P = 0.01$) sites (Appendix B). Raccoons were also nearly 30.0% less active at night than coyotes in the same urban environments ($W = 6.17$, $P = 0.013$; Appendix B). Additionally, red foxes were 15.4% more active during the diel period than raccoons in semiurban settings ($W = 8.85$, $P = 0.003$; Appendix B). Red foxes generally exhibited higher nocturnal activity levels in the same urban and semiurban areas than raccoons, but the differences were not significant (Figure 4; Appendix B).

When detected at the same camera sites, the temporal overlap between coyote and red fox was lowest in urban areas ($\hat{\Delta}_1 = 0.67$, 95% CI = 0.51–0.85) and highest in semiurban areas ($\hat{\Delta}_1 = 0.81$, 95% CI = 0.76–0.98), representing a 14% difference (Figure 5). Coyote and raccoon had the lowest overlap when detected in the same

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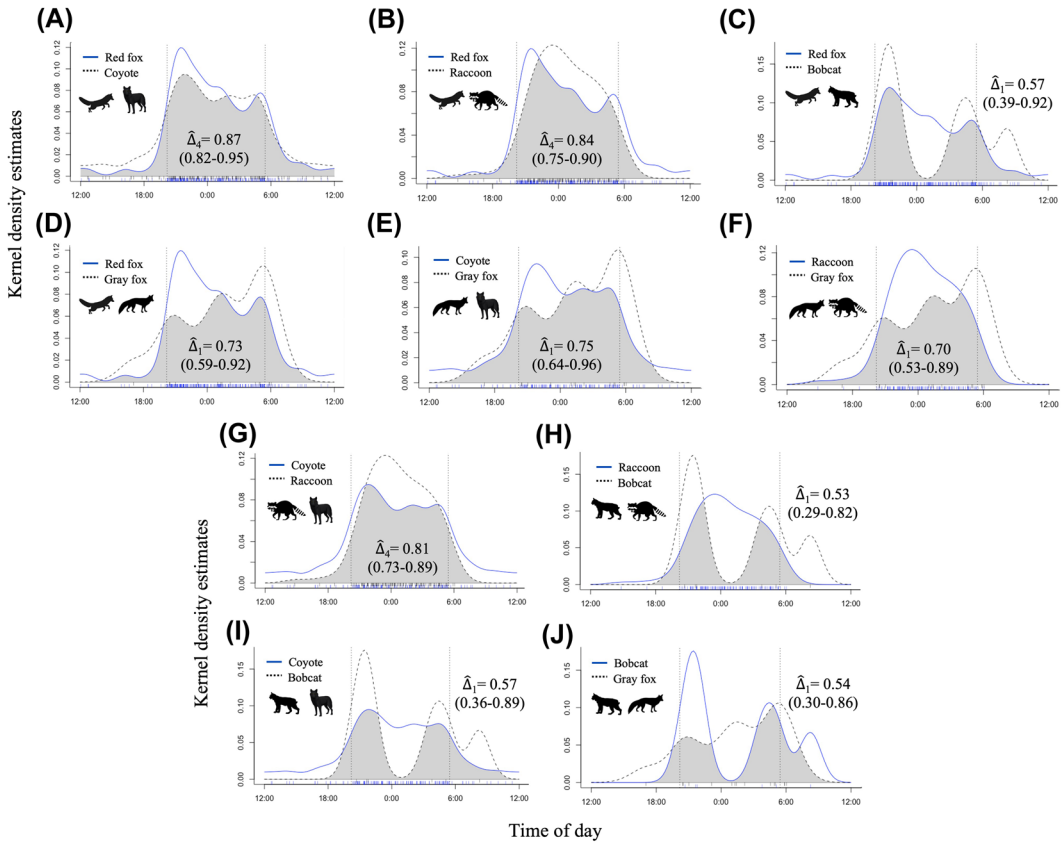


**FIGURE 3** Temporal activity overlap estimates ($\hat{\Delta}$) between bobcat, coyote, gray fox, raccoon, and red fox across all sites based on the number of independent detections from 40 motion-sensitive cameras in eastern Orange County, New York, USA, May to September 2021. We applied the overlap coefficient estimator $\hat{\Delta}_1$ for $n < 50$ and $\hat{\Delta}_4$ for $n > 50$. The vertical dotted lines represent the mean times of dusk (2041) and dawn (0515) throughout the survey period. The independent camera detections for each species are displayed at the bottom of each figure.

semiurban sites ($\hat{\Delta}_1$ = 0.66, 95% CI = 0.47–0.83) and the highest temporal overlap when detected in the same rural areas ($\hat{\Delta}_1$ = 0.78, 95% CI = 0.65–0.91; Figure 5). Raccoon and red fox exhibited a similar amount of overlap in the same urban, semiurban, and rural locales (Figure 5).

## DISCUSSION

We explored the spatiotemporal dynamics of a diverse mesocarnivore community in urban, semiurban, and rural sites near Newburgh, New York. This research adds to a growing body of literature examining carnivore distribution and abundance along an urbanization gradient (Schuette et al. 2013, Goad et al. 2014, Šálek et al. 2015, Wang et al. 2015, Moll et al. 2018). Mesocarnivore responses to anthropogenic landscape factors and potential competitors vary by species, but dominant and subordinate predators are likely finding mechanisms to coexist with each other next to increased human development.

Consistent with our predictions, larger mesocarnivores (coyote and bobcat) were associated with natural habitat features, while smaller mesocarnivores (red fox and raccoon) were more commonly detected in medium to

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**TABLE 5** Summary of 24-hour and nocturnal activity level estimates for red fox, coyote, and raccoon across all urban (U), semiurban (SU), and rural (R) sites based on the number of independent detections from 40 motion-sensitive cameras in eastern Orange County, New York, USA, May to September 2021.

| Species | Sample size | Activity estimate[a] | SE | 95% CIs | |
|---|---|---|---|---|---|
| | | | | CI lower | CI upper |
| 24-hour activity[a] | | | | | |
| U. red fox | 80 | 0.344 | 0.051 | 0.243 | 0.440 |
| SU. red fox | 98 | 0.403 | 0.033 | 0.300 | 0.429 |
| R. red fox | 45 | 0.293 | 0.061 | 0.185 | 0.408 |
| U. coyote | 28 | 0.484 | 0.070 | 0.265 | 0.537 |
| SU. coyote | 45 | 0.493 | 0.062 | 0.295 | 0.538 |
| R. coyote | 57 | 0.384 | 0.064 | 0.250 | 0.494 |
| U. raccoon | 56 | 0.375 | 0.039 | 0.263 | 0.416 |
| SU. raccoon | 29 | 0.270 | 0.042 | 0.173 | 0.333 |
| R. raccoon | 34 | 0.350 | 0.048 | 0.212 | 0.397 |
| Nocturnal activity[b] | | | | | |
| U. red fox | 51 | 0.622 | 0.091 | 0.454 | 0.802 |
| SU. red fox | 84 | 0.871 | 0.078 | 0.589 | 0.889 |
| R. red fox | 36 | 0.512 | 0.101 | 0.367 | 0.753 |
| U. coyote | 18 | 0.855 | 0.093 | 0.500 | 0.856 |
| SU. coyote | 32 | 0.729 | 0.110 | 0.466 | 0.878 |
| R. coyote | 44 | 0.647 | 0.098 | 0.459 | 0.841 |
| U. raccoon | 47 | 0.839 | 0.084 | 0.544 | 0.872 |
| SU. raccoon | 29 | 0.708 | 0.084 | 0.518 | 0.833 |
| R. raccoon | 31 | 0.808 | 0.078 | 0.538 | 0.834 |

[a]The percentage of the 24-hour day that an animal is active.

[b]The percentage of the period between dusk (2041) and dawn (0515) that an animal is active.

highly developed areas. As expected, coyotes increased nocturnal activity in more urbanized areas, whereas red foxes and raccoons were more consistently nocturnal despite our expectations that these smaller species would shift their activity patterns to avoid larger species. Lastly, although the diel and nocturnal activity levels of coyote, raccoon, and red fox overlapped the least in semiurban and urban sites, we cannot conclude whether these differences were due to the presence of coyote or another ecological variable.

## Red fox

Globally, the red fox has become one of the most prevalent urban carnivores owing to its plasticity to inhabit natural and built-up areas and use a variety of food in different landscapes (Harris and Rayner 1986, Marks and Bloomfield 1999, Gosselink et al. 2003, Bateman and Fleming 2012, Duduś et al. 2014). Not surprisingly, red foxes were strongly associated with more urbanized study areas and were likely to use habitat close to roads. Along the

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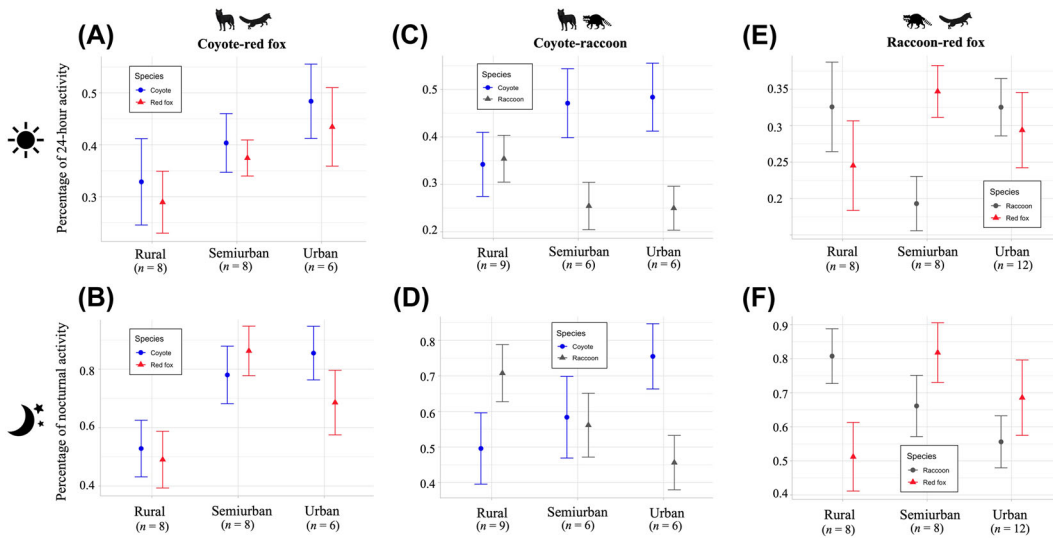


**FIGURE 4** Daily (percentage of time spent active over the 24-hr day) and nocturnal (percentage of time between dusk [2041] and dawn [0515] that an animal is active) activity level estimates for coyote-red fox (A, B), coyote-raccoon (C, D), and raccoon-red fox (E, F) comparisons when each species pair was detected at the same urban, semiurban, and rural sites based on the number of independent detections from 40 motion-sensitive cameras in eastern Orange County, New York, USA, May to September 2021. Bars represent ± the standard errors for each activity estimate.

urbanization spectrum, red foxes often reach the highest population sizes in areas of lower to intermediate residential density, including open landscapes like fields or managed green spaces (Soulsbury et al. 2010, Mueller et al. 2018). These areas often maintain sufficient access to relatively undisturbed natural areas while allowing wildlife to take advantage of human subsidies (Larson et al. 2020). The preference for intermediate development may explain why most red fox detections ($n = 98$) occurred in semiurban areas of our gradient.

Red foxes also exhibited notably higher nocturnal activity levels at semiurban sites compared to rural and urban locations. This may be an avoidance response to increased nighttime human activity as suggested elsewhere (e.g., Moll et al. 2018, Gil-Fernández et al. 2020). Yet it is possible that another unmeasured ecological or environmental factor may be influencing red fox temporal activity in suburban landscapes, such as the availability of diurnal versus nocturnal prey resources (i.e., small mammals and birds) that affect foraging rates (Newsome et al. 2015, Handler et al. 2020). Additionally, although red fox diel and nocturnal activity levels were not significantly different from coyote levels in any part of our gradient, red fox nocturnal activity did differ the most from coyote activity in urban areas (−17%). Other studies have reported that red foxes shift their temporal behavior to avoid interference and intraguild competition with coyotes at higher urbanization levels (Gosselink et al. 2003, Berger 2007, Kuijper et al. 2016, Moll et al. 2018). Thus, future research should assess if red foxes may adjust their activity patterns in urbanized settings as a response to human activity, apex predators, prey abundance, or other ecological variables. Lastly, camera detection distance increased red fox detection likelihood, further underscoring the importance of this variable in future studies (Moeller et al. 2022).

## Coyote

Coyotes were fairly ubiquitous throughout our study region, supporting their adaptability to various landscapes, including urbanized areas (Ordeñana et al. 2010, Dodge and Kashian 2013, Lesmeister et al. 2015). Coyotes were

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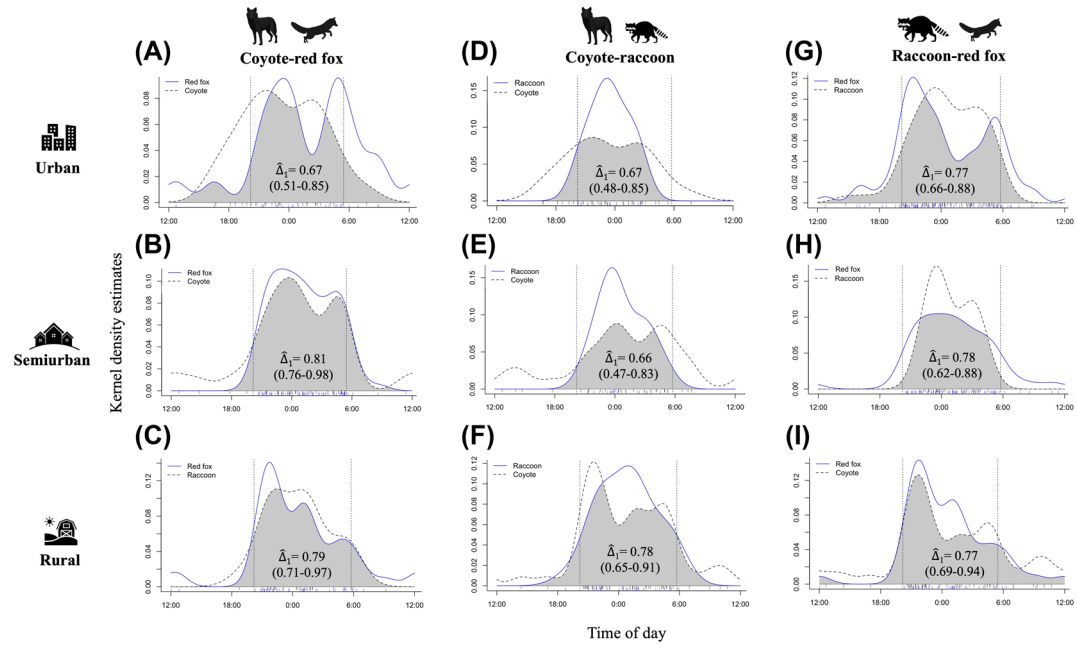


**FIGURE 5** Temporal activity overlap estimates ($\hat{\Delta}$) for coyote-red fox (A, B, C), coyote-raccoon (D, E, F), and raccoon-red fox (G, H, I) comparisons when each species pair was detected at the same urban, semiurban, and rural sites based on the number of independent detections from 40 motion-sensitive cameras in eastern Orange County, New York, USA, May to September 2021. We applied the overlap coefficient estimator $\hat{\Delta}_1$ for $n < 50$ and $\hat{\Delta}_4$ for $n > 50$. The vertical dotted lines represent the mean times of dusk (2041) and dawn (0515) throughout the survey period. The independent camera detections for each species are displayed at the bottom of each figure.

more likely to use settings with higher elevations, which may suggest that coyotes still prefer rural areas with larger amounts of natural cover and less human disturbance (Atwood et al. 2004, Poessel et al. 2013, Ellington and Gehrt 2019, Franckowiak et al. 2019, Kellner et al. 2020) or a potential change in neophobia at increased distances from human developments (Mettler and Shivik 2007). Additionally, the detection probability of coyote was positively correlated with the weekly capture rate of American black bears. Bears were principally detected in rural areas, suggesting the 2 species mostly overlapped in forests rather than developed landscapes. This result aligns with research performed in the Adirondacks of New York, in which black bear and coyote abundance were strongly predicted by similar habitat variables (e.g., woody debris abundance, canopy openness; Gompper et al. 2016). As such, landscape composition may be the main factor affecting coyote and black bear presence in this region of New York, but additional research is needed to evaluate other ecological factors (e.g., prey availability). Furthermore, in the western United States, Moll et al. (2021) reported that coyotes did not use the same areas as black bears, but subordinate species like foxes did, perhaps to reduce interspecific competition. Thus, it may be insightful for future work to also explore whether black bears alter carnivore guild dynamics in northeastern ecosystems.

Coyotes did not demonstrate a significant difference in diel and nocturnal activity patterns between urban, semiurban, and rural areas, but the general trend of our results showed higher nighttime activity levels for coyotes as urbanization intensified. Greater nocturnal activity in anthropogenic settings has been seen in coyote populations elsewhere (Tigas et al. 2002, Riley et al. 2003, Gese et al. 2012, Wang et al. 2015, Reilly et al. 2017), possibly owing to increased foraging and traveling time to meet energetic needs (Ellington et al. 2020). This change in activity could also emphasize coyotes' perceptions of humans as super predators (Darimont et al. 2015, Clinchy

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et al. 2016, Suraci et al. 2019). Increased nocturnality in response to human disturbance has been more frequently recorded in mammalian carnivores across the globe, and likely has negative implications for species' fitness, relative abundance, and long-term survival (Gaynor et al. 2018).

## Raccoon

In line with our hypotheses, raccoons were common across all landscapes in our survey area. As observed elsewhere in New York (Gompper et al. 2016), raccoon habitat use was not significantly influenced by any survey- or site-specific variables, further supporting their characterization as a highly generalist species. Consistent with previous research (Prange et al. 2004), raccoon daily and nocturnal activity levels were relatively stable across the gradient; however, raccoons were significantly less active during the diel period when detected at the same semiurban sites as coyotes and red foxes. Raccoons also generally exhibited the lowest nocturnal activity levels in semiurban areas. Evidence suggests that raccoon densities and survival increase in urban and semiurban environments compared to rural areas, potentially because anthropogenic food and structures are more readily available (Riley et al. 1998, Prange et al. 2003). The decline in overall raccoon activity in our semiurban study region may mean that human food subsidies or another preferred resource were less abundant, leading raccoons to spend less time and energy foraging compared to other mesocarnivores (Hoffmann and Gottschang 1977).

Although raccoon activity levels were, on average, highest at night across all urban locales, raccoons significantly reduced their percentage of nighttime activity at urban sites with coyotes also detected. This result may marginally support that subordinate species like the raccoon shift their temporal activity patterns in more fragmented anthropogenic areas to avoid negative encounters with dominant competitors like coyotes (Gosselink et al. 2003, Mueller et al. 2018). Nevertheless, prior research suggests that coyotes do not influence the spatial use or temporal activity patterns of raccoons (Gehrt and Prange 2007, Lesmeister et al. 2015, Gompper et al. 2016), though raccoon mortality from coyotes has been documented in rare occurrences (Gehrt and Clark 2003, Prange et al. 2003). Alternatively, raccoons may be exploiting an unmeasured resource in urban locations where coyotes are absent, resulting in reduced nocturnal detections at sites with coyotes. More research is needed to evaluate which variables may influence the temporal dynamics between raccoons and coyotes across gradients of urbanization.

## Bobcat

Although the small bobcat sample size limited the inference of our results, some general trends can be shared. Bobcats largely avoided more urbanized environments, as they were only found in semiurban and rural parts of the study area. As a larger mesocarnivore, bobcats commonly have a negative response to increasing urbanization proximity and intensity (George and Crooks 2006, Ordeñana et al. 2010), and maintain home ranges with primarily natural habitat (Riley 2006). Our results broadly support bobcats' documented sensitivities to landscape fragmentation, especially when compared to coyotes (Crooks 2002, Riley et al. 2003, Riley 2006). Temporally, bobcats exhibited the lowest percentage of diel activity of all 5 mesocarnivores. Yet, consistent with other research, their activity levels were highest at night (Witmer and deCalesta 1986, Tigas et al. 2002, Farias et al. 2012). Additionally, while bobcats were not detected in the most urbanized sections of our study area, researchers have reported conflicting conclusions on the species' temporal responses to anthropogenic landscapes. For example, like coyotes, bobcats have been reported to increase their nocturnal activity levels in some urban landscapes, likely to avoid human disturbance (Riley et al. 2003, George and Crooks 2006), whereas other researchers reported no change in their nocturnal activity when compared to natural environments (Bradley and Fagre 1988, Young et al. 2019).

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## Gray fox

The apparent rarity of gray fox in our study area may highlight the need for additional research on gray fox ecology, particularly in the eastern, midwestern, and western United States where gray fox populations appear to be declining (Egan et al. 2021). Although still considered an abundant mesocarnivore, the combined pressures of coyote competition, urban growth, and the spread of disease (i.e., canine distemper virus) are cause for heightened concern about gray fox conservation and management (Farias et al. 2005, Levi and Wilmers 2012, Rich et al. 2018, Parsons et al. 2022, Morin et al. 2022). We encourage future research to measure how habitat characteristics (i.e., vegetation type, canopy cover), prey availability (i.e., small mammal and bird abundance), and carnivore community structure influence gray fox abundance and distribution across local, state, and regional scales.

## Study limitations

We acknowledge that several limitations of the dataset and analyses could influence the application and conclusions of our research. First, given the smaller scale and single-season survey period of our study, our results on mesocarnivore habitat use may differ from studies that occurred across larger landscape scales and over longer timelines (Lesmeister et al. 2015, Allen et al. 2022). Though the results of our work provide species-specific information at the local or microhabitat level, which will help support multi-scale perspectives within the field of urban ecological research (Moll et al. 2020). Additionally, the areas we defined as rural were smaller forested patches closely surrounded by urban areas of varying intensity. This may affect the observed habitat use, activity, and distribution of our focal mesocarnivores, especially when compared to study areas that also contained larger patches of contiguous forest within the urbanization gradient. For example, Mueller et al. (2018) reported that coyotes near larger natural areas rarely used surrounding developed landscapes, whereas coyotes near smaller natural sites were more likely to venture into urban regions. Consequently, habitat patch size may influence the way wildlife use human landscapes, which was a potentially influential variable that we did not measure in our study. Researchers should continue to carefully evaluate the scale, timeline, and landscape composition of similar studies to overcome potential shortcomings and ensure appropriate interpretation of results.

# MANAGEMENT IMPLICATIONS

As the conversion of natural landscapes to urbanized environments grows, city planners and wildlife managers will likely need to conserve sufficient habitat to support landscape connectivity and species diversity, while mitigating human–wildlife conflict. Our research highlights that red foxes and raccoons may be particularly concentrated at intermediate to high levels of urbanization, which may have implications for managing human–carnivore interactions in residential neighborhoods and agricultural communities that are characteristic to the suburbs of Orange County, New York. Human encounters with urban wildlife are increasing in frequency and gathering knowledge of people's current and future attitudes toward these species will likely help support wildlife management in the area.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## ETHICS STATEMENT

Capture and handling protocols were approved by the Columbia University Institutional Animal Care and Use Committee (AABN0560) and all experiments were conducted in alignment with relevant regulations and guidelines. Additionally, all field protocols and access were approved and permitted by the New York State Department of Environmental Conservation (#2645) and the New York State Office of Parks, Recreation and Historic Preservation (2020-MP8-003).

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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## REFERENCES

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267–281 *in* B. N. Petrov and F. Csaki, editors. Second international symposium on information theory. Akademiai Kiado, Budapest, Hungary.

Alexander, J. S., J. J. Cusack, C. Pengju, S. Kun, and P. Riordan. 2016. Conservation of snow leopards: spill-over benefits for other carnivores? Oryx 50:239–243.

Allen, M. L., A. M. Green, and R. J. Moll. 2022. Modelling the distribution and intraguild associations of an understudied mesocarnivore across the contiguous United States. Diversity and Distributions 28:1022–1033.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Atwood, T. C., H. P. Weeks, and T. M. Gehring. 2004. Spatial ecology of coyotes along a suburban-to-rural gradient. Journal of Wildlife Management 68:1000–1009.

Bateman, P. W., and P. A. Fleming. 2012. Big city life: carnivores in urban environments. Journal of Zoology 287:1–23.

Bekoff, M. 1977. Canis latrans. Mammalian Species 79:1–9.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letters 3: 620–623.

Bradley, L. C., and D. B. Fagre. 1988. Coyote and bobcat responses to integrated ranch management practices in south Texas. Journal of Range Management 41:322–327.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Burton, A. C., E. Neilson, D. Moreira, A. Ladle, R. Steenweg, J. T. Fisher, E. Bayne, and S. Boutin. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology 52: 675–685.

Clare, J. D. J., E. M. Anderson, and D. M. MacFarland. 2015. Predicting bobcat abundance at a landscape scale and evaluating occupancy as a density index in central Wisconsin. Journal of Wildlife Management 79:469–480.

Clinchy, M., L. Y. Zanette, D. Roberts, J. P. Suraci, C. D. Buesching, C. Newman, and D. W. Macdonald. 2016. Fear of the human "super predator" far exceeds the fear of large carnivores in a model mesocarnivore. Behavioral Ecology 27: 1826–1832.

Cozzi, G., F. Broekhuis, J. W. McNutt, L. A. Turnbull, D. W. Macdonald, and B. Schmid. 2012. Fear of the dark or dinner by moonlight? Reduced temporal partitioning among Africa's large carnivores. Ecology 93:2590–2599.

Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology 16: 488–502.

19372817, 2023, 7, Downloaded from https://wildlife.onlinelibrary.wiley.com/doi/10.1002/jwmg.22474 by Columbia University Libraries, Wiley Online Library on [05/09/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Crooks, K. R., C. L. Burdett, D. M. Theobald, S. R. B. King, M. Di Marco, C. Rondinini, and L. Boitani. 2017. Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. Proceedings of the National Academy of Sciences 114:7635–7640.

Crooks, K. R., C. L. Burdett, D. M. Theobald, C. Rondinini, and L. Boitani. 2011. Global patterns of fragmentation and connectivity of mammalian carnivore habitat. Philosophical Transactions of the Royal Society B: Biological Sciences 366:2642–2651.

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

Curveira-Santos, G., N. M. Pedroso, A. L. Barros, and M. Santos-Reis. 2019. Mesocarnivore community structure under predator control: unintended patterns in a conservation context. PLoS One 14:e0210661.

Curveira-Santos, G., C. Sutherland, S. Tenan, A. Fernández-Chacón, G. K. H. Mann, R. T. Pitman, and L. H. Swanepoel. 2021. Mesocarnivore community structuring in the presence of Africa's apex predator. Proceedings of the Royal Society B: Biological Sciences 288:20202379.

Darimont, C. T., C. H. Fox, H. M. Bryan, and T. E. Reimchen. 2015. The unique ecology of human predators. Science 349: 858–860.

Deuel, N. R., L. M. Conner, K. V. Miller, M. J. Chamberlain, M. J. Cherry, and L. V. Tannenbaum. 2017. Gray fox home range, spatial overlap, mated pair interactions and extra-territorial forays in southwestern Georgia, USA. Wildlife Biology 2017:1–10.

Dewitz, J., and U.S. Geological Survey. 2021. National Land Cover Database (NLCD) 2019 products (version 2.0). U.S. Geological Survey data release, Reston, Virginia, USA. <https://doi.org/10.5066/P9KZCM54>

Dodge, W. B., and D. M. Kashian. 2013. Recent distribution of coyotes across an urban landscape in southeastern Michigan. Journal of Fish and Wildlife Management 4:377–385.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46.

Duduś, L., A. Zalewski, O. Kozioł, Z. Jakubiec, and N. Król. 2014. Habitat selection by two predators in an urban area: the stone marten and red fox in Wrocław (SW Poland). Mammalian Biology 79:71–76.

Du Preez, B. D., A. J. Loveridge, and D. W. Macdonald. 2014. To bait or not to bait: a comparison of camera-trapping methods for estimating leopard Panthera pardus density. Biological Conservation 176:153–161.

Egan, M. E., C. C. Day, T. E. Katzner, and P. A. Zollner. 2021. Relative abundance of coyotes (*Canis latrans*) influences gray fox (*Urocyon cinereoargenteus*) occupancy across the eastern United States. Canadian Journal of Zoology 99: 63–72.

Ellington, E. H., and S. D. Gehrt. 2019. Behavioral responses by an apex predator to urbanization. Behavioral Ecology 30: 821–829.

Ellington, E. H., E. M. Muntz, and S. D. Gehrt. 2020. Seasonal and daily shifts in behavior and resource selection: how a carnivore navigates costly landscapes. Oecologia 194:87–100.

Farias, V., T. K. Fuller, and R. M. Sauvajot. 2012. Activity and distribution of gray foxes (*Urocyon cinereoargenteus*) in southern California. Southwestern Naturalist 57:176–181.

Farias, V., T. K. Fuller, R. K. Wayne, and R. M. Sauvajot. 2005. Survival and cause-specific mortality of gray foxes (*Urocyon cinereoargenteus*) in southern California. Journal of Zoology 266:249–254.

Fedriani, J. M., T. K. Fuller, R. M. Sauvajot, and E. C. York. 2000. Competition and intraguild predation among three sympatric carnivores. Oecologia 125:258–270.

Fiske, I., and R. Chandler. 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Flores-Morales, M., J. Vázquez, A. Bautista, L. Rodríguez-Martínez, and O. Monroy-Vilchis. 2019. Response of two sympatric carnivores to human disturbances of their habitat: the bobcat and coyote. Mammal Research 64:53–62.

Fox, C. H. 2006. Coyotes and humans: can we coexist? Page 287–293 *in* Proceedings of the 22nd Vertebrate Pest Conference. University of California, 6 March–9 March 2006, Berkeley, California, USA.

Franckowiak, G. A., M. Perdicas, and G. A. Smith. 2019. Spatial ecology of coyotes in the urbanizing landscape of the Cuyahoga Valley, Ohio. PloS ONE 14:e0227028.

Frankham, R. 2005. Genetics and extinction. Biological Conservation 126:131–140.

Fritzell, E. K., and K. J. Haroldson. 1982. Urocyon cinereoargenteus. Mammalian Species 189:1–8.

Gálvez, N., F. Hernández, J. Laker, H. Gilabert, R. Petitpas, C. Bonacic, A. Gimona, A. Hester, and D. W. Macdonald. 2013. Forest cover outside protected areas plays an important role in the conservation of the Vulnerable guiña Leopardus guigna. Oryx 47:251–258.

Gaynor, K. M., C. E. Hojnowski, N. H. Carter, and J. S. Brashares. 2018. The influence of human disturbance on wildlife nocturnality. Science 360:1232–1235.

19372817, 2023, 7, Downloaded from https://wildlife.onlinelibrary.wiley.com/doi/10.1002/jwmg.22474 by Columbia University Libraries, Wiley Online Library on [05/09/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Gehrt, S. D., C. Anchor, and L. A. White. 2009. Home range and landscape use of coyotes in a metropolitan landscape: conflict or coexistence? Journal of Mammalogy 90:1045–1057.
Gehrt, S. D., and W. R. Clark. 2003. Raccoons, coyotes, and reflections on the mesopredator release hypothesis. Wildlife Society Bulletin 31:836–842.
Gehrt, S. D., and S. Prange. 2007. Interference competition between coyotes and raccoons: a test of the mesopredator release hypothesis. Behavioral Ecology 18:204–214.
George, S. L., and K. R. Crooks. 2006. Recreation and large mammal activity in an urban nature reserve. Biological Conservation 133:107–117.
Gerber, B. D., S. M. Karpanty, and M. J. Kelly. 2012. Evaluating the potential biases in carnivore capture–recapture studies associated with the use of lure and varying density estimation techniques using photographic-sampling data of the Malagasy civet. Population Ecology 54:43–54.
Gese, E. M., P. S. Morey, and S. D. Gehrt. 2012. Influence of the urban matrix on space use of coyotes in the Chicago metropolitan area. Journal of Ethology 30:413–425.
Gil-Fernández, M., R. Harcourt, T. Newsome, A. Towerton, and A. Carthey. 2020. Adaptations of the red fox (*Vulpes vulpes*) to urban environments in Sydney, Australia. Journal of Urban Ecology 6:juaa009.
Goad, E. H., L. Pejchar, S. E. Reed, and R. L. Knight. 2014. Habitat use by mammals varies along an exurban development gradient in northern Colorado. Biological Conservation 176:172–182.
Gompper, M. E., D. B. Lesmeister, J. C. Ray, J. R. Malcolm, and R. Kays. 2016. Differential habitat use or intraguild interactions: what structures a carnivore community? PloS One 11:e0146055.
Gosselink, T. E., T. R. Van Deelen, R. E. Warner, and M. G. Joselyn. 2003. Temporal habitat partitioning and spatial use of coyotes and red foxes in east-central Illinois. Journal of Wildlife Management 67:90–103.
Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1:e1500052.
Handler, A. M., E. V. Lonsdorf, and D. R. Ardia. 2020. Evidence for red fox (*Vulpes vulpes*) exploitation of anthropogenic food sources along an urbanization gradient using stable isotope analysis. Canadian Journal of Zoology 98:79–87.
Harris, S., and J. M. V. Rayner. 1986. Urban fox (*Vulpes vulpes*) population estimates and habitat requirements in several British cities. Journal of Animal Ecology 55:575–591.
Haswell, P. M., J. Kusak, K. A. Jones, and M. W. Hayward. 2020. Fear of the dark? A mesopredator mitigates large carnivore risk through nocturnality, but humans moderate the interaction. Behavioral Ecology and Sociobiology 74:1–9.
Hody, J. W., and R. Kays. 2018. Mapping the expansion of coyotes (*Canis latrans*) across North and Central America. ZooKeys 759:81–97.
Hoffmann, C. O., and J. L. Gottschang. 1977. Numbers, distribution, and movements of a raccoon population in a suburban residential community. Journal of Mammalogy 58:623–636.
Holinda, D., J. M. Burgar, and A. C. Burton. 2020. Effects of scent lure on camera trap detections vary across mammalian predator and prey species. PloS One 15:e0229055.
Hooke, R. L., and J. F. Martín-Duque. 2013. Land transformation by humans: a review. GSA Today 12:4–10.
Kamler, J. F., U. Stenkewitz, U. Klare, N. F. Jacobsen, and D. W. Macdonald. 2012. Resource partitioning among cape foxes, bat-eared foxes, and black-backed jackals in South Africa. Journal of Wildlife Management 76:1241–1253.
Karelus, D. L., J. W. McCown, B. K. Scheick, M. van de Kerk, and B. M. Bolker. 2017. Effects of environmental factors and landscape features on movement patterns of Florida black bears. Journal of Mammalogy 98:1463–1478.
Kays, R., A. Hody, D. S. Jachowski, and A. W. Parsons. 2021. Empirical evaluation of the spatial scale and detection process of camera trap surveys. Movement Ecology 9:article 41.
Kays, R., B. Kranstauber, P. Jansen, C. Carbone, M. Rowcliffe, T. Fountain, and S Tilak. 2009. Camera traps as sensor networks for monitoring animal communities. IEEE Conference on Local Computer Networks 34:811–818.
Kellner, K. F., J. E. Hill, M. G. Gantchoff, D. W. Kramer, A. M. Bailey, and J. L. Belant. 2020. Responses of sympatric canids to human development revealed through citizen science. Ecology and Evolution 10:8705–8714.
Kitchen, A. M., E. M. Gese, and E. R. Schauster. 2000. Changes in coyote activity patterns due to reduced exposure to human persecution. Canadian Journal of Zoology 78:853–857.
Kolowski, J. M., J. Oley, and W. J. McShea. 2021. High-density camera trap grid reveals lack of consistency in detection and capture rates across space and time. Ecosphere 12:e03350.
Kuijper, D. P. J., J. W. Bubnicki, M. Churski, and J. P. G. M. Cromsigt. 2016. Multi-trophic interactions in anthropogenic landscapes: the devil is in the detail. Proceedings of the Royal Society B: Biological Sciences 283:20152375.
Larivière, S., and M. Pasitschniak-Arts. 1996. Vulpes vulpes. Mammalian Species 537:1–11.
Larson, C. L., S. E. Reed, A. M. Merenlender, and K. R. Crooks. 2016. Effects of recreation on animals revealed as widespread through a global systematic review. PloS One 11:e0167259.

19372817, 2023, 7, Downloaded from https://wildlife.onlinelibrary.wiley.com/doi/10.1002/jwmg.22474 by Columbia University Libraries, Wiley Online Library on [05/09/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Larson, R. N., J. L. Brown, T. Karels, and S. P. Riley. 2020. Effects of urbanization on resource use and individual specialization in coyotes (*Canis latrans*) in southern California. PLoS One 15:e0228881.

Lesmeister, D. B., C. K. Nielsen, E. M. Schauber, and E. C. Hellgren. 2015. Spatial and temporal structure of a mesocarnivore guild in midwestern north America. Wildlife Monographs 191:1–61.

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

Lombardi, J. V., C. E. Comer, D. G. Scognamillo, and W. C. Conway. 2017. Coyote, fox, and bobcat response to anthropogenic and natural landscape features in a small urban area. Urban Ecosystems 20:1239–1248.

Long, R. A., T. M. Donovan, P. MacKay, W. J. Zielinski, and J. S. Buzas. 2011. Predicting carnivore occurrence with noninvasive surveys and occupancy modeling. Landscape Ecology 26:327–340.

Lotze, J. H., and S. Anderson. 1979. Procyon lotor. Mammalian Species 119:1–8.

Lozano, J., A. Olszańska, Z. Morales-Reyes, A. A. Castro, A. F. Malo, M. Moleón, J. A. Sánchez-Zapata, A. Cortés-Avizanda, H. von Wehrden, I. Dorresteijn, et al. 2019. Human-carnivore relations: a systematic review. Biological Conservation 237:480–492.

Lucherini, M., J. I. Reppucci, R. S. Walker, M. L. Villalba, A. Wurstten, G. Gallardo, A. Iriarte, R. Villalobos, and P. Perovic. 2009. Activity pattern segregation of carnivores in the High Andes. Journal of Mammalogy 90:1404–1409.

MacKenzie, D. I. 2006. Modeling the probability of resource use: the effect of, and dealing with, detecting a species imperfectly. Journal of Wildlife Management 70:367–374.

MacKenzie, D. I., L. L. Bailey, and J. D. Nichols. 2004. Investigating species co-occurrence patterns when species are detected imperfectly. Journal of Animal Ecology 73:546–555.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2017. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier, London, United Kingdom.

Magioli, M., M. Z. Moreira, R. C. B. Fonseca, M. C. Ribeiro, M. G. Rodrigues, and K. M. Ferraz. 2019. Human-modified landscapes alter mammal resource and habitat use and trophic structure. Proceedings of the National Academy of Sciences 116:18466–18472.

Marks, C. A., and T. E. Bloomfield. 1999. Distribution and density estimates for urban foxes (*Vulpes vulpes*) in Melbourne: implications for rabies control. Wildlife Research 26:763–775.

Marzluff, J. M. 2001. Worldwide urbanization and its effects on birds. Pages 19–47 *in* J. M. Marzluff, R. Bowman, and R. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Springer, Boston, Massachusetts, USA.

McKinney, M. L. 2002. Urbanization, biodiversity, and conservation: the impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. Bioscience 52:883–890.

Meredith, M., and M. Ridout. 2021. Estimates of coefficient of overlapping for animal activity. <https://cran.r-project.org/web/packages/overlap/overlap.pdf>. Accessed 25 Feb 2021.

Mettler, A. E., and J. A. Shivik. 2007. Dominance and neophobia in coyote (*Canis latrans*) breeding pairs. Applied Animal Behaviour Science 102:85–94.

Mitchell, N., M. W. Strohbach, R. Pratt, W. C. Finn, and E. G. Strauss. 2015. Space use by resident and transient coyotes in an urban–rural landscape mosaic. Wildlife Research 42:461–469.

Moeller, A. K., S. J. Waller, N. J. DeCesare, M. C. Chitwood, and P. M. Lukacs. 2022. Best practices to account for capture probability and viewable area in camera-based abundance estimation. Remote Sensing in Ecology and Conservation 9:152–164.

Moll, R. J., J. D. Cepek, P. D. Lorch, P. M. Dennis, T. Robison, J. J. Millspaugh, and R. A. Montgomery. 2018. Humans and urban development mediate the sympatry of competing carnivores. Urban Ecosystems 21:765–778.

Moll, R. J., J. D. Cepek, P. D. Lorch, P. M. Dennis, T. Robison, and R. A. Montgomery. 2020. At what spatial scale (s) do mammals respond to urbanization? Ecography 43:171–183.

Moll, R. J., P. J. Jackson, B. F. Wakeling, C. W. Lackey, J. P. Beckmann, J. J. Millspaugh, and R. A. Montgomery. 2021. An apex carnivore's life history mediates a predator cascade. Oecologia 196:223–234.

Morin, D. J., D. B. Lesmeister, C. K. Nielsen, and E. M. Schauber. 2022. Asymmetrical intraguild interactions with coyotes, red foxes, and domestic dogs may contribute to competitive exclusion of declining gray foxes. Ecology and Evolution 12:e9074.

Mueller, M. A., D. Drake, and M. L. Allen. 2018. Coexistence of coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) in an urban landscape. PloS One 13:e0190971.

National Weather Service. 2022. Montgomery Orange County AP, New York: NOAA online weather data <https://www.weather.gov/wrh/Climate?wfo=okx>. Accessed 30 Jan 2021.

Newsome, S. D., H. M. Garbe, E. C. Wilson, and S. D. Gehrt. 2015. Individual variation in anthropogenic resource use in an urban carnivore. Oecologia 178:115–128.

19372817, 2023, 7, Downloaded from https://wildlife.onlinelibrary.wiley.com/doi/10.1002/jwmg.22474 by Columbia University Libraries, Wiley Online Library on [05/09/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Nouvellet, P., G. S. A. Rasmussen, D. W. Macdonald, and F. Courchamp. 2012. Noisy clocks and silent sunrises: measurement methods of daily activity pattern. Journal of Zoology 286:179–184.

Orange County New York Geographic Information System Division. 2022. Orange County G.I.S. <http://ocgis.orangecountygov.com/mra>. Accessed 10 Feb 2021.

Ordeñana, M. A., K. R. Crooks, E. E. Boydston, R. N. Fisher, L. M. Lyren, S. Siudyla, C. D. Haas, S. Harris, S. A. Hathaway, G. M. Turschak, A. K. Miles, and D. H. Van Vuren. 2010. Effects of urbanization on carnivore species distribution and richness. Journal of Mammalogy 91:1322–1331.

Parsons, A. W., K. F. Kellner, C. T. Rota, S. G. Schuttler, J. J. Millspaugh, and R. W. Kays. 2022. The effect of urbanization on spatiotemporal interactions between gray foxes and coyotes. Ecosphere 13:e3993.

Parsons, A. W., C. T. Rota, T. Forrester, M. C. Baker-Whatton, W. J. McShea, S. G. Schuttler, J. J. Millspaugh, and R. Kays. 2019. Urbanization focuses carnivore activity in remaining natural habitats, increasing species interactions. Journal of Applied Ecology 56:1894–1904.

Pluemer, M., S. Dubay, D. Drake, S. Crimmins, T. Veverka, H. Hovanec, M. Torkelson, and M. Mueller. 2019. Red foxes (*Vulpes vulpes*) and coyotes (*Canis latrans*) in an urban landscape: prevalence and risk factors for disease. Journal of Urban Ecology 5:juz022.

Poessel, S. A., S. W. Breck, and E. M. Gese. 2013. Spatial ecology of coyotes in the Denver metropolitan area: influence of the urban matrix. Journal of Mammalogy 97:1414–1427.

Prange, S., S. D. Gehrt, and E. P. Wiggers. 2003. Demographic factors contributing to high raccoon densities in urban landscapes. Journal of Wildlife Management 67:324–333.

Prange, S., S. D. Gehrt, and E. P. Wiggers. 2004. Influences of anthropogenic resources on raccoon (*Procyon lotor*) movements and spatial distribution. Journal of Mammalogy 85:483–490.

Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The rise of the mesopredator. BioScience 59:779–791.

R Core Team. 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Randa, L. A., and J. A. Yunger. 2006. Carnivore occurrence along an urban-rural gradient: a landscape-level analysis. Journal of Mammalogy 87:1154–1164.

Reilly, M. L., M. W. Tobler, D. L. Sonderegger, and P. Beier. 2017. Spatial and temporal response of wildlife to recreational activities in the San Francisco Bay ecoregion. Biological Conservation 207:117–126.

Rich, M., C. Thompson, S. Prange, and V. D. Popescu. 2018. Relative importance of habitat characteristics and interspecific relations in determining terrestrial carnivore occurrence. Frontiers in Ecology and Evolution 6:78.

Ridout, M. S., and M. Linke. 2009. Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural, Biological, and Environmental Statistics 14:322–337.

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

Riley, S. P., J. Hadidian, and D. A. Manski. 1998. Population density, survival, and rabies in raccoons in an urban national park. Canadian Journal of Zoology 76:1153–1164.

Riley, S. P., R. M. Sauvajot, T. K. Fuller, E. C. York, D. A. Kamradt, C. Bromley, and R. K. Wayne. 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. Conservation Biology 17:566–576.

Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, and B. Elmhagen. 2014. Status and ecological effects of the world's largest carnivores. Science 343:1241484.

Roemer, G. W., M. E. Gompper, and B. Van Valkenburgh. 2009. The ecological role of the mammalian mesocarnivore. BioScience 59:165–173.

Rowcliffe, M. 2021. Animal activity statistics. <https://cran.r-project.org/web/packages/activity/activity.pdf>. Accessed 10 Mar 2021.

Rowcliffe, M., R. Kays, B. Kranstauber, C. Carbone, and P. Jansen. 2014. Quantifying animal activity level using camera trap data. Methods in Ecology and Evolution 5:1170–1179.

Šálek, M., L. Drahníková, and E. Tkadlec. 2015. Changes in home range sizes and population densities of carnivore species along the natural to urban habitat gradient. Mammal Review 45:1–14.

Sargeant, A. B., S. H. Allen, and J. O. Hastings. 1987. Spatial relations between sympatric coyotes and red foxes in North Dakota. Journal of Wildlife Management 51:285–293.

Schuette, P., A. P. Wagner, M. E. Wagner, and S. Creel. 2013. Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. Biological Conservation 158:301–312.

Seveque, A., L. K. Gentle, J. V. López-Bao, R. W. Yarnell, and A. Uzal. 2020. Human disturbance has contrasting effects on niche partitioning within carnivore communities. Biological Reviews 95:1689–1705.

Shores, C. R., J. A. Dellinger, E. S. Newkirk, S. M. Kachel, and A. J. Wirsing. 2019. Mesopredators change temporal activity in response to a recolonizing apex predator. Behavioral Ecology 30:1324–1335.

19372817, 2023, 7, Downloaded from https://wildlife.onlinelibrary.wiley.com/doi/10.1002/jwmg.22474 by Columbia University Libraries, Wiley Online Library on [05/09/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Sirami, C., P. Caplat, S. Popy, A. Clamens, R. Arlettaz, F. Jiguet, L. Brotons, and J.-L. Martin. 2017. Impacts of global change on species distributions: obstacles and solutions to integrate climate and land use. Global Ecology and Biogeography 26:385–394.

Smith, J. A., A. C. Thomas, T. Levi, Y. Wang, and C. C. Wilmers. 2018. Human activity reduces niche partitioning among three widespread mesocarnivores. Oikos 127:890–901.

Socioeconomic Data and Applications Center. 2010. NASA Socioeconomic Data and Applications Center. U.S. Census Grids. <https://sedac.ciesin.columbia.edu/data/collection/usgrid> Accessed 12 Jan 2023.

Sollmann, R. 2018. A gentle introduction to camera-trap data analysis. African Journal of Ecology 56:740–749.

Soulsbury, C. D., P. J. Baker, G. Iossa, and S. Harris. 2010. Red foxes (*Vulpes vulpes*). Pages 63–75 *in* S. D. Gehrt, S. P. D. Riley, and B. L. Cypher, editors. Urban carnivores: ecology, conflict, and conservation. Johns Hopkins University Press, Baltimore, Maryland, USA.

Stewart, F. E., J. P. Volpe, and J. T. Fisher. 2019. The debate about bait: a red herring in wildlife research. Journal of Wildlife Management 83:985–992.

Suraci, J. P., M. Clinchy, L. Y. Zanette, and C. C. Wilmers. 2019. Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. Ecology Letters 22:1578–1586.

Temple, D. L., M. J. Chamberlain, and L. M. Conner. 2010. Spatial ecology, survival and cause-specific mortality of gray foxes (*Urocyon cinereoargenteus*) in a longleaf pine ecosystem. American Midland Naturalist 163:413–422.

Tigas, L. A., D. H. Van Vuren, and R. M. Sauvajot. 2002. Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. Biological Conservation 108:299–306.

U.S. Census Bureau. 2020. United States Census Bureau: Newburgh City, New York. <https://www.census.gov/en.html>. Accessed 30 Jan 2021.

U.S. Forest Service. 1992. New York-New Jersey Highlands regional study. Report to Congress. U.S. Department of Agriculture, Washington, D.C., USA.

U.S. Geological Survey. 2019. 1-arc second resolution digital elevation model (DEM). The National Map. <https://nationalmap.gov/>. Accessed 10 Feb 2021.

Vazquez, C., J. M. Rowcliffe, K. Spoelstra, and P. A. Jansen. 2019. Comparing diel activity patterns of wildlife across latitudes and seasons: time transformations using day length. Methods in Ecology and Evolution 10:2057–2066.

Wagenmakers, E. J., and S. Farrell. 2004. AIC model selection using Akaike weights. Psychonomic Bulletin & Review 11: 192–196.

Wang, Y., M. L. Allen, and C. C. Wilmers. 2015. Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. Biological Conservation 190:23–33.

Wei, T., and V. Simko. 2021. R package "corrplot": visualization of a correlation matrix. <https://github.com/taiyun/corrplot>. Accessed 25 Feb 2022.

White, L. A., and S. D. Gehrt. 2009. Coyote attacks on humans in the United States and Canada. Human Dimensions of Wildlife 14:419–432.

Wilson, M. W., A. D. Ridlon, K. M. Gaynor, S. D. Gaines, A. C. Stier, and B. S. Halpern. 2020. Ecological impacts of human-induced animal behaviour change. Ecology Letters 23:1522–1536.

Witmer, G. W., and D. S. DeCalesta. 1986. Resource use by unexploited sympatric bobcats and coyotes in Oregon. Canadian Journal of Zoology 64:2333–2338.

Young, J. K., J. M. Golla, D. Broman, T. Blankenship, and R. Heilbrun. 2019. Estimating density of an elusive carnivore in urban areas: use of spatially explicit capture-recapture models for city-dwelling bobcats. Urban Ecosystems 22: 507–512.

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## SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

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## APPENDIX A: WALD TEST RESULTS FOR COYOTE, RACCOON, AND RED FOX ACROSS ALL CAMERA SITES

Table A1

**TABLE A1** Results of Wald tests used to compare the 24-hour and nocturnal activity levels of coyote, raccoon, and red fox across all urban (U), semiurban (SU), and rural (R) camera sites deployed in eastern Orange County, New York, USA, May to September 2021.

| Species | Difference[a] | SE[b] | *W*[c] | *P*[d] |
|---|---|---|---|---|
| 24-hour activity[e] | | | | |
| U. red fox − SU. red fox | −0.059 | 0.061 | 0.959 | 0.327 |
| U. red fox − R. red fox | 0.051 | 0.079 | 0.411 | 0.522 |
| SU. red fox − R. red fox | 0.110 | 0.069 | 2.542 | 0.111 |
| U. raccoon − SU. raccoon | 0.105 | 0.058 | 3.330 | 0.068 |
| U. raccoon − R. raccoon | 0.025 | 0.062 | 0.168 | 0.682 |
| SU. raccoon − R. raccoon | −0.080 | 0.064 | 1.579 | 0.209 |
| U. coyote − SU. coyote | −0.009 | 0.094 | 0.008 | 0.927 |
| U. coyote − R. coyote | 0.100 | 0.095 | 1.103 | 0.294 |
| SU. coyote − R. coyote | 0.109 | 0.090 | 1.480 | 0.224 |
| Nocturnal activity[f] | | | | |
| U. red fox − SU. red fox | −0.249 | 0.121 | 4.238 | 0.040 |
| U. red fox − R. red fox | 0.110 | 0.137 | 0.650 | 0.420 |
| SU. red fox − R. red fox | 0.359 | 0.128 | 7.822 | 0.005 |
| U. raccoon − SU. raccoon | 0.131 | 0.178 | 1.228 | 0.268 |
| U. raccoon − R. raccoon | 0.031 | 0.113 | 0.074 | 0.785 |
| SU. raccoon − R. raccoon | −0.100 | 0.114 | 0.764 | 0.382 |
| U. coyote − SU. coyote | 0.126 | 0.143 | 0.773 | 0.379 |
| U. coyote − R. coyote | 0.208 | 0.135 | 2.358 | 0.125 |
| SU. coyote − R. coyote | 0.082 | 0.147 | 0.305 | 0.581 |

[a]Differences between activity estimates of 2 site types.

[b]Standard errors of the differences.

[c]Wald statistics.

[d]*P*-values ($P < 0.05$ is a significant difference between species).

[e]The percentage of the 24-hour day that an animal is active.

[f]The percentage of the period between dusk (2041) and dawn (0515) that an animal is active.

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## APPENDIX B: WALD TEST RESULTS FOR COYOTE, RACCOON, RED FOX DETECTED AT SAME CAMERA SITES

Table B1

**TABLE B1** Results of a Wald test used to compare the 24-hour and nocturnal activity levels between coyote-red fox, coyote-raccoon, and raccoon-red fox when each species pair was detected at the same urban (U), semiurban (SU), and rural (R) camera sites deployed in eastern Orange County, New York, USA, May to September 2021.

| Species | Difference[a] | SE[b] | *W*[c] | *P*[d] |
|---|---|---|---|---|
| 24-hour activity[e] | | | | |
| U. red fox − U. coyote | −0.049 | 0.104 | 0.225 | 0.635 |
| SU. red fox − SU. coyote | −0.039 | 0.066 | 0.344 | 0.558 |
| R. red fox − R. coyote | −0.049 | 0.102 | 0.237 | 0.627 |
| U. raccoon − U. coyote | −0.234 | 0.084 | 7.715 | 0.005 |
| SU. raccoon − SU. coyote | −0.217 | 0.087 | 6.186 | 0.013 |
| R. raccoon − R. coyote | 0.012 | 0.084 | 0.020 | 0.887 |
| U. raccoon − U. red fox | 0.031 | 0.064 | 0.240 | 0.624 |
| SU. raccoon − SU. red fox | −0.154 | 0.052 | 8.850 | 0.003 |
| R. raccoon − R. red fox | 0.081 | 0.087 | 0.858 | 0.354 |
| Nocturnal activity[f] | | | | |
| U. red fox − U. coyote | −0.169 | 0.144 | 1.375 | 0.241 |
| SU. red fox − SU. coyote | 0.027 | 0.131 | 0.042 | 0.838 |
| R. red fox − R. coyote | −0.048 | 0.140 | 0.116 | 0.734 |
| U. raccoon − U. coyote | −0.299 | 0.120 | 6.170 | 0.013 |
| SU. raccoon − SU. coyote | −0.023 | 0.147 | 0.023 | 0.879 |
| R. raccoon − R. coyote | 0.212 | 0.127 | 2.768 | 0.096 |
| U. raccoon − U. red fox | −0.217 | 0.124 | 3.063 | 0.080 |
| SU. raccoon − SU. red fox | −0.191 | 0.115 | 2.730 | 0.098 |
| R. raccoon − R. red fox | 0.196 | 0.140 | 1.975 | 0.162 |

[a]Differences between activity estimates of 2 mesocarnivore species.

[b]Standard errors of the differences.

[c]Wald statistics.

[d]*P*-values ($P < 0.05$ is a significant difference between species).

[e]The percentage of the 24-hour day that an animal is active.

[f]The percentage of the period between dusk (2041) and dawn (0515) that an animal is active.

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