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Authors

Veon, JT
Lassiter, EV
Johansson, E
et al.

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ORIGINAL RESEARCH

Influence of human development and predators on patterns of Virginia opossum occupancy, abundance, and activity

J. T. Veon¹ , E. V. Lassiter¹, E. Johansson¹, M. Shaw¹, L. McTigue¹, A. Massey^{1,*}, R. Gibson¹ & B. A. DeGregorio²

¹Department of Biological Sciences, University of Arkansas, Fayetteville, AR, USA

²US Geological Survey, Arkansas Cooperative Fish and Wildlife Research Unit, University of Arkansas, AR, Fayetteville, USA

Keywords

animal behavior; bobcat; coyote; *Didelphis virginiana*; camera trapping; urbanization; anthropogenic environments; urban ecology.

Correspondence

John T. Veon, Department of Wildlife, Fish, and Conservation Biology, University of California-Davis, Davis, CA 95616, USA.

Email: jtveon@ucdavis.edu

*Current address: Center for Environmental Management of Military Lands, Colorado State University, Fort Polk, LA, USA

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Abstract

As human development continues to expand, wildlife must relocate or adapt to survive. Many mammalian mesopredators, such as the Virginia opossum (*Didelphis virginiana*), have adapted to living alongside human development. Furthermore, top-down predation pressure may be altered in nuanced ways within the human environment. Species such as opossums may be shielded from predation by human development or behavioral changes in predators. Understanding how dominant and subordinate mesopredators co-exist across natural and developed areas will provide insight into how wildlife communities are structured. Our objective was to evaluate how opossum occupancy, abundance, and activity were associated with human development and the relative abundance of their predators. We used data from a nationwide camera trapping study, Snapshot USA, to estimate opossum occupancy, abundance, and activity. We related these measures to the surrounding landscape and urbanization variables. We found that opossum occupancy was positively associated with anthropogenic sound (a surrogate for human activity). Furthermore, opossums in heavily forested areas were more likely to be detected in locations with higher predicted anthropogenic sounds. In areas with a high density of human housing, opossum relative abundance increased when predator abundance increased. We also found opossums were strictly nocturnal and shifted their activity to earlier in the evening in the presence of high predator abundance. Our results suggest that humans and their urban development can have multidimensional impacts on opossum behavior and occurrence, and could facilitate changes in predator-prey dynamics. Future research should evaluate if the association of opossums with urban areas is due to human-subsidized resources or caused by reduced mortality from altered predator-prey dynamics.

Introduction

As urban sprawl continues to expand, human development radically displaces and transforms ecosystems (Tian et al., 2022). Human development can be referred to as areas that have some degree of human modification of the environment which can range from low density housing to high density urban development (Wang et al., 2015). While many species of wildlife avoid developed spaces, other species have adapted their behavior to co-exist within humans (Bozek et al., 2007; Greenspan et al., 2018). These urban adapted species modify their behavior (e.g. habitat use, activity patterns, diets) to exist within environments that are frequently loud, bright, and dominated by human development (Gese et al., 2012; Magle et al., 2016). Those species that do successfully adapt to

human-dominated environments are rewarded with access to human-subsidized resources, such as supplemental food, water, and shelter sites (Belaire et al., 2015; Demeny et al., 2019; Wright et al., 2012).

Mammalian mesopredators, which are medium-sized carnivores, are frequent human adapters capable of existing along a continuum of human development and activity (Greenspan et al., 2018; Magle et al., 2016; Tucker et al., 2021). Mesopredators often attain high densities in human-dominated areas and can constitute a large proportion of the mammal community (Bateman & Fleming, 2012; Tucker et al., 2021). Mesopredators take advantage of food, refugia, and water left or created by humans and may persist in yards, parks, cemeteries, and riparian areas (McKinney, 2002; Nickel et al., 2020; Wright et al., 2012). Often, mesopredators occurring in

developed areas will attain increased body size, survival rates, and higher population densities than in natural areas due to the combined effects of reduced predation, access to resources provided by humans, and habitat restriction that elevates local density and reduces home ranges (Bateman & Fleming, 2012; Kanda *et al.*, 2009; Prange *et al.*, 2003; Wright *et al.*, 2012).

Mesopredator responses to human development are often complicated and can lead to interesting patterns of occupancy and behavior. Larger-bodied mesopredators that outcompete or depredate smaller mesopredators are often referred to as dominant over the smaller-bodied subordinate species (Gámez & Harris, 2021; Moll *et al.*, 2018). Many dominant mesopredators are less likely to occur in developed areas due to harassment by humans (e.g. Ordeñana *et al.*, 2010). In such cases, subordinate urban mesopredators may benefit through a reduction in predation risk from their natural predators, a phenomenon referred to as the Human Shield Hypothesis (HSH; Gámez & Harris, 2021; Moll *et al.*, 2018). The human shield effect can be spatial if dominant predators avoid urban areas and structures, or it can be a more complicated spatio-temporal effect whereby dominant and subordinate species use the same areas but at different times (Moll *et al.*, 2018; Vanak *et al.*, 2013). However, some dominant mesopredators can be urban adapted and can take advantage of the same human-provided resources as the subordinate mesopredators and attain high densities in developed areas (Gehrt *et al.*, 2011; Larson *et al.*, 2020). This can lead to increased agonistic interactions for subordinate mesopredators. However, in other cases the higher density of predators in urban areas may not lead to a corresponding increase in predation pressure as human-provided resources may disrupt top-down predator–prey interactions, a phenomenon referred to as the Urban Predation Paradox (reviewed in Fischer *et al.*, 2012).

In addition to complex changes in the occurrence and relative abundance of mesopredators and their predators in response to development, wildlife often shift their behavior to better persist in urban areas (Gaynor *et al.*, 2018). A common response is a shift in activity patterns toward the night when humans are least active (Hubbard *et al.*, 2022). However, when dominant mesopredators shift to a primarily nocturnal existence, subordinate mesopredators are faced with the pressure of either being active during the day when humans are active or at night when their predators are most active.

Here, we investigate how patterns of occupancy, relative abundance, and daily activity patterns of a widespread mesopredator, the Virginia opossum (hereafter, opossum: *Didelphis virginiana*), change in response to human development (i.e. developed open space, development, housing unit density, anthropogenic sound) and the relative abundance of their predators (coyote, *Canis latrans* and bobcat, *Lynx rufus*). We chose to use coyotes and bobcats because they most frequently depredate or kill opossums (Gipson & Kamler, 2001; Rose & Prange, 2015). Due to their adaptability, human-tolerance, and susceptibility to predation, the opossum makes for an excellent candidate to study distributional and behavioral responses of wildlife to development and predators. We used data from a coordinated, nationwide camera trapping study (Snapshot USA; Cove *et al.*, 2021; Kays *et al.*, 2022) to evaluate if opossum

occurrence, abundance, and behavior vary based on human development or predator abundance. We predicted that opossum will be more likely to occur and attain higher relative abundances in areas of human development due to their documented ability to take advantage of resources left behind by humans. However, we also predicted that patterns in the relative abundance of their primary predators (i.e. coyote and bobcat) will influence their occurrence, relative abundance, and behavior. We predicted that opossums likely experience a reduction in predation pressure in developed areas and thus opossum abundance and occurrence will increase with human development regardless of the relative abundance of their predators. Conversely, because human development may disrupt predator–prey interactions or provide opossums with a human shield, we predicted that opossum occupancy and relative abundance will be low in areas of high relative predator abundance without human development. Furthermore, we anticipated that opossums would alter their activity patterns in the presence of human development, such that opossums in developed areas will be more active during the night than those in natural areas.

Materials and methods

Data collection

We used data from a coordinated, nationwide camera trapping study, Snapshot USA. The majority of data from 2019 and 2020 were collected by Snapshot USA contributors during Sept–Nov 2019 and 2020 (Cove *et al.*, 2021; Kays *et al.*, 2022). However, some project contributors provided data spanning July–Dec. All contributors collected data following a standardized camera deployment protocol (refer to Cove *et al.*, 2021 for full details). Each contributor deployed between 8 and 40 motion-triggered game cameras at a chosen study site referred to as a subproject. Cameras were placed a minimum of 200 m apart and a maximum of 5 km. Cameras should not have been deployed along travel corridors or associated with particular landscape features that could artificially increase wildlife detections, but rather deployment sites should have been chosen to represent the surrounding environment. We imported coordinates of all cameras from the Snapshot USA contributors into a geographic information system (GIS) (ESRI, 2011). We only included Snapshot USA subprojects that occurred within the geographic distribution of the opossum ($n = 168$ of 212 subprojects) determined by the geographic distribution of occurrence records of the species from the Biodiversity Information Serving Our Nation (BISON) database (USGS, 2015 accessed October 2021; Fig. 1).

We first created 500 m buffers around each camera included in the study. We chose 500 m because it is a commonly used spatial scale for camera trap studies and represents the biologically meaningful home range of the opossum (Fidino *et al.*, 2016; Gallo *et al.*, 2017; Magle *et al.*, 2016). Furthermore, we chose to only analyze variables at the 500 m buffer scale to avoid data-dredging biases associated with analyzing variables at multiple scales that may not be as biologically relevant (Erasmus *et al.*, 2022). Within these buffers, we

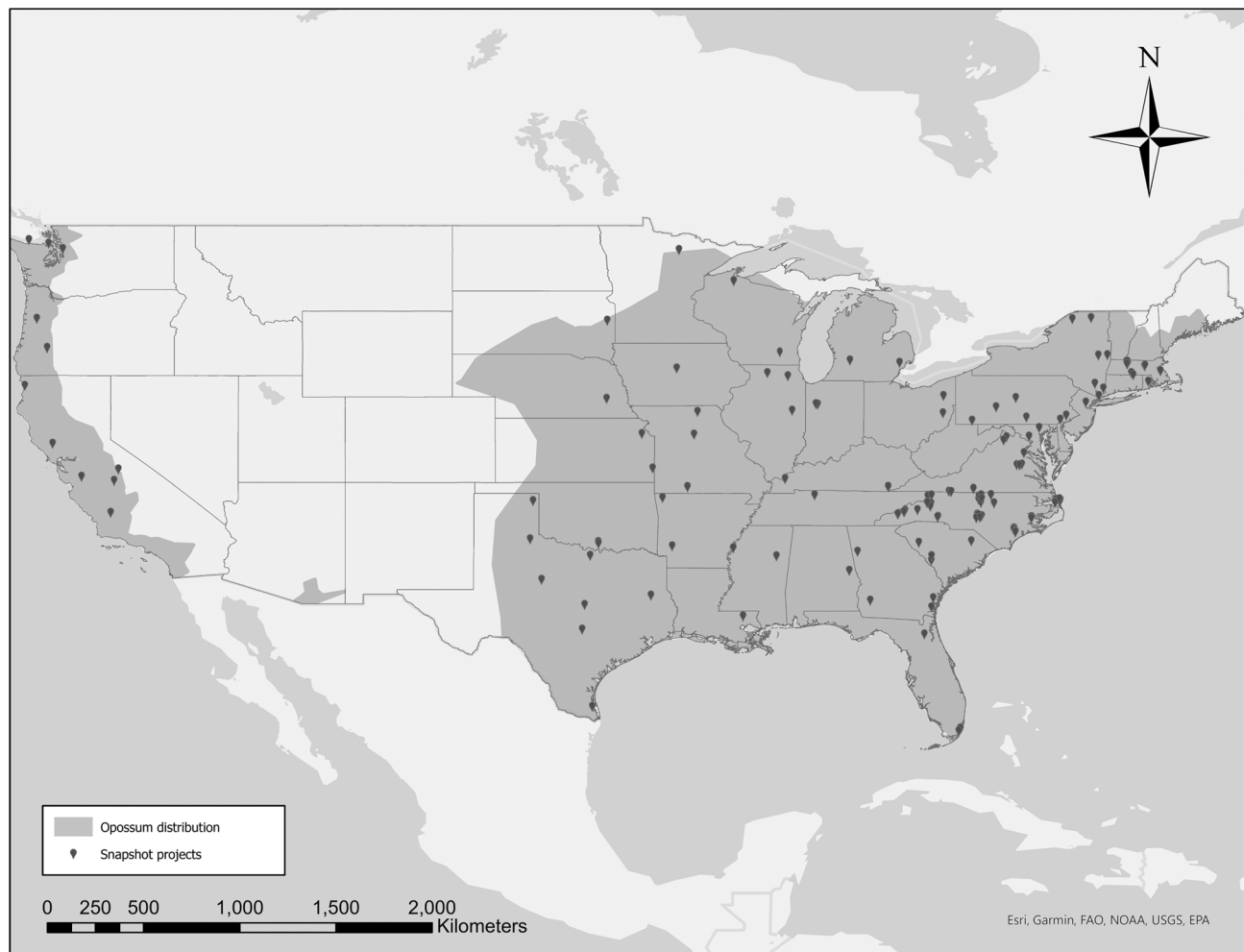


Figure 1 A map of the Virginia opossum (*Didelphis virginiana*) geographic range in the United States, as well as camera subprojects used within analyses containing camera traps from Snapshot USA data during 2019 and 2020. Geographic range was determined by occurrence data from the Biodiversity Information Serving Our Nation (BISON) database (USGS, 2015 accessed October 2021).

calculated a number of landscape variables that would later be used in analyses of opossum occupancy, abundance, and activity. Within each buffer, we calculated the total area (m^2) of forest cover, developed open space (hereafter, DOS; cemeteries, parks, and lawns), and developed areas using the 2016 National Land Cover Database (Dewitz, 2019). We combined the moderate and high development categories within the National Land Cover Database to calculate our development variable because both represent areas that contain greater than 50% impervious surface. We also quantified the maximum housing unit density (hereafter, HUD; km^2) around each camera using the SILVIS Housing Data Layer (Hammer *et al.*, 2004). Finally, we calculated the estimated anthropogenic sound around each camera location using the US National Park Service 250 m^2 Geospatial Model (Buxton *et al.*, 2017; Mennitt & Frstrup, 2016). To create this data, acoustic recordings from 2000 to 2014 scattered across the United States in urban and rural areas were used as response

variables for a random forest machine learning algorithm, and 45 landscape and environmental variables were used as predictors (Buxton *et al.*, 2017). Anthropogenic sound levels were calculated by systematically minimizing contributions from all anthropogenic model inputs, leaving only biotic and abiotic sources of sound. Here, we used the 'L50' anthropogenic sound level estimate, which is defined as the sound level exceeded 50% of times during an average summer daytime hour. We assumed that higher levels of L50 sound correspond to higher human presence and activity in an area. Because this anthropogenic sound layer incorporates a large number of landscape, landscape, and anthropogenic factors, it often differs substantially from the distribution of simple human development.

At each camera site, we calculated the relative abundance (or detection rate) of coyotes and bobcats, which are two known predators of opossums (Gipson & Kamler, 2001) present throughout the geographic scope of the study. We define a

unique sighting as a camera detection by a species within a one-minute window, while relative abundance represents the total number of sightings of each species divided by the number of days the camera was active. The relative abundance of coyotes and bobcats were then combined to create a relative abundance of predators variable.

For all covariates used for each subsequent analysis, we checked collinearity via Spearman's rank correlation (r) using 0.5 as a cut-off (Shaker & Sirodoev, 2016) (Table 1). No covariates were removed from analysis, though correlated covariates were not included within a single candidate model. Covariates were then standardized by centering on the mean and scaling by standard deviation.

Opossum occupancy

We constructed single-season occupancy models (MacKenzie *et al.*, 2002) to estimate the probability of opossum occurrence and to explore the influence of covariates on occupancy. We combined 2019 and 2020 data into a single analysis creating unique site \times year combinations. We adopted this approach because sites were sampled during the same time frame during both years and, while some subprojects were used in both years, the camera locations were not always kept the same between years. Thus, this approach allowed us to use the most available data without removing cameras from any of the resampled sites that were in different locations in 2020 than in 2019. To ensure site closure during the sampling period, we restricted analysis to a 9-week period during Sept–Oct when the majority of cameras were active (e.g. Allen *et al.*, 2022).

Therefore, we included 1873 cameras across 134 subprojects in occupancy analyses. We created a detection history for each camera by consolidating data into one-week segments. One-week segments are frequently used to delineate survey periods in camera trap analyses and considered to be an appropriate length of time by balancing over-compressing and under-compressing for statistical power (Fidino *et al.*, 2019; Rodriguez *et al.*, 2021; Trolle & Kéry, 2003). Camera locations were not uniformly active during the entire sampling period; thus, we kept all camera locations in the analysis, but censored observations as necessary by using 'NA' instead of 0 when we constructed the observation histories for the analysis. We also excluded any cameras that were not active for at least one full sampling period.

For occupancy covariates, we included forest cover, development, DOS, HUD, anthropogenic sound, predator relative abundance, and year. We used total number of days a camera was active as the covariate of detection. Our candidate model set included each possible pair of landscape covariates, including both additive and interactive effects, as well as year. We performed all model fitting in R Computing Software (R Core Team, 2022) with the 'unmarked' package (Fiske & Chandler, 2011). Model selection was conducted using Akaike's Information Criterion (AIC) approach to improve accuracy and reduce potential model overfitting (Burnham & Anderson, 2002). To improve clarity in presenting model selection tables, we display only models that were competitive within 4 Δ AIC. However, full results are presented in supplementary information (Table S1). Similarly, when applicable, parameter estimates were derived by model averaging all models within

Table 1 Spearman's rank correlation between covariates (r) used in occupancy, relative abundance, and activity analyses of Virginia opossum (*Didelphis virginiana*)

	Sound	DOS	Development	Forest	HUD	Predators
Occupancy						
Sound	1.00	0.61	0.41	-0.24	0.34	-0.01
DOS	0.61	1.00	0.50	-0.16	0.52	0.01
Development	0.41	0.50	1.00	-0.12	0.34	-0.01
Forest	-0.24	-0.16	-0.12	1.00	-0.09	0.01
HUD	0.34	0.52	0.34	-0.09	1.00	0.02
Predators	-0.01	0.01	-0.01	0.01	0.02	1.00
Abundance						
Sound	1.00	0.76	0.57	-0.22	0.77	0.00
DOS	0.76	1.00	0.65	-0.11	0.71	-0.02
Development	0.57	0.65	1.00	-0.14	0.52	-0.06
Forest	-0.22	-0.11	-0.14	1.00	-0.13	-0.03
HUD	0.77	0.71	0.52	-0.13	1.00	0.01
Predators	0.00	-0.02	-0.06	-0.03	0.01	1.00
Activity						
Sound	1.00	0.82	0.56	0.00	0.83	0.01
DOS	0.82	1.00	0.65	-0.01	0.80	0.00
Development	0.56	0.65	1.00	-0.08	0.56	-0.11
Forest	0.00	-0.01	-0.08	1.00	-0.05	-0.16
HUD	0.83	0.80	0.56	-0.05	1.00	-0.04
Predators	0.01	0.00	-0.11	-0.16	-0.04	1.00

DOS, developed open space; HUD, housing unit density.

4 Δ AIC (Burnham & Anderson, 2002). If the top model(s) included an interactive effect, visualization of the relationship was facilitated by binning one of the covariates into low, medium, and high categories. Categories were determined using minus one standard deviation as low, the mean as medium, and plus one standard deviation as high. Additionally, we tested model goodness-of-fit on the global model using the MacKenzie and Bailey (2004) goodness-of-fit test for occupancy models.

Opossum abundance

For each game camera included in the study, we calculated the rate of opossum detection defined as the number of opossum detections divided by the number of days the camera was deployed. While this detection rate should not be confused with true abundance, it is a commonly used index of relative abundance derived and reported from camera trapping studies and is often reliable (Gerber *et al.*, 2010; O'Brien, 2011; Palmer *et al.*, 2018).

To explore variables that affected opossum relative abundance, we used generalized linear mixed models in R Computing Software using the 'lme4' package (Bates *et al.*, 2015). Because generalized linear mixed models do not make closure assumptions, we included data from all 1923 cameras spread across all 168 subprojects. Because the distribution of our response was right skewed and thus violated normality assumptions, we fitted models using a gamma distribution with a log link function (Robinson *et al.*, 2006). We created a set of candidate models using all two-way additive and interactive combinations of forest cover, development, DOS, HUD, anthropogenic sound, and predator relative abundance. We used opossum relative abundance as our response variable, and subproject as our random variable on the intercept to account for climatic and landscape similarities between cameras within subproject. If the top model(s) included an interactive effect, visualization of the relationship was facilitated by applying the same methods used for occupancy model figures. However, in cases where the HUD independent variable occurred in top models, we used zero HUD for the low category because HUD was right skewed and using minus one standard deviation would result in associating a negative low HUD value to opossum relative abundance, which is biologically unrealistic. Therefore, because minus one standard deviation of HUD and a biologically realistic value of zero HUD hold very similar trends with opossum relative abundance in our top model set, we present low HUD as zero HUD for visualization purposes. Finally, we assessed goodness-of-fit on a set of global models for relative abundance, to avoid the inclusion of correlated covariates, using residual plots.

Opossum activity

To explore the daily activity patterns of opossums, we recorded the timing of each individual opossum detection. We converted all times of detection for each opossum to 'minutes after sunset'. We calculated the time of each sunset for each

camera for each day of the study using the R package 'suncalc' meaning that our sunset times varied across the season and reflected the true sunset time for that day and that location (Thieurmel & Elmarhraoui, 2022).

To explore variables that influenced opossum activity, we used generalized linear mixed models in R Computing Software using the 'lme4' package (Bates *et al.*, 2015). Because the distribution of our response was right skewed and thus violated normality assumptions, we fitted models using a gamma distribution with a log link function (Robinson *et al.*, 2006). We used the minutes after sunset for each opossum detection as our response variable because this provided a biologically meaningful reference point by which to assess the timing of opossum activity. Because 91.7% of opossum activity occurred after sunset, we excluded points that occurred before sunset because doing so allowed our data to better fit the model assumptions. We used the same candidate models and random variable used in the relative abundance analyses described above. Model goodness-of-fit was assessed on a set of activity global models using the same methods as relative abundance models. For the activity analysis, we included data from 639 cameras spread across 125 subprojects.

Results

Cameras used in the occupancy analysis, collected a total of 71 827 trap nights and 1666 opossum detections. Cameras used in the abundance analysis collected a total of 66 193 trap nights and 5000 opossum detections. These cameras collected a total 5000 opossum detections (although we use only the 4804 opossum detections in the activity analysis). We used 2397 coyote detections and 407 bobcat detections to calculate subproject and camera-specific predator detection rates.

Opossum occupancy

Naïve occupancy (proportion of surveys in which opossums were detected) of opossums across the study was 0.32. Predicted opossum occupancy was 0.32 (95% CI = 0.29–0.35) and detection probability was 0.44 (95% CI = 0.41–0.46). Occupancy probability was best predicted by the interaction between anthropogenic sound and forest cover ($\beta = 0.26$; 95% CI = 0.13–0.38) (Fig. 2). This top model received 99% of the weight of evidence, and no other models were within 4 Δ AIC units (Table S1). The interactive model indicated that when anthropogenic sound levels were high (11.53 dB), opossum occupancy probability increased with increased forest cover, whereas in areas with low (2.67 dB) and medium (7.10 dB) levels of anthropogenic sound, opossums were negatively associated with forest cover (Fig. 2).

Opossum abundance

Opossum relative abundance was best explained by the interaction between HUD and predator abundance ($\beta = 0.08$; 95% CI = 0.02–0.15). This top model received 99% of the weight of evidence and the next competing model was 10.77 Δ AIC

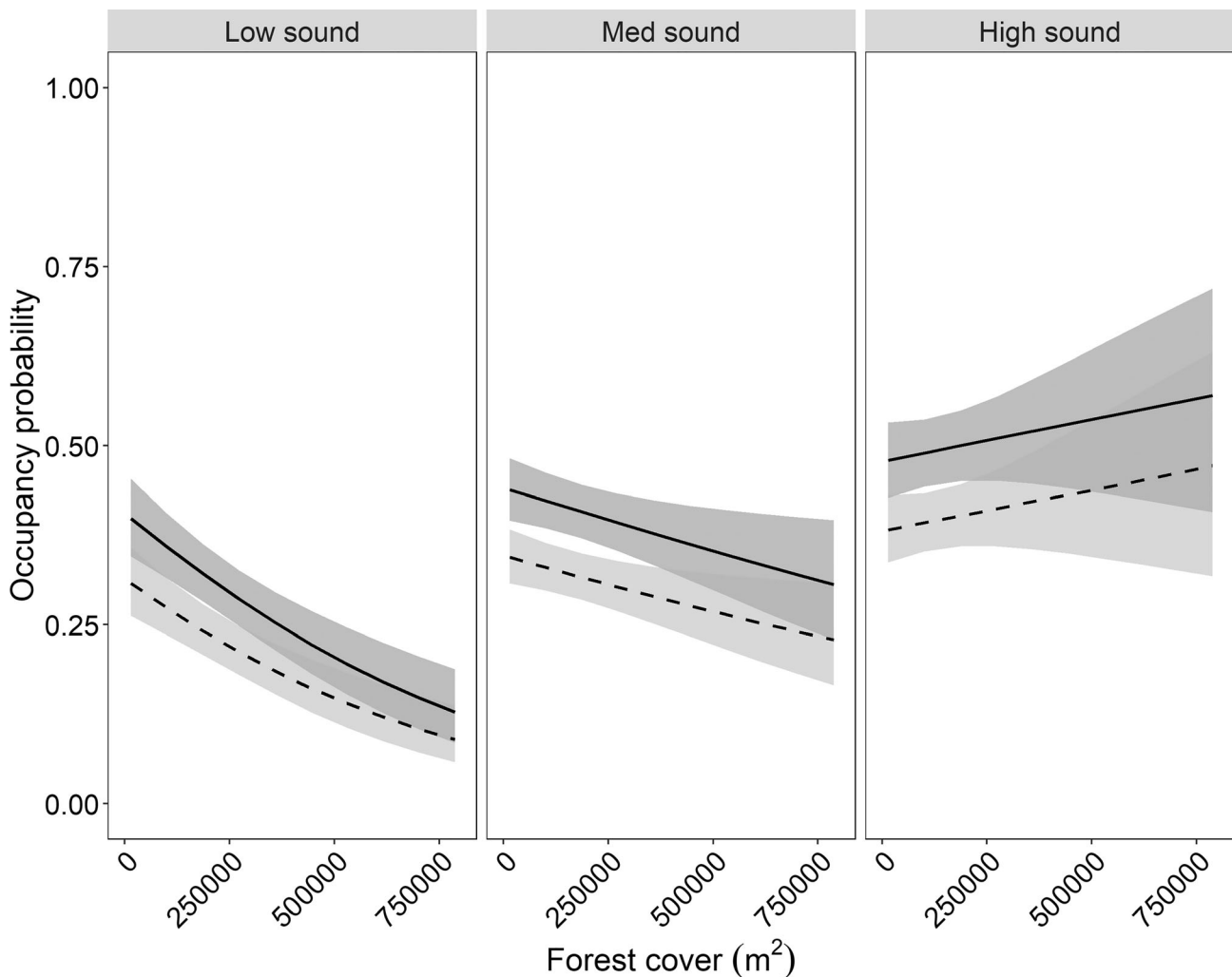


Figure 2 The interactive effects of anthropogenic sound and forest cover on Virginia opossum (*Didelphis virginiana*) occupancy probability across the species' geographic range in the United States. Sound was binned using minus one standard deviation (low [2.67 dB]), mean (medium [med; 7.10 dB]), and plus one standard deviation (high [11.53 dB]) for ease of visualization. 95% confidence intervals are presented using a gray band. Site occupancy was assessed using camera traps from Snapshot USA data during 2019 (dashed line) and 2020 (solid line).

below it (Table S2). This model indicated that at high levels of HUD (2991.78 km²), opossum relative abundance increased even in situations where predator abundance was high, whereas at low (0 km²) or moderate (440.27 km²) levels of HUD, opossum abundance barely increased when predator abundance did (Fig. 3).

Opossum activity

Of our 5000 opossum detections, 4587 (91.7%) occurred during the night (Fig. 4). Although opossums were detected at varying times throughout the night, the average time of activity was 298 min (approximately 5 h) after sunset.

Opossum activity, the time of night an opossum was detected on camera, was best predicted by predator relative abundance (model averaged $\beta = -0.03$; 95% CI = -0.05 to

-0.01), with predator relative abundance in all 10 top models paired with development, sound, forest, DOS, and HUD (Table 2; Table S3). Collectively, all 10 models that included predator abundance accounted for 94% of the weight of evidence. As the relative abundance of predators increased, we found that opossums were more likely to be detected closer to sunset (Fig. 5).

To provide the reader the extent to which top model continuous variables ranged, we have included histograms of each in the supplementary documentation (Figs S1–S7).

Discussion

The opossum is a well-documented urban-associated mesopredator that can take advantage of human-provided resources, such as compost piles, refuse, and denning sites in buildings

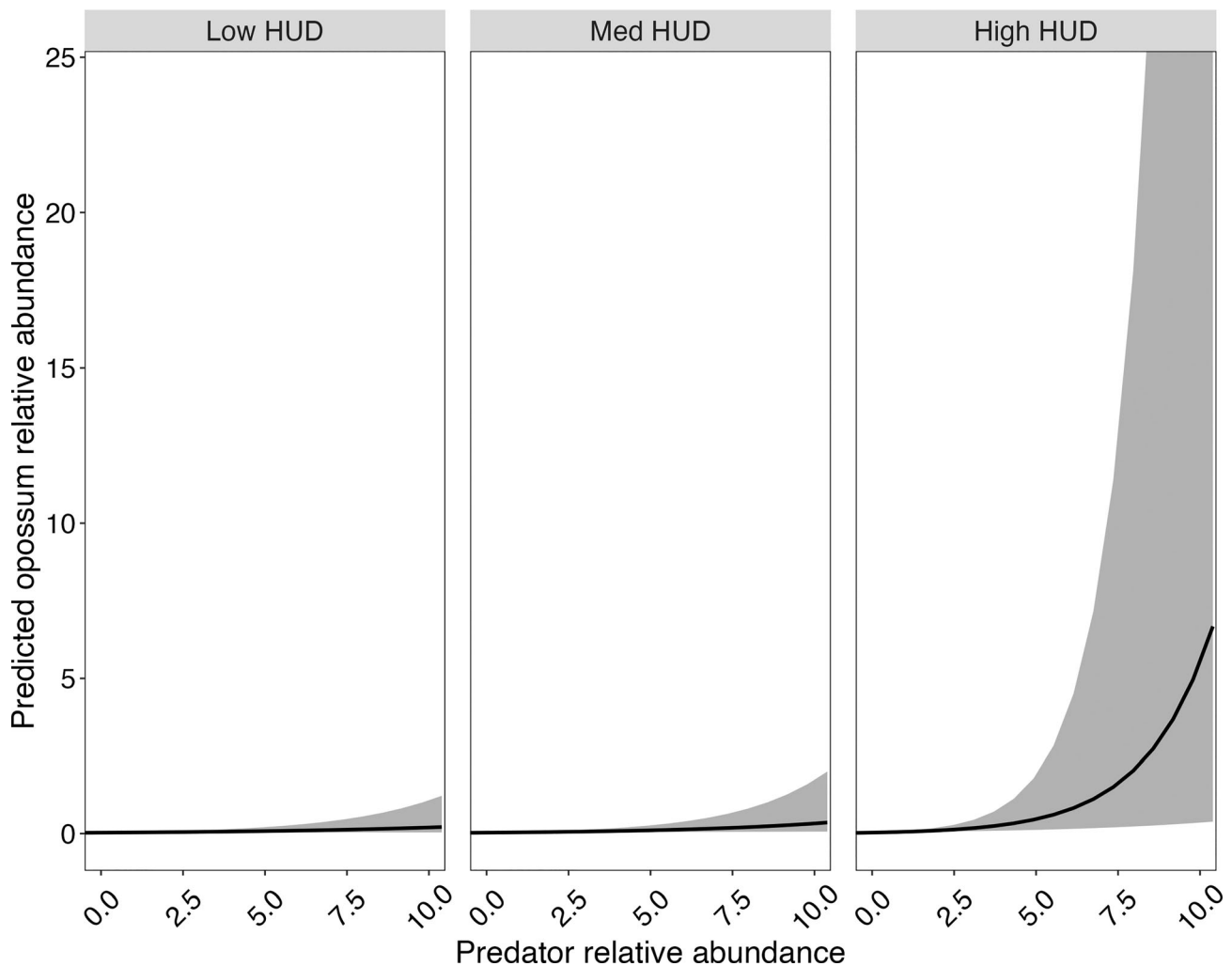


Figure 3 The interactive effects of housing unit density (HUD) and predator abundance on Virginia opossum (*Didelphis virginiana*) relative abundance across the species' geographic range in the United States. HUD was binned using zero HUD (low [0 km²]), mean (medium [med; 440.27 km²]), and plus one standard deviation (high [2991.78 km²]) for ease of visualization. We used zero HUD for low HUD because HUD was right skewed and using minus one standard deviation would result in associating a negative low HUD value to opossum relative abundance, which is biologically unrealistic. Therefore, because minus one standard deviation of HUD and a biologically realistic value of zero HUD hold a similar trend with opossum relative abundance, we present low HUD as zero HUD for visualization purposes. 95% confidence intervals are presented using a gray band. Relative abundance was derived using camera traps from Snapshot USA data during 2019 and 2020.

(Kanda et al., 2006; Markovchick-Nicholls et al., 2008; Nickel et al., 2020). In addition to access to human-associated resources, opossums may benefit from reduced predation risk in human-dominated environments due to a human shield effect (Lesmeister et al., 2015; Muhly et al., 2011; Suraci et al., 2019). We found that opossums were more abundant with increased housing unit density and more likely to occur in areas with higher predicted human activity (anthropogenic sound), trends consistent with the behavior of an urban-adapted mesopredator that takes advantage of numerous food, water, and shelter resources associated with humans. Although opossums were nearly exclusively nocturnal (91.7% of detections occurred after sunset), we found that the timing of their

activity varied in response to predator abundance. Here, we discuss our findings in terms of occupancy, abundance, and activity in turn.

We found a nuanced relationship between the effects of opossum occupancy, land cover, and anthropogenic sound (Fig. 2). Opossums were generally positively related to anthropogenic sound and negatively related to forest cover, suggesting that opossums were more likely to occupy areas with high levels of human activity. This is almost certainly in response to the resources located in areas that correspond to humans. However, when anthropogenic sound was high, opossum occupancy showed a positive relationship with forest cover (Fig. 2). We believe these results indicate that in more

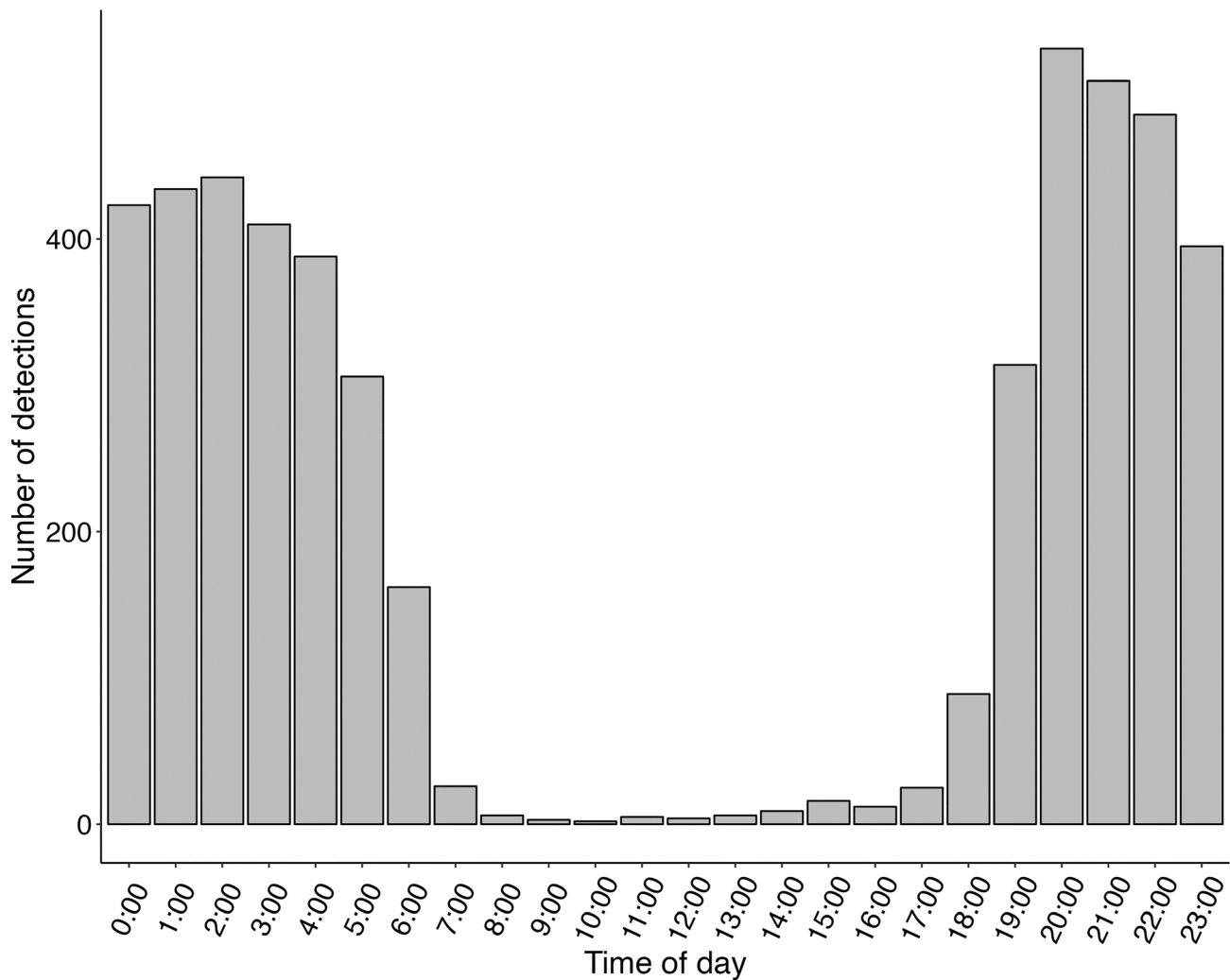


Figure 4 Activity patterns of Virginia opossum (*Didelphis virginiana*) calculated from number of independent detections over a 24-h cycle presented in 1-h bins. Time of day is represented in military format. Activity was derived using camera traps from Snapshot USA data during 2019 and 2020.

naturally wooded environments, opossums are more likely to occupy areas with human activity (such as trails, roads or human structures) as measured by anthropogenic sound. These areas may provide food or water (e.g. gardens, bird feeders, compost piles, roadkill) or structures in which to den (e.g. out-buildings, sheds). It is also possible that the presence of human activity, even in predominantly natural areas, may confer some level of protection from predators consistent with a human shield effect. However, we did not directly test for whether predation on opossums was lower near human infrastructure, nor did we find that opossum occupancy was influenced by the relative abundance of predators. Studies conducted on finer spatial scales may be able to better elucidate the causal mechanism driving these observed patterns in opossum occupancy.

We found that patterns of opossum relative abundance were nuanced in relation to residential development and predator abundance. We found that at low or moderate housing density,

opossum abundance was relatively low regardless of predator abundance. However, in the presence of high levels of housing unit density, both opossum and predator abundance tended to be higher (Fig. 3). There was large uncertainty around opossum abundance in high levels of HUD, likely because Snapshot USA tends to be biased toward more rural sampling locations and results in a right-skewed distribution in HUD (Fig. S1). There are several possible explanations for the correlated increase in abundance of predators and opossums. Both opossums and coyotes (the more abundant predator included in analyses) likely exploit abundant resources located in the human-dominated environment. Coyotes in urban areas often prey on rats, lagomorphs, and other small mammals that proliferate in the human environment, whereas opossum likely increased in abundance due to human-subsidized food, water, and shelter. One might expect that as predator abundance increases in these areas, that opossum abundance could

Table 2 Model selection statistics for activity estimation of Virginia opossum (*Didelphis virginiana*)

Model	<i>K</i>	AIC	ΔAIC	AICwt	LL
Development+Predators	5	63 886.83	0.00	0.19	−31 938.42
Sound+Predators	5	63 887.38	0.55	0.14	−31 938.69
Forest+Predators	5	63 887.71	0.88	0.12	−31 938.86
DOS+Predators	5	63 887.77	0.94	0.12	−31 938.88
HUD+Predators	5	63 888.32	1.49	0.09	−31 939.16
Sound*Predators	6	63 888.65	1.81	0.08	−31 938.32
Development*Predators	6	63 888.76	1.93	0.07	−31 938.38
DOS*Predators	6	63 889.05	2.22	0.06	−31 938.52
Forest*Predators	6	63 889.71	2.88	0.04	−31 938.86
HUD*Predators	6	63 890.18	3.34	0.04	−31 939.09

Activity is derived from camera trap data across the geographic range of the opossums in the United States during 2019 and 2020 (using data from Snapshot USA). Only top candidate models, models within 4 ΔAIC, are presented here although all model rankings are shown in the supplemental materials. Covariates of activity included surrounding landscape and urbanization variables (HUD represents housing unit density and DOS represents developed open space). Models were ranked using Akaike's Information Criterion (AIC) and included with each model is the number of parameters (*K*), difference from best model (ΔAIC), model weight (AICwt) and log-likelihood estimate (LL).

decrease. The correlated increase in abundance of predators and opossums indicates that opossum may have derived some protection from living alongside humans (i.e. a human shield) or that the normal predator–prey interactions between coyotes and opossums are disrupted in this environment. Alternatively, it is possible that both opossums and their predators congregate in green spaces as development increases, such that they are naturally correlated by being confined to fragmented habitat within a developed matrix (Parsons *et al.*, 2019, 2022). In areas with high density human housing, opossums may use structures that provide safety from predators such as seeking refuge in buildings, under decks, or in other structures. Alternatively, high densities of human structures (and thus humans) may cause behavioral changes in predators such that there are times or areas of relative safety for opossums to be active. Coyotes that inhabit areas of human development are often active in the early hours of the morning when human activity is lowest (Gese *et al.*, 2012), thus animals less wary of humans may have reduced predation risk from coyotes when active earlier in the night. Habitat partitioning may also occur on small spatial scales. While both predators and opossums can co-occur in high abundances in developed areas, opossums may be using areas in very close proximity to humans that predators may be wary of using, and thus contact rates are lower as has been shown for interactions between coyote and red fox (*Vulpes vulpes*: Moll *et al.*, 2018). Evidence indicates that opossum forage in yards and other areas very close to humans (Hansen *et al.*, 2020).

We predicted that opossums occurring in human-dominated areas might have different patterns in activity than opossums occurring in more natural areas. It has been shown that predators such as coyote occurring near humans often shift their activity to avoid being active when humans are most active (Gese *et al.*, 2012). We expected that opossums may shift their activity to take advantage of this change in predator behavior. Alternatively, opossums may also become more nocturnal in the presence of humans as they too seek to avoid contact with humans. In our study, and in others (Reilly *et al.*, 2017;

Ryser, 1995), opossums were almost exclusively nocturnal (Fig. 4). We found that opossums that occurred in areas with high predator abundance shifted their activity to be active earlier in the night (closer to sunset). This likely indicates that opossums show a behavioral response to perceived predation risk.

Our results indicate that human development and activity could cause complex responses from wildlife and potentially disrupt predator–prey interactions. Humans (intentionally or unintentionally) provide food, water, and shelter resources that opossums can use, leading to opossums being more likely to occur in areas near people and to attain higher relative abundances near humans. While their predators also can increase in abundance near humans, this increase in abundance did not lead to decreased abundance of opossums, indicating that they are either shielded by the presence of humans from predators or that the normal interactions between these species are disrupted. Our analyses relied upon relative abundance as measured by detection rate of cameras. While this is a commonly used metric from camera studies, it may not always be indicative of true abundance (O'Brien, 2011; Sollmann *et al.*, 2013). Furthermore, we used data from sites ranging from natural rural sites to heavily urbanized sites, which could influence detection rates. We believe that using data from a large number of locations (≥ 125 subprojects) and the standardized camera deployment protocols of Snapshot USA likely reduced much of this potential bias. Because Snapshot USA data are weighted toward rural sampling locations, with fewer locations classified as urban (Figs S1 and S2), it is possible that increased variability from fewer samples among the highly urban subprojects could have biased results toward increases in opossum abundance and occupancy as development and anthropogenic sound increased. However, we do not believe this is the case due to our large sample size and because generalized linear mixed-effects models do not make assumptions about the fixed effects (Bates *et al.*, 2015). Finally, we recognize that because human development is occurring rapidly, many of the remote sensing layers used to

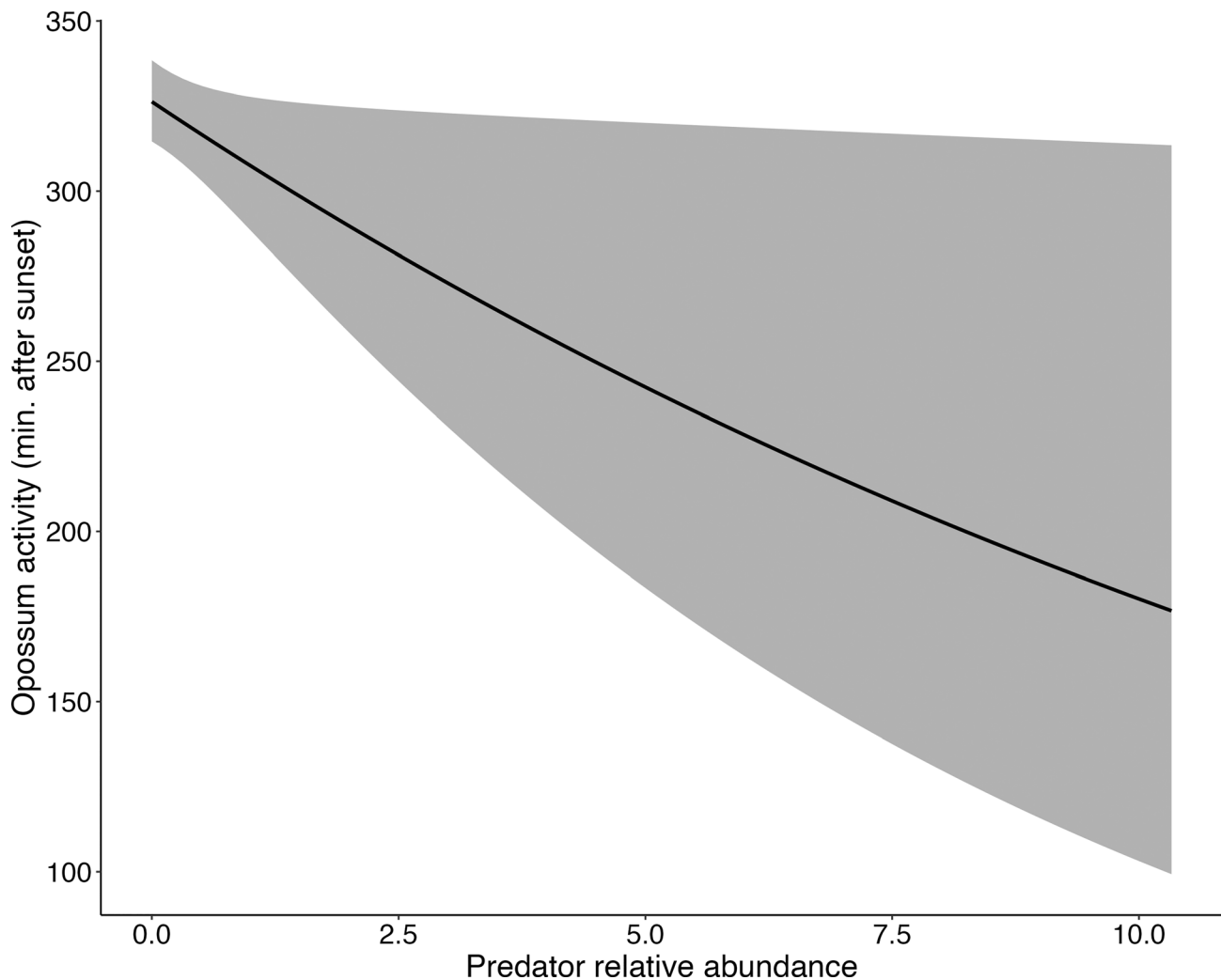


Figure 5 Effects of predator relative abundance on Virginia opossum (*Didelphis virginiana*) activity (measured in minutes after sunset). 95% confidence intervals are presented using a gray band. Relative abundance was derived using camera traps from Snapshot USA data during 2019 and 2020.

quantify human development are older than the data collected and may not be fully reflective of the current extent of human development.

As we continue to modify the planet, we create novel and unique ecosystems. Wildlife capable of adapting and taking advantage of this novel environment will continue to be models for ecological and behavioral research. Recent research suggests that conservation policy and management might fail if they do not comprehensively account for the multidimensional impacts that humans have on wildlife, as well as their trophic interactions (Moll *et al.*, 2021). Our results further emphasize these effects, and we suggest that future work continue to take a holistic approach in considering the human niche as a part of the greater ecosystem. Likewise, the opossum, and other behaviorally flexible mesopredators will continue to be an important part of the human-modified landscape. We suggest that future research should investigate if opossums benefit

primarily from subsidized resources associated with humans or if they have increased survival due to the presence of a human shield or a disruption of predator–prey interactions.

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Conflict of interest

The authors have no conflict of interest to report.

Data Availability Statement

This article used publicly available data from Snapshot USA located at <https://esajournals.onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1002%2Fecy.3353&file=ecy3353-sup-0001-DataS1.zip> (Kays et al., 2021). Data specific to these analyses will be available by request to any of the authors.

Author contributions

BD, JV, EL, RG, MS, LM, AM, and EJ conceived the ideas and designed methodology; BD, JV, EL, RG, MS, LM, AM, and EJ collected, organized, cleaned, proofed, and manipulated data for analyses and visualization; JV and EL analyzed the data; All authors contributed to interpretation and contextualization of the results; BD led the writing of the manuscript with contributions from all other authors, particularly JV and EL. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Frequency and distribution of housing unit density (km²) data used in occupancy and abundance analyses derived from camera trap data (using all 168 subprojects) across the geographic range of the opossums in the United States during 2019 and 2020 (using data from Snapshot USA).

Figure S2. Frequency and distribution of anthropogenic sound (dB) data used in occupancy and abundance analyses derived from camera trap data (using all 168 subprojects) across the geographic range of the opossums in the United States during 2019 and 2020 (using data from Snapshot USA).

Figure S3. Frequency and distribution of forest cover (m²) data used in occupancy and abundance analyses derived from camera trap data (using all 168 subprojects) across the geographic range of the opossums in the United States during 2019 and 2020 (using data from Snapshot USA).

Figure S4. Frequency and distribution of the relative abundance of Virginia opossum (*Didelphis virginiana*) used in abundance analyses derived from camera trap data (using all 168 subprojects) across the geographic range of the opossums in the United States during 2019 and 2020 (using data from Snapshot USA).

Figure S5. Frequency and distribution of predator relative abundance data (i.e. only coyotes and bobcats) used in occupancy and abundance analyses derived from camera trap data (using all 168 subprojects) across the geographic range of the opossums in the United States during 2019 and 2020 (using data from Snapshot USA).

Figure S6. Frequency and distribution of predator relative abundance data (i.e. only coyotes and bobcats) used in activity analyses derived from camera trap data across the geographic range of the opossums in the United States during 2019 and 2020 (using data from Snapshot USA).

Figure S7. Frequency and distribution of Virginia opossum (*Didelphis virginiana*) activity data used in activity analyses derived from camera trap data across the geographic range of the opossums in the United States during 2019 and 2020 (using data from Snapshot USA).

Table S1. Full model selection statistics for detection (p) and occupancy probability (Ψ) of Virginia opossum (*Didelphis virginiana*).

Table S2. Full model selection statistics for relative abundance estimation of Virginia opossum (*Didelphis virginiana*).

Table S3. Full model selection statistics for activity estimation of Virginia opossum (*Didelphis virginiana*).