

ARTICLE

Effect of species-level trait variation on urban exploitation in mammals

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Abstract

Identifying drivers of urban association in wildlife is a central challenge in conservation biology. Traits facilitating access to novel resources and avoiding humans often correspond with urban exploitation in mammal species, but these relationships differ by taxa and trophic guild. Variation among or within traits may be a yet untested explanation for the non-generality of species-trait relationships in cities. Using camera trap data from 1492 sites throughout the contiguous USA in 2019, we investigated if mammal species with greater intra-specific trait variation have higher degrees of urban occupancy. We hypothesized that intraspecific trait variation would correspond with urban occupancy, but that the strength of these relationships would vary by taxonomic order due to expected phylogenetic constraints. Mean trait values (average home range size, body mass, group size, weaning age, litter size, and diet composition) varied widely across orders. The only traits that affected urban association across all species corresponded with demography (litter size), while responses across orders were more variable and informative. Mean trait values associated with home range and body size had informative relationships with urbanization for Cetartiodactyla, Rodentia, and Carnivora, while intraspecific variation in traits corresponding with diet (Carnivora), demography (Cetartiodactyla, Carnivora, Rodentia), and temporal responses to humans (Carnivora) had informative relationships to urbanization. This is the first study investigating mammalian species-level trait variation and its relationship to urban exploitation across many traits and taxa. Since natural selection requires trait variation, the variation of demographic traits, like litter size, can have significant implications for wildlife management and conservation. Our results also provide further evidence for omnivory as a form of dietary plasticity supporting urban accessibility in higher trophic guilds (e.g., Carnivora). Using this information, we can better manage and understand which species occupy and adapt to cities, thereby promoting human-wildlife coexistence.

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KEYWORDS

demography, mammal, occupancy, traits, urbanization, variation, wildlife

INTRODUCTION

Due to rapid changes on Earth from human activity and development, identifying drivers of urban exploitation and avoidance by wildlife has emerged as a central challenge in conservation biology (Aronson et al., 2016; Fischer et al., 2015; Hansen et al., 2020; Suraci et al., 2021). Substantial trends in land use change via urban development (Homer et al., 2020; Venter et al., 2016) and the human occupation of cities (United Nations, 2018) are particularly pronounced in North America (Güneralp et al., 2020). Landscape fragmentation and environmental degradation from urbanization can affect wildlife by limiting resources (e.g., fragmenting territories, reducing native prey species), limiting access to mates (Bateman & Fleming, 2012; McKinney, 2006), and displacing non-human animals into pockets of greenspace more frequently populated by people (e.g., parks and neighborhoods; Mueller et al., 2018; Moll et al., 2018), all of which can perpetuate human-wildlife conflicts (Ditchkoff et al., 2006; Schell et al., 2020). Nonetheless, cities also provide many services to wildlife, such as resource supplementation and refuge from predators (Fischer et al., 2012; Moll et al., 2018; Shochat et al., 2006). Since an organism's traits influence its ability to occupy urban environments (Aronson et al., 2016), identifying which traits support urban persistence has become a foundational question for both science and management, particularly among mammals that experience conflicts with humans (Schell et al., 2020).

Urban mammals are often defined by traits that allow a species to persist in fragmented landscapes, access novel resources, and avoid direct confrontations with humans (Bateman & Fleming, 2012; Schell et al., 2020). For example, broad-scale, global range expansion (Pacifi et al., 2020) and urban occupancy and association (Rega-Brodsky et al., 2023; Suraci et al., 2021) have been observed in mammal species with smaller body sizes, higher reproductive rates, and more generalist diets, though these results are not ubiquitous within trophic guilds or taxonomic groups (Nickel et al., 2020; Santini et al., 2019). Conversely, other studies have found mammal body sizes to increase (Hantak et al., 2021; Yom-Tov, 2003) or approach a moderate size (Guralnick et al., 2020) in anthropogenic environments. Similarly, some studies have identified mammal activity patterns to converge toward nocturnality in cities (Gaynor et al., 2018), while others have observed variation in activity among urban mammals (Frey et al., 2020; Gallo et al., 2022). In addition, some mammals may occupy cities

not because they are predisposed to urban environments, but instead due to a misreading of environmental cues (e.g., ecological traps; Hale & Swearer, 2016), to exploit anthropogenic food resources (Larson et al., 2020; Shochat et al., 2006), or as a result of inflated population densities along the less-developed peripheries of urban centers (Crooks et al., 2010; Riley et al., 2006). Other individuals may disperse through or near cities after reaching sexual maturity, but fail to establish territories within these spaces (e.g., Beier, 1995). As such, flexibility to and continued persistence (i.e., population growth) under anthropogenic conditions may further contribute to urban exploitation (Fischer et al., 2015).

Variation among or within traits may reflect a species' capacity to adapt to meet the dynamic pressures of urban living and, thus, explain the non-generalizability of species-trait relationships in urban environments better than the average values of the traits themselves (Thompson et al., 2022). For example, a mammal species' ability to be more active at night in developed compared to wildland areas (Gaynor et al., 2018) suggests underlying variation in within-species temporal activity that is flexible to urban conditions (e.g., Gallo et al., 2022; Green et al., 2022; Lamb et al., 2020). Further, intraspecific variation influences interactions between species, and this relationship, in some cases, is more significant in defining community structure than direct species effects (Des Roches et al., 2018). However, not all species exhibit trait variation in the same traits or to the same degree, and trait variation also differs among populations due to local evolution (adaptive and non-adaptive [population-level]; Des Roches et al., 2018), physiological or anatomical constraints (species-level), and phylogenetic history (lineage-level; Cheverud et al., 1985; Wilkes et al., 2020). Further, finer-scale trait-environment relationships can result in animals with the same genotypes expressing different phenotypes (i.e., phenotypic plasticity; Miner et al., 2005). Nonetheless, intraspecific trait variation may support a species' ability to navigate the novel and fast-changing ecological conditions of a city (Des Roches et al., 2018), thereby promoting environmental filtering from regional to urban species pools (Aronson et al., 2016). In other words, species with fewer anatomical, physiological, phylogenetic, or behavioral constraints and more flexibility to city-living may have an advantage in urban environments.

We investigated if mammal species with greater trait variation also exhibit higher degrees of urban occupancy by analyzing a large set of standardized camera trap data

collected throughout the contiguous United States in 2019. We defined urban exploitation as occurring when a species exhibits higher rates of species occupancy in urban compared to less urbanized spaces (Fischer et al., 2015). We hypothesized that variation among traits expected to confer resilience to landscape fragmentation, increase reproductive success, support the acquisition of novel food sources, and allow a species to avoid or respond to human presence would correspond with urban occupation (see Table 1 for traits assessed and predictions). Due to expected phylogenetic constraints on trait variation (e.g., differences in and interactions between nutritional requirements, home range, and body size in Carnivores vs. Cetartiodactyls vs. Rodents), we hypothesized that these responses would differ between taxonomic orders (e.g., Cherverud et al., 1985; Wilkes et al., 2020). We also investigated how the average value of each trait overall and across taxonomic orders corresponds with urban occupancy to identify if different

relationships exist between each measure and urban exploitation (i.e., does variation in body mass correspond with urban exploitation, while average body mass does not?). We predicted traits that allow animals to better access fragmented environments, inflate demographic rates, facilitate the consumption of novel resources, or help animals to better avoid humans would relate to increased occupancy in urban compared to rural environments (e.g., Santini et al., 2019; Suraci et al., 2021; see Table 1 for predictions and traits assessed).

METHODS

Study area

To understand how variation in traits corresponds with urban occupancy, we used a large-scale data set from 107 communities in all 48 states across the contiguous

TABLE 1 Hypotheses and predictions for how each variable is expected to influence mammal urban occupancy.

Rationale and traits	Measure of trait variation	Predictions for species in urban areas
Responses to fragmentation		
Home range	(Maximum reported individual home range – minimum reported individual home range)/average reported individual home range	Variation: + Mean: –
Sociality	(Maximum no. individuals in single observation – minimum no. individuals in single observation)/average no. individuals across observations within the Snapshot USA dataset	Variation: + Mean: –
Body mass	(Maximum reported body mass – minimum reported body mass)/average reported body mass	Variation: + Mean: –
Demography		
Litter size	(Maximum reported litter size – minimum reported litter size)/average reported litter size	Variation: + Mean: –
Weaning age	(Maximum reported weaning age – minimum reported weaning age)/average reported weaning age	Variation: + Mean: –
No. litters	(Maximum reported annual litters – minimum reported annual litters)/average reported annual litters	Variation: + Mean: –
Responses to changes in food resources		
Degree of omnivory	Percent of diet categories listed for each species within the EltonTraits database that contain meat	Variation: +
Diet breadth	No. diet categories within the EltonTraits database that listed for each species	Variation: +
Responses to humans		
Total diel activity	95% isopleth value	Variation: +
Diel activity potential	50% isopleth value/95% isopleth value	Variation: +
Core diel activity	50% isopleth value	Mean: –

Note: Rationale for trait selection is in bold, with corresponding traits nested underneath. + and – indicate a positive or negative effect is predicted (i.e., increased/decreased variance or increased/decreased mean values associated with urban occupancy). Some traits are only indicative of variation (i.e., diet breadth, degree of omnivory, total diel activity, and diel activity potential), while core diel activity is solely a mean trait value.

USA (Figure 1, Appendix S1: Figure S1; Cove et al., 2021; 25.17° to 48.14° latitude, -124.02° to -69.10° longitude). These data were collected as a part of the Snapshot USA program in 2019 (Cove et al., 2021). Snapshot USA is a coordinated, national effort across all 50 U.S. states to assess mammalian biodiversity in a snapshot in time using camera traps (Cove et al., 2021). We did not include data collected within Hawaii and Alaska in our analyses due to their unique community compositions compared to other data collected within the contiguous United States. Given the size, diversity, and geographic scope of this dataset, the communities represented a wide variety of climates, landscape types, and wildlife communities (Cove et al., 2021).

Field methods

Un-baited camera traps were deployed from approximately September–October 2019, with a minimum of 400 trap nights per array, totaling 51,684 survey days (Cove et al., 2021). Although camera traps were deployed for an average of 34.18 survey days (SD = 18.62, minimum = 1, maximum = 92), it takes approximately 2-weeks for a camera trap to detect most species present at a site, and species accumulation curves tend to asymptote after approximately 30 days, even in the more biodiverse tropics (Kays et al., 2020). All camera trap locations (latitude/longitude) were recorded upon deployment. Methods for standardization of camera arrays, settings,

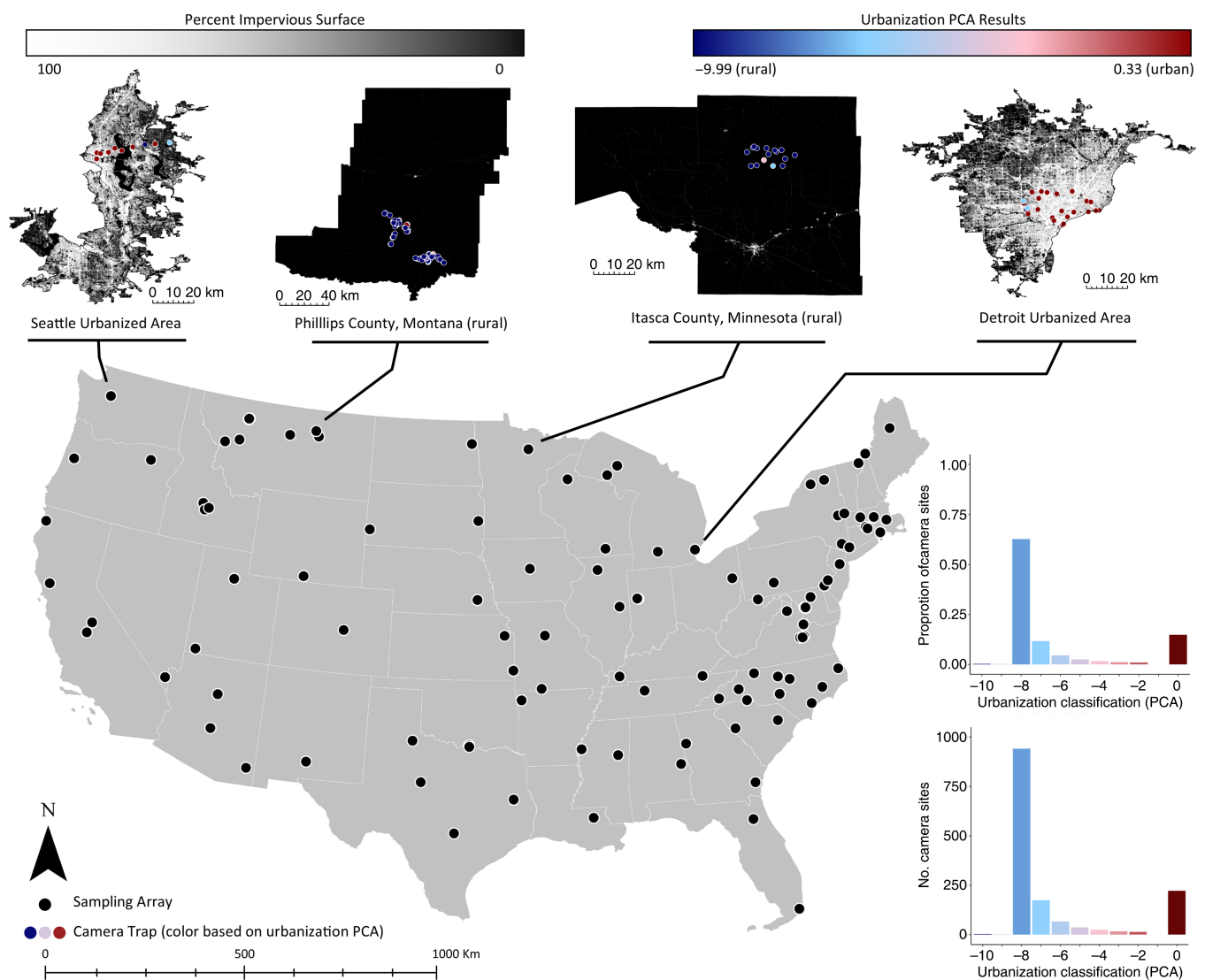


FIGURE 1 Map of research area for Snapshot USA 2019 initiative (Cove et al., 2021). Each black dot signifies the location of a camera trap array in the contiguous United States of America, while dots in each inset map signify a single camera trap. Camera points are colored based on their urbanization principal component analysis (PCA) result and illustrate the variation in array types (urban–rural gradient) across the study area. Histograms show the proportion (top) and number (bottom) of camera sites with each urbanization PCA result across the entire study area.

and models can be found in Cove et al. (2021). Each sampling occasion consisted of 7 days of continuous sampling at an individual site. For example, if a camera was active for exactly 28 days, it would have gathered four repeat samples. Photos were sorted and identified within eMammal (<https://emammal.si.edu/>). We defined a detection as a single eMammal aggregated sequence, grouped as (a) consecutive images with individuals of the same or different species at the same site, and (b) images that were taken within 1 min of the previous image. Individuals within each detection were counted and adults and juveniles were counted separately whenever differentiation was possible.

Of the species detected from the 2019 Snapshot USA deployment, we analyzed data from 53 mammal species with >28 detections to have enough data for model convergence. Of the species with >28 detections, we excluded detection data for mountain cottontail (*Sylvilagus nuttallii*) and Mexican woodrats (*Neotoma mexicana*) from our analyses, due to insufficient data availability on their traits. We also excluded data for human-associated mammals, such as domestic dogs (*Canis familiaris*), horses (*Equus caballus*), and livestock species (i.e., domestic cows, *Bos taurus*, and sheep, *Ovis aries*). However, we included domestic cats (*Felis catus*) in our analysis. Though domestic cats tend to associate with human-occupied landscapes (e.g., Cove et al., 2023), we included them in our analyses due to their unique ecological influence, position as free-roaming throughout much of the USA (Cove et al., 2018, 2023; Loss et al., 2013), and frequent presence in wildland areas, as well as across the rural-to-urban gradient (Crowley et al., 2020; Herrera et al., 2022; Lepczyk et al., 2003). Nonetheless, to confirm that our results were not significantly influenced by the inclusion of domestic cats, we conducted a secondary analysis of our dataset excluding domestic cats and found nearly identical results and unchanged model interpretations when cats were included versus excluded. As such, we continued with the inclusion of domestic cats in our analyses due to their ecological importance on the landscape (Cove et al., 2018, 2023; Loss et al., 2013).

Trait data

We compiled trait variation data for 10 traits and the average values of seven traits for each species (Table 1) based on data reported in existing literature (Appendix S1: Table S1) or derived from Snapshot USA camera trap data (Appendix S1: Table S2). We included traits expected to facilitate urban exploitation, including those related to species-level demographic rates (e.g., litter size, weaning age, number of litters), hypothesized responses to

fragmentation (e.g., home range, sociality, body mass), hypothesized responses to novel food resources (e.g., degree of omnivory, diet breadth), and hypothesized responses to human activity (e.g., activity patterns). The traits selected were also largely informed by other studies (e.g., Pacifici et al., 2020; Santini et al., 2019; Suraci et al., 2021). For continuous traits, we defined intraspecific trait variation as the range of known values of a trait (e.g., the range of body sizes documented in a species) divided by the average value of that trait, for a given species. We defined a species' diet breadth as the number of diet categories listed in EltonTraits (Wilman et al., 2014). Likewise, we defined omnivory as the proportion of prey items reported in each species' diet (Wilman et al., 2014), with a value of 0.5 indicating true omnivory and both 0 (complete herbivory) and 1 (complete carnivory) indicating no omnivory. We did not include carrion in this proportion, since EltonTraits places consuming carrion and anthropogenic refuse in the same category, which may not contain meat (Wilman et al., 2014). We used the number of adult individuals of each species observed together in camera trap data from Cove et al. (2021) as a proxy for socialization, and calculated variation by dividing the range of the number of adults observed together by the average number of adults observed together. In cases where traits were not reported in the literature ($n = 27$, 3% of trait values), we performed a single imputation using the package "Hmisc" in R (Harrell, 2021). The imputed values for diet breadth were nonsensical, despite high R^2 values for the imputations across the dataset. For this reason, we gave missing values in diet breadth the average value for other species within the same genus, rounded to the nearest multiple of 10, for data consistency.

We determined diel activity patterns for each species using the detection times recorded across four USA time zones across the camera trap data from Cove et al. (2021). We anchored detection times to sunrise and sunset events based on location and date using National Oceanic and Atmospheric Administration (NOAA) calculations, and then converted sunrise and sunset times to radians via the "transtime" function in the package "activity" (Rowcliffe, 2021), expressing detection times relative to the two solar events. We used the "modal.region.circular" function in the package "circular" (Lund et al., 2017) to calculate the 50% and 95% isopleths (Appendix S1: Table S2) with a smoothing parameter (k) of 5 to describe each mammal species' activity range (Oliveira-Santos et al., 2013). The 95% isopleth is the smallest time interval of the day in which 95% of the species' activity occurs (Oliveira-Santos et al., 2013), representing the potential proportion of the day a species can utilize (i.e., existing activity variation). In contrast, the 50% isopleth is the smallest time interval of the day in which 50% of the species' activity occurs, representing

the proportion of the day that the species actually uses (analogous to a mean trait value), and is referred to as the “core diel activity.” Finally, we divided the 50% isopleth value by the 95% isopleth value to calculate a value representative of the relative variation observed in each species’ temporal activity (i.e., potential activity variation). We excluded North American beaver (*Castor canadensis*) data from the temporal activity analysis, as cameras were not placed in such a way as to reliably detect semi-aquatic mammal activity. Finally, we compared how trait variation differed across orders using one-way analysis of variance (ANOVA), with significance assessed at $\alpha = 0.05$. We used program R version 4.02 or 2.0.3 (R Core Team, 2022) for all our statistical analyses.

Occupancy modeling

We modeled how both species-level mean trait values and trait variation predicted response to urbanization using a two-step analysis methodology consisting of (1) a Bayesian multi-species occupancy model predicting each target species’ urbanization response and (2) a series of Bayesian generalized linear models to elucidate the effect of species’ mean traits and trait variation values on urbanization response (measured as the urbanization beta coefficient from the aforementioned occupancy model) across both species and orders.

To test whether variation in species-level trait values correspond to urban specialization, we extracted urbanization variables within 100 m buffers around each camera trap location, including human population density (Doxsey-Whitfield et al., 2015) and percent impervious surface cover (Homer et al., 2020), using ArcMap v10.8 (ESRI, Redlands, CA) and QGIS v3.12 (QGIS Development Team). Per the Snapshot USA study protocol, camera trap sites must be a minimum of 200 m apart (Cove et al., 2021). We therefore investigated urbanization at the 100 m-scale to ensure independence of sites and to capture more site-specific relationships. Though it is the case that different results or relationships could be identified at broader scales, other investigations using Snapshot USA data have not identified significant differences in species occupancy between finer and larger scales (e.g., Allen et al., 2022). Since composite measures of urbanization have been described as most representative of the complexities of urban matrices (Moll et al., 2019), we ran a principal component analysis (PCA) using values of mean population density and percent impervious surface cover calculated at each camera trap site to construct a continuous “urbanization metric” used in our multi-species occupancy model. We then extracted the first principal component (PC1; hereafter referred to as “urbanization”), describing axes of

increasing population density and percent impervious surface cover, which accounted for 83% of the total variation in the two predictors, for each camera trap site (Figure 1; Appendix S1: Table S3). Due to a lack of data on population density and/or percent impervious surface cover from some of the sites present in the full Snapshot USA dataset, this restricted our final dataset to 1492 sites. Using this truncated dataset, we created detection histories for each of the species meeting the analysis criteria outlined in the field methods above (Appendix S1: Table S4). This resulted in 53 species-specific matrices where rows represented sites, columns represented sampling occasions, and cells represented whether the species was detected (1) or not (0) at a site during each sampling occasion. Each occasion represented a weeklong interval of continuous sampling. We created all detection histories using the “camtrapR” package in program R (version 2.0.3; Niedballa et al., 2016).

We constructed a hierarchical Bayesian multi-species, single-season occupancy model to describe the patterns of species detection/non-detection data in response to urbanization (Kéry & Royle, 2015; MacKenzie et al., 2017; Rich et al., 2016). We investigated the effects of site-level urbanization (PC1 from the above PCA) and latitude and longitude (to account for variability across sites that may be dependent on a particular site’s location; Allen et al., 2022) on both species-specific and community occupancy, while allowing detection probability to vary across species (Rich et al., 2016). Since we are investigating if trait variation or mean trait values correspond with urban exploitation, or specialization, we did this by modeling the linear effect of each covariate on the logit-transformed occupancy parameter (Dorazio & Royle, 2005; Zipkin et al., 2009, 2010) where, before analysis, we scaled each covariate to a mean = 0 and standard deviation (SD) = 1 to improve numerical optimization (Schielzeth, 2010). Following the approach of Rich et al. (2016), we linked species-specific parameters to a community hyperparameter. In this context, the hyperparameter represented the mean response across all species, and we modeled species-specific responses as random effects from the given hyperparameter (Kéry & Royle, 2015; Rich et al., 2016; Zipkin et al., 2010). The final model structure was as follows:

$$z_{i,j} \sim \text{Bern}(\Psi_{i,j}),$$

$$\text{logit}(\Psi_{i,j}) = \beta_{0i} + \beta_{1i} \times \text{Urb}_j + \beta_{2i} \times \text{Lat}_j + \beta_{3i} \times \text{Long}_j,$$

$$\beta_i \sim \text{Normal}(\mu_\beta, \sigma_\beta^2),$$

$$y_{i,j,k} \sim \text{Bern}(p_{i,j,k} \times z_{i,j}),$$

$$\text{logit}(p_{i,j,k}) = \alpha_{0i},$$

$$\alpha_i \sim \text{Normal}(\mu_\alpha, \sigma_\alpha^2),$$

where $z_{i,j}$ represents the occurrence of species i at site j ; $\Psi_{i,j}$ the probability species i occurred at site j ; β_{0i} the logit occurrence probability of species i at average covariate values, $\beta_{1i}, \dots, \beta_{3i}$ species-specific covariate effects of urbanization, latitude, and longitude, respectively; μ_β the community hyperparameters; and σ_β^2 the associated variances. For the detection model, $y_{i,j,k}$ represents the detection of species i at site j during sampling occasion k ; $p_{i,j,k}$ the detection probability of species i at site j during occasion k , given that species i actually occurred at site j ; α_{0i} the logit detection probability of species i ; μ_α the average detection probability across all species; and σ_α^2 the associated variance across species.

We estimated posterior distributions for all species-specific and community-wide coefficients using Markov Chain Monte Carlo (MCMC) methods implemented in JAGS through program R using the “R2jags” and “jagsUI” packages (Kellner & Meredith, 2021; Yu-Sung & Yajima, 2021). We ran three chains in parallel, each 20,000 iterations in length. We discarded the initial 10,000 draws from each chain as burn-in, and we thinned resultant samples by five, leaving a total of 6000 draws to craft all parameters’ posterior distributions. We used flat uniform priors from -5 to 5 for each beta coefficient and a flat uniform prior from 0 to 10 for all SDs. We assessed parameter convergence by visually inspecting individual traceplots and by calculating the Gelman-Rubin statistic, where values <1.1 indicate convergence across chains (Gelman, 2004). We extracted the posterior mean, median, SD, and 95% Bayesian credible interval for each parameter.

Trait and trait variation modeling

Using the species-specific urbanization beta coefficients from our occupancy model, we adopted a Bayesian generalized linear modeling (bGLM) framework for assessing the effects of average traits and trait variation on species-specific urbanization response. However, as our response variable (urbanization response) was itself estimated from a previous model, we had to account for this error in our second stage model. We therefore propagated the error from our species-specific parameter estimates through each bGLM by modeling urbanization response as a random variable with associated “observation” error,

$$\text{Urb}_i \sim \text{Normal}(\mu_i, 1/\sigma_i^2).$$

where Urb_i denotes the occupancy response of species i to urbanization, μ_i is the mean estimated occupancy

response of species i to urbanization, and σ_i is the posterior SD of species i ’s occupancy response to urbanization (Barnick et al., 2022; Kéry & Royle, 2015; Suraci et al., 2021). We then modeled urbanization response as a function of species average traits and trait variation using a Gaussian linear model, incorporating order-specific intercepts and slopes,

$$\mu_i = \gamma_k + \beta_k \times \text{trait}_i + \epsilon_i,$$

$$\epsilon_i \sim \text{Normal}(0, 1/\theta_i^2),$$

$$\theta \sim \text{Uniform}(0, 10),$$

where species i belongs to order k and γ_k is an order-specific intercept term, β_k is an order-specific slope term, trait_i is the species-specific trait value from the list of average trait and trait variation values (Table 1), and ϵ_i is a species-specific error term. Finally, since we were interested in order-specific responses, as well as the community as a whole, we modeled order-specific slope and intercepts as random variables using,

$$\gamma_k \sim \text{Normal}(\mathbf{Y}, 1/\Phi^2),$$

$$\beta_k \sim \text{Normal}(\mathbf{B}, 1/\Omega^2),$$

where \mathbf{Y} and \mathbf{B} denote the mean intercept and slope for the entire community, respectively, and Φ and Ω their respective SDs. We again used MCMC through JAGS in program R to estimate posterior distributions for all parameters. As before, we scaled all covariates to a mean = 0 and SD = 1 for ease of comparison across covariates. Variation in body mass, average body mass, variation in home range size, average home range size, variation in weaning age, and average weaning age were all log-transformed before scaling. We ran models across three parallel chains, each with 10,000 iterations. We discarded the initial 5000 draws from each chain as burn-in, and thinned the resultant samples by two, leaving 7500 iterations per posterior for each parameter. We assigned Beta parameters a flat uniform prior from -5 to 5 and their SDs were assigned a flat uniform prior from 0 to 10 . Convergence was assessed in the same way as for the occupancy model described above. We measured “significant” differences using posterior probability, where we expressed “strongly significant” effects as parameters with $>95\%$ posterior probability of a negative or positive response (i.e., our model estimates that the probability the parameter effect is more extreme than 0 is $>95\%$), and expressed “moderately significant” effects as parameters with $>85\%$ but $<95\%$ posterior probability of a negative or positive response. We included the 85% threshold

to capture both order and community effects that exhibit a strong trend toward either a negative or positive association, but were limited by high variation in community hyperparameters, which can lead to overall “shrinkage” of order-specific effects toward the community mean effect (Mata et al., 2017; Suraci et al., 2021).

RESULTS

Dataset summary

Our truncated dataset resulted in 92,285 detections of 53 mammal species across 52,828 camera trap days and 1492 camera trap sites. Individual camera trap sites were active for an average of 35 camera trap days (SD = 18).

Mean trait values varied widely across orders (Appendix S1: Table S1). Average home range was greatest in Carnivora (n species = 14, mean = 52.58 km², SD = 90.2), followed by Cetartiodactyla (n species = 8, mean = 17.3 km², SD = 20.42), Lagomorpha (n species = 6, mean = 1.03 km², SD = 1.92), Didelphimorphia (n species = 1, mean = 0.51 km²), Rodentia (n species = 23, mean = 0.09 km², SD = 0.18), and Cingulata (n species = 1, home range = 0.03 km²). Average adult body mass was largest in Cetartiodactyla (205.0 kg, SD = 222.84; 1.70 individuals, SD = 1.00). Didelphimorphia displayed the largest average litter size (8.62 individuals), while Lagomorphs had both the youngest weaning age (24.81 days, SD = 4.02) and greatest annual number of litters (3.69 litters, SD = 0.79). Carnivora and Didelphimorphia were the only orders whose diets were relatively omnivorous on average (Carnivora = 69.29% meat consumption, SD = 29.99; Didelphimorphia = 50% meat consumption), with the diets of all other orders trending toward 0% or 100% meat consumption. Diet breadth was greatest in Didelphimorphia (four diet categories) and Rodentia (3.22 diet categories; SD = 1.20).

The degree of trait variation displayed by each order was similarly variable. Reported variation in home range was greatest for Rodentia (mean = 15.03, SD = 55.68) and smallest in Lagomorpha (mean = 1.72, SD = 0.68), but there were no measured significant differences across orders ($f = 0.23$, $p = 0.95$). Similarly, rodents displayed the greatest variation in adult body mass (mean = 24.93, SD = 69.20), while ungulates displayed relatively little variation (mean = 0.05, SD = 0.05). As with home range, there was no significant variation in adult body mass across orders ($f = 1.20$, $p = 0.33$). In contrast, Cetartiodactyla displayed significantly greater variation in social group size (mean = 7.31, SD = 3.85) than Rodentia (mean = 0.91, SD = 1.73; $p \leq 0.001$), Carnivora (mean = 0.09, SD = 0.44, $p \leq 0.001$), and Lagomorpha (mean = 0.25, SD = 0.75,

$p \leq 0.001$). Variation in litter size was greatest in Didelphimorphia (1.74), but did not differ across orders ($f = 2.07$, $p = 0.09$). Cetartiodactyla displayed the greatest variation in weaning age (mean = 0.96, SD = 1.59), which also did not differ across orders ($f = 0.70$, $p = 0.63$), and Carnivora showed the greatest variation in annual litters (mean = 0.81, SD = 1.91), albeit not significantly ($f = 0.40$, $p = 0.85$). Litter size varied most within Cetartiodactyla (mean = 0.47, SD = 0.32), but did not differ significantly across orders ($f = 2.07$, $p = 0.09$). Finally, diet breadth was greater in Rodentia than Lagomorpha ($p = 0.006$), and Carnivora were more omnivorous than Cetartiodactyla ($p \leq 0.001$), Cingulata ($p \leq 0.001$), Lagomorpha ($p \leq 0.001$), and Rodentia ($p \leq 0.001$); Cingulata were more omnivorous than both Lagomorpha ($p \leq 0.001$) and Rodentia ($p \leq 0.001$).

Occupancy model

Community occupancy probability was low and highly variable across species (mean = 0.09, SD = 0.14), ranging from 0.0001 in bushy-tailed woodrat (*Neotoma cinerea*) to 0.70 in white-tailed deer (*Odocoileus virginianus*). Community detection probability was high and also varied across species (mean = 0.38, SD = 0.16), ranging from 0.04 in American badger (*Taxidea taxus*) to 0.73 in white-tailed deer. There was a strong, negative community response to urbanization (mean = -0.92, SD = 0.26, ~100% posterior probability density [PD] <0). Across species, urbanization response ranged from -3.01 in elk (*Cervus canadensis*, SD = 1.05, ~100% PD <0) to 1.78 in domestic cat (*Felis catus*, SD = 0.20, ~100% PD >0; Figure 2). Full occupancy model results can be found in Appendix S1: Tables S5 and S6.

Trait variation

Across all species, only variation in litter size significantly affected community urbanization response, with variation in litter size having a moderately positive response to urbanization (mean = 0.33, SD = 0.34, 89% PD >0; Table 2). No other trait variation values had a significant effect on community urbanization response (Appendix S1: Table S7).

Within orders, the effect of trait variation values on urbanization response varied (Table 2, Figure 3). Variation in litter size had a strong positive relationship with Cetartiodactyla urbanization response (mean = 0.47, SD = 0.32, 95% PD >0). Cetartiodactyla was also the only order whose urbanization response was positively associated with variation in weaning age, albeit

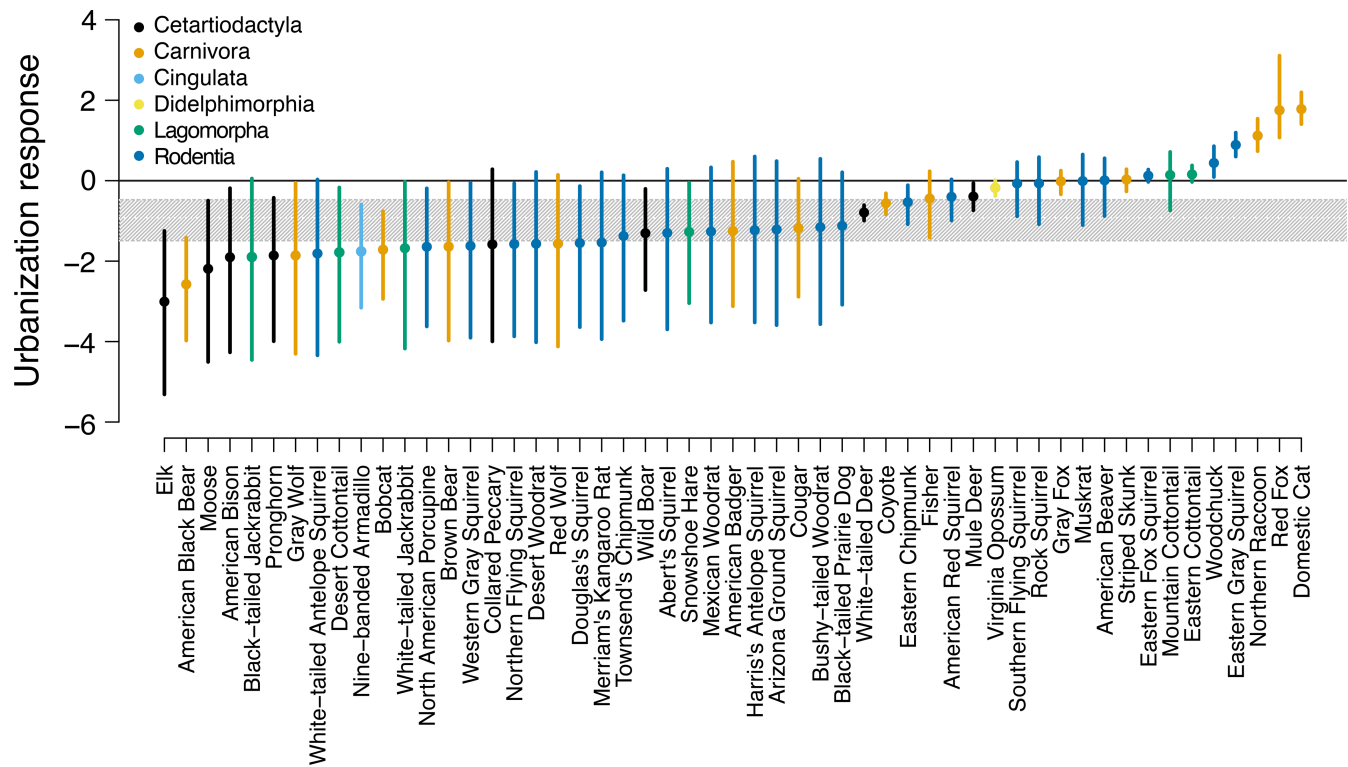


FIGURE 2 Species modeled occupancy response to urbanization. Points represent individual species' posterior mean occupancy response to the measured urbanization metric, with error bars denoting Bayesian 95% credible intervals. White, dashed line and gray bands represent the community mean response and Bayesian 95% credible Intervals, respectively.

non-significantly (mean = 0.04, SD = 0.19, 60% PD >0). Carnivora urbanization response was affected by multiple trait variation values; specifically, litter size variation had a strong positive effect (mean = 0.42, SD = 0.28, 95% PD >0), and total diel activity length had a strong negative effect (mean = -0.51, SD = 0.31, 96% PD <0), while variation in the number of litters (mean = -0.26, SD = 0.18, 93% PD <0) and variation in weaning age (mean = -0.43, SD = 0.33, 92% PD <0) had a moderately negative effect, and omnivory (mean = 0.33, SD = 0.26, 91% PD >0) had a moderately positive effect (Figure 3). Lagomorpha showed no significant associations between trait variation and urbanization response, nor did Cingulata and Didelphimorphia, although each of the latter two orders were represented by only one species in the target species pool. Finally, variation in litter size had a moderate positive effect on Rodentia urbanization response (mean = 0.26, SD = 0.20, 90% PD >0), while variation in weaning age had a moderately negative effect (mean = -0.26, SD = 0.18, 93% PD <0; Figure 3). Potential activity variation (i.e., core diel activity divided by total diel activity), diet breadth, variation in body mass, variation in home range size, and variation in sociality were not significantly associated with urbanization response for any order (Appendix S1: Table S7).

Mean trait values

Across all species, only mean litter size had a significant effect on community urbanization response (Table 2). Specifically, litter size had a moderately positive effect on urbanization response (mean = 0.27, SD = 0.29, 88% PD >0). No other trait values had a significant response on community urbanization response (Appendix S1: Table S8).

Across orders, the effect of mean trait values on urbanization response varied (Table 2, Figure 3). Litter size (mean = 0.34, SD = 0.30, 90% PD >0) and sociality (mean = -0.22, SD = 0.22, 85% PD <0) each had a moderately positive effect on Cetartiodactyla urbanization response, while average body mass (mean = -0.78, SD = 0.53, 94% PD <0), average home range size (mean = -0.75, SD = 0.52, 93% PD <0), and weaning age (mean = -0.41, SD = 0.39, 86% PD <0) each had a moderately negative effect. Average body mass (mean = -1.47, SD = 0.52, ~100% PD <0) and average home range size (mean = -1.43, SD 0.53, ~100% PD <0) had a strong negative effect on Carnivora urbanization response, while core diel activity (mean = -0.36, SD = 0.36, 87% PD <0) had a moderately negative effect and litter size (0.27, SD = 0.27, 86% PD >0) and number of litters

TABLE 2 Results of variation and mean trait value analyses for traits hypothesized to predispose species to urban exploitation.

Rationale and traits	Community trait variation effect	Community mean trait effect	Order-level trait variation effect	Order-level mean trait effect
Responses to fragmentation				
Home range	Cetartiodactyla: – Carnivora: – – Rodentia: +
Sociality	Cetartiodactyla: +
Body mass	Cetartiodactyla: – Carnivora: – – Rodentia: +
Demography				
Litter size	+	+	Cetartiodactyla: ++ Carnivora: ++ Rodentia: +	Cetartiodactyla: + Carnivora: + Lagomorpha: +
Weaning age	Carnivora: – Rodentia: –	Cetartiodactyla: –
No. litters	Carnivora: –	Carnivora: +
Responses to changes in food availability				
Degree of omnivory	Carnivora: +	NA
Diet breadth	NA
Responses to humans				
Total diel activity	Carnivora: – –	NA
Diel activity potential	NA
Core diel activity	NA	Carnivora: –

Note: Rationale for trait selection is in bold, with corresponding traits nested underneath. + or – indicate moderately significant (85%–95% Posterior distribution probability density [PD] > 0) positive/negative association with urbanization; ++ or – – indicate strongly significant (>95% PD > 0) positive/negative association with urbanization; ... indicates no relationship observed. Community-level responses refer to the urbanization response observed across all species for each trait assessed, while order-level responses reflect the urbanization response of particular taxonomic orders to each tested trait. Some traits were only indicative of variation (i.e., diet breadth, degree of omnivory, total diel activity, and diel activity potential), while core diel activity was solely a mean trait value. These cells have therefore been given “NA” designations in their respective columns.

(mean = 1.43, SD = 1.23, 93% PD > 0) had a moderately positive response. Litter size had a moderately positive effect on Lagomorph urbanization response (mean = 0.42, SD = 0.47, 88% PD > 0), while no trait values significantly affected Cingulata or Didelphimorphia urbanization response. Contrary to all other orders, average home range size (mean = 0.36, SD = 0.32, 87% PD > 0) and average body mass (mean = 0.38, SD = 0.32, 89% PD > 0) had a moderately positive effect on Rodentia urbanization response.

DISCUSSION

The only trait assessed that affected urban exploitation across all species was litter size (both mean of and variation within), a demographic trait that had a moderately

significant, positive community urbanization response (Table 2, Figure 3). This result supports other species-level mean trait analyses (Pacifiçi et al., 2020; Santini et al., 2019; Suraci et al., 2021) that suggest urban-exploiting mammals may exhibit faster life-history strategies or pace of life syndromes (Dammhahn et al., 2018; Promislow & Harvey, 1990). It is possible that flexibility in litter sizes allows a species to more efficiently respond to the heterogeneous availability of resources in cities (i.e., producing greater or fewer offspring when resources are more or less abundant, respectively) (e.g., Gamelon et al., 2014). Trait variation and mean trait values more broadly did not correspond with urban exploitation across species at the community-level, suggesting that pre-existing, species-level trait variation did not predispose mammal species assessed in our study to urban environments, overall.

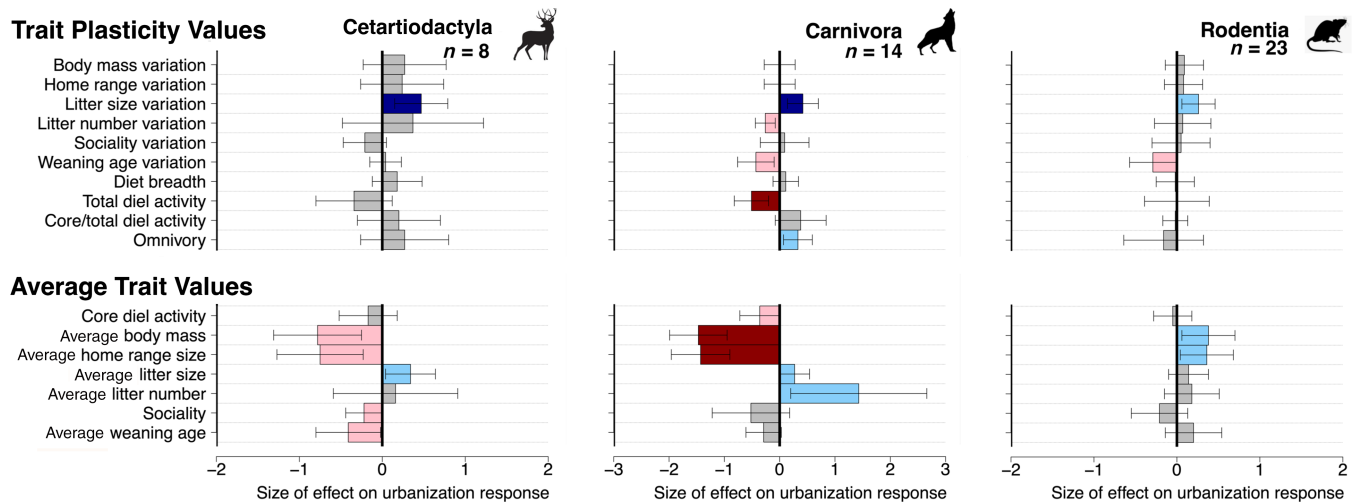


FIGURE 3 Trait variation and average trait value effects on order-specific urbanization response. Bars represent estimated mean effect size in response to urbanization, with error bars denoting 1 posterior standard deviation. The color of the bars signifies both the direction and strength of the association. Specifically, dark red = strong negative association (>95% posterior probability density [PD] <0), pink = moderate negative association (85%–95% PD <0), dark blue = strong positive association (>95% PD >0), light blue = moderate positive association (85%–95% PD >0), and gray = no association. Note the difference in scale between x-axes.

Some species well-known to persist in developed areas, such as coyotes (*Canis latrans*; Bateman & Fleming, 2012) and white-tailed deer (Parsons et al., 2017), were not found to disproportionately occupy urban compared to rural environments in our analyses (Figure 2). As landscape characteristics (e.g., forest cover, road and housing density) and species-interactions often modulate both deer and coyote occupancy in urbanized environments (Jones et al., 2016; Magle et al., 2014; but see Gallo et al., 2019), it is possible that spatial avoidance of predators (e.g., of coyotes by deer or of people by coyotes) better explains urban species occupancy than trait variation. However, it is also possible that trait variation in these species is still important, but that variation supports habitat selection in a broad array of environments, as opposed to habitat specialization in cities. For example, white-tailed deer had the highest occupancy (0.70) across all sites, and so were relatively ubiquitous across both rural and urban land use types in our study. Additionally, future work could investigate if trait variation has stronger effects on other metrics (e.g., species abundance, detection rates) in urbanizing environments compared to species occupancy.

At the order-level, mean trait values associated with home range size and body size had moderately informative relationships for certain taxonomic groups. For example, rodents were found to more likely persist in cities compared to rural areas when they were bigger in size or had larger home ranges (Table 2, Figure 3). This is in contrast with carnivores and ungulates, both of which exhibited the predicted, negative relationship of mean

home range size and mean body size with urbanization. Since body size and home range size are often correlated (Lindstedt et al., 1986), the consistency of these relationships corroborates with prior evidence. However, differences in the direction of these relationships between carnivores and ungulates (often larger species) and rodents (comparatively smaller species) might be due to an overall benefit of moderate body sizes in urban systems. On the other hand, small rodents can be difficult to detect on remote wildlife cameras, due to their body size, speed, and body temperature (Jacobs & Ausband, 2018). It is therefore also possible that larger rodents were simply more detectable than smaller ones in our study.

Variation in traits relating to diet and avoiding people had significant relationships to urbanization within certain taxonomic orders. For example, omnivory—a measure of dietary plasticity—was found to be positively associated with carnivore occupancy in urban areas. This matched our predictions and past evidence (e.g., Suraci et al., 2021). For non-taxonomic carnivores, it is possible that anatomy and physiology (e.g., the digestive system of ruminants and hind-gut fermenters) or lifestyle (e.g., fossorial species) constrains dietary flexibility. Additionally, human-mediated landscapes often provide supplemental forage (Shochat et al., 2006), while also limiting apex predators (Moll et al., 2018; Shochat et al., 2006). This may explain why mammal orders with predominantly herbivorous species (e.g., Rodentia, Lagomorpha, and Cetartiodactyla) did not require dietary plasticity to persist in urban systems. We also expected a negative relationship between sociality and urbanization, as more social species may require more

space to accommodate their social networks. In line with this hypothesis, we found a moderately negative association between sociality and urban exploitation among ungulates. However, these results differ from other studies, which have found some species exhibit increased group sizes in urbanized areas as a behavioral response to increased vigilance (e.g., key deer, *Odocoileus virginianus clavium*, Maurer et al., 2022). It is possible that humans shield populations of ungulates from carnivores in some anthropogenic environments but not in others (Berger, 2007), or that habituation (e.g., Found, 2016) among ungulate populations differs with urban context or other ecological conditions (Aronson et al., 2016), which could explain the moderately negative relationship we found in urban ungulate sociality compared to other studies.

Relationships between demographic traits (e.g., litter size, weaning age, number of litters) and urban occupancy did not always occur as predicted. For example, although ungulates, carnivores, and rodents all expressed positive relationships with urbanization given variation in litter size, carnivores and rodents also exhibited negative associations with other demographic variation values (i.e., variation in weaning age). Similarly, urban occupancy for Carnivora species decreased with variation in the number of litters. This may be because variation in weaning age or litter number could have high energetic costs in heterogeneous urban landscapes. On the other hand, the mean number of litters had a moderately positive association with urbanization among carnivores, which could support the hypothesis that higher reproductive rates are a prerequisite for urban exploitation (Fischer et al., 2015). Alternatively, relationships between urbanization, mean litter number, and other demographic traits (e.g., increased mean litter size across Carnivora, Lagomorpha, and Cetartiodactyla and decreased mean weaning age in ungulates) could indicate that faster life history strategies are needed for urban persistence (Gamelon et al., 2014).

Contrary to our predictions, total diel activity (a measure of trait variation) had a strongly negative relationship among carnivores and no relationship with other taxonomic orders. Similarly, and in line with our predictions, core diel activity (i.e., average diel activity) had a moderately significant, negative association with carnivore occupancy in urban areas. Diel activity among mammals has been found to shift toward nocturnality in cities (Gaynor et al., 2018; but see Frey et al., 2020; Maurer et al., 2022), and some juvenile carnivores may learn to shift their activity in response to urbanization (e.g., brown bears, *Ursus arctos*; Lamb et al., 2020). Further, recent evidence suggests that temporal activity can vary significantly within and across species and in response to urbanization (Gallo et al., 2022). Although

this indicates that flexibility in diel behaviors does exist among urban mammals, there is also evidence that the degree or direction to which mammals alter their activity in response to anthropogenic disturbance differs across species (Allen et al., 2022; Frey et al., 2020). It is possible that these shifts are too small to show a strong signal in our analyses for most species. Since many carnivores already exhibit crepuscular or nocturnal activity patterns (Prugh & Golden, 2014), it is also possible that species with more constrained nocturnal activity may better exploit urban environments than those whose activity varies more widely.

CONCLUSION

Increased variation among demographic traits can support more rapid evolution (Des Roches et al., 2018; Jump et al., 2009). Since we found variation in litter size as indicative of urban association across mammals, our results suggest that urban exploiting species may be predisposed to stronger selective pressures, provided this variation translates to intraspecific fitness variation within local populations (Thompson et al., 2022). These results also have significant implications for human-wildlife conflict (Schell et al., 2020), as species with higher average-values and variation in litter size may also be more adept at avoiding human extirpation and management interventions by responding as needed to environmental constraints. Additionally, our results add to a growing body of evidence that indicates faster life-history strategies or pace of life syndromes may support mammal species to occupy cities (Pacifi et al., 2020; Santini et al., 2019; Suraci et al., 2021). However, our results also suggest that relationships between traits and urban exploitation are often not ubiquitous. It is possible that anatomical or physiological constraints (e.g., energetic requirements, digestive physiology, circadian rhythms) contribute to these differences. Since coexistence theory suggests that intraspecific competition must be greater than interspecific competition for coexistence to occur (Chesson, 2000, although also note commentary in Adler et al., 2018 on the complex discourse surrounding coexistence theory), it makes sense that species interactions might preclude taxa from responding in the same way to city life. Selective pressures may therefore also exist for variation in or the differentiation of strategies among individuals in urban environments. Future research that compares trait variation and mean trait values between urban and rural mammal populations—and at differing scales (see Adler et al., 2018)—could help elucidate competition, coexistence, and subsequent eco-evolutionary processes in cities.

To our knowledge, this is the first study investigating species-level trait variation and its relationship to urban exploitation across multiple traits and mammal species. Since natural selection requires trait variation, the variation of demographic traits, such as litter size, can have significant implications for wildlife management and conservation. Additionally, our results provide further evidence for omnivory as a form of dietary plasticity that supports urban accessibility among species in higher trophic guilds (e.g., order Carnivora). Using this information, we can better manage and understand which species might occupy and adapt to cities, thereby promoting human-wildlife coexistence.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Previously published data sets were utilized for this research and are available as follows: Cove et al. (2021) (<https://doi.org/10.1002/ecy.3353>); Wilman et al. (2014) (<https://doi.org/10.1890/13-1917.1>); Jones et al. (2009) (<https://doi.org/10.1890/08-1494.1>).


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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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