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Land cover mediates predator effects on urban deer mouse abundance

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ABSTRACT

Urbanization alters biodiversity, contributing to habitat loss and fragmentation and non-native species introductions. Despite these changes, urban environments provide habitat for many species and could be managed to support diverse wildlife communities. However, we do not fully understand species' responses to urban environments or the mechanisms that drive them, particularly how species interactions (e.g., predation) affect urban populations. This lack of understanding restricts our ability to manage urban habitats to support wildlife communities rather than individual species. We sought to understand how urbanization affects and interacts with predator distributions to influence the abundance of small mammalian prey. We identified the impacts of urban land cover and predator occurrence on population persistence and recruitment of deer mice (*Peromyscus* spp.) using a hierarchical Bayesian abundance model. Mouse population persistence was lower when domestic cat (*Felis catus*) occupancy was high. However, persistence probabilities increased as native vegetation cover increased, even when cat occupancy was high at those naturally-vegetated sites. In contrast, mouse persistence was unrelated to red fox (*Vulpes vulpes*) occupancy. Our results strengthen mounting evidence that free-ranging cats negatively affect native prey populations, especially where human-modified land cover is high, and demonstrate a loss of prey population regulation for urban native mammalian predators. We further provide the first evidence that urban mouse populations exhibit low persistence and high recruitment, and thus are spatially and temporally dynamic. Managing free-ranging cats and providing structural heterogeneity in vegetation are critical for maintaining urban small mammalian prey and trophic systems in cities.

1. Introduction

Urbanization is a leading cause of environmental change worldwide and thus poses a significant challenge to wildlife conservation globally. For example, urbanization leads to vegetation loss and fragmentation (Seto et al., 2012) and the introduction of non-native species (Francis and Chadwick, 2015) which, in turn, alters habitat availability and wildlife distributions. Wildlife respond differently to urbanization such that some species thrive (e.g., edge species, dietary generalists) while others (e.g., habitat and dietary specialists) decline or disappear (Hensley et al., 2019). It is increasingly apparent that wildlife responses to urbanization result from a complex interplay between the characteristics of urban environments and species biology (e.g., body size; Haight et al., 2023), but we still do not fully understand the driving mechanisms behind many species' responses to urban environments. This knowledge gap complicates our efforts to sustain urban biodiversity, given that, despite negative ecological impacts, cities can have significant conservation value as habitat for some species (Lepczyk et al., 2023) and that the maintenance of native species in cities is critical for urban ecosystem function (Tartaglia and Aronson, 2024).

Interactions with other taxa are important aspects of a species' biology that strongly influence occurrence and abundance. Predatory interactions are an important determinant of wildlife space use (Sih, 2005), and urbanization can alter predator-prey relationships (Faeth et al., 2005). For example, anthropogenic subsidies—food items intentionally or unintentionally provided by humans (e.g., food waste, bird seed)—can reduce predation pressure as predators switch to these more easily acquired food items (Rodewald et al., 2011). Alternatively, the removal of large predators from urban systems can "release" smaller predators from competition and increase predation pressure, leading to local extinction of prey species (Crooks and Soulé, 1999). Introduced species may further affect predation pressure in urban systems. Introduced prey species can augment predator numbers and increase predation pressure on native prey (Cava et al., 2012). Moreover, introduced predators can reduce prey abundance through direct consumption (Loss et al., 2013) or through changes in prey behavior (Bonnington et al.,

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2013). Urbanization thus changes how interactions such as predation shape wildlife communities.

The majority of research on predator-prey interactions in urban areas focuses on songbirds or invertebrates as the prey taxon of interest. Small mammals (i.e., mammals weighing <120 g as adults) are key prey species in non-urban ecosystems (Dickman, 1999) and are likely of similar importance in urban systems, yet the compounding effects urbanization and predation have on small mammal distributions and abundance is understudied (reviewed in Eötvös et al., 2018). Mammalian prey species generally do not spatially segregate from their predators in urban areas, but rather alter other aspects of their behavior such as vigilance rates (Gallo et al., 2019), activity levels (Moll et al., 2020), or foraging strategies (Fardell et al., 2021) to avoid encountering predators. However, we do not know how predation affects population-level parameters such as persistence (i.e., the continued presence of a population) and recruitment (i.e., the addition of new individuals through births and immigration). These parameters in turn affect metapopulation dynamics and are important indicators of local extinction risk. Given the importance of small mammals for ecosystem function (e.g., as prey, as seed predators), it is imperative to understand how changes to species interactions as a result of urbanization alter their distributions and abundance and potentially impact the ability of urban ecosystems to support wildlife communities.

We identified the impacts of predator occurrence on common North America native prey species, deer mice (*Peromyscus leucopus* and *P. maniculatus*; hereafter “mice”), in an urban ecosystem. by quantifying changes in mouse population persistence and recruitment across an urban intensity gradient and under varying occupancy probabilities of common predator species (domestic cat, *Felis catus*, hereafter “cat”; red fox, *Vulpes vulpes*, hereafter “fox”; coyote *Canis latrans*; and American mink *Neogale vison*, hereafter “mink”) in the Iowa City metropolitan area of Iowa, USA. Under the predation risk hypothesis (Prugh and Golden, 2014; Taylor et al., 2023), increased predator occupancy probabilities should correlate with increased predation risk; thus, we predicted mouse population persistence to decrease as cat occupancy probability increased, as cats have previously been shown to depredate significant numbers of small mammals (Loss and Marra, 2017). We also predicted the presence of native mammalian predators to reduce mouse population persistence given that these species can reach high densities in urban ecosystems due to resource subsidization (Gehrt et al., 2010) and could thus depredate more individuals. However, under the habitat-mediated predation risk hypothesis (Prugh and Golden, 2014; Taylor et al., 2023), the local habitat can reduce the suppressive effects of increased predation risk. We predicted that mouse persistence in the presence of predators would be greater with increasing native vegetation cover, as urban mouse persistence in general is greater on sites with more natural vegetation cover (Larson and Sander, 2024). This study is among the first to examine the role of predation in regulating native rodent populations in urban environments via concurrent sampling of predator and prey populations. As such, this research will help support the management of urban landscapes to maintain urban prey populations and trophic systems.

2. Material and methods

2.1. Study area

This study was conducted in the Iowa City, Iowa, USA metropolitan area and surrounding rural areas (Fig. 1). Iowa City is relatively small (213 km^2) with a human population of 175,732 (U.S. Census Bureau, 2021). The metropolitan area is 31 % impervious and 38 % turfgrass, with the remaining 29 % native and naturalized vegetation and agriculture. Green spaces consist of riparian corridors, sports complexes, nature preserves, city parks and trails, and private properties (e.g., business campuses; large-lot residential properties). The dominant land cover outside of Iowa City is row-crop agriculture with small remnants of eastern deciduous forest and tallgrass prairie (Homer et al., 2015).

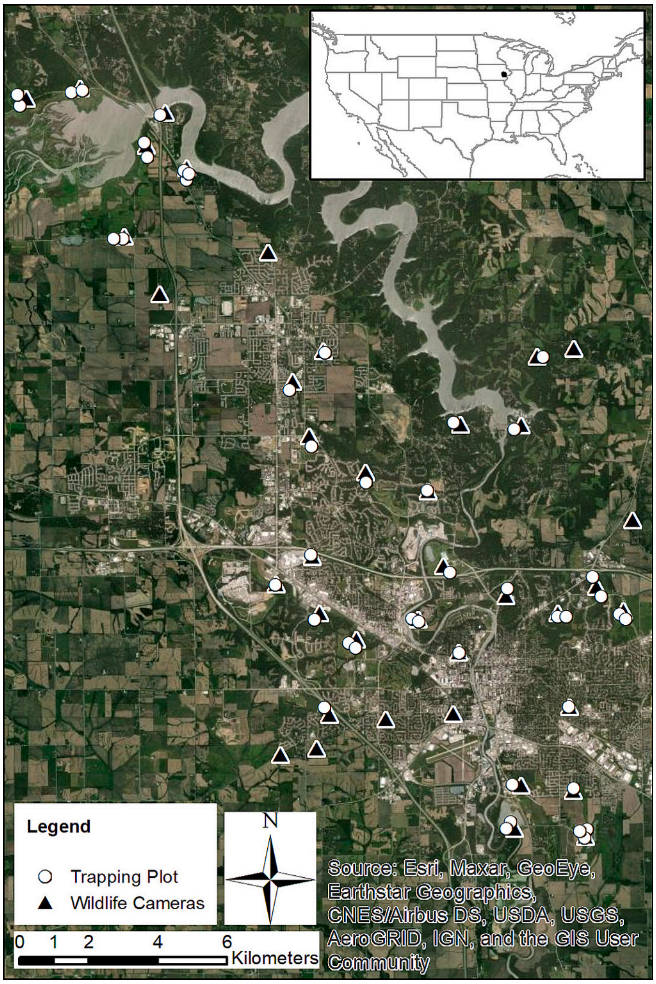

Fig. 1. Map of study area, the Iowa City metropolitan area of Iowa, USA, and the locations of the small mammal trapping plots and wildlife cameras. Inset map shows the study location in the context of the continental United States. Note that in some instances the symbols for the trapping plots mask the location of their associated wildlife camera.

2.2. Site selection

This study is part of a larger study of urban wildlife in Iowa City, and camera and mouse trapping site selection methods are detailed elsewhere (Larson and Sander, 2024; MacDougall and Sander, 2022; Magle et al., 2019). Briefly, we delineated three transects to capture a gradient of urban intensity (i.e., impervious cover) throughout the study area. Potential camera sites were randomly established along the transects, separated by ≥1 km to reduce the chances of detecting the same individual animal on multiple cameras. Potential camera sites that were not suitable (e.g., in parking lots, for which landowner permission was not granted) were excluded, for a total of 39 sampling locations (Fig. 1).

To track the number of unique individuals in an area, we selected smaller sampling plots surrounding each camera on which to live-trap and mark mice. A 1 km buffer was delimited around each camera and three to four random points (separated by ≥150 m) were generated. A 50 m radius area surrounding each of these points was designated as the trap plot to capture several potential mouse home ranges within a single plot (Stickel, 1968). We used *k*-means analysis to group mouse survey plots into distinct cover types based on land-cover classes in the 2016 National Land Cover Database (NLCD; Dewitz and U.S. Geological Survey, 2019). Details of the k-means analysis are described elsewhere

(Larson and Sander, 2024) but briefly, dimension 1 (45.3 % of variation) separated sites with high developed (i.e., impervious surfaces; cluster 1) or a mix of developed and herbaceous cover (cluster 5) from sites with other cover (remaining clusters). Dimension 2 (30.2 % of variation) separated sites dominated by herbaceous cover (cluster 3) or a mix of herbaceous cover and crops (cluster 6), from sites with predominantly forest (cluster 4) or mixed forest and herbaceous cover (cluster 2). We selected one plot per cluster per camera to ensure representative sampling. Thus, cameras in large tracts of homogenous land cover had one trapping plot associated with them, whereas cameras with a mix of land covers nearby had more than one trapping plot associated with them. Potential plots that were in areas that threatened animal safety (e.g., parking lots) or where landowners would not provide property access were excluded, for a total of 45 mouse survey plots (Fig. 1).

2.3. *Animal sampling*

2.3.1. *Carnivore sampling*

We attached one motion-triggered trail camera (Bushnell Outdoor Products, Overland Park, KS) approximately 1 m off the ground to a tree or other stationary object at each camera location for at least 28 days in 4 separate months: January, April, July, and October (i.e., “seasons”). We set the cameras to run continuously and take one, time-stamped photograph per trigger, with a 30 s quiet period between photos if the motion sensor was continuously triggered. We downloaded photographs from cameras at the end of each season. Two trained observers independently identified species in photographs, and a third trained observer validated identifications in cases where observers disagreed. We analyzed data collected from October 2019 through October 2022 to model average predator site occupancy over multiple years preceding and concurrent with small mammal trapping, as mice respond most strongly to long-term predation risk (Moll et al., 2020). We compiled binary detection/non-detection histories (1/0) for cat, coyote, fox, and mink. Although potentially important mouse predators, bobcats (*F. rufus*), long-tailed weasels (*Mustela frenata*), and badgers (*Taxidea taxus*) were not included due to low sample sizes (< 20 detections each). Raccoons (*Procyon lotor*) were also not included due to their ubiquity; raccoons are estimated to occur at every camera site (MacDougall and Sander, 2022).

2.3.2. *Mouse sampling*

We delineated a 100 m transect, oriented to capture the greatest variation in vegetation types, through the centroid of each 50 m radius survey plot. A trapping station was located every 11 m along each transect for a maximum of 10 trap stations per plot. Trap stations that were unsuitable (e.g., on a bike path) were excluded, reducing the number of trap stations for that plot. During each sampling bout, one small folding Sherman Trap (H.B. Sherman Traps Inc., Tallahassee, FL) was placed within 1 m of each trap station. Bait and bedding were provisioned according to standard small mammal trapping protocols (Paull et al., 2020). Trapping took place in the spring (10 Apr – 26 May), summer (3 Jul – 14 Aug), and fall (20 Sep – 6 Nov) from spring 2021 to fall 2022. No trapping occurred during the winter (7 Nov – 9 Apr) due to logistical complications and potential mortality when trapping animals in cold, snowy conditions.

Each site was trapped for three consecutive nights in each sampling season. We opened traps at sunset and checked traps at dawn. We recorded the number of disturbed traps (i.e., displaced, missing, or closed with no capture) as a measure of effort (total number of traps set – number of traps disturbed = trap effort). Captured animals were identified to the lowest taxonomic group and marked with a three-digit ear tag (National Band & Tag Company, Newport, KY) in their right ear. Due to the difficulty of reliably distinguishing *P. leucopus* from *P. maniculatus* based on morphological characteristics (Feldhamer et al., 1983), and the ecological similarity of these two species (Wolff, 1985), we combined counts of individuals of these two species into a single “mouse” count. All mortalities (24 northern short-tailed shrews *Blarina brevicauda*, 16 mice, and 4 masked shrews *Sorex cinereus*) were weighed, measured, and stored in individual zipper-top bags at 0 °C before being deposited as voucher specimens at the University of Iowa Museum of Natural History. All trapping protocols were approved by the University of Iowa Animal Care and Use Committee (protocol #0022288) and the Iowa Department of Natural Resources (permit #SC1419).

2.4. *Urban environmental variables*

2.4.1. *Land-cover variables*

We used multiple land-cover types as covariates in the predator occupancy model to identify predators’ occurrence probabilities across our study area. We delimited a 500 m radius buffer around each camera location and calculated the proportional cover of each 2019 NLCD landcover product (Dewitz and U.S. Geological Survey, 2021) landcover type in ArcMap version 10.7.1. We combined similar land-cover classes prior to these calculations, resulting in four classes: crops (Cultivated Cropland), “prairie” (Herbaceous/Grassland; Hay/Pasture; Emergent Herbaceous Wetland), forest (Coniferous, Deciduous, and Mixed Forest; Woody Wetlands), and impervious surfaces (Developed, Medium Intensity; Developed, High Intensity). We also calculated the average housing density surrounding each camera location as, in contrast to other carnivores, cat occurrence is more closely linked to residential development than land cover (Cove et al., 2023). We determined the number of residential buildings in each buffer from the building footprint database from Johnson County (Iowa Counties Information Technology Association, 2022) and divided that number by the plot area. Because mink are semi-aquatic (Larivière, 1999), we calculated the distance in meters from each camera location to the centerline of the nearest stream or river to produce a ‘distance to water’ covariate.

In the mouse model, landscape connectivity surrounding trapping sites could impact mouse population persistence and recruitment on a plot. We thus included a connectivity estimate for a 100 m radius buffer around each survey plot to approximate the average dispersal distance of mice (Stickel, 1968). We first used the 2019 NLCD to calculate the proportion of vegetated (Developed, Open Space; Developed, Low Intensity; all forest classes; Shrub/Scrub; Grassland/Herbaceous; all planted/cultivated classes; all wetlands classes) classes that might facilitate mouse movement and non-vegetated (Open Water; Developed, Medium Intensity; Developed, High Intensity; Barren Land) cover that may restrict movement within each plot and its buffer. We used the ‘lsm_l_contag’ function in the R package “landscapemetrics” (Hesselbarth et al., 2019) to calculate the contagion index, a measure of interspersion and dispersion of land-cover types in a landscape (here a “landscape” is each plot and its buffer). This metric ranges from 0 to 100, with low values indicate low dispersion of different landcover types (i.e., spatial clumping; high connectivity) and high values indicating high interspersion (i.e., equal, near-random distributions; low connectivity).

2.4.2. *Field surveys*

We used field surveys to identify attributes of mouse trapping plot vegetation. We delimited four, evenly-spaced 50 m transects from the centroid to the perimeter of each. At points located every 10-m along each transect, we recorded the occurrence of turfgrass, non-turfgrass vegetation (in three height classes: 0–75 cm, 76–150 cm, and 151–500 cm), and impervious cover. We calculated the percentage of points along each transect covered by each vegetation and/or impervious cover type then averaged percent cover values for all transects on a plot to identify plot-level coverage. We measured canopy closure at the mid-point of each transect four times (facing north, south, east, and west) using a spherical densitometer, then averaged all measurements to identify the percent tree canopy closure for each plot.

Because many of these variables were colinear (e.g., canopy closure and turfgrass; Pearson’s $r = -0.5$), we combined structurally similar vegetation types and performed a principal components analysis. First, we combined the 76–150 cm and 151–500 cm height classes into a single variable called “shrub cover”, as most of the plants in these height classes in our study area are woody shrubs and combined the impervious and turfgrass cover types into a single “human-modified land cover”. We then used the ‘prcomp’ function in the R package ‘psych’ (Revelle, 2022) to create a composite variable. The first component (PC1) explained 49.5 % of the variation, separating “naturally vegetated” and “human modified” sites. Canopy closure (0.509), shrub cover (0.184), and tall herbaceous cover (the 0–75 cm height class; 0.619) loaded positively on this axis while human-modified land cover loaded negatively (−0.569). The scores of each plot were saved to include as a covariate (“PC1”) in our mouse model.

2.5. Statistical modeling

2.5.1. Predator occupancy model

We used a multi-species autologistic occupancy model (Kass et al., 2020) to determine the average site occupancy probability of each predator species through time. We chose a multi-species modeling approach to assess whether coyotes influence the occupancy of the other carnivores, as both cats (Gehrt et al., 2013) and foxes (Mueller et al., 2018) spatially avoid coyotes in urban environments. This model contains first-order parameters that are associated with each species and second-order parameters associated with the co-occurrence of species pairs; detailed explanations of model specifications are available in Supplementary file 1.

We modeled the latent occupancy state $z_{s,j,t}$, of species s at site j during sampling period t by assuming it was a categorical random variable with modeled categories corresponding to different possible occupancy states of the predator community (Eq. (1)). As an example, the natural parameter specification for foxes is

$$f_{fox,t} = \beta_0 + \boldsymbol{\beta} \boldsymbol{x}_j + \theta I\left(z_{j,t-1}\right) \tag{1}$$

where β_0 is the intercept, $\boldsymbol{\beta}$ is a vector of slope coefficients, $\mathbf{x}_j$ is a vector of conformable environmental predictor variables for site j, θ is a temporal autologistic term to account for temporal dependence in our data (i.e., correlated occupancy states across seasons), and $I()$ is an indicator function that equals 1 if the community state in the previous timestep includes the species of interest and is otherwise 0. We included housing density and crop cover as occupancy covariates for cats, prairie and crop cover for coyotes, forest cover for foxes, and forest cover and distance to water for mink. Species-specific occupancy covariates were selected based on significant findings from a previous study (MacDougall and Sander, 2022) and known habitat relationships (e.g., cat association with housing and agriculture, Cove et al., 2023; mink associated with water; Larivière, 1999). For species co-occurrence parameters (e.g., $f_{cat \times coyote}$, $f_{cat \times fox}$, $f_{cat \times mink}$, etc.), we included impervious cover as we were primarily interested in how co-occurrence of these species varies as a function of increasing urban intensity (i.e., greater impervious cover). We added a temporal autologistic term to account for temporal dependence in our data because we lacked sufficient observations to model colonization and extinction rates across sites (Mckann et al., 2013).

We modeled detection probabilities $\rho_{s,t}$ for species s in sample period t as a function of the climatological season of sampling (i.e., spring, summer, fall, winter) to account for changes in animal activity levels due to weather and life-history events (e.g., denning; Eq. (2))

$$logit\left(\rho_{s,t}\right) = r_{0_s} + r_{1_s} \times spring_t + r_{2_s} \times summer_t + r_{3_s} \times winter_t \tag{2}$$

where r_{0_s} is the species-specific intercept, r_{1_s} the species-specific slope for species s, and “$spring_t$”, “$summer_t$”, and “$winter_t$” are dummy variables that equal 1 if sample period t is associated with that season and 0 otherwise. We treated fall as the baseline category for comparison.

To assess the relationship between predator occurrence and mouse populations, we used the results of this model to estimate site-specific occupancy for each predator. We logit-transformed these estimates and derived two quantities from 10,000 posterior draws: 1) the average occupancy of a predator at each site across all sampling periods and 2) the standard deviation of these average occupancies. These two components were then used to propagate uncertainty in predator occupancy in the subsequent mouse abundance model by using the mean and standard deviation as site-specific priors for the predator covariates in the mouse model (cat_j, fox_j; see Section 2.5.2 and Supplementary file 1).

All predator model parameters were given vague normal priors (e.g., $\overline{\beta_0} \sim \text{Normal}(0, 100)$). Following a 500-step adaptation and a 1000 step burn-in, we sampled all predator model parameters 5000 times across 3 chains for a total of 15,000 samples.

2.5.2. Mouse abundance model

Because we collected counts of individual mice, we used a dynamic abundance model (Kéry and Royle, 2021) to investigate trends in mouse abundance and population dynamics through time. Briefly, dynamic abundance models are hierarchical models with two submodels: the latent abundance submodel and the data submodel that relates the number of captured individuals to the true number of individuals and a capture probability; full details of the model specification are available in Supplementary file 1.

Initial abundance ($N_{i,j,t=1}$) on site j of 1, …,45 sites for time $t = 1$ was calculated with a log-predictor of λ (Eq. (3)):

$$\log\left(\lambda_{j,t=1}\right) = l_0 + l_1 \times PC1_j \tag{3}$$

where $PC1_j$ is the principal component score of each site (as described above). In each sampling period $t > 1$, abundance was calculated as the sum of apparent survivors ($\boldsymbol{S_{jt}}$) and recruits ($\boldsymbol{R_{jt}}$) at site j. To quantify changes in population persistence, the number of apparent survivors in the population was estimated from abundance in the previous time step $N_{j,t-1}$ and a persistence probability φ for site j for time t: $S_{jt} \sim Binomial(\varphi_{j,t}, N_{j,t-1})$. The logit-link predictor of φ was (Eq. (4)):

$$\begin{aligned} \text{logit}\left(\varphi_{j,t}\right) = p_0 + p_1 PC1_j + p_2 cat_j + p_3 fox_j + p_4\left(cat_j \times PC1_j\right) + \\ p_5\left(fox_j \times PC1_j\right) + p_6 CONTAG_j \end{aligned} \tag{4}$$

where cat_j and fox_j are occupancy probabilities for cats and foxes, respectively, and $CONTAG_j$ is the contagion index as described above (see Section 2.4.1). The cat and fox covariates were drawn from a normal distribution specified by the mean log-odds of site occupancy and the standard deviation around this mean as calculated in the predator model (see Section 2.5.1 and Supplementary file 1). These draws were then transformed to create occupancy probabilities for each predator. This specification preserves the uncertainty from the predator model and serves as an estimate of predators’ occupancy probability on each site across all sampling periods and thus long-term predation risk. Cats and foxes were selected because of the high likelihood that they depredate mice; while coyotes do consume small mammals, mice are not preferred prey (Hayward et al., 2023). Coyotes thus are unlikely to significantly affect mouse abundance and we did not include them in our model. Although mink are important predators of small mammals (Larivière, 1999), mink were ultimately not included in the mouse model due to their low detection probability.

The number of recruits (defined as both animals born and immigrating into the population) was estimated from a Poisson distribution with a mean of γ. The log-predictor of γ at site j for time t was (Eq. (5)):

$$\log\left(\gamma_{j,t}\right) = g_0 + g_1 CONTAG_j + g_2 \times spring_t + g_3 \times summer_t \tag{5}$$

where $season_t$ is a categorical variable that represents the meteorological season of sampling (spring, summer, or fall; fall was the reference category to which other seasons were compared). Season was included to account for population growth as young are born throughout the year.

In our capture probability submodel, the number of individuals captured each night was a function of the estimated true abundance at each site N_{jt} and a capture probability c. The logit-link function for c for site j, for nights 1, …,k, for season t was (Eq. (6)):

$$\text{logit}\left(c_{j,k,t}\right) = \alpha_0 + \alpha_1 \boldsymbol{moon}_{j,k,t} + \alpha_2 \boldsymbol{date}_{j,k,t} + \alpha_3 \boldsymbol{effort}_{j,k,t} \tag{6}$$

where $moon_{j,k,t}$ is moon illumination, $date_{j,k,t}$ was the ordinal date, and $effort_{j,k,t}$ was the number of available (i.e., open, undisturbed) traps at site j on night k in season t. We used the 'getMoonIllumination' function from the R package "suncalc" (Thieurmel and Elmarhraoui, 2019) to record moon illumination (proportion full) for each trap-night.

2.5.3. Model convergence, and interpretation

To assess model convergence for both models, we inspected traceplots of all model parameters to evaluate proper mixing and ensured that all Gelman-Rubin diagnostics for each parameter were < 1.10 (Gelman et al., 2013). All data processing and modeling was conducted in R version 4.2.2 (R Core Team, 2022) and JAGS 4.3.1 (Plummer, 2003). For each covariate effect for both models, we used the proportion of the posterior estimates sharing a sign (positive or negative) with the median estimate to represent the probability of a substantial parameter-covariate relationship. We denote this statistic as "Pr(relationship)" throughout the results. We refer to distributions for which ≥85 % of their posterior distribution share the same sign as the median as 'likely' and ≥ 95 % as 'highly likely' following Haight et al. (2023).

3. Results

3.1. Predator occupancy and co-occurrence

We captured 568 images of cats, 564 of foxes, 327 of coyote, and 60 of mink. Cats had the highest detection probability at an average site ($r_{0_{cat}} = 0.16$, 95 % CI: 0.14, 0.18), followed by foxes ($r_{0_{fox}} = 0.12$, 95 % CI: 0.10, 0.13), coyotes ($r_{0_{coyote}} = 0.04$; 95 % CI: 0.03, 0.05), and mink ($r_{0_{mink}} = 0.02$; 95 % CI: 0.01, 0.03). Coyotes had the highest marginal occupancy probability on average ($\beta_{0_{coyote}} = 0.33$, 95 % CI: 0.21, 0.50), followed by cats ($\beta_{0_{cat}} = 0.16$, 95 % CI: 0.07, 0.28), foxes ($\beta_{0_{fox}} = 0.15$, 95 % CI: 0.07, 0.25), and mink ($\beta_{0_{mink}} = 0.08$, 95 % CI: 0.03, 0.20). It was highly likely that cat occupancy increased with increasing crop cover ($\beta_{crop} = 0.40$, 95 % CI: 0.15, 0.68; Pr(relationship) = 100 %) and likely that cat occupancy increased with increasing housing density ($\beta_{house} = 0.29$, 95 % CI: −0.11, 0.68; Pr(relationship) = 92.3 %). It was likely that prairie cover had a positive effect on coyote occupancy ($\beta_{prairie} = 0.16$, 95 % CI: −0.08, 0.42; Pr(relationship) = 90.7 %) but there was less evidence that crop cover influenced coyote occupancy ($\beta = -0.13$, 95 % CI: −0.39, 0.13; Pr(relationship) = 83.0 %). There was little evidence that forest cover had an effect on fox occupancy ($\beta_{forest,fox} = -0.12$, 95 % CI: −0.38, 0.15; Pr(relationship) = 80.7 %). The autologistic terms were positive for all four species, indicating occupancy status in the previous season was correlated with occupancy in the current season (i.e., occupied sites tend to stay occupied from one season to the next).

Both cats ($\beta_{0,cat\times coyote} = 0.91$; 95 % CI: 0.11, 1.81; Pr(relationship) = 98.9 %) and foxes ($\beta_{0,fox\times coyote} = 0.43$; 95 % CI: −0.27, 1.22; Pr(relationship) = 89.0 %) were more likely to occur with coyotes than expected. Coyote and cat co-occurrence was not influenced by impervious cover ($\beta_{1,cat\times coyote} = 0.07$; 95 % CI: −0.49, 0.63; Pr(relationship) = 59.0 %), however, it is highly likely that coyotes and foxes ($\beta_{1,fox\times coyote} = -0.47$; 95 % CI: −1.08, 0.05; Pr(relationship) = 96.2 %) co-occurred less frequently as impervious cover increased. We concluded cats do not avoid coyotes at the site occupancy scale in our system. While foxes appear to co-occur less frequently with coyotes as impervious cover increases, the credible intervals of expected and actual co-occurrence rates overlap significantly (Supplementary file 2). We therefore conclude that, at the site occupancy scale, smaller carnivores do not appear influenced by coyote occurrence. Full predator model results are available in Supplementary file 2.

3.2. Mouse abundance

We undertook a total of 6418 trap-nights across 45 trap lines. However, on some nights, traps were unavailable to mice (e.g., disturbed by another animal), which reduced the total effort to 5209 trap-nights. At the individual plot level, trapping effort ranged from 0 to 10 traps (mean ± standard deviation; $\bar{x} = 6.6 \pm 2.4$ SD). A total of 1424 mice were captured. Capture probability on an average night was 0.43 (95 % CI: 0.38, 0.48). Capture probability increased with decreasing moon illumination ($\alpha_1 = -0.14$, 95 % CI: −0.25, −0.04; Pr(relationship) = 99.8 %) and increasing ordinal date ($\alpha_2 = 0.30$, 95 % CI: 0.17, 0.44; Pr(relationship) = 100 %) and trap effort ($\alpha_3 = 0.66$, 95 % CI: 0.54, 0.79; Pr(relationship) = 100 %) (Table 1, Supplementary file 3).

Initial abundance was approximately 1.2 mice on the average site. Initial abundance was highly likely to be greater at sites with greater natural vegetation cover (i.e., more positive PC1 scores; $\beta_1 = 0.63$; 95 % CI: 0.33, 0.92; Pr(relationship) = 100 %). In subsequent seasons, persistence probability on an average site was relatively high ($p_0 = 0.74$; 95 % CI: 0.56, 0.87). It was highly likely that the interaction between cat occupancy and land cover influenced persistence ($p_4 = 1.97$, 95 % CI: −0.37, 4.87; Pr(relationship) = 95.8 %). Mouse persistence tended to increase as local land cover shifted from human-modified to more naturally-vegetated (i.e., increasing PC1 values), however, the magnitude of this effect was significantly greater when predicted cat occupancy was high compared to when it was low (Fig. 2). There was some evidence that the effect of fox occupancy was related to land cover ($p_5 = 1.62$, 95 % CI: −1.16, 4.57; Pr(relationship) = 88.0 %). Mouse persistence decreased as human-modified cover increased when fox occupancy was high, similar to cat occupancy; however, the uncertainty around this estimate is much greater for foxes than for cats (Fig. 2). Persistence was not correlated with connectivity (i.e., contagion; p_6 =

Table 1

Intercept and slope coefficient estimates of a hierarchical abundance model for deer mice (*Peromyscus* spp.) from the Iowa City metropolitan area. Terms are presented with their median estimate, upper and lower limits of the 95 % credible interval, and the "probability of a relationship", which is defined as the percent of the posterior distribution of each estimate that matches the sign (positive or negative) of the median estimate.

Parameter	Median	Lower 95 % CI	Upper 95 % CI	Probability of relationship
Initial abundance ($N_{j,t=1}$)				
Intercept (β_0)	0.21	−0.22	0.61	83.8 %
PC1 (β_1)	0.63	0.33	0.92	100 %**
Persistence ($\varphi_{j,t}$)				
Intercept (p_0)	1.07	0.27	1.93	99.9 %**
PC1 (p_1)	−0.63	−1.33	−0.01	98.8 %**
Cat (p_2)	−2.68	−5.20	−0.59	99.5 %**
Fox (p_3)	0.82	−1.03	2.82	81.0 %
Cat × PC1 (p_4)	1.97	−0.37	4.87	95.8 %**
Fox × PC1 (p_5)	1.62	−1.16	4.57	88.0 %*
Contagion (p_6)	0.02	−0.47	0.55	52.3 %
Recruitment ($\gamma_{j,t}$)				
Intercept (g_0)	0.18	−0.28	0.61	80.1 %
Contagion (g_1)	0.16	0.00	0.33	97.3 %**
Season, spring (g_2)	−1.41	−3.16	−0.02	99.0 %**
Season, summer (g_2)	0.77	0.34	1.24	100 %**
Detection ($p_{j,k,t}$)				
Intercept (α_0)	−0.28	−0.50	−0.08	99.8 %**
Moon illumination (α_1)	−0.14	−0.25	−0.04	99.8 %**
Julian date (α_2)	0.30	0.17	0.44	100 %**
Effort (α_3)	0.66	0.54	0.79	100 %**

[*] A 'likely' relationship (≥85 % probability).

[**] A 'highly likely' relationship (≥95 % probability).

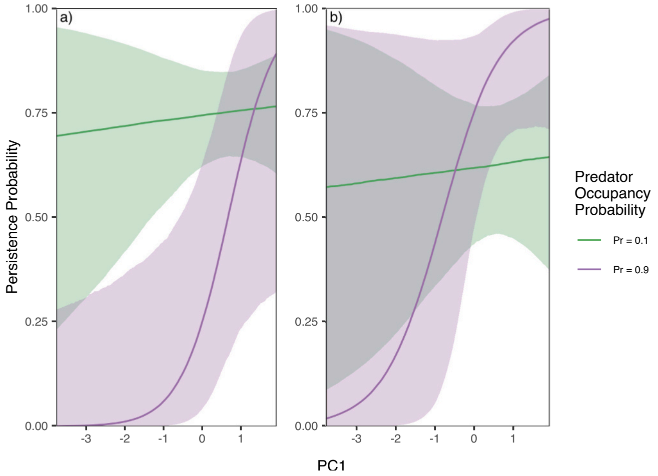

Fig. 2. Deer mouse (*Peromyscus* spp.) persistence probability is related to both land cover (PC1) and predator occupancy of a) cats (*Felis catus*) and b) red fox (*Vulpes vulpes*). PC1 is the first dimension of a principal components analysis on site vegetation characteristics and roughly represents a human-modified land cover (impervious surfaces and turfgrass; negative values) to natural vegetation cover (high canopy closure, shrub cover, and tall herbaceous cover; positive values) continuum. Solid lines are median estimates and shaded ribbons are 95 % credible intervals.

0.02; 95 % CI: −0.47, −0.55; Pr(relationship) = 52.3 %).

Recruitment was relatively low; 1.2 individuals (95 % CI: 0.8, 1.8) were recruited into the population between sampling periods at the average site. Recruitment was highly likely to increase at sites with lower connectivity (g_1 = 0.16; 95 % CI: 0.00, 0.33; Pr(relationship) = 97.3 %; Fig. 3). Recruitment was lower in the spring ($g_{2,spring}$ = −1.41, 95 % CI: −3.16, −0.02; Pr(relationship) = 99.0 %) and greater in the summer ($g_{2,summer}$ = 0.77, 95 % CI: 0.34, 1.24; Pr(relationship) = 100 %) compared to the fall.

4. Discussion

4.1. Relationships between predators, land cover, and mouse abundance

We sought to identify how local land cover and mammalian predators affected mammalian prey populations in an urban environment. Overall, we found that different attributes of mouse populations were affected by different features of urban environments. Persistence was significantly reduced on sites with greater human-modified land cover when cats were likely to be present. However, this relationship did not occur on sites with greater natural vegetation cover. Conversely, mouse persistence tended to increase when foxes were likely to be present, potentially because the presence of foxes correlates with higher-quality habitat (e.g., safe distances from human structures; Fardell et al., 2021). Recruitment was greater on sites with greater habitat fragmentation and was correlated with season, coinciding with the birth of offspring in the summer and fall. Urban mouse populations in our study system are thus characterized by low persistence and high recruitment, and their presence and abundance in the urban environment may be temporally dynamic.

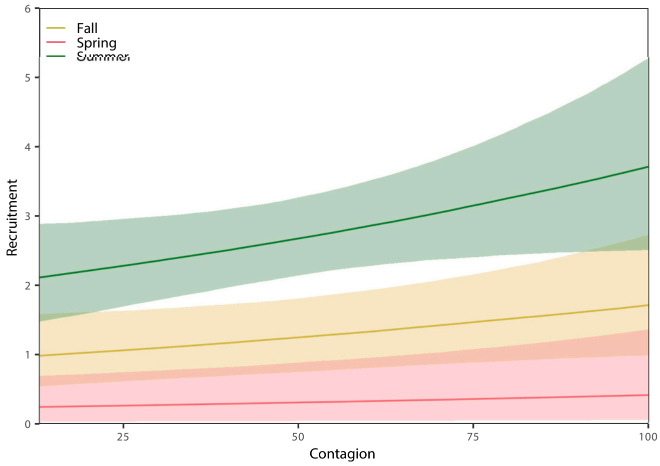

Fig. 3. Recruitment of deer mouse (*Peromyscus* spp.) individuals into a population is related to both habitat fragmentation (contagion) and season. Contagion ranges from 0 (continuous habitat) to 100 (completely fragmented habitat). Solid lines are median estimates and shaded ribbons are 95 % credible intervals.

Our findings support our prediction that mouse persistence would decrease as the probability of cat occurrence increased. Our results are in alignment with previous research indicating cats can have a negative effect on native wildlife (Loss and Marra, 2017; Sims et al., 2007), and small mammals in particular (Herrera et al., 2022; Kauhala et al., 2015). Cats often occur at high densities within urban environments because humans provision food and shelter. This high-density presence, combined with cats' tendency to engage in hunting behavior regardless of hunger level (Cecchetti et al., 2021), may increase predation pressure and decrease population persistence of urban mice. However, high levels of natural vegetation appear to increase mouse persistence, as mice appear to have roughly equal persistence on heavily vegetated sites regardless of the occurrence of cats. Previous research in Perth, Western Australia has also found cat presence to not be correlated with small mammal at urban sites with more dense vegetation (Lilith et al., 2010). Cats generally occur at lower densities in these environments (e.g., forest remnants; Cove et al., 2023), reducing predation risk, and the presence of vegetation such as shrubs and tall herbaceous plants provide refuges where mice can escape predation (McGregor et al., 2015; Persons and Eason, 2017). However, we were unable to observe the fates of individual mice to confirm cat predation. It is possible that cat occurrence is correlated with another aspect of the environment to which mice respond, such as the use of rodenticides, or that cats are more likely to occupy habitat with lower mouse abundances. Additional data regarding resident attitudes towards mice and their inclination to use pest control measures (e.g., traps, poison) could help to further assess this relationship. Additionally, surveying cat owners to document returned prey or deploying animal-mounted video collars could further elucidate the effects of direct cat predation on urban mice.

Our results did not support our prediction that foxes significantly reduce mouse persistence. In general, mouse persistence increased as natural vegetation cover increased regardless of fox occupancy. Similarly to cats, our study design precluded observation of fox predation events and fox presence may be related to other environmental variables to which mice respond. For example, previous research suggests some small mammals use fox presence as a cue to indicate relative safety from human disturbance (Fardell et al., 2021), as foxes avoid human-disturbed locations (Moll et al., 2018). Mice may also use fox presence as a habitat quality cue in our system, however, this hypothesis warrants further testing. Foxes, as omnivores, can also take advantage of multiple food sources (including anthropogenic subsidies; Soulsbury et al., 2010), potentially reducing predation pressure on urban small mammals and decoupling predator-prey relationships. Future studies should investigate whether more obligately-carnivorous mammalian predators (e.g., bobcats) or non-mammalian predators (e.g., owls) affect urban prey persistence, as mice are known to exhibit predator-specific behavioral responses (Moll et al., 2020).

We also identified a positive relationship between recruitment and contagion, such that recruitment was greater on sites with lower connectivity. Mice tend to move more often and travel further distances in fragmentated habitat (Diffendorfer et al., 1995); thus, mice in landscapes fragmentated by urbanization may also "wander" more frequently, increasing the likelihood that they enter habitat patches and are counted as new individuals in those populations. Additionally, our low-connectivity plots tended to have more human-modified land cover and increased cat-occurrence probability, which were correlated with lower persistence probabilities as discussed above. Given low persistence probabilities under these conditions, these plots may often be "available" (i.e., no resident mice with established territories) for dispersing individuals. Alternatively, given that our study design did not allow us to distinguish immigration from births in the recruitment metric, low connectivity sites may have lower competition from other species or additional resources that increase birth rates and/or juvenile survival on those sites. Mice born on these sites must then experience high mortality and/or emigration rates, leading to the low observed persistence rates. Low persistence and high recruitment imply that mouse populations in urban habitat patches function as "sinks" where new individuals appear but do not persist for long periods of time. This hypothesis requires further examination in other urban environments. There may also be a scale mismatch between the data we used to measure connectivity and the actual features that mice use to traverse urban landscapes. In New York City, for example, important gene flow corridors for mice include narrow features such as road medians and forest strips (Munshi-South, 2012)—features that are not preserved in the 30x30m resolution of the NLCD. Future studies could use high-resolution GPS collar data to identify connections between populations and further tease out the importance of dispersal/immigration and juvenile survival to population dynamics. Although individual behaviors are unknown, our data still indicate that mouse population presence in urban environments in our system are dynamic in space and time. Long-term monitoring would elucidate the stability of any source-sink dynamics.

5. Conclusions

We found that urban mouse populations in the Iowa City metropolitan area are small and temporally dynamic, particularly where cats are present, which could alter urban predator-prey interactions. Our findings thus lend support to the hypothesis that urban carnivores consume anthropogenic subsidies in part because prey are scarce, decoupling predator-prey interactions and potentially indicating poor urban food web functioning. However, the impact of cats on mouse populations in our study also appears to be landscape dependent, as the relationship between cat occurrence and mouse persistence varied with urban intensity and vegetation complexity. Our work has important implications for managing urban ecosystems to support small mammals and the ecosystem functions they carry out. Providing structurally-complex vegetation in cities, such as tall herbaceous and shrub cover, could allow prey to escape predation attempts and increase the persistence probability of local populations. Given that urban ecosystems are key areas for biodiversity conservation (Ives et al., 2016), understanding how urbanization affects processes such as predator-prey relationships can help maintain biodiversity in and beyond cities.

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CRediT authorship contribution statement

Rachel N. Larson: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Heather A. Sander:** Writing – review & editing, Supervision, Project administration, Conceptualization. **Mason Fidino:** Writing – review & editing, Validation, Methodology.

Declaration of competing interest

The authors declare no conflicts of interest.

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Data availability

Data and code of the analyses are available on GitHub: https://github.com/RLarson92/UrbFoodChain

UrbMouseAbund (Original data) (GitHub)

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