RESEARCH ARTICLE

Journal of Animal Ecology | BRITISH ECOLOGICAL SOCIETY

Urbanization alters predator-avoidance behaviours

Travis Gallo[†] (iD) | **Mason Fidino[†]** (iD) | **Elizabeth W. Lehrer** | **Seth Magle**

Department of Conservation and Science, Urban Wildlife Institute, Lincoln Park Zoo, Chicago, Illinois

Correspondence
Travis Gallo
Email: tgallo@lpzoo.org

Abstract

1. Urbanization is considered the fastest growing form of global land-use change and can dramatically modify habitat structure and ecosystem functioning. While ecological processes continue to operate within cities, urban ecosystems are profoundly different from their more natural counterparts. Thus, ecological predictions derived from more natural ecosystems are rarely generalizable to urban environments.

2. In this study, we used data from a large-scale and long-term camera trap project in Chicago IL, USA, to determine whether urbanization alters predator-avoidance behaviour of urban prey species.

3. We studied three behavioural mechanisms often induced by the fear of predation (spatial distribution, daily activity patterns and vigilance) of white-tailed deer (*Odocoileus virginianus*) and eastern cottontail (*Sylvilagus floridanus*) when coyote (*Canis latrans*)—an urban apex predator—was present.

4. We found no evidence of spatial segregation between coyote and either prey species. Furthermore, neither white-tailed deer nor eastern cottontail changed their daily activity or increased vigilance in urban areas when coyotes were present. Eastern cottontail, however, had their uppermost level of vigilance in highly urban sites when coyotes were absent.

5. Our study demonstrates that predator–prey dynamics might be modified in urban ecosystems—moving from what is traditionally thought of as a two-player system (predator and prey) to a three-player system (predator, prey and people).

KEYWORDS

Bayesian two-species occupancy model, behaviour, daily activity overlap, predator–prey dynamics, spatial distribution, urban wildlife, urbanization, vigilance

1 | INTRODUCTION

Urbanization is the fastest growing form of land-use change and can be considered the greatest anthropogenic impact on Earth's ecosystems (Foley et al., 2005; Grimm et al., 2008). Land-use changes that accompany urbanization dramatically modify habitat structure and ecosystem function through the conversion of natural habitats to impervious surfaces and altering hydrological and nutrient cycling

(Beninde, Veith, & Hochkirch, 2015; Farinha-Marques, Lameiras, Fernandes, Silva, & Guilherme, 2011; Ibáñez-Álamo, Rubio, Benedetti, & Morelli, 2017). Despite these profound changes, ecological processes continue to operate within urban landscapes (Forman, 2016; Grimm et al., 2008; Pickett & Cadenasso, 2017). Cities also support a significant number of ecologically important species (e.g., keystone species) and species of conservation concern (Aronson et al., 2017; Ives et al., 2016). Thus, cities are an important venue for the management and conservation of biodiversity (Dearborn & Kark, 2010).

[†]Authors contributed equally.

wileyonlinelibrary.com/journal/jane

As urban ecosystems distinctively vary from their more natural counterparts (Forman, 2016), ecological models derived from more natural ecosystems may not generalize to urban environments (Rodewald, Kearns, & Shustack, 2011; Shochat, Warren, Faeth, McIntyre, & Hope, 2006). For example, the classic river continuum model (Vannote, Minshall, Cummins, Sedell, & Cushing, 1980) for urban watersheds must be modified to consider engineered infrastructure and disconnections from floodplains (Kaushal & Belt, 2012). Similarly, top-down and bottom-up trophic dynamics in urban ecosystems often differ from those in more natural ecosystems due to the multitude of maintained parks and yards, which increase and stabilize primary productivity throughout the system (Imhoff, Tucker, Lawrence, & Stutzer, 2000). Understanding the parallels and disconnects between well-founded ecological principles in natural and urban ecosystems is essential to understanding how human activities alter ecological and evolutionary processes in cities (Grimm et al., 2008; Pickett & Cadenasso, 2017; Shochat et al., 2006).

The presence of predators typically influences the behaviour and distribution of prey species (Brown & Kotler, 2007; Laundre, Hernandez, & Ripple, 2010). Predators not only impact prey through direct predation but also influence prey behaviour through fear (an organism's perceived cost of injury or mortality; Brown & Kotler, 2007). These costs are at odds with the prey's needs to acquire resources, and therefore, prey species must make trade-offs between food and safety to survive (Brown & Kotler, 2007). For example, prey may use resource rich habitat patches less than expected or avoid some habitats altogether if the risk of predation is too high (McArthur, Banks, Boonstra, & Forbey, 2014; van der Merwe & Brown, 2008). However, unique characteristics of urban ecosystems may alter expected behavioural outcomes. For example, the presence of novel resources may reduce the need for prey to forage in environments with predators (Brown & Kotler, 2007; Rodewald et al., 2011). Further, available habitat is generally reduced and disconnected in urban areas, limiting a species' ability to distribute freely across the landscape (Magle, Simoni, Lehrer, & Brown, 2014).

Habitat patches are smaller and more rare in highly urbanized areas, creating highly fragmented and spatially disjunct habitats (Gehrt, 2010b). Patchy arrangements of habitats may constrain the prey's ability to spatially avoid predators (Magle et al., 2014) and force them to occupy the same habitat patches as predators (McKinney, 2002; Ordeñana et al., 2010). In these cases, we would expect prey species to possess behavioural adaptations that allow them to co-exist in the same habitat patch as a predator. For example, prey species may alter the amount of time they allocate to foraging or increase their vigilance to avoid predation (Brown & Kotler, 2007). The inability of a prey species to respond to predators would inevitably result in their extirpation from the patch (Carthey & Banks, 2014). Human development also presents novel threats to wildlife—for example, vehicular traffic or increased potential for human–wildlife conflict—that may be perceived as a greater risk compared to non-human predators (Bleicher & Rosenzweig, 2017; Frid & Dill, 2002; Polfus & Krausman, 2012). Therefore, the addition of anthropogenic risks may increase the complexity of trade-offs that

must be made by prey species to persist in urban habitat patches (e.g., Coleman, Richardson, Schechter, & Blumstein, 2008; Valcarcel & Fernández-Juricic, 2009).

Additionally, prey species should continually respond to changes in predator habitat use (Brown & Kotler, 2007) and behaviour (Brown, Laundré, & Gurung, 1999; Fretwell, 1969; Lima & Dill, 1990)—although this is not always the case (Bleicher, Brown, Embar, & Kotler, 2016). Yet, urban predators may also be constrained in their movement or daily activity patterns due to human activity or features of the built environment (Gese, Morey, & Gehrt, 2012), thus lowering the impact they hold on prey. Urban predators may also supplement their diet through anthropogenic resources which would reduce their need to hunt risky prey and further reduce their impact on prey populations (Morey, Gese, & Gehrt, 2007; Murray & St. Clair, 2017). In many cases, larger-bodied predators avoid areas of high human activity (e.g., Shannon, Cordes, Hardy, Angeloni, & Crooks, 2014; Waser et al., 2014). However, some predators have adapted behaviours that allow them to persist in human-dominated ecosystems—for example, increased nocturnality (Gaynor, Hojnowski, Carter, & Brashares, 2018). These nuanced behavioural changes of urban predators—facilitated by urbanization—may induce behavioural cascades that further alter predator-avoidance behaviour of urban prey species.

The goal of this study was to better understand how urbanization influences predator-avoidance behaviours in urban prey species, and inform urban wildlife management and conservation through an improved knowledge of predator–prey dynamics in urban ecosystems. To assess how predators influence the behaviour of prey species in urban environments, we studied three behavioural mechanisms often manifested by the fear of predation—the spatial distribution, daily activity patterns and vigilance of prey species. First, we assessed the spatial co-occurrence of coyotes (*Canis latrans*) and two common prey species—white-tailed deer (*Odocoileus virginianus*) and eastern cottontail (*Sylvilagus floridanus*). We then assessed changes in temporal prey behaviour by comparing the daily activity patterns of each prey species when coyotes were present or absent within a habitat patch. Finally, we assessed photographs of prey species to determine whether prey vigilance behaviour increased when coyotes were present in a habitat patch.

Coyotes (*C. latrans*) are highly adaptable carnivores that have become more nocturnal to avoid humans (Gehrt, 2010a; Riley et al., 2003) and supplement their diet with anthropogenic resources in urban ecosystems (Morey et al., 2007; Murray & St. Clair, 2017; Newsome, Garbe, Wilson, & Gehrt, 2015). While urban coyotes are often misrepresented as eating mostly anthropogenic refuse, they are, in fact, actively engaged in predatory roles in urban systems (Gehrt, 2010a) and prey on both eastern cottontails and young white-tailed deer (Newsome et al., 2015). With the absence of most large-bodied predators in urban ecosystems, coyotes are the closest equivalent to apex predators and likely influence the distribution and behaviour of urban prey (Crooks & Soulé, 1999).

White-tailed deer and eastern cottontails are known to spatially avoid coyotes in more remote (Lingle, 2002) and suburban (Jones,

Cove, Lashley, & Jackson, 2016) areas. However, we hypothesized that these prey species would not demonstrate a pattern of spatial segregation from coyotes, because habitat patches are limited in highly urban environments (Magle et al., 2014). Thus, each prey species would be forced to occupy the same habitat patches as coyote. If prey species were unable to avoid coyotes, but continue to persist within the same patch as coyotes, we predicted that they would alter their daily activity patterns and increase vigilance to lessen their risk of predation (Brown & Kotler, 2007).

2 | MATERIALS AND METHODS

2.1 | Study site

This study was conducted in Chicago, IL, USA, as part of an ongoing biodiversity monitoring survey in the greater Chicago Metropolitan area. Chicago is the third most populous city in the United States with approximately 2.7 million residents, an average population density of 7,355 people per km^2 (U.S. Census Bureau, 2015b), and an

estimated 8.6 million people (U.S. Census Bureau, 2015a) in the metropolitan area. The Chicago region is highly urbanized, but contains a significant portion of protected lands (i.e., forest preserves and natural areas). Although small in size and fragmented, these protected areas, along with other urban green spaces (e.g., city parks, cemeteries and golf courses), provide habitat for urban wildlife (Aronson et al., 2017; Magle, Lehrer, & Fidino, 2016).

2.2 | Data collection

The Chicago Biodiversity Monitoring Project consists of three sampling transects originating in Chicago's urban centre and continuing 50 km in three cardinal directions (Figure 1a). Each transect was divided into ten 5-km-long sections within which we randomly selected sampling sites (Magle et al., 2016). To spatially distribute sampling evenly along each transect, a maximum of four sites were selected within each section, and locations were separated from one another by at least 1 km (Magle et al., 2016). All sampling sites (n = 102) were placed in urban natural areas, city parks, golf courses
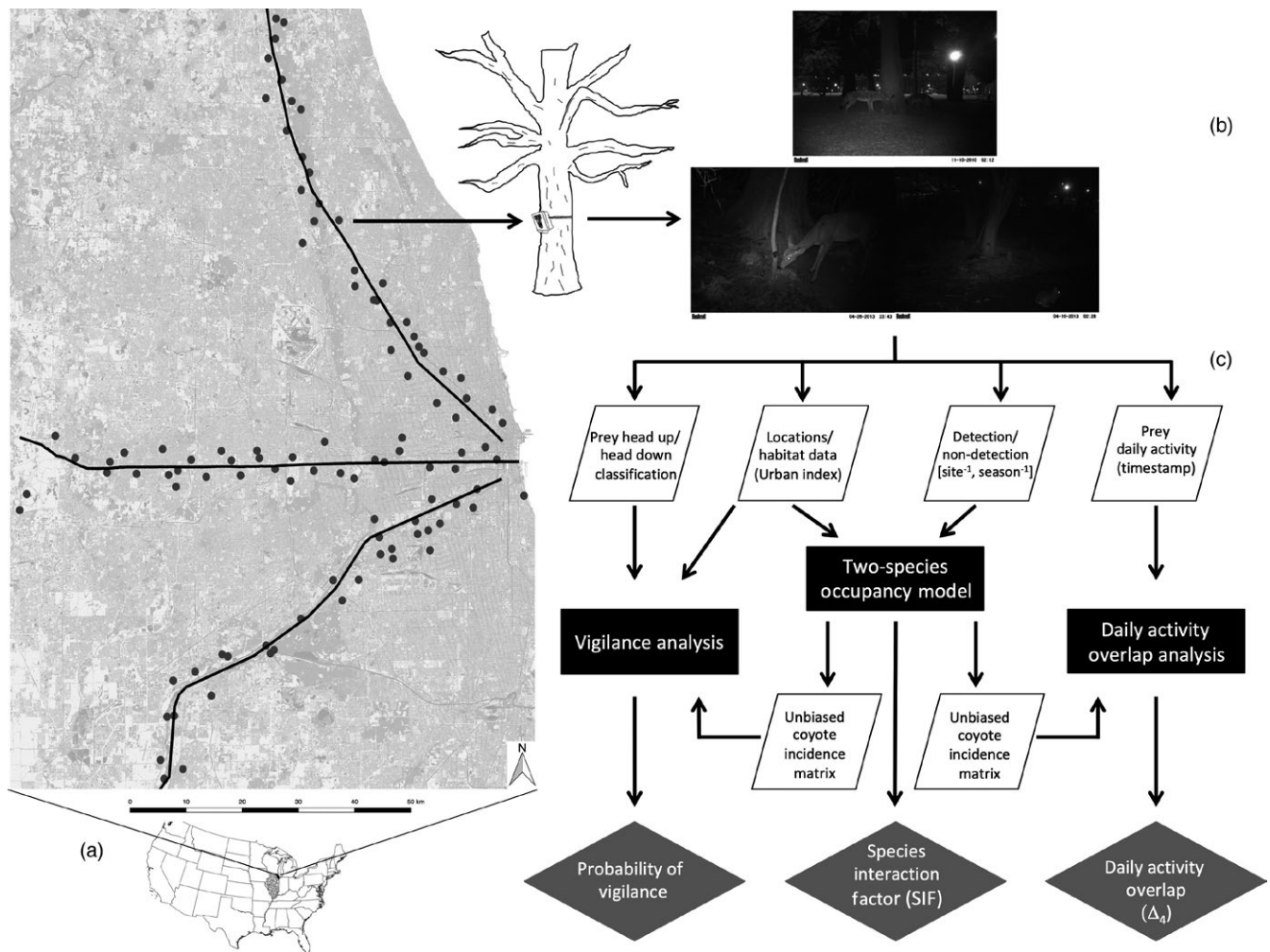

FIGURE 1 Location and design of the Chicago Biodiversity Monitoring Project (a), example of data collected from remotely triggered cameras (b), and the hierarchical model formulation used to assess predator-avoidance behaviour of white-tailed deer and eastern cottontail in Chicago, IL USA (c). Within figure (c), white boxes represent data, black boxes indicate analysis, and grey diamonds represent results. Note: Habitat data are calculated using GIS and are not collected from camera images

and cemeteries. We placed one Bushnell motion-triggered infrared Trophy Cam (Bushnell Corp., Overland Park, KS, USA; see Supporting Information Appendix S1 for camera settings) at each site (Figure 1b) for 28 days per season (i.e., spring, summer, fall and winter). Each season we placed one synthetic fatty acid scent lure in the line of sight of the camera to increase the detection probability of each species (Gerber, Karpanty, & Kelly, 2012). Lures were replaced on a 2-week interval, if missing, to remain consistent. For this analysis, we used data from fall 2010 to spring 2013 for a total of 11 sampling seasons. Due to malfunctioning cameras, vandalism and logistical constraints, not all sites were sampled equally across each season; however, most cameras were active for the entire sampling period (median days active = 27). For each sampling period, we calculated (1) the number of days each species was detected at each sampling location and (2) the number of days a camera was operational at each sampling location. Further details about study design and species identification procedures are described in Magle et al. (2016).

Our study design follows an urban to suburban gradient (Figure 1a). To characterize the varying levels of urbanization surrounding a site, we calculated an urbanization index using a principal components analysis consisting of the per cent tree cover, per cent impervious cover and mean housing density, each within a 500 m fixed-radius buffer around a sampling site (Gallo, Fidino, Lehrer, & Magle, 2017). Tree cover and impervious cover were included in the urbanization index calculation because together they represent the conversion of natural habitats to impervious surfaces (Grimm et al., 2008). Housing density was also included as it represents the inherent human element of urban ecosystems (Foley et al., 2005; Grimm et al., 2008). We chose a 500 m radius because it encompasses the home range of eastern cottontail (Hunt et al., 2014) and the majority of white-tailed deer home range (Etter et al., 2002) without creating

significant overlap between independent sampling sites (Gallo et al., 2017). We calculated these metrics using QGIS ver 2.14 (QGIS Development Team, 2009). We used the first principal component for each site as an index or urbanization (URB), which accounted for 77.31% of the variation in the data. Index values that are positive indicate sites with higher mean tree cover (less urban), while negative values indicate sites with higher housing densities and impervious cover (more urban).

2.3 | Statistical analysis

To quantify how coyote presence influences the spatial distribution and behaviour of white-tailed deer and eastern cottontail, we took a 3-tier approach underpinned by a Bayesian hierarchical multi-season occupancy model. Using this approach, we estimated (1) spatial overlap of coyote and each prey species, (2) changes in the daily activity patterns of each prey species in the presence and absence of coyote, and (3) changes in vigilance behaviour of each prey species in the presence and absence of coyote (Figure 1c).

To determine whether site-level occupancy of coyote influenced the occupancy of white-tailed deer and eastern cottontail, we adapted a Bayesian single season occupancy model (Waddle et al., 2010) to a dynamic occupancy model (MacKenzie et al., 2006). This model formulation allowed us to estimate detection-corrected colonization and persistence rates (MacKenzie et al., 2006) for coyote as well as detection-corrected colonization and persistence rates of a prey species given the presence or absence of coyotes at a site (Table 1). We define colonization as the probability that a site is occupied by the focal species given that it was unoccupied in the previous sampling season, and persistence as the probability a site is occupied by the focal species given it was occupied in the previous

TABLE 1 Parameters used to estimate latent co-occurrence rates between prey species (*A*) and coyote (*B*) within a hierarchical multi-season occupancy model. Underpinning our analyses with a Bayesian two-species occupancy model allowed us to propagate the uncertainty of when coyotes were present or absent across all three components of our analyses[a]

Parameter	Probability	Definition
ψ^A	$\Pr\left(z^A_{t=1}=1\right)$	Initial probability of occupancy of subordinate species *A* at time *t* = 1
ψ^B	$\Pr\left(z^B_{t=1}=1\right)$	Initial probability of occupancy of dominant species *B* at time *t* = 1
γ^B	$\Pr\left(z^B_t=1\mid z^B_{t-1}=0\right)$	Conditional probability of colonization of dominant species *B* given its absence in the previous time step
$\gamma^{A\mid B}$	$\Pr\left(z^A_t=1\mid z^A_{t-1}=0, z^B_{t-1}=1\right)$	Conditional probability of colonization of species *A* given their absence in the previous time step and presence of dominant species *B* in previous time step
$\gamma^{A\mid B^-}$	$\Pr\left(z^A_t=1\mid z^A_{t-1}=0, z^B_{t-1}=0\right)$	Conditional probability of colonization of species *A* given their absence in the previous time step and absence of dominant species *B* in the previous time step
ϕ^B	$\Pr\left(z^B_t=1\mid z^B_{t-1}=1\right)$	Conditional probability of persistence of dominant species *B* given its presence in the previous time step
$\phi^{A\mid B}$	$\Pr\left(z^A_t=1\mid z^A_{t-1}=1, z^B_{t-1}=1\right)$	Conditional probability of persistence of species *A* given their presence in the previous time step and the presence of dominant species *B* in the previous time step
$\phi^{A\mid B-}$	$\Pr\left(z^A_t=1\mid z^A_{t-1}=1, z^B_{t-1}=0\right)$	Conditional probability of persistence of species *A* given their presence in the previous time step and the absence of dominant species *B* in the previous time step

[a]All of the above parameters may be transformed via a variety of link functions (e.g., the logit link) such that they may be made a linear function of covariates.

sampling season (MacKenzie et al., 2006). We further hypothesized that urbanization would influence these interactions. Therefore, all parameters in Table 1 were made a function of the URB covariate (see Supporting Information Appendix S2 for a detailed description of our model formulation, prior specifications and posterior distribution). This model formulation allowed us to estimate a detection-corrected presence/absence matrix (hereafter "incidence matrix") for coyote that we leveraged across the remaining analyses.

2.3.1 | Deriving species interaction factors: Predator–prey spatial overlap

To estimate the spatial overlap of our target predator and prey species, we derived species interaction factors (SIF) between coyote and each prey species from our occupancy model (MacKenzie, Bailey, & Nichols, 2004; Richmond, Hines, & Beissinger, 2010). Species interaction factors demonstrate if species co-occur more or less frequently than would be expected if they co-occurred independently of one another (MacKenzie et al., 2004). Any estimated SIF < 1 indicates that the two species co-occur less frequently than expected by chance (segregation/avoidance), while a SIF > 1 indicates that the species are co-occurring more often than expected by chance (aggregation). Following Richmond et al. (2010), we reparameterized the traditional SIF formula from MacKenzie et al. (2006), to fit our conditional dynamic occupancy model such that SIF = $\psi^B\psi^{A|B}/\psi^B(\psi^B\psi^{A|B} + (1 - \psi^B)\psi^{A|B^-})$, where ψ^B is the unconditional occupancy probability of coyote (species B), $\psi^{A|B}$ is the probability of occupancy for the prey species (species A) given coyote is present and $\psi^{A|B^-}$ is the probability of occupancy for the prey species given coyote is absent. As future occupancy states are a function of local colonization and persistence rates, we used the recursive equation described by MacKenzie et al. (2006), $\psi_{t+1} = \psi_t\phi_t + (1 - \psi_t)\gamma_t$, to derive each of the subsequent occupancy probabilities using the parameters estimated by our occupancy model (Table 1) and calculate SIFs between coyote and a given prey species for each sampling season. See Supporting Information Appendix S2 for a detailed description of SIF calculations at each time step.

2.3.2 | Changes in daily activity patterns: Temporal behaviour

To assess the influence that coyotes have on the temporal behaviour of white-tailed deer and eastern cottontail, we used the time stamp data from each photo and compared the daily activity patterns of each species given the presence or absence of coyote (Figure 1c). An exploratory analysis (T. Gallo, unpublished data) showed neither seasonal difference in species-specific daily activity nor difference across the urban gradient. Therefore, photos were pooled together across seasons and sites. We separated photos of prey species into two groups: (a) photos taken when coyotes were estimated to be present at the respective site during the same sampling period and (b) photos taken when coyotes were estimated to be absent from

the respective site during the same sampling period. To account for the imperfect detection of coyotes, we conducted this photo classification at each step (n = 100,000) of the coyote incidence matrix's posterior distribution (Supporting Information Appendix S2). At each Markov chain Monte Carlo (MCMC) step, we used the *overlap* package (Meredith & Ridout, 2016) in R ver 3.3.2 (R Core Team, 2016) to estimate a coefficient of overlap ($\hat{\Delta}$) comparing daily activity patterns under both coyote scenarios (present or absent). The overlap package estimates $\hat{\Delta}$ by fitting a kernel density function to the time of day each prey species was detected under each scenario, and calculates the proportion of area of overlap of each activity curve. $\hat{\Delta}$ is a quantitative measure ranging from 0 (no overlap) to 1 (identical patterns) (Ridout & Linkie, 2009). Following Ridout and Linkie (2009), we made inference with the $\hat{\Delta}_4$ estimator (Schmid & Schmidt, 2006) recommended for large sample sizes (n > 75 photos).

2.3.3 | Changes in vigilance behaviour in the presence or absence of coyote

Camera traps are predominately used to collect detection/non-detection data. However, because camera traps take photos independent of the behaviour of an organism, behavioural data (e.g., vigilance or foraging) can be collected from camera trap images (e.g., Abu Baker & Brown, 2013; Arias-Del Razo, Hernández, Laundré, & Velasco-Vázquez, 2012; Lashley et al., 2014; Schuttler et al., 2017). To assess prey vigilance when coyotes were present or absent, we coded a random subset of prey photos (deer = 4,847 photos at 49 sites; eastern cottontail = 2,229 photos at 90 sites) as "vigilant" if the individual in a photo had its head above its shoulders in an apparent alert posture or as "non-vigilant" if the individual's head was down in a foraging posture (Supporting Information Figure S1). If the individual's head was even with its shoulders, the photo was considered inapplicable and removed from the dataset (Supporting Information Figure S1). Photos were coded only if the prey species head was visible. The data generated in this way would arise in a similar manner to more traditional approaches in behavioural ecology such as scan-sampling (Altmann, 1974). Given that our dynamic occupancy model estimated the presence of coyote, we incorporated an additional binomial model into our hierarchical model to determine the influence that coyote presence had on the vigilance rates (proportion of photos in alert posture) of each prey species (Figure 1c). Here, $\text{vig}_{i,t}$ was the number of images in which the prey species was vigilant at site i and primary sampling period t, and $\text{photo}_{i,t}$ denotes the total number of images of the prey species at site i and primary sampling period t that were coded as vigilant or non-vigilant. We then modelled the probability that the prey species was displaying vigilance in a photo, $\eta_{i,t}$, as a binomial process: $\text{vig}_{i,t} \sim \text{Binomial}(\text{photo}_{i,t}, \eta_{i,t})$. To account for the level of urbanization at a sampling location and the presence of coyote, we modelled $\eta_{i,t}$ as a function of covariates, $\text{logit}(\eta_{i,t}) = \left(1 - z_{i,t}^B\right)(v_0 + v_1\text{URB}_i) + z_{i,t}^B(v_2 + v_3\text{URB}_i)$. When coyotes

are absent, v_0 is the vigilance rate at average levels of urbanization (URB) and v_1 is the effect of a 1-unit change in URB on $\eta_{i,t}$. When coyotes are present, v_2 is the average vigilance rate and v_3 is the slope of URB. The presence of coyote, $z_{i,t}^B$, is estimated from the occupancy model (Supporting Information Appendix S2). When a coyote is estimated to be present, $z_{i,t}^B$ equalled 1, otherwise it is 0.

2.3.4 | Model implementation

Marginal posterior distributions of model parameters were estimated using a MCMC algorithm implemented in ver 4.2.0 of JAGS (Plummer, 2003) using the *runjags* package (Denwood, 2016) in R. See Supporting Information Appendix S2 for a detailed description of JAGS settings, model specifications, priors and model assessment.
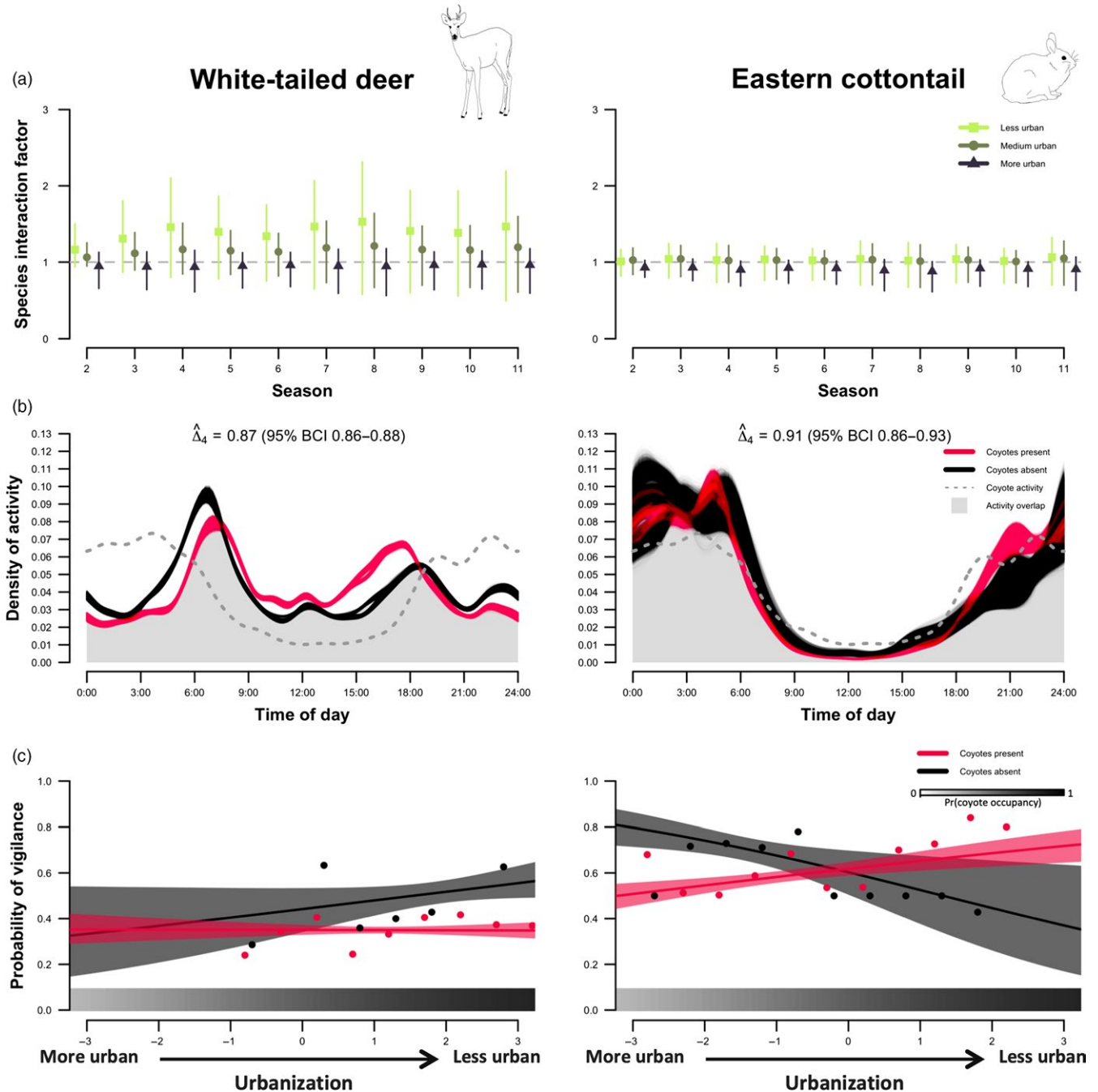
FIGURE 2 The spatial overlap of coyote and prey species and the daily activity and vigilance of each prey species when coyotes were present or absent. Median coefficient values (points) and 95% Bayesian credible intervals (BCI; vertical lines) for species interaction factors between each prey species and coyote across 10 sampling seasons (a), daily activity curves (overlay of 100,000 iterations) for each prey species when coyotes are present (red) and absent (black) (b), and the rate of vigilance behaviour (solid line), 95% BCI (shaded area), and the mean proportion of prey photos displaying vigilance behaviour (points) given coyotes were present (red) or absent (black) along an urban gradient. The probability of occupancy for coyote across the urban gradient is illustrated by the lower gradient strip (c). See Supporting Information Table S3 for mean proportion and standard error values of photos of vigilance posture

3 | RESULTS

In total, we captured 3,941 photographs of coyote, 4,604 of eastern cottontail, and 11,262 of white-tailed deer from a total of 23,861 trap nights.

3.1 | Predator–prey spatial overlap

All Bayesian Credible Intervals (BCI) of $\gamma^{A|B^-} - \gamma^{A|B}$ and $\phi^{A|B^-} - \phi^{A|B}$ overlapped 0, indicating no significant difference in γ or ϕ for prey species given the presence of coyote (see Supporting Information Table S1). Spatial overlap between coyote and each prey species was measured using the SIF for each predator–prey pair at high (URB = −1), medium (URB = 0) and low (URB = 1) levels of urbanization. The SIF 95% BCI between coyote and both prey species bounded 1 across all sampling seasons and all levels of urbanization, indicating each prey species was spatially distributed independent of coyote through space and time (Figure 2a).

3.2 | Daily activity patterns: Temporal behaviour

The daily activity overlap of deer when coyotes were present and when coyotes were absent was $\hat{\Delta}_4$ = 0.87 (95% BCI 0.86–0.88) with evidence of a slight increase in activity during the earlier evening when coyotes were present (Figure 2b). Deer were most active around 06:00 and again around 18:00. The daily activity overlap of eastern cottontail when coyotes were present and when coyotes were absent was $\hat{\Delta}_4$ = 0.91 (95% BCI 0.85–0.93) with no noticeable shift in daily activity when coyotes were present. Eastern cottontails were most active between 00:00 and 06:00. Coyotes were primarily nocturnal and were most active between 19:00 and 04:00 (Figure 2b).

3.3 | Vigilance behaviour in the presence or absence of coyote

On average, deer vigilance rates were lower in sites with coyote than sites without, though the difference was not significant (95% BCI of deer $v_0 - v_2$ overlapped 0; Supporting Information Table S2). There was weak evidence that deer vigilance rates increased with a decrease in urbanization when coyotes were not present (deer v_1 = 0.16, 95% BCI = −0.02 to 0.35); however, deer vigilance rates were constant in the presence of coyote across all levels of urbanization (deer v_3 = 0, 95% BCI = −0.07 to 0.07; Figure 2b). At average levels of urbanization, eastern cottontail vigilance rates did not significantly differ in the presence or absence of coyote (95% BCI of eastern cottontail $v_0 - v_2$ overlapped 0; Supporting Information Table S2). However, cottontail vigilance rates varied significantly in opposite directions along an urbanization gradient in habitat patches with and without coyote. In the urban core, cottontail vigilance was highest in habitat patches without coyote (cottontail v_1 = −0.32, 95% BCI = −0.55 to −0.07). At low levels of urbanization, cottontail vigilance rates were highest in habitat patches with coyote (cottontail v_3 = 0.15, 95% BCI = 0.07–0.24; Figure 2c).

4 | DISCUSSION

Our results demonstrate that urbanization alters predator-avoidance behaviour in white-tailed deer and eastern cottontails. We found, across our study area, that neither white-tailed deer nor eastern cottontail were spatially segregated from coyotes, nor did we find a pronounced change in their daily activity patterns. While deer did not increase vigilance when coyotes were present, eastern cottontails had higher vigilance when coyotes were present in less urban sites, but lower vigilance when coyotes were present in more urban sites. Conversely, eastern cottontails had their highest vigilance rates in more urban sites when coyotes were absent, indicating an alternative source of fear that may be "forcing" cottontails to be vigilant even when coyotes are absent.

If all other factors are equal (e.g., food availability and social standing), prey species should display increased anti-predator behaviour where predation pressures exist (Caro, 2005). White-tailed deer in less urban ecosystems have been shown to avoid habitat occupied by coyotes (Jones et al., 2016; Lingle, 2002). Although coyotes depredate eastern cottontails and young white-tailed deer in the greater Chicago region (Gehrt, 2010a; Morey et al., 2007), we found that neither white-tailed deer nor eastern cottontail demonstrated spatial segregation from coyotes across our study area (Figure 2a). These results are similar to previous findings in the Chicago metropolitan area (Magle et al., 2014). Coyote and deer occupancy rates were positively linked, and the authors suggested that the need for limited habitat may outweigh any spatial predator avoidance by deer (Magle et al., 2014). We too expect that habitat limitation constrained prey species' ability to spatially avoid coyotes across the landscape.

Because white-tailed deer and cottontail did not spatially avoid coyotes, we expected to observe a change in prey species temporal activity patterns to minimize the frequency of interactions with coyotes. Yet, we found only minor changes in daily activity patterns of prey species in sites with or without coyote (Figure 2b). White-tailed deer slightly increased their activity to be active later in the morning and earlier in the evening when coyotes were present at a site (Figure 2b). However, peak activity of coyotes did not track high levels of deer activity. White-tailed deer are generally crepuscular or diurnal (Feldhamer, Thompson, & Chapman, 2003), and our results show that this behaviour does not change for urban deer (Figure 2b). Previous studies have also shown that urban coyotes become more nocturnal to avoid human activity (Gehrt, 2010a; Grubbs & Krausman, 2009; Riley et al., 2003; Tigas, Van Vuren, & Sauvajot, 2002), and our results support this evidence (Figure 2b). Perhaps the risk from humans outweighs the benefits of overlapping activity patterns with deer and has decoupled the temporal interactions between deer and coyotes.

This potential decoupling may have important implications for urban predator–prey dynamics. Within human-dominated systems, especially cities, predators are often extirpated or removed from the system if they interact with humans (Curtis & Hadidian, 2010). Thus, urban apex predators, who previously faced little risk while hunting, now face new mortality risks when choosing when and where to forage given the presence of humans (Blecha, Boone, & Alldredge, 2018). For coyote, aligning their activity pattern with that of deer may be too risky at most times, especially given that other food sources are seemingly available (Newsome et al., 2015). Thus, our results may indicate the influential role of a "third player" (i.e., humans) in urban predator–prey dynamics.

Just as urban coyotes become more nocturnal to avoid humans, eastern cottontail may similarly concentrate their activity patterns to late hours to avoid human activity. We found that coyote and cottontail had similar daily activity patterns (Figure 2b), yet cottontails did not change their activity patterns when coyotes were present. Anthropogenic pressures, such as humans, vehicles and domestic dogs, that are more abundant during daytime hours (Lowry, Lill, & Wong, 2013) may be perceived as a greater risk than coyotes. Thus, eastern cottontail is forced to temporally overlap with coyote. It could also be that coyote pose less of a risk to eastern cottontail due to a hyperabundance of prey items (Brown & Kotler, 2007). Eastern cottontails and other small-bodied mammals have high intrinsic growth rates (Feldhamer et al., 2003), and eastern cottontails do exist in high densities within smaller, isolated urban habitat patches (Hunt et al., 2014). At high levels of prey density, coyotes could become satiated and a fear-driven system would switch to a mortality-driven system (Brown & Kotler, 2007). When this is the case, predators will have little effect on the behaviour of prey (Brown & Kotler, 2007; Holt, 1977).

Predation pressures may also be reduced due to a surplus of resources provided by anthropogenic sources (e.g., refuse, fruit trees, pet food). Coyotes are generalist predators (Morey et al., 2007), and urban coyotes have greater access to a variety of supplemental resources throughout the year (Morey et al., 2007; Murray & St. Clair, 2017; Newsome et al., 2015; Poessel, Mock, & Breck, 2017). A potential increase in prey items combined with the supplementation of anthropogenic food sources may reduce the overall predation rates on cottontails and deer by coyotes across the urban landscape, thus reducing the need for either species to increase their predator-avoidance behaviour.

We also expected prey species to express increased vigilance in the presence of coyote, and we found that eastern cottontail vigilance rates, in the presence of coyote, positively covaried with coyote occupancy. Vigilance rates were higher in less urban sites with coyote present where coyote occupancy is also high (Figure 2c). Conversely, eastern cottontail vigilance was highest in urban sites without coyotes. These varying results may suggest different sources that induce vigilance behaviour in eastern cottontails along an urbanization gradient. In Chicago, cottontail rabbits are likely to occupy green spaces in the urban core (e.g., city parks; Gallo et al., 2017) where coyote occupancy is low

(Figure 2c, Supporting Information Table S4) but visitation by humans and their pets is high. While these urban locations may provide potential refuge for eastern cottontails from coyote (i.e., human-shield effect), they potentially come with trade-offs in the form of increased interactions with humans and their pets. As a result, their vigilance rates are high in urban sites without coyote. As sites become less urban, we begin to see more expected anti-predator behaviour towards a native predator as cottontails have higher vigilance rates in less urban sites with coyote than those without (Figure 2c).

In regards to white-tailed deer, our results may indicate that white-tailed deer are at their limits of behavioural plasticity in urban ecosystems, and cannot afford to change their predator-avoidance behaviour (Lowry et al., 2013). Deer vigilance rates at sites with coyote did not vary as a function of urbanization. However, vigilance rates appeared higher in less urban sites without coyote, though this trend was not significant (Figure 2c). Alternatively, the separation in temporal interaction between coyote and deer due to changes in urban coyote daily activity (Figure 2b) may have reduced the need for deer to be vigilant of coyote.

It is important to note that detecting within-patch dynamics was not possible within our study design, as we had only one camera placed within each habitat patch. However, we found that detection rates were higher for both prey species when coyotes were present (Supporting Information Table S1). These findings could indicate that coyotes are influencing within-patch activity and movement patterns of both prey species (Bowers & Dooley, 1993). Future research should assess within-patch spatial avoidance or behavioural changes by including multiple sampling sites within a single habitat patch or collecting fine-scale movement data using GPS collars on individual animals.

Our results add to a growing body of literature that indicates interactions between predators and prey in human-dominated landscapes may be better understood by considering the interplay between three players instead of two: predators, prey and people (Berger, 2007; Blecha et al., 2018; Magle et al., 2014). Given our findings, we believe it would be of value to assess fine-scale behaviours at the individual level (e.g., forager's perception of risk, internal state of predator and prey). Conducting fine-scale diet and behavioural analysis, such as measuring giving up densities, (Brown & Kotler, 2004; Kotler, Brown, & Bouskila, 2004) would be a natural progression to further assess our postulates about behavioural plasticity, the use of anthropogenic resource by predators and novel threats within urban ecosystems. Additionally, we assessed patterns of predator-avoidance behaviour based on the presence of coyote, yet predator abundance may have a stronger influence on predator–prey dynamics (Power, Matthews, & Stewart, 1985). Future studies that measure population dynamics, such as mark-recapture, would help elucidate the influence predator abundance has on prey behaviour in novel ecosystems.

Our findings have greater implications for urban wildlife management. Conservation and management actions are often based on predictions about population dynamics and species interactions

generated from ecological models derived in more natural or rural settings. Changes in the impact that urban predators have on the behaviour of urban prey can alter or reduce top-down trophic effects causing further changes in prey behaviour (Waser et al., 2014). Changes in predator-avoidance behaviour may have further cascading effects on both plant and animal communities, ultimately changing the community composition of urban ecosystems (Kuijper et al., 2016; Waser et al., 2014). For example, urban and suburban white-tailed deer often modify understory plant communities and alter forest ecology through uncontrolled herbivory (Côté, Rooney, Tremblay, Dussault, & Waller, 2004; DeNicola, VerCauteren, Curtis, & Hyngstrom, 2000). Thus, recognizing how urbanization alters the behaviour of both urban predators and urban prey is a key component to understanding urban wildlife communities and managing and conserving biodiversity on an urbanizing planet.

AUTHORS' CONTRIBUTIONS

T.G. and M.F. performed modelling work, analysed output data and wrote the manuscript. E.W.L. collected data, contributed to the study design and contributed to the writing of this manuscript. S.M. created the study design, collected data and contributed to the writing of this manuscript.

DATA ACCESSIBILITY

Data and R scripts available from the Dryad Digital Repository https://doi.org/10.5061/dryad.2hm27nc (Gallo, Fidino, Lehrer, & Magle, 2019).

ORCID

Travis Gallo https://orcid.org/0000-0003-2877-9848

Mason Fidino https://orcid.org/0000-0002-8583-0307

REFERENCES

Abu Baker, M. A., & Brown, J. S. (2013). Foraging and habitat use of common duikers, *Sylvicapra grimmia*, in a heterogeneous environment within the Soutpansberg, South Africa. *African Journal of Ecology*, *52*(3), 318–327. https://doi.org/10.1111/aje.12122

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*(3), 227–266. https://doi.org/10.1163/156853974X00534

Arias-Del Razo, I., Hernández, L., Laundré, J. W., & Velasco-Vázquez, L. (2012). The landscape of fear: habitat use by a predator (*Canis latrans*) and its main prey (*Lepus californicus* and *Sylvilagus audubonii*). *Canadian Journal of Zoology*, *90*(6), 683–693. https://doi.org/10.1139/z2012-036

Aronson, M. F., Lepczyk, C. A., Evans, K. L., Goddard, M. A., Lerman, S. B., MacIvor, J. S., … Vargo, T. (2017). Biodiversity in the city: Key challenges for urban green space management. *Frontiers in Ecology and the Environment*, *15*(4), 189–196. https://doi.org/10.1002/fee.1480

Beninde, J., Veith, M., & Hochkirch, A. (2015). Biodiversity in cities needs space: A meta-analysis of factors determining intra-urban biodiversity variation. *Ecology Letters*, *18*(6), 581–592. https://doi.org/10.1111/ele.12427

Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters*, *3*(6), 620–623. https://doi.org/10.1098/rsbl.2007.0415

Blecha, K. A., Boone, R. B., & Alldredge, M. W. (2018). Hunger mediates apex predator's risk avoidance response in wildland–urban interface. *Journal of Animal Ecology*, *87*(3), 609–622. https://doi.org/10.1111/1365-2656.12801

Bleicher, S. S., Brown, J. S., Embar, K., & Kotler, B. P. (2016). Novel predator recognition by Allenby's gerbil (*Gerbillus andersoni allenbyi*): Do gerbils learn to respond to a snake that can "see" in the dark? *Israel Journal of Ecology & Evolution*, *62*(3–4), 178–185. https://doi.org/10.1080/15659801.2016.1176614

Bleicher, S. S., & Rosenzweig, M. L. (2017). Too much of a good thing? A landscape-of-fear analysis for collared peccaries (*Pecari tajacu*) reveals hikers act as a greater deterrent than thorny or bitter food. *Canadian Journal of Zoology*, *96*(4), 317–324. https://doi.org/10.1139/cjz-2017-0158

Bowers, M. A., & Dooley, J. L. (1993). Predation hazard and seed removal by small mammals: Microhabitat versus patch scale effects. *Oecologia*, *94*(2), 247–254. https://doi.org/10.1007/BF00341324

Brown, J. S., & Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, *7*(10), 999–1014. https://doi.org/10.1111/j.1461-0248.2004.00661.x

Brown, J. S., & Kotler, B. P. (2007). Foraging and the ecology of fear. In D. W. Stephens, J. S. Brown, & R. C. Ydendberg (Eds.), *Foraging behavior and ecology* (pp. 437–480). Chicago, IL: University of Chicago Press.

Brown, J. S., Laundré, J. W., & Gurung, M. (1999). The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, *80*(2), 385–399. https://doi.org/10.2307/1383287

Caro, T. (2005). *Antipredator defenses in birds and mammals*. Chicago, IL: University of Chicago Press.

Carthey, A. J. R., & Banks, P. B. (2014). Naïveté in novel ecological interactions: Lessons from theory and experimental evidence. *Biological Reviews*, *89*(4), 932–949. https://doi.org/10.1111/brv.12087

Coleman, A., Richardson, D., Schechter, R., & Blumstein, D. T. (2008). Does habituation to humans influence predator discrimination in Gunther's dik-diks (*Madoqua guentheri*)? *Biology Letters*, *4*(3), 250–252. https://doi.org/10.1098/rsbl.2008.0078

Côté, S. D., Rooney, T. P., Tremblay, J.-P., Dussault, C., & Waller, D. M. (2004). Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics*, *35*(1), 113–147. https://doi.org/10.1146/annurev.ecolsys.35.021103.105725

Crooks, K. R., & Soulé, M. E. (1999). Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, *400*, 563–566. https://doi.org/10.1038/23028

Curtis, P. D., & Hadidian, J. (2010). Repsonding to human-carnivore conflict in urban areas. In S. D. Gehrt, S. P. D. Riley & B. L. Cypher, (Eds.), *Urban carnivores: Ecology, conflict, and conservation* (pp. 201–211). Baltimore, MD: The Johns Hopkins University Press.

Dearborn, D. C., & Kark, S. (2010). Motivations for conserving urban biodiversity. *Conservation Biology*, *24*(2), 432–440. https://doi.org/10.1111/j.1523-1739.2009.01328.x

DeNicola, A. J., VerCauteren, K. C., Curtis, P. D., & Hyngstrom, S. E. (2000). *Managing white-tailed deer in suburban environments*. Cornell Cooperative Extension. Retrieved from https://hdl.handle.net/1813/65

Denwood, M. J. (2016). runjags: An R package providing interface utilities, model templates, parallel computing methods and additional distributions for MCMC models in JAGS. *Journal of Statistical Software*, *71*(9), 25.

Etter, D. R., Hollis, K. M., Van Deelen, T. R., Ludwig, D. R., Chelsvig, J. E., Anchor, C. L., & Warner, R. E. (2002). Survival and movements of white-tailed deer in suburban Chicago, Illinois. *The Journal of Wildlife Management*, *66*(2), 500–510. https://doi.org/10.2307/3803183

Farinha-Marques, P., Lameiras, J. M., Fernandes, C., Silva, S., & Guilherme, F. (2011). Urban biodiversity: a review of current concepts and contributions to multidisciplinary approaches. *Innovation: The European Journal of Social Sciences*, *24*(3), 247–271.

Feldhamer, G. A., Thompson, B. C., & Chapman, J. A. (2003). *Wild mammals of North America: Biology, management, and conservation*. Baltimore, MD: JHU Press.

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., … Snyder, P. K. (2005). Global consequences of land use. *Science*, *309*(5734), 570–574. https://doi.org/10.1126/science.1111772

Forman, R. T. T. (2016). Urban ecology principles: Are urban ecology and natural area ecology really different? *Landscape Ecology*, *31*(8), 1653–1662. https://doi.org/10.1007/s10980-016-0424-4

Fretwell, S. D. (1969). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, *19*(1), 45–52. https://doi.org/10.1007/BF01601955

Frid, A., & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, *6*(1), 11. https://doi.org/10.5751/ES-00404-060111

Gallo, T., Fidino, M., Lehrer, E. W., & Magle, S. B. (2017). Mammal diversity and metacommunity dynamics in urban green spaces: Implications for urban wildlife conservation. *Ecological Applications*, *27*(8), 2330–2341. https://doi.org/10.1002/eap.1611

Gallo, T., Fidino, M., Lehrer, E. W., & Magle, S. B. (2019). Data from: Urbanization alters predator avoidance behaviors. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.2hm27nc

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, *360*(6394), 1232–1235. https://doi.org/10.1126/science.aar7121

Gehrt, S. D. (2010a). Coyote (*Canis latrans*). In S. D. Gehrt, S. P. D. Riley & B. L. Cypher (Eds.), *Urban carnivores: Ecology, conflict, and conservation* (pp. 97–98). Baltimore, MD: The Johns Hopkins University Press.

Gehrt, S. D. (2010b). The urban ecosystem. In S. D. Gehrt, S. P. D. Riley & B. L. Cypher (Eds.), *Urban carnivores: Ecology, conflict, and conservation* (pp. 3–12). Baltimore, MD: The Johns Hopkins University Press.

Gerber, B. D., Karpanty, S. M., & Kelly, M. J. (2012). Evaluating the potential biases in carnivore capture–recapture studies associated with the use of lure and varying density estimation techniques using photographic-sampling data of the Malagasy civet. *Population Ecology*, *54*(1), 43–54. https://doi.org/10.1007/s10144-011-0276-3

Gese, E. M., Morey, P. S., & Gehrt, S. D. (2012). Influence of the urban matrix on space use of coyotes in the Chicago metropolitan area. *Journal of Ethology*, *30*(3), 413–425. https://doi.org/10.1007/s10164-012-0339-8

Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., & Briggs, J. M. (2008). Global change and the ecology of cities. *Science*, *319*(5864), 756–760. https://doi.org/10.1126/science.1150195

Grubbs, S. E., & Krausman, P. R. (2009). Observations of coyote-cat interactions. *The Journal of Wildlife Management*, *73*(5), 683–685. https://doi.org/10.2193/2008-033

Holt, R. D. (1977). Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology*, *12*(2), 197–229. https://doi.org/10.1016/0040-5809(77)90042-9

Hunt, V. M., Magle, S. B., Vargas, C., Brown, A. W., Lonsdorf, E. V., Sacerdote, A. B., … Santymire, R. M. (2014). Survival, abundance, and capture rate of eastern cottontail rabbits in an urban park. *Urban Ecosystems*, *17*(2), 547–560. https://doi.org/10.1007/s11252-013-0334-z

Ibáñez-Álamo, J. D., Rubio, E., Benedetti, Y., & Morelli, F. (2017). Global loss of avian evolutionary uniqueness in urban areas. *Global Change Biology*, *23*(8), 2990–2998. https://doi.org/10.1111/gcb.13567

Imhoff, M. L., Tucker, C. J., Lawrence, W. T., & Stutzer, D. C. (2000). The use of multisource satellite and geospatial data to study the effect of urbanization on primary productivity in the United States. *IEEE Transactions on Geoscience and Remote Sensing*, *38*(6), 2549–2556. https://doi.org/10.1109/36.885202

Ives, C. D., Lentini, P. E., Threlfall, C. G., Ikin, K., Shanahan, D. F., Garrard, G. E., … Kendal, D. (2016). Cities are hotspots for threatened species. *Global Ecology and Biogeography*, *25*(1), 117–126. https://doi.org/10.1111/geb.12404

Jones, B. M., Cove, M. V., Lashley, M. A., & Jackson, V. L. (2016). Do coyotes *Canis latrans* influence occupancy of prey in suburban forest fragments? *Current Zoology*, *62*(1), 1–6. https://doi.org/10.1093/cz/zov004

Kaushal, S. S., & Belt, K. T. (2012). The urban watershed continuum: Evolving spatial and temporal dimensions. *Urban Ecosystems*, *15*(2), 409–435. https://doi.org/10.1007/s11252-012-0226-7

Kotler, B. P., Brown, J. S., & Bouskila, A. (2004). Apprehension and time allocation in gerbils: The effects of predatory risk and energetic state. *Ecology*, *85*(4), 917–922. https://doi.org/10.1890/03-3002

Kuijper, D. P. J., Sahlén, E., Elmhagen, B., Chamaillé-Jammes, S., Sand, H., Lone, K., & Cromsigt, J. P. G. M. (2016). Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, *283*(1841), 20161625. https://doi.org/10.1098/rspb.2016.1625

Lashley, M. A., Chitwood, M. C., Biggerstaff, M. T., Morina, D. L., Moorman, C. E., & DePerno, C. S. (2014). White-tailed deer vigilance: The influence of social and environmental factors. *PLoS One*, *9*(3), e90652. https://doi.org/10.1371/journal.pone.0090652

Laundre, J. W., Hernandez, L., & Ripple, W. J. (2010). The landscape of fear: Ecological implications of being afraid. *The Open Ecology Journal*, *3*(3), 1–7. https://doi.org/10.2174/1874213001003030001

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, *68*(4), 619–640. https://doi.org/10.1139/z90-092

Lingle, S. (2002). Coyote predation and habitat segregation of white-tailed deer and mule deer. *Ecology*, *83*(7), 2037–2048. https://doi.org/10.1890/0012-9658(2002) 083[2037:CPAHSO]2.0.CO;2

Lowry, H., Lill, A., & Wong, B. B. M. (2013). Behavioural responses of wildlife to urban environments. *Biological Reviews*, *88*(3), 537–549. https://doi.org/10.1111/brv.12012

MacKenzie, D. I., Bailey, L. L., & Nichols, J. (2004). Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology*, *73*(3), 546–555. https://doi.org/10.1111/j.0021-8790.2004.00828.x

MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., & Hines, J. E. (2006). *Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence*. London, UK: Academic Press.

Magle, S. B., Lehrer, E. W., & Fidino, M. (2016). Urban mesopredator distribution: Examining the relative effects of landscape and socio-economic factors. *Animal Conservation*, 19(2), 163–175. https://doi.org/10.1111/acv.12231

Magle, S. B., Simoni, L. S., Lehrer, E. W., & Brown, J. S. (2014). Urban predator–prey association: Coyote and deer distributions in the Chicago metropolitan area. *Urban Ecosystems*, 17(4), 875–891. https://doi.org/10.1007/s11252-014-0389-5

McArthur, C., Banks, P. B., Boonstra, R., & Forbey, J. S. (2014). The dilemma of foraging herbivores: Dealing with food and fear. *Oecologia*, 176(3), 677–689. https://doi.org/10.1007/s00442-014-3076-6

McKinney, M. L. (2002). Urbanization, biodiversity, and conservation. *BioScience*, 52(10), 883–890. https://doi.org/10.1641/0006-3568(2002) 052[0883:UBAC]2.0.CO;2

Meredith, M., & Ridout, M. (2016). *overlap: estimates of coefficient of overlapping for animal activity patterns*. R package version 0.2.6. Retrieved from https://CRAN.R-project.org/package=overlap

van der Merwe, M., & Brown, J. S. (2008). Mapping the landscape of fear of the cape ground squirrel (*Xerus inauris*). *Journal of Mammalogy*, 89(5), 1162–1169. https://doi.org/10.1644/08-MAMM-A-035.1

Morey, P. S., Gese, E. M., & Gehrt, S. (2007). Spatial and temporal variation in the diet of coyotes in the Chicago metropolitan area. *The American Midland Naturalist*, 158(1), 147–161. https://doi.org/10.1674/0003-0031(2007) 158[147:SATVIT]2.0.CO;2

Murray, M. H., & St. Clair, C. C. (2017). Predictable features attract urban coyotes to residential yards. *The Journal of Wildlife Management*, 81(4), 593–600. https://doi.org/10.1002/jwmg.21223

Newsome, S. D., Garbe, H. M., Wilson, E. C., & Gehrt, S. D. (2015). Individual variation in anthropogenic resource use in an urban carnivore. *Oecologia*, 178(1), 115–128. https://doi.org/10.1007/s00442-014-3205-2

Ordeñana, M. A., Crooks, K. R., Boydston, E. E., Fisher, R. N., Lyren, L. M., Siudyla, S., … Van Vuren, D. H. (2010). Effects of urbanization on carnivore species distribution and richness. *Journal of Mammalogy*, 91(6), 1322–1331. https://doi.org/10.1644/09-MAMM-A-312.1

Pickett, S. T. A., & Cadenasso, M. L. (2017). How many principles of urban ecology are there? *Landscape Ecology*, 32(4), 699–705. https://doi.org/10.1007/s10980-017-0492-0

Plummer, M. (2003). A program for analysis of Bayesian graphical models using Gibbs sampling. In Proceedings of the Third International Workshop on Distributed Statistical Computing (pp. 125–133). Vienna, Austria: R Foundations for Statistical Computing.

Poessel, S. A., Mock, E. C., & Breck, S. W. (2017). Coyote (*Canis latrans*) diet in an urban environment: Variation relative to pet conflicts, housing density, and season. *Canadian Journal of Zoology*, 95(4), 287–297. https://doi.org/10.1139/cjz-2016-0029

Polfus, J. L., & Krausman, P. R. (2012). Impacts of residential development on ungulates in the Rocky Mountain West. *Wildlife Society Bulletin*, 36(4), 647–657. https://doi.org/10.1002/wsb.185

Power, M. E., Matthews, W. J., & Stewart, A. J. (1985). Grazing minnows, piscivorous bass, and stream algae: Dynamics of a strong interaction. *Ecology*, 66(5), 1448–1456. https://doi.org/10.2307/1938007

QGIS Development Team. (2009). *QGIS Geographic Information System*. Open Source Geospatial Foundation. Retrieved from http://qgis.osgeo.org

R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Richmond, O. M. W., Hines, J. E., & Beissinger, S. R. (2010). Two-species occupancy models: A new parameterization applied to co-occurrence of secretive rails. *Ecological Applications*, 20(7), 2036–2046. https://doi.org/10.1890/09-0470.1

Ridout, M. S., & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, 14(3), 322–337. https://doi.org/10.1198/jabes.2009.08038

Riley, S. P. D., Sauvajot, R. M., Fuller, T. K., York, E. C., Kamradt, D. A., Bromley, C., & Wayne, R. K. (2003). Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. *Conservation Biology*, 17(2), 566–576. https://doi.org/10.1046/j.1523-1739.2003.01458.x

Rodewald, A. D., Kearns, L. J., & Shustack, D. P. (2011). Anthropogenic resource subsidies decouple predator–prey relationships. *Ecological Applications*, 21(3), 936–943. https://doi.org/10.1890/10-0863.1

Schmid, F., & Schmidt, A. (2006). Nonparametric estimation of the coefficient of overlapping—Theory and empirical application. *Computational Statistics & Data Analysis*, 50(6), 1583–1596. https://doi.org/10.1016/j.csda.2005.01.014

Schuttler, S. G., Parsons, A. W., Forrester, T. D., Baker, M. C., McShea, W. J., Costello, R., & Kays, R. (2017). Deer on the lookout: How hunting, hiking and coyotes affect white-tailed deer vigilance. *Journal of Zoology*, 301(4), 320–327. https://doi.org/10.1111/jzo.12416

Shannon, G., Cordes, L. S., Hardy, A. R., Angeloni, L. M., & Crooks, K. R. (2014). Behavioral responses associated with a human-mediated predator shelter. *PLoS One*, 9(4), e94630. https://doi.org/10.1371/journal.pone.0094630

Shochat, E., Warren, P. S., Faeth, S. H., McIntyre, N. E., & Hope, D. (2006). From patterns to emerging processes in mechanistic urban ecology. *Trends in Ecology & Evolution*, 21(4), 186–191. https://doi.org/10.1016/j.tree.2005.11.019

Tigas, L. A., Van Vuren, D. H., & Sauvajot, R. M. (2002). Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. *Biological Conservation*, 108(3), 299–306. https://doi.org/10.1016/S0006-3207(02)00120-9

U.S. Census Bureau. (2015a). *American Community Survey 1-Year Estimates*. Washington, DC: U.S. Department of Commerce.

U.S. Census Bureau. (2015b). *Annual Estimates of the Resident Population for Incorporated Places of 50,000 or More, Ranked by July 1, 2015 Population: April 1, 2010 to July 1, 2015 – United States – Places of 50,000 + Population*. Washington, DC: U.S. Department of Commerce.

Valcarcel, A., & Fernández-Juricic, E. (2009). Antipredator strategies of house finches: Are urban habitats safe spots from predators even when humans are around? *Behavioral Ecology and Sociobiology*, 63(5), 673. https://doi.org/10.1007/s00265-008-0701-6

Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., & Cushing, C. E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, 37(1), 130–137. https://doi.org/10.1139/f80-017

Waddle, J. H., Dorazio, R. M., Walls, S. C., Rice, K. G., Beauchamp, J., Schuman, M. J., & Mazzotti, F. J. (2010). A new parameterization for estimating co-occurrence of interacting species. *Ecological Applications*, 20(5), 1467–1475. https://doi.org/10.1890/09-0850.1

Waser, N. M., Price, M. V., Blumstein, D. T., Arózqueta, S. R., Escobar, B. D. C., Pickens, R., & Pistoia, A. (2014). Coyotes, deer, and wildflowers: Diverse evidence points to a trophic cascade. *Naturwissenschaften*, 101(5), 427–436. https://doi.org/10.1007/s00114-014-1172-4

SUPPORTING INFORMATION

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