



# An urban cast of characters: Landscape use and cover influencing mammal occupancy in an American midwestern city

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## HIGHLIGHTS

- Land cover influences occupancy of eight urban dwelling mammal species.
- More species negatively associated with anthropogenic land cover.
- Four species negatively associated with residential yards.
- Residential yards may be an unnecessary or unsuitable subsidizing resource.
- Green space and residential yards with vegetation heterogeneity may offset urbanization.

## ABSTRACT

With future human population growth concentrating in urban areas, cities are working to counterbalance ecological disturbances resulting from development by incorporating green space that supports greater biodiversity. An initial line of inquiry into designing wildlife-inclusive green space involves evaluating landscapes that are associated with the habitat use of urban species. In this study, we utilized occupancy modeling to estimate select terrestrial mammal presence in a fast-growing mid-sized midwestern city to determine possible taxa-specific associations with multiple land use and cover variables, specifically those associated with higher degrees of human activity. Using motion-triggered infrared trail cameras over eight seasons from winter 2017 to fall 2018, we applied a single-species, single-season stacked design to estimate occupancy for eight urban dwelling mammals. Taxa-specific models contained one of three possible detection variables (null, percent green space, or percent impervious surface) and combinations of three species-specific variables, natural and anthropogenic. We hypothesized that large species, coyote (*Canis latrans*) and white-tailed deer (*Odocoileus virginianus*), would exhibit the most positive association to natural land cover and the most negative association to anthropogenic land cover. We also hypothesized that small and medium sized species, eastern cottontail (*Sylvilagus floridanus*), gray squirrel (*Sciurus carolinensis*), opossum (*Didelphis virginiana*), raccoon (*Procyon lotor*), red fox (*Vulpes vulpes*), and striped skunk (*Mephitis mephitis*), would demonstrate a neutral association to land cover type, anthropogenic or natural. Our results indicated that the presence of anthropogenic features rather than any particular natural land cover may be driving wildlife distribution in our study area, as none of our species demonstrated a positive association to natural land cover (percent recreation, residential yards, vacant land, or woodland). Species with a wide range of body sizes, showed a negative association with residential yards, indicating that this type of green space may be an unnecessary or unsuitable subsidizing resource in our study area. With our results in mind, we recommend increasing the amount of natural or less manicured green space to offset the intensity of impervious surface as well as encouraging the establishment of native vegetation in existing and newly constructed residential development to better connect urban green space and residential yards to larger adjoining tracts of natural landscapes. For our study area and other cities in similar phases of development, these suggestions may be essential first steps to reduce biodiversity loss and strengthen community ecology as urban areas continue to grow.

## 1. Introduction

The expansion of a city's human population and its corresponding physical footprint reshapes terrestrial ecosystems and resources (Güneralp, Reba, Hales, Wentz, & Seto, 2020; Liu, He, & Wu, 2016;

Magle et al., 2021). With each urban landscape presenting a dynamic combination of unique structural, ecological, and demographic properties, cities are experiencing a variety of sustainable development challenges, including the consequences of urbanization on flora and fauna (Aronson et al., 2017; Beninde, Veith, & Hochkirch, 2015;

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Lepczyk et al., 2017). For wildlife, the transformation of a natural or vegetated area into an anthropogenic environment can lead to habitat degradation, loss, or fragmentation, as well as endemic biodiversity loss, particularly where natural areas become isolated from one another (Liu et al., 2016; Nielsen, van den Bosch, Maruthaveeran, & van den Bosch, 2014). In addition, environmental modifications, such as human structures, street lighting, and artificial acoustical amplification can alter a landscape's suitability for a broad range of taxa as well as inflict persistent and deleterious influences on ecosystem resilience and services, species dispersal patterns, and genetic and evolutionary responses to environmental change (Benitez-Lopez et al., 2010; Evans, Chamberlain, Hatchwell, Gregory, & Gaston, 2011; Haddad et al., 2015; Johnson & Munshi-South, 2017).

While many wildlife species' life cycles are incompatible with the sights and sounds endemic to human-altered landscapes, other species gravitate toward novel urban environments, finding opportunities unrealized in their natural environment (Breck, Poessel, Mahoney, & Young, 2019; Fleming & Bateman, 2018; Kark, Iwaniuk, Schalimtzek, & Banker, 2007). Even species thought to be maladapted to human dominated landscapes can succeed there, which is often attributed to heightened resource availability, behavioral plasticity, and ingenuity (Breck et al., 2019; Kark et al., 2007). Mexican free-tail bats (*Tadarida brasiliensis*) roosting under highway bridges and peregrine falcons (*Falco peregrinus*) nesting on the ledges of skyscrapers, cathedrals, and university buildings across the United States and Europe are two of the many examples of synanthropic species capitalizing on anthropogenic assets (Caballero, Bates, Hennen, & Ashley, 2016; Capoccia, Boyle, & Darnell, 2018; Keeley & Tuttle, 1999). In addition, recurring assemblages of species often appear across distinct geographic regions and along varying degrees of urbanization (Fidino et al., 2021; Magle et al., 2019). Commonly observed species, such as red fox (*Vulpes vulpes*) and American crow (*Corvus brachyrhynchos*) repeatedly occur across regional cities and have a distribution that aligns positively with human-dominated landscapes (Leong & Trautwein, 2019).

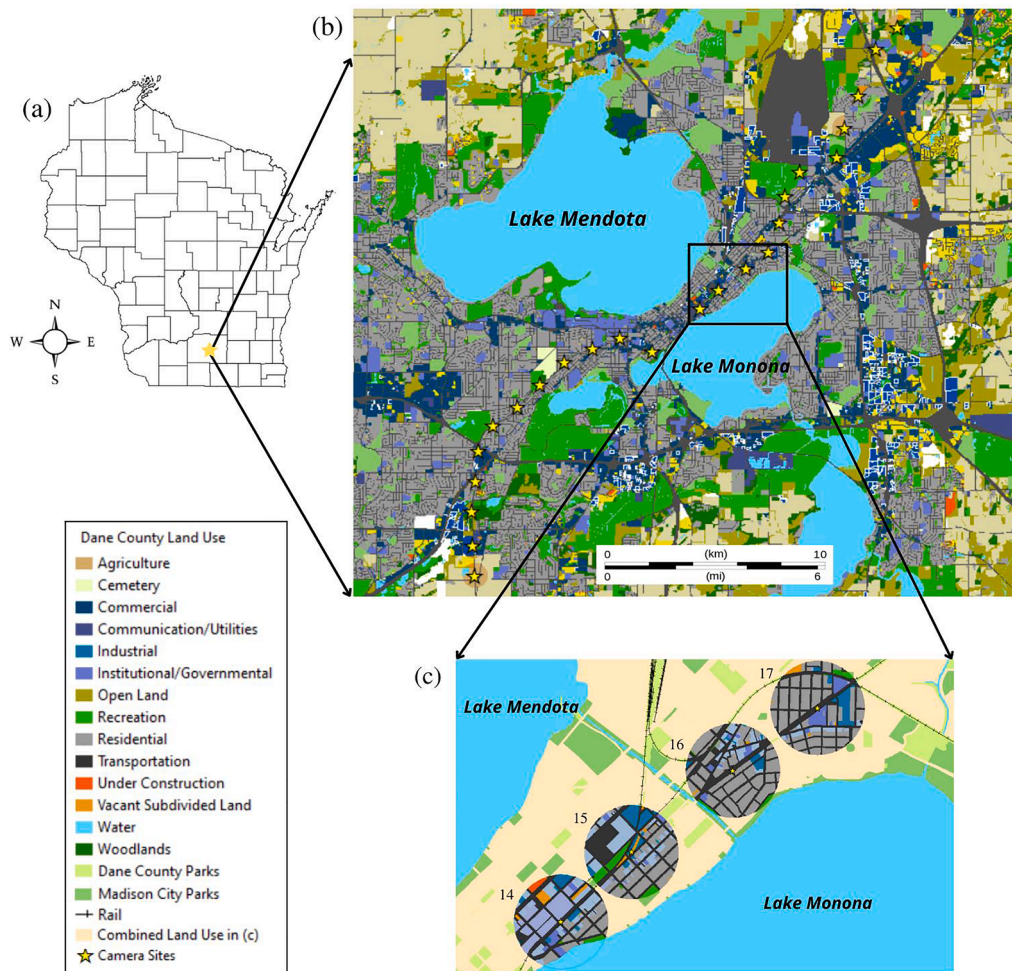
Urban dwelling and urban utilizing species are equipped to take advantage of anthropogenic features that imitate nature or enhance survival strategies and often adjust their behavior in response to heightened human activity (Beninde et al., 2015; Fischer, Schneider, Ahlers, & Miller, 2015; Kettel, Gentle, Quinn, & Yarnell, 2018). Individual skill sets vary by taxa, but species generally have advantageous niche positions or breadth and employ a broad range of behavioral strategies that are beneficial in multiple habitats or varying levels of disturbance, including cities (Devictor, Julliard, & Jiguet, 2008; Evans et al., 2011). Many urban avian species have adapted to exploit anthropogenic food and nesting resources and avoid urban risks, exhibiting broader habitat breadth, nesting habits, and greater breeding attempts than urban avoiding species (Sol, González-Lagos, Moreira, Maspons, & Lapiedra, 2014). One of the most prevalent attributes of urban dwelling and urban utilizing vertebrate species is lacking an aversion to environmental novelty, which allows those species to occupy a variety of modified habitats (Ducatez, Sayol, Sol, & Lefebvre, 2018). Although the repertoire of urban species is not limitless, there is a portion of species that not only survive but thrive in a multitude of environmental alterations (Aronson et al., 2014; Johnson & Munshi-South, 2017; Shochat, 2004).

Despite some species being able to make use of select urban resources, landscapes with greater habitat heterogeneity can provide increased opportunities for food, shelter, and space which may increase taxonomic diversity among urban wildlife and enhance ecosystem resilience (Aronson et al., 2014; Beninde et al., 2015; Lovell & Taylor, 2013; Stirnemann, Ikin, Gibbons, Blanchard, & Lindenmayer, 2015; Van Helden, Close, & Steven, 2020). In an effort to offset biodiversity loss and strengthen community ecology, there is a growing initiative to intentionally design urban green space to be wildlife-inclusive (Apfelbeck et al., 2020; Nilon et al., 2017; Weiss & Ray, 2019). Although competing interests in urban real estate can make this objective

challenging, cities are incorporating wildlife enhancing designs that promote greater biodiversity within existing urban areas and simultaneously deliver a broad range of benefits to humans (Ives et al., 2017; Twohig-Bennett & Jones, 2018). A springboard to understanding how anthropogenic landscapes shape wildlife community composition involves the synthesis of multiple lines of inquiry (Magle et al., 2021). Identifying resource preferences for multiple species to thrive in human-altered landscapes involves a comprehensive understanding of the complexities and nuances of individual species as well as the cities and surrounding areas where they reside (Fidino et al., 2021; Weiss & Ray, 2019). This can be a challenging and imperfect process. However, investigations comparing urban matrices of varying sizes are key to identifying environmental variables associated with synanthropic species (Aronson et al., 2014; Fidino et al., 2021; Greenspan, Nielsen, & Cassel, 2018). When applied collectively, these multi-taxa studies can have numerous applications, including how to modify cityscapes to be more inclusive for a broader range of taxa (Filazzola, Shrestha, & MacIvor, 2019; Pierce et al., 2020).

Exploring more specific associations in urban environments, such as distance to wooded areas, access to natural water sources, or density of roadways or buildings helps provide a more complete narrative of the factors influencing species presence (Fidino, Lehrer, & Magle, 2016; Stirnemann et al., 2015). For example, coyote (*Canis latrans*) and raccoon (*Procyon lotor*) are more likely to be present on golf courses compared to white-tailed deer (*Odocoileus virginianus*) (Gallo, Fidino, Lehrer, & Magle, 2017). For other common urban species, such as Virginia opossum (*Didelphis virginiana*, hereafter opossum) and striped skunk (*Mephitis mephitis*), the connectivity of green space to forest patches or access to water has a dominant effect on occupancy (Greenspan et al., 2018; Lesmeister, Nielsen, Schaubert, & Hellgren, 2015). Identifying the landscape features, both natural and anthropogenic, that are associated with urban dwellers can provide insight into landscape deficiencies that likely need to be addressed by urban practitioners to support urban avoiding species and increase biodiversity and resilience (Greenspan et al., 2018; Lesmeister et al., 2015; Sol et al., 2014). As each city has a unique history that has shaped its spatial configuration, human demographic, and in turn, its wildlife diversity, it is imperative to explore how species ecology differs in varying sized cities (Łopucki & Kitowski, 2017; Steele & Wolz, 2019). Studies based in larger cities generate a disproportionate share of urban wildlife research, while small and mid-sized cities remain largely underrepresented in the literature (Kendal et al., 2020). In conjunction with less representation, many of these smaller urban areas are also experiencing some of the fastest growth rates, further emphasizing the importance of identifying attributes that positively influence wildlife so they can be incorporated in planning decisions as growth occurs.

The goal of our study was to address knowledge gaps regarding the presence of terrestrial mammals in fast-growing mid-sized cities and identify the urban land use and cover associated with mammal presence. Our specific objective was to use occupancy models to estimate habitat use rates across terrestrial mammal species and determine possible species-specific associations with multiple land use and cover variables, particularly those associated with higher degrees of human presence. We hypothesized that coyote and white-tailed deer, the large species in our study, would most frequently use areas with high levels of green space and would have the strongest positive associations to natural land cover and the strongest negative associations to anthropogenic land cover. (Greenspan et al., 2018; Grund, McAninch, & Wiggers, 2002). Both of these species are known to have large home ranges and are more likely to be associated with wooded areas and larger vegetated corridor habitats that provide food and cover (Atwood, Weeks, & Gehring, 2004; Grund et al., 2002). We also hypothesized that small and medium sized urban dwelling species — eastern cottontail (*Sylvilagus floridanus*), gray squirrel (*Sciurus carolinensis*), opossum, raccoon, red fox, and striped skunk — would be widespread throughout our study area and have neither a strong positive nor a strong negative association with natural



**Fig. 1.** Map of state of Wisconsin and Dane County (starred) (a), camera site transect covering 29 km (b), and (c) land cover detail of four camera sites with 800-meter diameter buffers evaluated using ArcGIS 10.6.1 (Esri, Redlands, California), Dane LandUse 2015, Parks, City of Madison 2017, Dane County Parks 2018, and Transportation (MPO) Dane County, WI 2016 through Dane County's online geoportal at GeoData@Wisconsin (UW-Madison Robinson Map Library, Madison, WI).

or anthropogenic land cover (Fidino et al., 2021; Johnson & Munshi-South, 2017). As urban dwellers, these species are likely making multiple adjustments depending on landscape opportunities, utilizing food and shelter resources in natural areas, as well as anthropogenic substitutes found in urban areas (Abu Baker, Emerson, & Brown, 2015; Bonnington, Gaston, & Evans, 2014; Greenspan et al., 2018; Lesmeister et al., 2015). By examining the landscape associations of common and widespread North American mammals in a fast-growing mid-sized city, we hope that our findings will provide insight into mammal responses to current levels of urbanization, as well as provide guidance for offsetting a decline of wildlife diversity as urbanization expands.

## 2. Methods

Our study was conducted along a 29 km transect in Dane County, Wisconsin, USA, and extended through the greater Madison area (Fig. 1). The transect traversed a corridor containing varying proportions of land cover and use such as buildings, transportation, residential yards, impervious surfaces, and green space. Madison has a population of approximately 260,000 residents covering approximately 260 km<sup>2</sup> and is located in south central Wisconsin in the four county Madison Metropolitan Statistical Area (US Census Bureau, 2019). Madison is currently the fastest growing city in Wisconsin with population growth of 1.5 times the national average (US Census Bureau, 2019). Madison is home to the state capital and the University of Wisconsin-Madison and is within the Yahara Watershed, now largely

dominated by agricultural (65 %) and urban land cover (20 %), with the remainder in scattered remnants of forest, wetland, or open water (Carpenter et al., 2007). The area experiences four distinct seasons, with temperatures averaging 7.7C in spring (March/April/May), 20.7C in summer (June/July/August), 9.3C in autumn (September/October/November), and -5.7C in winter (December/January/February) (Wisconsin State Climatology Office, 2021). Rainfall and snowfall averages, respectively, are 7.75 cm and 8.46 cm in spring (March/April/May), 10.98 cm and 0 cm in summer (June/July/August), 6.71 cm and 4.24 cm in autumn (September/October/November), and 3.73 cm and 32.18 cm in winter (December/January/February) (Wisconsin State Climatology Office, 2010).

We placed twenty-four Bushnell TrophyCam® motion-triggered infrared trail cameras (Model #119436C, Overland Park, Kansas, USA) along the transect, with 17 cameras placed along shared-use paved trails, the Southwest Commuter Trail, Capital City Trail, and Starkweather Creek Path. Four cameras were placed north of the Starkweather Creek Path and the remaining three cameras were placed south of the Southwest Commuter Trail along the Badger State Trail. Cameras were positioned on public and private land and placed at a minimum of 800 m apart to reduce the probability of detecting the same individual at multiple cameras.

Camera traps were placed at each location for at least 28 consecutive days in January, April, July, and October in 2017 and 2018 (8 seasons total, details in Vernon, Sutherland, Young, & Hartley, 2014). Cameras were strapped approximately 1 m from the base of a tree, light post, or



**Table 1**  
Pearson's correlation coefficients between all covariates used in species-specific models, Madison, WI, 2017–2018. See Appendix A for a complete list of covariates and their descriptions.

	%buildings	%green space	%impervious	Distance to rail edge	%recreation	%residential yards	Distance to road edge	%transportation	%vacant land	Distance to water	%woodland
%buildings											
%green space	–0.65										
%impervious	0.83	–0.73									
Distance to rail edge	–0.44	0.51	–0.63								
%recreation	–0.48	0.16	–0.25	–0.13							
%residential yards	0.31	–0.58	0.25	–0.24	–0.13						
Distance to road edge	–0.46	0.45	–0.44	0.59	0.23	–0.57					
%transportation	0.75	–0.71	0.87	–0.46	0.03	0.39	–0.04				
%vacant land	–0.19	0.15	–0.34	0.22	0.03	–0.03	–0.01				
Distance to water	0.29	–0.30	0.37	–0.18	0.04	0.01	–0.38				
%woodlands	–0.41	0.56	–0.46	0.42	0.01	–0.38	0.73	–0.45	–0.06	–0.25	

utility pole and angled downward to contain the field of view to <8 m. Cameras were positioned away from areas of higher human activity (e. g., trail access points or parking lots) to reduce the incidences of vandalism or theft and to reduce the number of human images on the memory cards that result in rapid battery depletion. Batteries and memory cards were changed two weeks after each seasonal deployment. A synthetic fatty acid disk (United States Department of Agriculture, Pocatello, Idaho) was placed in a mesh bag and attached to vegetation approximately 30 cm from the ground and  $\leq 6$  m from the camera directly within the camera's field of view, resulting in the virtual presentation of the disk at the center of the photo images (Magle, Lehrer, & Fidino, 2016). As this lure likely does not increase the detectability of these species (Fidino, Barnas, Lehrer, Murray, & Magle, 2020), we did not expect the use of lure to influence the results of our analysis. Photo data were uploaded and evaluated with a customized Access (Microsoft, Redmond, Washington) database designed for camera imagery research (Ivan & Newkirk, 2016). We then created detection histories for each study species and site using each camera deployment day within the 28-day sampling period as a repeated site visit. A detection history was coded '1' if a species was detected during a given day, '0' if a species was not detected, and '.' if the camera was not operable or not present (i.e., stolen).


We calculated the percent coverage of ten land cover covariates within a 400-m and 800-m diameter buffer around each camera site using ArcGIS 10.6.1 (Esri, Redlands, California) and Dane LandUse 2015 and Dane Buildings YE2016 (NAD 83 HARN, Lambert conformal conic projection) through Dane County's online geoportal at GeoData@Wisconsin (UW-Madison Robinson Map Library, Madison, WI) (Appendix A). Using a *t*-test with  $p < 0.05$ , we found no significant differences when comparing our ten covariates across the two different buffer sizes, so we used the 800-meter diameter buffer size in order to examine the largest amount of area possible. We calculated percent impervious surface as the sum of percentage of buildings (%buildings), transportation (%transportation), sidewalks, and parking areas (Appendix A). We also calculated the percent of green space (%green space) as the sum of percentage of agriculture (%agriculture), recreation (%recreation), open land (%open land), vacant land (%vacant land), and woodland (%woodland) (Appendix A). Finally, we measured the Euclidean distance of each camera site to the nearest water, rail and road edge using ArcGIS 10.6.1 and GeoData@Wisconsin.

Our sample sizes were insufficient to evaluate a dynamic occupancy model estimating among-season colonization and extinction rates (Mckann, Gray, & Thogmartin, 2013). We therefore modeled data for our study species using single-species, single-season occupancy models and used a stacked design by including sampling site as a random effect for occupancy and detection to account for repeat sampling among sites (Crum, Fuller, Sutherland, Cooch, & Hurst, 2017; MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003). Because the habitat patches we surveyed were likely too small to permit site closure and may not be of sufficient size to house a local population of a given species, we interpreted occupancy and detection as habitat use and intensity of use, respectively. We fit our models using the package unmarked (Fiske & Chandler, 2011) in Program R (v. 3.6.1, R Core Team, 2019). We calculated a Pearson's correlation coefficient between all covariates and did not include variables with  $|r|$  greater than 0.60 in the same model (Table 1). All continuous covariates were z-score standardized before analysis.

We developed our models using a two-stage process for each species. In Stage 1, three detection models (null, percent green space, and percent impervious) were evaluated and ranked using Akaike's information criterion, adjusted for small sample size (AICc), to determine the optimal detection model. The best fit detection model was paired with the species-specific occupancy models generated in the next stage. In Stage 2, we modeled occupancy using two models (hereafter Yards & Transportation Model or Buildings Model), each of which contained all combinations of three species-specific variables. We selected the

**Table 2**

Species detection (dark squares) and absence (white squares) for eight mammal species at 24 camera sites within the greater Madison, Wisconsin area (2017–2018) and the associated percent impervious and percent green space. The state capitol (icon) is located at the center of the study transect between camera site 12 and camera site 14. See Appendix A for a complete list of covariates and their descriptions.



Camera Site	1	2	3	4	5	6	7	8	9	10	11	12	14	15	16	17	18	19	20	21	22	23	24	25
Species																								
Coyote																								
E. Cottontail																								
Gray Squirrel																								
Opossum																								
Raccoon																								
Red Fox																								
Striped Skunk																								
Wt. Deer																								
Percent Impervious	10.48	38.38	14.08	60.55	74.30	36.85	54.26	32.41	54.29	71.43	92.96	71.94	75.44	87.77	67.13	64.42	63.35	35.58	50.24	51.60	22.26	28.89	43.39	11.07
Percent Green Space	81.26	10.42	67.27	7.87	4.17	27.90	3.61	40.42	0.83	0.12	0.74	10.96	4.93	7.16	1.95	2.79	6.01	47.66	49.39	48.04	48.35	34.87	45.05	87.25

variables for each species based on previous research from natural and urban environments in combination with the local knowledge of our study area. We attempted to minimize model overfitting and the selection of inconsequential variables due to excessive model testing, particularly given our limited sample size (Appendix C, Burnham & Anderson, 2003). In order to include both anthropogenic and natural species-specific landscape features with  $|r| \leq 0.60$ , limit covariates to accommodate smaller sample sizes, examine the role of residential yards, and maximize model convergence, the Yards & Transportation Model contained percent residential yards and percent transportation along with a third species-specific covariate (percent woodland, distance to water, or percent recreation) and the Buildings Model contained percent buildings and two additional species-specific covariates (percent recreation, percent vacant land, distance to water, distance to road edge, or distance to rail edge). Percent transportation and percent buildings present different considerations for wildlife and as such were included in the Yards & Transportation Model and the Buildings Model, respectively (Elmore et al., 2021; van der Ree, Jaeger, van der Grift, & Cleverger, 2011). We therefore fit eight occupancy models (seven models with a detection variable and one to three occupancy variables, plus a null [i.e., random intercept-only] model for occupancy) from the Yards & Transportation Model and eight models from the Buildings Model for each species. We ranked models using AICc and excluded models that failed to converge. The models with an  $\Delta AICc \leq 2$  were selected as the models that best explained our data and model weights were calculated for all

competitive models. We drew inferences from covariates within competitive models whose 95 % CI excluded zero.

### 3. Results

We detected 14 mammal species but excluded eastern chipmunk (*Tamias striatus*), mink (*Neovison vison*), muskrat (*Ondatra zibethicus*), thirteen-lined ground squirrel (*Ictidomys tridecemlineatus*), woodchuck (*Marmota monax*), and mice (unknown species) from analysis due to inadequate numbers of detections. We recorded 11,565 detections of eight focal mammal species at 24 camera trap locations over 224 trap nights in 2017 and 2018: 5410 gray squirrel, 4379 eastern cottontail, 772 raccoon, 757 opossum, 107 white-tailed deer, 67 coyote, 48 striped skunk, and 25 red fox. The percentage of sites where focal species were detected at least once across the entire study varied: eastern cottontail (95.8 %), gray squirrel (91.7 %), opossum (91.7 %), raccoon (79.2 %), red fox (50.0 %), coyote (45.8 %), striped skunk (45.8 %), and white-tailed deer (37.5 %) (Table 2).

Components of impervious surface were in the top models for four of the eight species: coyote, eastern cottontail, striped skunk, and white-tailed deer (Table 3, Appendix A). Eastern cottontail and coyote had percent buildings in their top model, with percent buildings being positively associated with eastern cottontail ( $\beta = 1.60$ , 95 % CI = 0.69–2.52) and negatively associated with coyote ( $\beta = -3.28$ , 95 % CI = -4.44 — -2.13) (Table 4, Fig. 2). Eastern cottontail and red fox had

**Table 3**

Top model predicting occupancy ( $\psi$ ) and detection ( $p$ ) for eight mammal species within the greater Madison, Wisconsin area (2017–2018) based on Akaike's Information Criterion for small sample size (AICc). K is the number of estimable parameters. Wt. is the AICc weight of the top model. Cum. Wt. is the cumulative AICc weight of the competitive models ( $\Delta AICc \leq 2$ ) for each species. Variables with an asterisk (\*) specify covariates whose 95 % CI do not overlap zero. See Appendix A for a complete list of covariates and their descriptions.

Species	Top Model	K	AICc	Wt.	Cum. Wt.
Coyote	$\sim p(\text{site} + \% \text{impervious}^*) \sim \Psi(\text{site} + \% \text{buildings}^* + \% \text{recreation}^* + \text{distance to rail edge}^*)$	8	591.16	0.30	0.70
Eastern cottontail	$\sim p(\% \text{green space}) - \Psi(\% \text{buildings}^* + \text{distance to water}^* + \text{distance to road edge}^*)$	8	4645.81	0.55	0.55
Gray Squirrel	$\sim p(1 \text{site}) - \Psi(\% \text{residential yards}^*)$	5	4877.79	0.66	0.66
Opossum	$\sim p(\% \text{impervious}^*) - \Psi(\% \text{residential yards}^*)$	6	2436.87	0.87	0.87
Raccoon	$\sim p(1 \text{site}) - \Psi(1 \text{site})$	4	1993.04	0.84	0.84
Red Fox	$\sim p(1 \text{site}) - \Psi(\text{distance to water})$	5	369.49	0.46	0.70
Striped Skunk	$\sim p(\% \text{impervious}) - \Psi(\% \text{residential yards}^* + \% \text{transportation})$	7	399.83	0.36	0.64
White-tailed Deer	$\sim p(\% \text{green}) - \Psi(\% \text{residential yards}^* + \% \text{transportation})$	7	531.16	0.47	0.67

**Table 4**

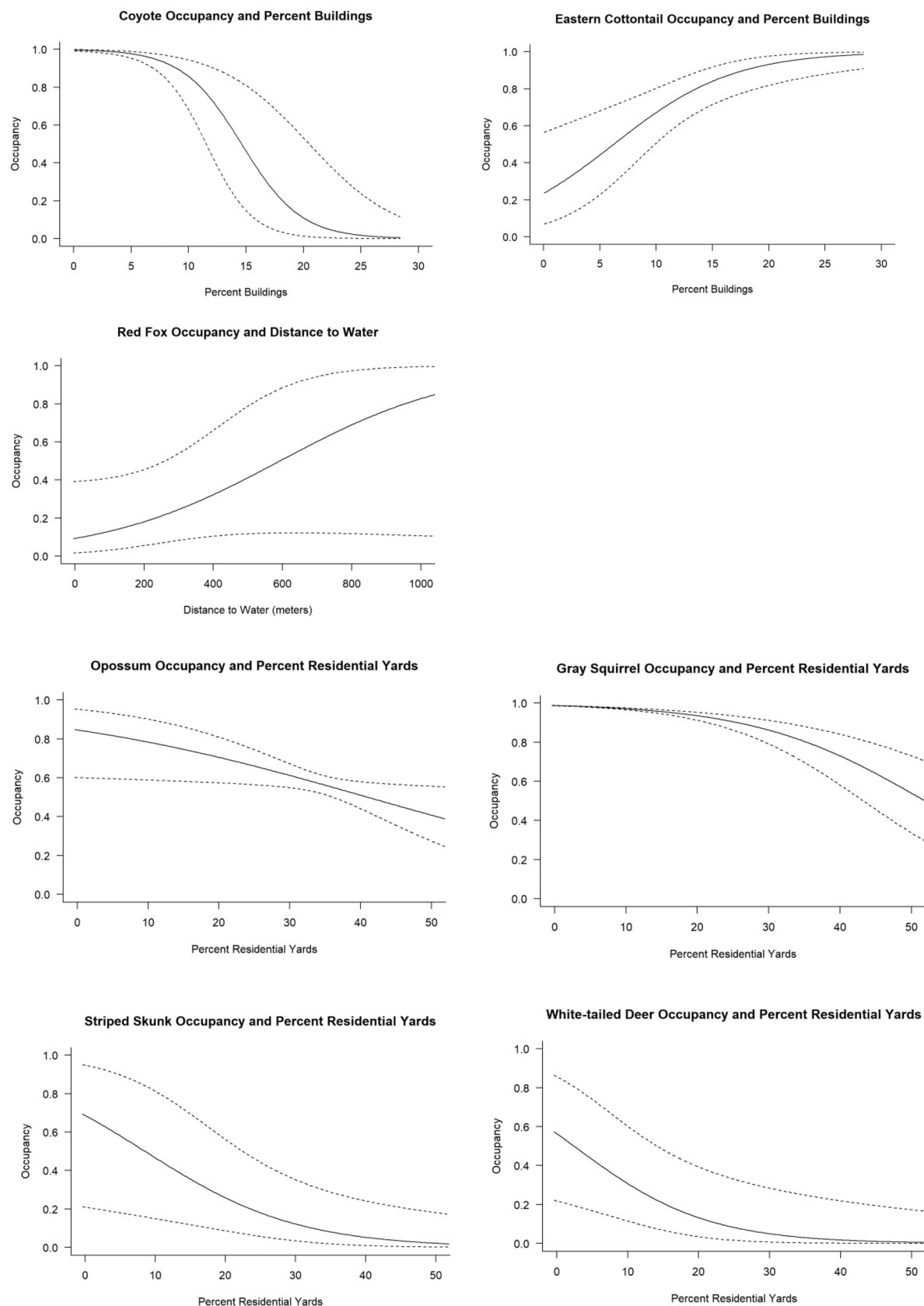
Top model for each of eight species within the greater Madison, WI area (2017–2018), along with coefficient estimates ( $\beta$ ), standard error (SE), and 95 % confidence intervals (CI). Symbols:  $p$  = detection probability,  $\Psi$  = occupancy, with abbreviations in parentheses indicating covariates included in the model. Variables with an asterisk (\*) specify covariates whose 95 % CI do not overlap zero. See Appendix A for a complete list of covariates and their descriptions.

Species	Top model and covariates	$\beta$	SE	CI
Coyote	$\sim p(\text{site} + \% \text{impervious}^*) - \Psi(\text{site} + \% \text{buildings}^* + \% \text{recreation}^* + \text{distance to rail edge}^*)$			
$\sim p$	(1 site)	-4.19	0.25	(-4.69, -3.68)
	%impervious	-0.40	0.17	(-0.73, -0.06)
$\sim \Psi$	(1 site)	0.37	0.73	(-1.07, 1.80)
	%buildings	-3.28	0.59	(-4.44, -2.13)
	%recreation	-1.64	0.31	(-2.24, -1.04)
	distance to rail edge	3.72	0.79	(2.16, 5.27)
Eastern cottontail	$\sim p(\text{site} + \% \text{green space}) - \Psi(\text{site} + \% \text{buildings}^* + \text{distance to water}^* + \text{distance to road edge}^*)$			
$\sim p$	(1 site)	-1.13	0.19	(-1.51, -0.076)
	%green space	-0.27	0.18	(-0.63, 0.09)
$\sim \Psi$	(1 site)	1.41	0.35	(0.60, 2.14)
	%buildings	1.60	0.47	(0.69, 2.52)
	distance to water	-0.86	0.37	(-1.58, -0.13)
	distance to road edge	1.04	0.48	(0.10, 1.98)
Gray Squirrel	$\sim p(1 \text{site}) - \Psi(\text{site} + \% \text{residential yards}^*)$			
$\sim p$	(1 site)	-0.96	0.05	(-1.06, -0.86)
$\sim \Psi$	(1 site)	2.55	0.18	(2.18, 2.90)
	%residential yards	-1.25	0.13	(-1.51, -1.00)
Opossum	$\sim p(\text{site} + \% \text{impervious}^*) - \Psi(\text{site} + \% \text{residential yards}^*)$			
$\sim p$	(1 site)	-2.53	0.20	(-2.92, -2.13)
	%impervious	-0.74	0.20	(-1.14, -0.33)
$\sim \Psi$	(1 site)	0.81	0.27	(0.29, 1.33)
	%residential yards	-0.62	0.28	(-1.18, -0.07)
Raccoon	$\sim p(1 \text{site}) - \Psi(1 \text{site})$			
$\sim p$	(1 site)	-3.22	0.02	(-3.26, -3.18)
$\sim \Psi$	(1 site)	2.44	0.04	(2.36, 2.52)
Red Fox	$\sim p(1 \text{site}) - \Psi(\text{site} + \text{distance to water})$			
$\sim p$	(1 site)	-4.29	0.44	(-5.14, -3.43)
$\sim \Psi$	(1 site)	-0.47	0.80	(-2.05, 1.10)
	distance to water	1.15	0.73	(-0.28, 2.58)
Striped Skunk	$\sim p(\text{site} + \% \text{impervious}^*) - \Psi(\text{site} + \% \text{residential yards}^* + \% \text{transportation})$			
$\sim p$	(1 site)	-4.15	0.54	(-5.21, -3.09)
	%impervious	-1.24	0.38	(-1.99, -0.50)
$\sim \Psi$	(1 site)	-1.18	0.66	(-2.47, 0.10)
	%residential yards	-1.38	0.55	(-2.46, -0.30)
	%transportation	1.07	0.68	(-0.27, 2.40)
White-tailed Deer	$\sim p(\text{site} + \% \text{green space}) - \Psi(\text{site} + \% \text{residential yards}^* + \% \text{transportation})$			
$\sim p$	$\sim p(\text{site})$	-4.46	0.85	(-6.11, -2.80)
	%green space	0.75	0.53	(-0.28, 1.79)
$\sim \Psi$	(1 site)	-2.03	0.77	(-3.54, -0.52)
	%residential yards	-1.61	0.65	(-2.88, -0.34)
	%transportation	-1.29	0.85	(-2.95, 0.37)

distance to water in their top model, with distance to water being negatively associated with eastern cottontail occupancy ( $\beta = -0.86$ , 95 % CI =  $-1.58 - -0.13$ ), and weakly but positively associated with fox occupancy ( $\beta = 1.15$ , 95 % CI =  $-0.28 - 2.58$ ) (Table 4, Fig. 2). Eastern cottontail and coyote had distance to road edge or distance to rail edge in their top model, with distance to road edge positively associated with Eastern cottontail occupancy ( $\beta = 1.04$ , 95 % CI =  $0.10 - 1.98$ ) and distance to rail edge positively associated with coyote occupancy ( $\beta = 3.72$ , 95 % CI =  $2.16 - 5.27$ ) (Table 4). Both striped skunk and white-tailed deer had percent transportation in their top model, with striped skunk having a weak but positive association ( $\beta = 1.07$ , 95 % CI =  $-0.27 - 2.40$ ) and white-tailed deer having a weak but negative association ( $\beta = -1.29$ , 95 % CI =  $-2.95 - 0.37$ ) (Table 4).

Percent residential yards was present in the top model for four of our eight species: gray squirrel, opossum, striped skunk, and white-tailed

deer (Table 4). The relationship between percent residential yards and species occupancy was negative for all species, gray squirrel ( $\beta = -1.25$ , 95 % CI =  $-1.51 - -1.00$ ), opossum ( $\beta = -0.62$ , 95 % CI =  $-1.18 - -0.07$ ), striped skunk ( $\beta = -1.38$ , 95 % CI =  $-2.46 - -0.30$ ), and white-tailed deer ( $\beta = -1.61$ , 95 % CI =  $-2.88 - -0.34$ ) (Table 4, Fig. 2). Coyote was the only species with percent recreation in the top model and that association was negative ( $\beta = -1.64$ , 95 % CI =  $-2.24 - -1.04$ ) (Table 4). For raccoon, the null model was the top explanatory model with high estimated occupancy (mean = 0.92, 95 % CI =  $0.91 - 0.93$ ) (Table 4). Coyote, red fox, striped skunk, and white-tailed deer had more than one competitive model. Cumulative AICc weights across competitive models ranged from 0.30 to 0.70 for coyote, 0.46 to 0.70 for red fox, 0.36 to 0.64 for striped skunk, and 0.47 to 0.67 for white-tailed deer (Table 3, Appendix B). The remaining four focal species had a single competitive model whose weight ranged from 0.55 for



**Fig. 2.** Estimated occupancy probability for top models with covariates for coyote and eastern cottontail as a function of percent buildings, red fox as a function of distance to water, and opossum, gray squirrel, striped skunk, and white-tailed deer as a function of percent residential yards, Madison, WI, 2017–2018. The solid line represents the average predicted occupancy, and the dashed lines represent 95% confidence intervals.

eastern cottontail to 0.87 for opossum (Table 3).

The top model evaluating covariate effects on detection included either percent green space or percent impervious for five of the eight focal species (Table 3). Gray squirrel, raccoon, and red fox each had the null model with a site random effect as the top detection model. Coyote, opossum, and striped skunk detection probability decreased with increasing percent impervious, whereas eastern cottontail detection probability decreased and white-tailed deer detection probability increased with increasing percent green space (Table 3).

#### 4. Discussion

Eight urban dwelling mammal species common throughout Madison, WI had dramatic differences in their landscape associations, including an unexpected negative association with residential yards. As predicted, the two large species, coyote and white-tailed deer, persisted in areas of our transect with the highest degree of green space, with each species having a negative association to anthropogenic land cover. However, neither species had a positive association to natural land cover, which may indicate that the presence of urban development rather than any particular natural land cover is the primary driver of urban distribution of these species. Coyote showed the strongest negative association with both percent buildings and percent recreation among our study species. In addition, white-tailed deer demonstrated a negative association with percent transportation and percent residential yards. As both of these species are known to utilize low disturbance areas that provide food and cover, the lack of a positive association with recreation areas or residential yards may be a result of lesser habitat quality or connectivity within these types of green spaces (Mueller, Drake, & Allen, 2018; Potapov, Bedford, Bryntesson, & Cooper, 2014). It is also possible that increased human activity associated with recreation areas and residential yards may be contributing to a lack of coyote and white-tailed deer presence. However, these species, as well as many other urban dwelling species, are known to utilize areas with relatively high human density by developing a habituation to humans or through temporal avoidance (Gaynor, Hojnowski, Carter, & Brashares, 2018).

Our hypothesis that small and medium urban dwelling species would be present throughout our transect, having neither a strong positive nor strong negative association with any particular natural or anthropogenic land cover, was only supported by raccoon. Raccoon were nearly ubiquitous throughout our transect. Madison still has a low human population density relative to its area combined with a high amount of greenspace, so development intensities may be insufficient to affect raccoon habitat use (Fidino et al., 2021). Given the pervasive nature of raccoon in anthropogenic landscapes along with a lack of competition for food resources utilized by guild members, this species is provided with a wide range of opportunities that allow them to successfully occupy a diverse range of habitats (Gehrt & Prange, 2007; Gross, Elvinger, Hungerford, & Gehrt, 2012; Lesmeister et al., 2015). Interestingly, for three of the remaining four species in this group, gray squirrel, opossum, and striped skunk, we found a strong negative association to residential yards, a contradiction with the many studies showing the subsidizing role of residential yards to urban wildlife (Lerman et al., 2021; Van Helden et al., 2020).

Six of our eight focal species (gray squirrel, opossum, raccoon, red fox, striped skunk and white-tailed deer) had no strong association with impervious cover and were detected at sites with impervious cover ranging from 10 to 93 %, an outcome that corresponds with the ability of these urban dwelling species to utilize a broad range of available natural

and anthropogenic resources (Table 2) (Fidino et al., 2021; Greenspan et al., 2018). Eastern cottontail and striped skunk demonstrated a positive relationship corresponding to the percent buildings and percent transportation, respectively, and occurred at sites with the highest percent impervious surface. For eastern cottontail, this association may be attributed to supplementary food, shelter, and nesting resources that often accompany buildings in the form of canopy cover or landscaping in addition to a reduction in predator presence in areas with higher percentages of buildings (Abu Baker et al., 2015; Gallo et al., 2017). For striped skunk, a positive, albeit weak, association with percent transportation may also be attributed to supplementary resources associated with buildings, as the percent transportation and percent buildings had a correlation coefficient of  $|r| = 0.75$  (Table 1). Our study did not evaluate specific qualities of roadways and further investigation into road ecology may provide a stronger explanation of striped skunk association with areas containing higher percentages of transportation (Barthelmess, 2014; Lesmeister et al., 2015; van der Ree et al., 2011). However, striped skunk are known to be urban dwellers so their lack of detection at nearly 60 % of our sites may be due to our camera placement as opposed to any pronounced landscape variables (Fisher & Stankowich, 2018; Prange & Gehrt, 2007).

None of our species demonstrated a positive association with natural land cover, percent recreation, residential yards, vacant land, or woodland. In fact, one of the most pronounced outcomes of our study was the negative association with residential yards for four species with a wide range of body sizes (gray squirrel, opossum, striped skunk, and white-tailed deer). Initially, this finding seems to contradict evidence corroborating the supportive role of residential yards, especially given that these species are common denizens of residential landscapes (Bonnington et al., 2014; Lerman et al., 2021; Van Helden et al., 2020). However, additional studies have found that residential development can have a negative association with mammal occupancy because natural areas that provided understory and canopy cover are replaced with new or expanding housing developments and associated roadways (Haskell, Webster, & Flaspohler, 2013; Murray & Clair, 2017; Ossola, Locke, Lin, & Minor, 2019). Although beyond the scope of this study, further investigation into the size, vegetative heterogeneity, and connectivity of residential yards may explain the negative association our species had to residential resources. For example, residential yards that are less manicured and contain greater amounts of native vegetation and cover have been shown to have higher biodiversity, including species that generally avoid urban environments (Farr et al., 2020; Lerman et al., 2021). Residential green space in rapidly expanding cities like Madison may lack these design qualities and instead contain higher amounts of manicured lawns, less established vegetation because of the young age of newly constructed residential areas, and non-native vegetation that provides inadequate food and shelter resources.

Although the quality of residential yards may explain the lack of positive association to this type of green space for four of our species, the outcome may also be a result of green space availability in Madison. Throughout the city's development, there has been a commitment to increasing and preserving natural drainageways and natural area acreage (City of Madison Parks Division, 2022). Today, the City of Madison Parks Division oversees more than 270 parks that comprise more than 5600 acres of land, including over 1750 acres of conservation areas that are largely managed to preserve native landscapes, wildlife, and vegetation (City of Madison Parks Division, 2022). Madison and cities of similar size and development are currently experiencing more dispersed forms of expansion and likely have different types and sizes of



natural and semi-natural green spaces, relative to larger cities experiencing higher rates of infill development (Vogler & Vukomanovic, 2021). Wildlife species that may commonly use residential yards in other cities may not be obligated to do so in Madison because much of the green space is interspersed throughout the city, in close proximity to residential areas, or connected by way of natural and anthropogenic corridors, such as waterways or shared-use paved trails.

Although our study was able to identify landscape features associated with use by several urban dwelling mammals, our results are limited by a relatively small sample size. As such, our model development required us to broadly categorize green space, such as percent recreation and percent residential yards, and did not allow us to incorporate less abundant land cover classes such as agricultural areas and open land, where our target species were detected. In addition, we did not evaluate the quality or connectivity of green spaces, which are known to influence species presence (Greenspan et al., 2018; Lesmeister et al., 2015; Markovchick-Nicholls et al., 2008). Small sample sizes and model convergence issues also prevented us from assessing seasonal variation in mammal-landscape associations, which could occur given Madison's seasonal differences. Finally, evaluating relationships between urban landscape features and wildlife behaviors, such as foraging, mating, or transitory movements, could provide additional insights into how wildlife use urban environments yet was beyond the scope of our study.

## 5. Conclusions

Overall, our findings present valuable information toward understanding the taxa-specific landscape features associated with highly adaptable urban species as well as underscore the shortcomings of generalizing the potential benefit of green space, particularly residential yards. As Madison and cities in similar phases of development continue to grow, they have a time sensitive opportunity to proactively plan for and strategically incorporate green space that is functional, connected, and designed to expand urban biotic assemblages (Apfelbeck et al., 2020; Nilon et al., 2017; Weiss & Ray, 2019). In particular, if urban species are responding more negatively to anthropogenic land cover

than positively to natural land cover, as was found in our study, reducing the intensity of impervious surface through the integration of natural or less manicured green space may be an essential first step. In conjunction with increasing the quality of green space, incentivizing the coordination of neighborhood initiatives that incorporate landscapes containing native vegetation can help to establish more contiguous wildlife habitat, connecting urban green space and residential yards to larger adjoining tracts of natural landscapes (Farr, Pejchar, & Reed, 2017; Lerman et al., 2021; Ossola et al., 2019; Van Helden et al., 2020). These types of suggestions will likely necessitate a change in the narrative of traditional thinking and practices across city collaborators and will require ecologists, landscape architects, and urban planners to work together to demonstrate the possibilities of blending aesthetics and ecology into multifunctional spaces (Connop et al., 2016; Gobster, Nassauer, Daniel, & Fry, 2007).

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A

Table A1.

Table A1

List of covariates and their descriptions used in the occupancy models for Madison, WI, 2017–2018. Each description is calculated within an 800-meter buffer for individual camera sites. Range (R), mean (X), and standard deviation (SD) are listed. Covariate descriptions (\*) are derived from Dane LandUse 2015 and Dane Buildings YE2016 at GeoData@Wisconsin (UW-Madison Robinson Map Library, Madison, WI).

Covariate	Description	Range (R)	Mean (X)	Standard Deviation (SD)
%agriculture*	Agriculture: Combined percent of areas designated as grain farming, animal production, or food production.	0 % to 75.76 %	6.32 %	17.33
%buildings*	Buildings: Combined percent of building footprints, including commercial, industrial, institutional, and residential.	0.32 % to 28.97 %	13.67 %	8.46
%green space*	Greenspace: Combined percent of areas designated as recreation, open land, vacant land, woodland, or agriculture.	0.13 % to 87.25 %	18.06 %	17.88
%impervious*	Impervious surface: Combined percent of areas designated as buildings or transportation, as well as percent sidewalks and percent parking not included in transportation.	10.48 % to 92.96 %	52.12 %	24.33
%openland*	Open land: Percent area not subdivided, not cultivated, and not pasture.	0 % to 28.01 %	3.31 %	7.99
distance to rail edge	Distance to rail: Euclidean distance of each camera to the nearest rail edge.	10.30 m to 5761.6 m	2058.40 m	1910.51
%recreation*	Recreation: Combined percent of areas designated as greenways, drainageways, playgrounds, playfields, athletic fields, golf courses, or conservation areas	0 % to 51.39 %	12.70 %	16.38
%residential yards*	Residential: Percent parcel after removal of single, two, and multi-family housing units.	0.02 % to 51.34 %	21.42 %	15.02
distance to road edge	Distance to road: Euclidean distance of each camera to the nearest paved road edge.	2.20 m to 294.50 m	65.50 m	66.47
%transportation*	Transportation: Combined percent of areas designated as public roadway, road right-of-way, rail right-of-way, bicycle path or right-of-way for bicycle path, or automobile parking.	0 % to 37.22 %	24.61 %	9.97
%vacant land*	Vacant land: Percent undeveloped and unused subdivided land area.	0 % to 10.95 %	1.53 %	2.52
distance to water	Distance to water: Euclidean distance of each camera site to nearest perennial water source; lakes, rivers, ponds, and streams	4.05 m to 1097.30 m	469.41 m	298.92
%woodland*	Woodland: Percent wooded area designated as 80 % or more canopy coverage of 0.81 + ha (2 + acres) of connectivity	0 % to 40.59 %	2.85 %	8.73

## Appendix B

Table B1.

Table B1

Results of occupancy model testing for four species of terrestrial mammals in Madison, Wisconsin resulting in more than one explanatory model with AICc delta  $\leq 2$  ( $\Delta AICc$ ) are listed. K is the number of estimable parameters. Wt. is the cumulative weights of  $\Delta AICc$ . Symbols:  $p$  = detection probability,  $\Psi$  = occupancy, with abbreviations in parentheses indicating covariates included in the model. Variables with an asterisk (\*) specify covariates whose 95 % CI do not overlap zero. See Appendix A for a complete list of covariates and their descriptions.

Species	Top models with $\Delta AICc \leq 2$	K	AICc	$\Delta AICc$	Wt.
Coyote	$\sim p(\text{site} + \% \text{impervious}^*)$	8	591.16	0.00	0.30
	$\sim \Psi(\text{site} + \% \text{buildings}^* + \% \text{recreation}^* + \text{distance to rail edge}^*)$				
	$\sim p(\text{site} + \% \text{impervious}^*)$	5	592.42	1.25	0.46
	$\sim \Psi(\text{site})$				
	$\sim p(\text{site} + \% \text{impervious}^*)$	6	592.90	1.74	0.58
	$\sim \Psi(\text{site} + \text{distance to water})$				
Red Fox	$\sim p(\text{site} + \% \text{impervious}^*)$	6	592.96	1.80	0.70
	$\sim \Psi(\text{site} + \% \text{recreation})$				
	$\sim p(\text{site})$	5	369.49	0.00	0.46
	$\sim \Psi(\text{site} + \text{distance to water})$				
Striped Skunk	$\sim p(\text{site})$	6	370.78	1.29	0.70
	$\sim \Psi(\text{site} + \text{distance to water}^* + \% \text{vacant land})$				
	$\sim p(\text{site} + \% \text{impervious}^*)$	7	399.83	0.00	0.36
	$\sim \Psi(\text{site} + \% \text{residential yards}^* + \% \text{transportation})$				
White-tailed Deer	$\sim p(\text{site} + \% \text{impervious}^*)$	6	400.36	0.53	0.64
	$\sim \Psi(\text{site} + \% \text{residential yards})$				
	$\sim p(\text{site} + \% \text{green space})$	7	531.16	0.00	0.47
	$\sim \Psi(\text{site} + \% \text{residential yards}^* + \% \text{transportation})$				
	$\sim p(\text{site} + \% \text{green space})$	8	532.92	1.76	0.67
	$\sim \Psi(\text{site} + \% \text{residential yards} + \% \text{transportation} + \% \text{recreation})$				

## Appendix C

Table C1.

Table C1

Yards & Transportation Model and Buildings Model for eight mammal species in Madison, Wisconsin, 2017–2018. Sampling site was used as a random effect for detection ( $p$ ) and occupancy ( $\Psi$ ). See Appendix A for a complete list of covariates and their descriptions.

Species	Yards & Transportation Model	Buildings Model
Coyote	$\sim p(\text{site}) - \Psi(\text{site} + \% \text{residential yards} + \% \text{transportation} + \text{distance to water})$	$\sim p(\text{site}) - \Psi(\text{site} + \% \text{buildings} + \% \text{recreation} + \text{distance to rail edge})$
Eastern Cottontail	$\sim p(\text{site}) - \Psi(\text{site} + \% \text{residential yards} + \% \text{transportation} + \% \text{recreation})$	$\sim p(\text{site}) - \Psi(\text{site} + \% \text{buildings} + \text{distance to water} + \text{distance to road edge})$
Gray Squirrel	$\sim p(\text{site}) - \Psi(\text{site} + \% \text{residential yards} + \% \text{transportation} + \% \text{woodland})$	$\sim p(\text{site}) - \Psi(\text{site} + \% \text{buildings} + \text{distance to water} + \% \text{recreation})$
Opossum	$\sim p(\text{site}) - \Psi(\text{site} + \% \text{residential yards} + \% \text{transportation} + \text{distance to water})$	$\sim p(\text{site}) - \Psi(\text{site} + \% \text{buildings} + \% \text{recreation} + \% \text{vacant land})$
Raccoon	$\sim p(\text{site}) - \Psi(\text{site} + \% \text{residential yards} + \% \text{transportation} + \% \text{recreation})$	$\sim p(\text{site}) - \Psi(\text{site} + \% \text{buildings} + \text{distance to water} + \% \text{vacant land})$
Red Fox	$\sim p(\text{site}) - \Psi(\text{site} + \% \text{residential yards} + \% \text{transportation} + \% \text{recreation})$	$\sim p(\text{site}) - \Psi(\text{site} + \% \text{buildings} + \text{distance to water} + \% \text{vacant land})$
Striped Skunk	$\sim p(\text{site}) - \Psi(\text{site} + \% \text{residential yards} + \% \text{transportation} + \% \text{recreation})$	$\sim p(\text{site}) - \Psi(\text{site} + \% \text{buildings} + \text{distance to water} + \% \text{vacant land})$
White-tailed Deer	$\sim p(\text{site}) - \Psi(\text{site} + \% \text{residential yards} + \% \text{transportation} + \% \text{recreation})$	$\sim p(\text{site}) - \Psi(\text{site} + \% \text{buildings} + \text{distance to water} + \% \text{vacant land})$

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