

Scales of Effect for Urban Mammals Vary Among Species and Environmental Attributes

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Abstract

Context.

Cities are increasingly recognized for their biodiversity conservation potential. Incomplete understanding of urban species habitat requirements and of the areal extents over which species-habitat interactions occur (“scale of effect”), however, restricts such conservation.

Objectives.

Better-understanding scales of effect for urban species could improve urban conservation by identifying areal extents to target in management. We sought to identify scales of effect for urban mammals and if and how these scales differ among species and environmental covariates.

Methods.

We constructed Eastern fox squirrel (*Sciurus niger*), red fox (*Vulpes vulpes*), and Virginia opossum (*Didelphis virginianus*) occupancy models using data from trail cameras in Iowa City, Iowa, USA. We compared models constructed using environmental covariates estimated over different extents and identified appropriate scales of effect for each covariate based on model fit.

Results.

Scales of effect varied among species and covariates. Environmental covariates based on home ranges sometimes provided the best model fit; however, best-fit model covariates were often estimated over other extents. The best-fit fox squirrel model included covariates estimated at different, but relatively local scales (<250 m). Both opossum and red fox models included local to landscape-level covariates. Thus, scales of effect differed among species, possibly with body size, and environmental attributes, offering clear evidence that urban mammals exhibit a multi-scalar response to their environments.

Conclusions.

Our findings suggest that habitat models should include covariates estimated over a range of biologically-informed extents to more accurately identify habitat relationships. Such modeling will inform the choice of extent in urban habitat management.

Introduction

Urban expansion (Chen et al. 2020) coupled with the increased landscape complexity of urban environments (Jenerette and Potere 2010) challenges the persistence of global biodiversity (Aronson et al. 2014, Snep and Clergeau 2020). Management of urban areas to counteract these challenges and support biodiversity conservation requires a theoretical understanding of the diverse habitat requirements of urban species (Magle et al. 2019), including how landscape composition affects species distributions

(Beninde et al. 2015). Identifying the areal extent within which environmental variables best explain patterns in species occupancy or abundance, termed the “scale of effect” (Jackson and Fahrig 2012), can build understanding of spatial scale at which wildlife interact with attributes of the environment (Moll et al. 2020). Such understanding is key to species habitat modeling given that models that include variables estimated for inappropriate extents may miss key relationships between species and urban environmental attributes, leading to inaccurate assessment of species-habitat relationships (Jackson and Fahrig 2012). Similarly, accurate scales of effect are critical to the implementation of management practices to ensure the management is implemented over extents needed to support urban species. Thus, accurately identifying scales of effect for urban wildlife is key to delineating both the spatial extent at which management for an individual species should occur and the attributes of urban environments that should be managed.

Species-habitat modeling thus requires careful consideration of scale of extent in model specification. Models that fail to account for scale of effect and rely on a single spatial scale selected *a priori* can mischaracterize the strength and direction of relationships (Miguet et al. 2016, Moll et al. 2020), or find no relationship where one may truly exist over a smaller or bigger spatial extent than used in modeling (Holland and Yang 2016). For example, multiple studies have reported a negative relationship between coyote (*Canis latrans*) occupancy and urban intensity as measured by housing density (Fidino et al. 2020) or proportional impervious cover (Wait et al. 2018) within 1 km buffers, yet a study that measured urban intensity over a larger extent (3 km) identified a positive relationship (3 km, Ordeñana et al. 2010). A conservation practitioner relying on only one of these studies to direct land management practices might undertake actions both over an inappropriate extent and of an inappropriate form. It is difficult to say which of these studies is correct and, indeed, they all may be in different contexts, without constructing and comparing the fit of models estimated using variables calculated for range of extents to identify an appropriate scale of effect.

Scales of effect are often predicted to increase proportionally with species attributes such as body size or mobility, and while a diverse body of evidence supports this assumption in birds (Thornton and Fletcher Jr 2014), empirical evidence for other taxa does not typically conform to this assumption (Jackson and Fahrig 2015), including for urban mammals (e.g., Moll et al. 2020). Further studies incorporating covariates estimated at multiple extents are warranted to build basic urban ecological theory, for example, by corroborating the lack of relationship between scale of effect and body size and mobility in mammals. Multivariate models that include covariates estimated across different spatial scales and that account for imperfect detection allow for more accurately identifying the scale of effect in ecological relationships (Stuber and Gruber 2020) and provide further evidence for or against hypothesized associations.

Despite recommendations for using a multiscale approach in estimating species-habitat relationships (McGarigal et al. 2016, Stuber and Gruber 2020), until recently most common approaches to species-habitat modelling have not addressed scale of effect. Instead, a conventional modelling approach estimates all model covariates using a single buffer area surrounding study sites (typically denoted by

the radius used, e.g., 100 m). For example, for medium to large-bodied urban mammals, 500 or 1000 m buffers are commonly employed (Fidino et al. 2016, Wait et al. 2018, Monterroso et al. 2020). Such a choice is often rooted in expert-knowledge, for example, assuming that a 500 m buffer represents an average home range across many mesocarnivores based on past experience with these species (Magle et al. 2016, Moreira-Arce et al. 2016). However, this extent is three times the median home range for the one mesocarnivore, the Virginia opossum (*Didelphis virginiana*, hereafter 'opossum') (Wright et al. 2012), and its use may thus miss important relationship for that species. Other approaches rely on extents selected based on biological attributes of species, for example, buffers based on home-range estimates for individual mesopredator species (e.g., Beatty et al. 2016, MacDougall et al. *In Review*). Such biologically-informed analysis extents are generally recommended for studies of species-habitat relationships (Boyce et al. 2017); however, they may still miss important relationships with environmental attributes that operate beyond home range extents or over smaller extents within them. Very often, extents are not derived based on expert knowledge or biological attributes of species, however, such as when extents are selected for the ease of computation and reporting (e.g., 100 m, 500 m) (Wheatley and Johnson 2009), and may thus fail in identifying species-habitat relationships and scales of effect.

It has long been recognized that there is no single scale (spatial or otherwise) at which an organism responds (Levin 1992) and that species responses often occur over multiple special scales. Birds, for example, are well-known to respond to their environments at multiple spatial scales (Pennington and Blair 2011, Smith et al. 2011, Litteral and Shochat 2017, Hallman and Robinson 2020). However, the existence of multiple scales of effect for urban mammals is less established. While some studies of urban mammals do explore relationships at multiple spatial scales, these analyses are often restricted to just a few extents (e.g., Moreira-Arce et al. 2016, Gallo et al. 2018) or focus on a particular set of extents, such as only landscape-level extents (e.g., Crimmins et al. 2016). Some studies have employed a hierarchical approach that relates species responses to environmental variation at plot, patch, and landscape scales (e.g., through a partial canonical ordination, Cushman and McGarigal 2004); however, these studies must still select a range of buffer zones to represent these extents and may do so following any one of the approaches detailed above. Thus, the use of such multiple extents, when not connected to ecologically sound assumptions, can lead to improper identification of the scale of effect (Jackson and Fahrig 2015).

While a growing number of studies, among them analyses of urban mammals (Moll et al. 2020), use multiple spatial extents selected in a biologically-informed manner to more accurately pinpoint scales of effect in species-habitat investigations (e.g., Chandler and Hepinstall-Cymerman 2016, Galán-Acedo et al. 2018, Stevens and Conway 2020), they do not yet indicate clear patterns regarding the appropriate scale or scales of effect for urban mammals. We sought to build understanding of these scales of effect by identifying whether single or multiple scales of effect best characterize habitat relationships of urban mammals, and whether and how scales of effect vary among urban mammals and environmental attributes. We hypothesized that scales of effect would differ among species, such that scale of effect would increase with species body size and home range extent, and that the appropriate scale of effect for most species would approximate their home range extent. Given that past studies of many taxa (e.g., birds) demonstrate responses to urban environments at multiple spatial scales (see above), we also

hypothesized that environmental covariates would vary in their scales of effect for a given mammal species. We tested these hypotheses using single-species occupancy modeling (MacKenzie et al. 2002) and environmental covariates estimated over a range of extents to identify scales of effect for three common urban mammals, opossum, Eastern fox squirrel (*Sciurus niger*), and red fox (*Vulpes vulpes*), and three land-cover attributes (impervious, forest, and water cover) in the Iowa City metropolitan area of Iowa, USA. We followed the guidelines of Stuber and Gruber (2020) by estimating land-cover variables over multiple extents ranging from local (50 m radius) to landscape (1000 m radius) as well as biologically-informed extents that approximate species home ranges. We constructed a set of occupancy models for each species that included all three land-cover covariates but differed in the extents over which different covariates were estimated such that all possible extent combinations were represented. Our results highlight the importance of considering different scales of effect in modeling urban mammal habitat relationships and contribute to urban ecological theory by identifying relationships between biological traits (e.g., body size) and scale of effect. Furthermore, by answering questions as to which spatial extents best represent scales of effect for these species, and whether these scales of effect differ among environmental covariates, we provide guidance to support management decisions regarding where and what habitat attributes to manage in urban mammal conservation.

Methods

Study area

Our study focused on the Iowa City metropolitan area of Johnson County, Iowa, USA, in the Midwestern US (Fig. 1). This region is characterized by widespread monoculture agriculture (primarily corn and soybeans) with 57% of the terrestrial area of the county in cultivated cropland (Homer et al. 2020). Another 12% of Johnson County is in hay or pasture; 10% is forested; and 10% is developed land with smaller areas of waterways, wetlands, and grasslands (Homer et al. 2020). This diversity of land-cover types, especially within urban boundaries, situates our study area well to compare species responses to urban and other land covers at a variety of spatial scales, as individual study site buffers at different extents will be representative of the fine-scale heterogeneity of urban environments.

Mammal surveys

We deployed motion-triggered cameras across Johnson County, IA, from 2017 to 2020 to survey mammal species. Camera-trapping survey design and methodology followed protocols outlined by the Urban Wildlife Information Network (UWIN), a network of research institutions utilizing similar wildlife survey methods to facilitate among-city urban ecological investigations (Magle et al. 2019). Briefly, we identified three linear transects to capture the urbanization gradient in the study area, divided them into 5-km segments, and buffered them by 2-km on both sides, thereby delineating 39, 20 km² survey “squares” in which 3-4 locations were randomly selected as camera trap sites (Fig. 1). We deployed motion-triggered trail cameras (Bushnell; Models #119736 & #119836) with infrared capabilities at each site for approximately 30 days in July, October, January, and April, months that represent study seasons

(summer, fall, winter, spring) in each year. We downloaded photographs from cameras twice per survey season. A minimum of two trained observers independently identified wildlife in each photograph to species. Identified photos were then compiled into species occurrence tables by season, site, and species, with seasons split into weekly sub-samples to assist in modeling individual species detectability rates in occupancy modeling.

Environmental covariate estimation

We created 50, 100, 500, and 1000 m-radius buffer zones around study sites in a geographic information system (ArcGIS version 10.6; ESRI 2017), as well as buffers approximating male and female urban home range extents for each of the three species included in this analysis (Table 1). We selected two extents (50 m, 100 m) to represent small or ‘local’ scales as both are commonly used to characterize local environments in species habitat modeling (e.g., Parsons et al. 2018, Cassel et al. 2020). We selected a 500 m buffer, an extent often used to estimate environmental covariates in species habitat modeling with urban mammals (e.g., Magle et al. 2016, Gallo et al. 2017), to represent an intermediate spatial extent. Finally, we used an 1000 m extent, an extent that is also commonly used in urban mammal occupancy analyses (e.g., Lesmeister et al. 2015, Wait et al. 2018), to represent a large or ‘landscape’ scale.

To identify home-range extents for the three species in this analysis, we searched for published papers that delineated home-range areas for our focal species using Web of Science and the search string ([common name] OR [species name]) AND (urban OR suburban OR city) AND (home range OR home-range). From the papers returned by this search, we selected the published home-range extents for males and females of each focal species from the most comparable study location to our own, in this case other small to mid-sized cities in the Great Plains Ecoregion (Taylor et al. 2015). We then used home range areal extents to identify radii of circular buffer zones to approximate the average home range extents of males and females of all three species (Table 1).

Table 1 Home-range buffer extents, and buffer radii used to estimate environmental covariates and studies that identified them.

Species	Sex	Buffer radius (m)	Home range areal extent (Ha)	Study location
Fox squirrel	F	239	17.9	College Station, Texas, USA (McCleery and Parker 2011)
	M	411	53.1	
Virginia opossum	F	244	18.8	Kirksville, Missouri, USA (Wright et al. 2012)
	M	345	37.3	
Red fox	F	863	234.0	Madison, Wisconsin, USA (Mueller et al. 2018)
	M	1339	563.0	

Our land-cover composition estimate relied on a 1-m resolution land-cover dataset for the study area (Kollasch 2009). We first updated this dataset to better represent the landscape during the data collection period using 2017 planimetric and cadastral data from the Johnson County Tax Assessors Office to identify and update parcels that changed land use during this period. We used the resulting dataset to calculate areas of forest, water, and impervious land cover within buffer radii surrounding camera-trap sites (Table 2; see Fig. 1 for example of 50 and 500 m buffers). Past research has identified links between these land-cover covariates and the occupancy of our study species with positive relationships between impervious cover and opossum (Wait and Ahlers 2020, MacDougall et al. *In Review*) and red fox occupancy rates (Mueller et al. 2018, MacDougall et al. *In Review*), and between opossum (Wait and Ahlers 2020) and fox squirrel (McCleery et al. 2007) occupancy and forested land cover. Past red fox occupancy analyses in the study region have conflicting findings regarding relationships with forest cover; for example, forest cover was negatively linked to red fox occupancy in Madison, Wisconsin (Mueller et al. 2018), but exhibited a positive relationship to occupancy and colonization in Iowa City, Iowa (MacDougall and Sander *In Review*). Finally, past studies have identified positive associations between water cover and red fox (MacDougall and Sander *In Review*) and opossum (Wait and Ahlers 2020) occupancy.

Table 2 Summary data for three land-cover covariates within buffer zones surrounding study sites. Values are given as a percentage of the total land area covered by a given land-cover class.

	Buffer radii									
	50 m	100 m	239 m	244 m	345 m	411 m	500 m	863 m	1000 m	1339 m
<i>Water</i>										
Min	0.000	0.000	0.000	0.000	0.000	0.001	0.001	0.001	0.001	0.001
Max	0.124	0.289	0.385	0.385	0.434	0.429	0.398	0.383	0.406	0.446
Mean	0.010	0.032	0.042	0.042	0.049	0.054	0.058	0.070	0.071	0.070
S.D.	0.022	0.067	0.096	0.095	0.103	0.104	0.104	0.103	0.105	0.108
<i>Forest</i>										
Min	0.093	0.065	0.025	0.024	0.029	0.034	0.030	0.021	0.025	0.022
Max	0.999	0.997	0.906	0.906	0.892	0.847	0.774	0.667	0.644	0.632
Mean	0.708	0.558	0.419	0.416	0.377	0.358	0.338	0.310	0.303	0.299
S.D.	0.250	0.244	0.224	0.223	0.216	0.207	0.193	0.169	0.163	0.152
<i>Impervious surfaces</i>										
Min	0.000	0.000	0.003	0.003	0.002	0.001	0.002	0.017	0.017	0.019
Max	0.256	0.368	0.489	0.488	0.481	0.502	0.507	0.524	0.501	0.492
Mean	0.040	0.077	0.119	0.119	0.131	0.135	0.143	0.164	0.168	0.169
S.D.	0.063	0.087	0.121	0.121	0.134	0.136	0.135	0.134	0.133	0.126

Occupancy modeling

Occupancy modelling, which is often conducted using programs such as PRESENCE (Hines 2011) and the R package *unmarked* (Fiske and Chandler 2011), is a common methodology for examining relationships between organisms and their environments. Occupancy models estimate the probability of a species occupying a site, typically by relating presence/absence data to site characteristics, with the underlying assumption of imperfect detection (MacKenzie et al. 2002). These models consist of two submodels, a submodel that models detection probability, accounting for imperfect detection by including covariates to represent repeated sampling at study sites in models (e.g., season) and that represent factors that may affect detection of individuals, and an occupancy submodel that predicts the likelihood of a species occupying a site given a set of site attributes (MacKenzie et al. 2002). We constructed single-species occupancy models (MacKenzie et al. 2017) for each species in our analysis using the *occu* function within the R package *unmarked* (Fiske and Chandler 2011) to assess relationships between species occupancy and our three land-cover variables across a variety of spatial extents. We included seasonality (a combination of season and year) as a detection (p) and occupancy

(ψ) parameter in all models as we expected seasonal changes in foliage to influence whether an organism triggered a camera and yearly fluctuations in climate and animal abundances to impact both detectability and occupancy of a species across our study area. We then fitted models containing every possible combination ($n = 216$) of our three landscape covariates such that each environmental covariate was included in all models, but at varying extents (e.g., water at 50 m, forest at 50 m, impervious surfaces at 50 m; water at 50 m, forest at 50 m, impervious surfaces at 100 m, water at 50 m, forest at 100 m, impervious surfaces at 1000 m). Individual species model sets were ranked by Akaike Information Criterion (AIC)(Burnham and Anderson 2003) to select the best-fit model.

Results

We collected 12 seasons of data between July of 2017 and April of 2020, representing a potential 1,862 secondary (weekly) sample data points across 39 sites and 12 seasons. Occasional camera malfunctions, however, resulted in a true total of 1,744 weeks of data for each species. Our modeling dataset included 3,496 fox squirrel observations, 3,674 opossum observations, and 1,576 red fox observations. Overall naïve detection rates were 0.404 for fox squirrel, 0.711 for opossum, and 0.444 for red fox.

For all three species, occupancy model sets contained no competitive models ($\Delta AIC \leq 2.0$) other than the top model. We evaluated goodness-of-fit for each model using a Freeman-Tukey test with bootstrap resampling ($n = 100$), with $p > 0.05$ indicating adequate model fit (fox squirrel: $p = 0.962$, opossum: $p = 0.615$, red fox: $p = 0.615$). For each of the three species, detection submodels indicated significant differences in detectability among some seasons (for full model specification, see Online Resource 1).

The top fox squirrel model identified a positive relationship with water cover at the smallest spatial scale, 50 m ($\beta = 0.319$, SE = 0.145, $p = 0.028$), and a negative relationship with impervious cover at the next largest spatial scale, 100 m ($\beta = -1.912$, SE = 0.316, $p < 0.001$). This model also identified a positive relationship with forest cover at the extent of a female home range ($\beta = 1.034$, SE = 0.207, $p < 0.001$) (Table 3). The top opossum model identified a positive relationship between occupancy and impervious cover at 100 m ($\beta = 0.362$, SE = 0.163, $p = 0.027$) and with water cover at 500 m ($\beta = 0.959$, SE = 1.018, $p = 0.346$). This model also indicated a negative relationship between occupancy and forest cover at the largest spatial extent we examined, 1000 m ($\beta = -0.314$, SE = 0.144, $p = 0.030$). The top occupancy model for red fox identified positive relationships for all three covariates, but at varying spatial extents. This model indicated a scale of effect for water cover of 100 m ($\beta = 0.403$, SE = 0.112, $p < 0.001$), forest cover in urban female home ranges (863 m radius extent) ($\beta = 0.549$, SE = 0.116, $p < 0.001$), and impervious cover in urban male home ranges (1339 m radius extent) ($\beta = 0.391$, SE = 0.113, $p = 0.001$).

Table 3 Occupancy model parameters for individual species' top models

Covariate	Estimate	SE	z	P(> z)
Fox squirrel				
water50m	0.319	0.145	2.1934	*
forest239m	1.034	0.207	4.9937	***
impervious100m	-1.912	0.316	-6.0443	***
Virginia opossum				
water500m	0.959	1.018	0.942	
forest1000m	-0.314	0.144	-2.171	*
impervious100m	0.362	0.163	2.213	*
Red fox				
water100m	0.403	0.112	3.59	***
forest863m	0.549	0.116	4.73	***
impervious1339m	0.391	0.113	3.45	**

***p < 0.001, ** p < 0.01, * p < 0.05, • p < 0.10

Discussion

We found that scales of effect differed among the mammalian species and among land-cover covariates in our analysis. No two land-cover covariates included in our top models for individual species exhibited the same scale of effect. Although past studies have identified many urban taxa, such as birds (Hostetler and Holling 2000, Pennington and Blair 2011, Hallman and Robinson 2020) and arthropods (Bennett and Gratton 2012) as responding to the environment at multiple spatial scales, our results support recently described evidence for similar multi-scale relationships between mammal species and urban environments (Moll et al. 2020). Additionally, and in line with our expectations, of the nine scales of effect examined across these three species, we found only one shared scale of effect across species (fox squirrel and opossum), for impervious surface coverage at 100 meters. Thus, our results clearly indicate that, in agreement with our hypotheses, scales of effect vary among both species and environmental attributes.

We also hypothesized that scales of effect would differ among species and would increase with body size. Our results provided some support for this hypothesis. The occupancy rate of the smallest species we examined, fox squirrel, was best predicted by water, forest, and impervious cover over smaller extents (50 m, 100 m, and 239 m, respectively). While top occupancy models for the larger two species in our analysis, opossum and red fox, also included covariates measured at local scales (impervious surfaces within 100 m for opossum; water within 100 m for red fox), remaining landscape covariates included in

the top models for both species were measured at much greater extents (500 and 1000 m for opossum, 863 and 1339 m for red fox). Thus, the mean scale of effect identified in our study is smallest (~130 m) for our smallest-bodied species and largest for our largest species (~770 m). Examining these relationships with a larger suite of species, and within a greater number of cities, could help identify whether these patterns hold more broadly or if no relationship truly exists, as identified in a previous study (Moll et al. 2020).

Some past studies found links between scale of effect and species traits such as dispersal distance and reproductive rate (Jackson and Fahrig 2012), while others found little evidence of such links (Galán-Acedo et al. 2018). We thus predicted that land-cover variables measured within biologically-informed extents would best approximate scales of effect as indicated by their inclusion in our best fit models. However, our results did not clearly support this hypothesis. We found that covariates measured within our biologically-informed extents, male and female home ranges, while included in some models, were no more common in best-fit models than covariates estimated in different ways. Our top fox squirrel model included one such covariate, forest cover, while our top red fox model included two, forest and impervious cover. In the case of red fox, male home range size represented the maximum buffer extent (1339 m) assessed in our analysis. Thus, the inclusion of forest cover measured within this extent may simply indicate that this species responds to this covariate over a very broad extent, potentially even larger than the extents explored in this analysis. Similarly, the top red fox model also included impervious cover measured at the extent of a female home range (863 m). Because the next largest (1000 m) and smallest (500 m) analysis extents differed considerably from this extent in areal coverage, it may be that this extent is simply closer to the appropriate scale of effect for this covariate for this species than other extents. Future analyses could include additional broad-scale covariates estimated over narrower intervals to help identify whether home range extents truly better identify scales of effect for some species and covariates.

Given that past studies had identified multiple scales of effect for other taxa (Hostetler and Holling 2000, Pennington and Blair 2011, Smith et al. 2011, Bennett and Gratton 2012, Litteral and Shochat 2017), we hypothesized that urban mammals would also respond to different aspects of their environment over different extents. Our results provide clear support for this hypothesis as the three covariates included in top models for each species were always estimated at different scales. While this finding disagrees with the findings of some past studies of mammals (Galán-Acedo et al. 2018), it broadly agrees with recommendations that ecologists examine multiple scales of effect in estimating species-habitat relationship (Moll et al. 2020), reinforcing the importance of incorporating a range of scales in modeling. Species habitat modeling that relies on covariates estimated at a single spatial extent is likely to misidentify important species-environment relationships (Jackson and Fahrig 2015).

Our results differ from and are similar to results from past studies of the same species, shedding light on potential effects of analysis extent in species-habitat modeling. For example, a study of opossum occupancy in Manhattan, Kansas used covariates estimated for 500-m radius buffers (Wait and Ahlers 2020). This study identified a positive relationship between water and occupancy, while we found a non-

significant relationship at 50 m; a positive relationship between impervious cover and opossum occupancy, similar to the relationship we identified with a scale of effect of 100 m; and did not include forest cover in the top model (although this covariate was significant and negatively linked to extinction), while we found a negative relationship between forest cover estimated in 1000 m buffer. Previous research in our study area found no relationship between forested land cover and opossum occupancy at a spatial scale based on a home range extent of 282 m (MacDougall and Sander *In Review*). While it is possible that the scales of effect for these covariates differ between cities, Wait and Ahlers (2020) conducted their analysis at a single extent, precluding identification of similarities and differences in scales of effect for opossum between the two cities. Future studies could help to identify whether scales of effect vary among study areas or if they are similar, suggesting a common scale of effect for particular covariates may exist for a given species. Past work suggests that studies that rely on covariates estimated across a single extent may not accurately identify important relationships (Jackson and Fahrig 2015); thus, it is likely that results from such single-scale studies will be less-reliable than studies that evaluated relationships over multiple spatial scales.

Based on the findings of this study, we suggest a protocol for researchers and practitioners to utilize when conducting species-environment analyses related to urban mammals. First, a broad range of biologically-informed (e.g., based on home range sizes, dispersal distances) spatial scales (Jackson and Fahrig 2015) over which relationships are likely to occur should be identified. Researchers should estimate environmental covariates over a variety of extents (e.g., local, landscape) within that range. The intervals between extents should be spaced so as to capture differences across scales (e.g., evenly spaced by a given percentage of the full range) (Miguet et al. 2016). Large gaps among extents could make it difficult to accurately identify scales of effect, as was the case for our red fox model. These covariate estimates should be included in models in all possible combinations as we demonstrated in this study (Stuber and Gruber 2020) and resulting models should then be compared (e.g., by AIC) to identify the combination of variables and extents that best explain variance in species occupancy or abundance. As in the present study, the extents of estimation for covariates included in best-fit models then identify the scale of effect for those covariates. Utilization of this protocol will reduce the likelihood of missing or inaccurately identifying species-environment relationships and could both build theory regarding the scale(s) of effect of urban mammals and how they vary among species and environmental attributes. The understanding thus built could inform urban conservation efforts by identifying the scales at which specific environmental attributes should be managed to support mammal species. As such, more accurate identification of scales of effect could serve to avoid issues that may arise when conservation is implemented at incorrect spatial scales (Montgomery et al. 2018).

Our findings should be considered in light of certain limitations. First, the scale of effect identified for some relationships from our top models occurred at the greatest extent measured (forest in the 1000 m extent for opossum; impervious surfaces in the 1339 m extent for red fox). Thus, it is possible that the true scale of effect is even greater than the identified scale (Jackson and Fahrig 2015). Second, our research was conducted in only one city, and it is likely that the scales of effect found here for each land-cover covariate, as well as for each species, differ among cities. Multi-city studies have highlighted

inconsistent relationships between mammalian species and land cover covariates among cities (Fidino et al. 2020, MacDougall et al. *In Review*), and we expect similar differences in scales of effect. Multi-city studies that estimate models using the protocol we outline above could serve to identify whether generalizable patterns in scales of effect exist.

Declarations

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Conflicts of interest/Competing interests

The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethics approval

University of Iowa, Institutions Animal Care and Use Committee (IACUC) Approval #7052015

Consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and material

Data will be available from Iowa Research Online (<https://ir.uiowa.edu/>)

Code availability

Not applicable

Authors' contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Brandon MacDougall and Heather Sander. The first draft of the manuscript was written by Brandon MacDougall and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Figures

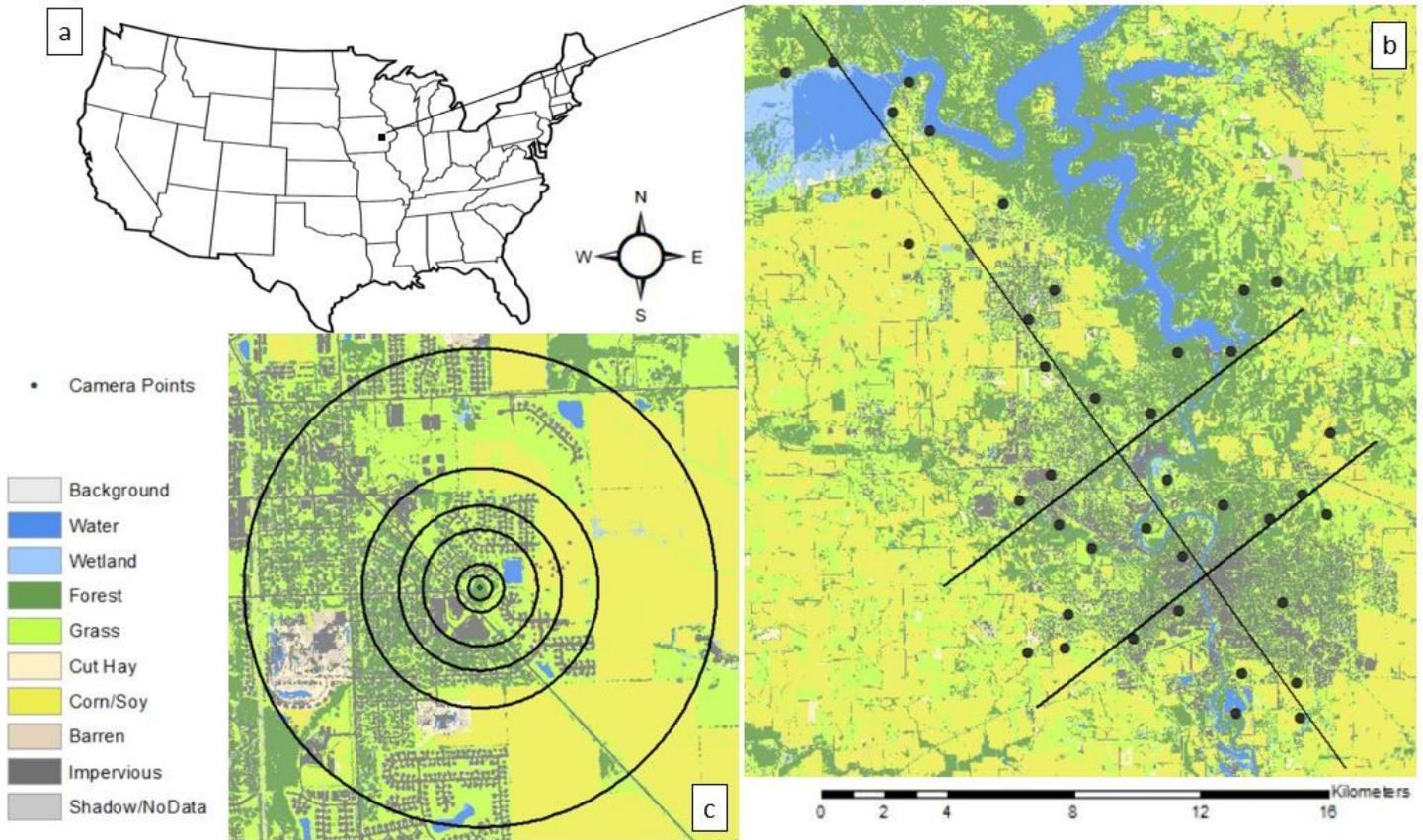


Figure 1

Location (a) and land cover (b, c) (based on Homer et al. 2020) of the study area, the Iowa City metropolitan area of Iowa, USA. Inset (b) identifies transect layout and location of individual study sites, while (c) highlights the degree of difference that may exist between the proportions of land cover within buffer sizes used for opossum in this study (50 m, 100 m, 244 m, 345 m, 500 m, 1000 m) Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

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