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Urban intensity predicts eastern gray squirrel (*Sciurus carolinensis*) and fox squirrel (*Sciurus niger*) occupancy and detection in St. Louis green spaces

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Abstract

Resource partitioning allows ecologically similar species to coexist, but human-altered landscapes such as cities change the availability and quality of resources. Tree squirrels are common in cities, yet the mechanisms that drive coexistence in urban habitats remain unclear. We explored how landscape features affect occupancy and detection of eastern gray squirrels (*Sciurus carolinensis*) and fox squirrels (*Sciurus niger*) along an urbanization gradient in St. Louis, Missouri. We conducted presence/absence surveys in 34 green spaces using seasonal camera trapping from fall 2018 to summer 2019. We examined the relationship between urbanization metrics (NDVI, % impervious surface, human population density) and estimates of occupancy and detection. We also investigated mean daily detection frequency among urban, suburban and rural green spaces and across seasons. Autologistic occupancy models with an urban intensity covariate yielded higher estimates of occupancy and detection for gray squirrels than fox squirrels. Fox squirrel occupancy and detection were negatively correlated with urban intensity, whereas gray squirrel occupancy and detection were positively correlated with it. Gray squirrel mean daily detection estimates were higher in urban sites than suburban and rural sites while fox squirrel mean daily detection rates were higher in rural than suburban sites. Both species had the highest mean daily detection rates in the fall and the lowest in the summer. Our results indicated that gray squirrels thrive in urban environments whereas fox squirrels are limited to more rural areas. Our results offer insight into the mechanisms influencing urban species' distribution and interactions, which are important for understanding the broader impacts on biodiversity.

Key words: squirrel; camera trap; occupancy; urbanization gradient; co-distribution

Introduction

Urbanization often reduces biodiversity (McKinney 2008), yet urban green spaces can provide important habitat for endemic wildlife (Boakes et al. 2024). As urban areas continue to grow, it is necessary to understand how urban green spaces affect species' distributions and interactions, and contribute to biodiversity within cities (McKinney 2002, Gallo et al. 2017). Human-altered landscapes can affect wildlife distributions through changes in the availability and quality of habitat and other resources (McKinney 2008). For example, species richness often declines in urban cores (Magle et al. 2021) but heterogeneity created by moderate human disturbance can enhance diversity of some taxa (McKinney 2008). Further, resource partitioning among species may become more pronounced in human-modified landscapes (Sovie et al. 2020, Casanelles-Abella et al. 2023, Cervantes et al. 2023). Ecological specialization combined with competition for limited resources, for example, may exclude one species over another and simplify species diversity (Devictor et al. 2008, Sovie et al. 2021). Questions that address how species coexist across

urban landscapes can reveal adaptive responses in novel environments and help inform efforts to manage and conserve biodiversity (McDonnell and Hahs 2015). Tree squirrels are found in cities worldwide and often have similar ecologies and overlapping distributions (Tranquillo et al. 2024). Introductions and range-expansions of some tree squirrels have occurred in urban areas across the globe, leading to the displacement of native species (Bertolino 2009, Tran et al. 2022). Thus, tree squirrels are excellent models to examine how urbanization affects the distribution and behavior of coexisting wildlife in urban green spaces.

Tree squirrels tend to be well-adapted to urban environments because life history and ecological characteristics of tree squirrels, such as short generation time and ability to use arboreal habitats to exploit resources, contribute to their success in urban environments (McDonnell and Hahs 2015, Tranquillo et al. 2024). Landscaping features, built structures and anthropogenic sources of food also alleviate the constraints of food limitation as well as predation risk (McCleery et al. 2007, Benson 2013, Fingland et al. 2022). Some tree squirrels, particularly *Sciurus* spp., thrive

in cities and their adaptability has led to successful introductions of populations in urban areas beyond their historical ranges where they then have negative impacts on native species (Gonzales et al. 2008, Bertolino 2009, Tranquillo et al. 2024). For example, the presence of introduced eastern gray squirrels (*Sciurus carolinensis*) resulted in widespread decline of native red squirrel (*S. vulgaris*) in Europe (Bertolino et al. 2014, Wauters et al. 2023). Similarly, in the western United States, introduced populations of eastern gray squirrel and fox squirrel (*S. niger*) have negatively impacted the native western gray squirrel (*S. griseus*) which are at risk of displacement in areas near human disturbances (Tran et al. 2022). Squirrels also form an important trophic link in urban ecosystems as a seed distributor and as prey species for urban predators such as canids and raptors (Koprowski 1994a). This link may be especially important in novel urban environments with homogenized functional diversity (El-Sabaawi 2018), further underscoring the importance of understanding interactions of co-distributed species in urban spaces. Here, we examine the co-distribution of two tree squirrel species, fox squirrel and eastern gray squirrel (hereafter referred to as gray squirrels), along an urbanization gradient within their historical range.

Gray and fox squirrels are native to and co-distributed over much of the eastern and central United States (Koprowski 1994a, b). Prior to the mid-19th century, both species were absent from American cities, but both species were actively released into city parks which facilitated their range expansion (King et al. 2010, Benson 2013). Supplemental feeding has also been correlated with increased abundance of gray squirrels in residential areas within and beyond their native range (Sexton 1990, Bonnington et al. 2014, Hansen et al. 2020). Fox and gray squirrels have similar ecological characteristics but may coexist through niche partitioning (Edwards et al. 1998, Sovie et al. 2019). In natural history accounts, gray squirrels tend to occur in contiguous forests with a woody understory (Koprowski 1994b) while fox squirrels are more abundant in ecotonal areas, edge habitats and forest patches with open understory (Koprowski 1994a). The distribution of these species may also be influenced by interspecific differences in foraging behavior, predation pressure, dispersal ability and territoriality (Goheen et al. 2003, Van Der Merwe et al. 2005). However, human-alteration of the natural landscape changes resource availability that can lead to the exclusion of congeners from realized niche space (Sovie et al. 2021). Fox and gray squirrels often co-occur in urban environments, but relative dominance of one species over the other varies across cities and mechanisms that drive coexistence are unclear (Van Der Merwe et al. 2005, Larson and Sander 2022, Larson et al. 2024). Much remains unexplored about the occupancy patterns of these two species in cities and how features of the urban environment drive the relative dominance of one squirrel species over the other in different metropolitan regions.

Our primary objective was to investigate how landscape features affect detection and occupancy of fox and gray squirrels in green spaces along an urbanization gradient in St. Louis, Missouri, USA. We explored (i) the relationship between urbanization metrics and occupancy and detection of both species and (ii) mean daily detection frequency of both species among urban, suburban and rural landscape categories along the gradient. Both species co-exist throughout Missouri with gray squirrels historically more common in the forested central and southern regions of the state and fox squirrels more common in the prairie region that comprises the northern and western portions of the state (Christisen and Kurzejeski 1988). However, statewide

hunting data suggests a concomitant decline in fox squirrels and increase in gray squirrels (Christisen and Kurzejeski 1988) and anecdotal evidence suggests displacement of fox squirrels by gray squirrels in a recently constructed subdivision in St. Louis (Sexton 1990). During the initial phases of our study, we routinely observed gray squirrels at green spaces throughout our transect, whereas fox squirrels were occasionally observed, and only in suburban or rural green spaces. Given previous studies and our own observations, we predicted that urban landscape variables, specifically the amount of built environment, human population density, and amount of vegetation structure, would be negatively correlated with fox squirrel occupancy and detection and that gray squirrel occupancy and detection would not change across the urbanization gradient. We predicted that gray squirrels mean daily detection estimates would be higher in urban habitats where tree cover is less dense and more concentrated (Engel et al. 2020) compared to less urban habitats. For fox squirrels, we expected mean daily detection to be greatest in the rural sites. For both species, we expected mean daily detection to be higher during the fall season, when tree squirrels actively forage and cache tree nuts to prepare for winter months, compared to the rest of the year.

Methods
Study area
The St. Louis Metropolitan area encompasses ~171 km^2 across Missouri and Illinois and contains ~2.8 million people (U.S. Census Bureau 2021). It includes large rivers such as the confluence of the Missouri and Mississippi Rivers and has a humid continental to humid subtropical climate (Peel et al. 2007). Underlying bedrock is mostly limestone and dolomite with karst features, and native vegetation is predominantly second growth, oak-hickory forest.

Camera trapping protocols and data collection
We established a 40 km transect along an urban-to-rural gradient in St. Louis, Missouri as part of a broader urban wildlife monitoring initiative, the St. Louis Wildlife Project (www.stlwildlifeproject.org) and conducted camera trapping following the standardized protocol developed by the Urban Wildlife Information Network (UWIN), a multi-city collaboration to monitor urban wildlife (Magle et al. 2016, Magle et al. 2019). Our transect was divided into 5 km segments with a 2 km buffer that started at the Gateway Arch National Park grounds in downtown St. Louis and extended to Route 66 State Park near Eureka, Missouri (Fig. 1). Segments along the gradient were categorized as urban, suburban, or rural based on the proportion of impervious surface (urban > 50%; suburban = 30%–50%, rural < 30%) within the 2 km buffer (Magle et al. 2016). We identified and randomly selected green spaces (e.g. parks, natural areas, golf courses, cemeteries) within the transect buffer to establish camera trapping stations. Final camera site selection was determined based on suitability of trees for camera placement and permission to access the location. We placed cameras at least 1 km away from each other such that there were at least four cameras within each buffered segment of the transect (Fig. 1). We established 34 total camera trapping stations (urban = 9, suburban = 16, rural = 9) across the transect.

Camera stations consisted of a motion-triggered infrared trail camera (Bushnell HD Trophy Cam, Overland Park, KS, USA) placed at a height of ~1 m and angled downward toward a scented lure (fatty acid scented disk, USDA Pocatello Supply) 3–5 m away on the
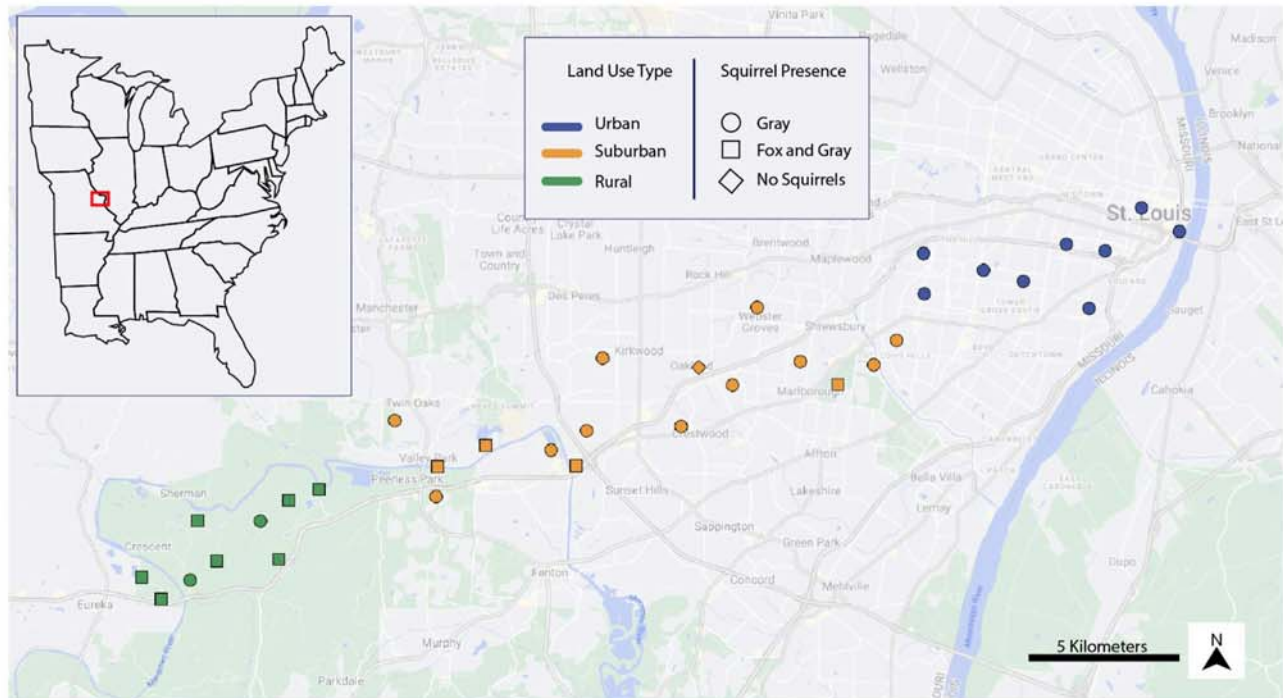
Figure 1. Map showing placement of 34 trail cameras in green spaces along a 40 km transect starting in downtown St. Louis and ending in Eureka, MO, USA. Camera placement was determined using the Urban Wildlife Information Network (UWIN) sampling protocol. Green spaces included urban ($n = 9$), suburban ($n = 16$), and rural ($n = 9$) sites. Gray squirrels (circles) were detected at all but one site. Fox squirrels (squares) were detected at 11 sites.

trunk of an adjacent tree. The lure was secured in a small pouch constructed of window screening and attached to a wire placed around the trunk of the tree. Following UWIN protocol, we programmed cameras to capture one photo at 30 sec intervals under the normal sensor level. Cameras were deployed seasonally for ~4-week sampling periods during 2018 (October) and 2019 (January, April and July). Images were uploaded to a customized database (UWIN) and photo-tagged for species identification. Each image was independently tagged by two individuals (students or local volunteers) who had undergone training to identify local wildlife species. In instances where tags or species identifications did not match, a third individual would review the image to determine the appropriate tag. Because gray squirrels and fox squirrels are distinguished in part by coat color, we excluded infrared images (those in black and white) from analyses. As both species are primarily diurnal, excluding infrared images should have had minimal impact on estimates of occupancy and detection. Additional details about study design and data collection protocols are provided in Magle et al. (2016).

Urban landscape variables

Three urban landscape variables, mean normalized difference vegetation index (NDVI), % impervious cover, and population density (1000 s of people km^{-2}) were determined based on a 1 km radius buffer around each camera station. Additional details for estimating these urban landscape variables are provided in Magle et al. (2021). Prior to analyses, raw data were log transformed. Following Magle et al. (2021), we performed a principal components analysis (PCA) to reduce dimensionality among the urban landscape variables. We conducted the PCA and visualized the results in R version 4.2.1 (R Development Core Team 2022) using the package FACTOEXTRA (Kassambara and Mundt 2020). The first principal component explained 79% of the variation and
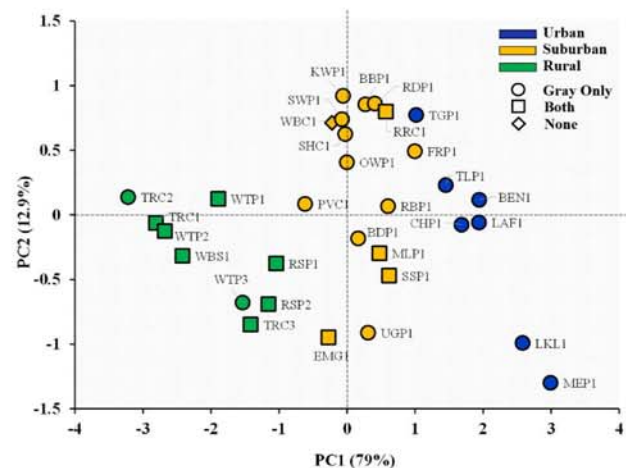
Figure 2. Separation of urban, suburban, and rural green spaces based on the "urban intensity" metric, the first principal component of the PCA. Landscape variables were based on a 1 km radius buffer around each camera station. Green spaces included urban ($n = 9$), suburban ($n = 16$), and rural ($n = 9$) sites. Gray squirrels (circles) were detected at all but one site. Fox squirrels (squares) were detected at 11 sites. Names of the green spaces along the urbanization gradient in St. Louis are provided in Supplementary Material.

clearly separated our sampling sites based on the urban, suburban, and rural categorizations of our transect gradient (Fig. 2). Loadings for variables were as follows: NDVI $= -0.58$, % impervious cover $= 0.59$, and population density $= 0.56$. We retained the first principal component (PC1) and interpreted it as an urban intensity metric (Magle et al. 2021), where increasing values in PC1 indicate an increase in urban intensity (Fig. 2). We then used the urban intensity metric as a covariate in occupancy analyses to

assess the role that urbanization has on the distribution of the two squirrel species along the urban-to-rural transect.

Occupancy modeling

We tabulated encounter histories for each squirrel species at each camera site and sampling period (i.e. fall 2018, winter 2019, spring 2019, and summer 2019). Each day of a given 4-week sampling period was considered a survey. Because we resampled sites over four sampling periods, we could not fit a standard single-season occupancy model, as that would result in pseudoreplication (Hurlbert 1984). Similarly, as we only sampled 33 sites, we had insufficient data to fit a standard dynamic occupancy model that separately estimates initial occupancy, colonization, extinction, and detection probabilities (Mckann et al. 2013). Instead, we fit autologistic occupancy models to these data, which are the simplest form of dynamic occupancy model, and can be used to estimate occupancy and detection probabilities through time (Royle and Dorazio 2008). What makes autologistic occupancy models unique is that they include one additional parameter, θ, in the occupancy logit-linear predictor to account temporal dependence in occupancy between subsequent sampling periods. Given our limited sample size, autologistic occupancy models were an ideal choice for our data.

We fit autologistic occupancy models using the AUTOOCC package (Fidino 2024) in R version 4.2.1 (R Development Core Team 2022). For each species we fit two models: an intercept-only model on both occupancy and detection and a model using our urban intensity covariate for both occupancy and detection. We compared models using AIC and considered all models within 2 ΔAIC of the best fit model to have substantial support (Burnham and Anderson 2002). To keep our significance testing in line with our model selection strategy, we assessed statistical significance by checking if 85% confidence intervals (CIs) of parameters crossed 0 (Sutherland et al. 2023). We report standard errors alongside parameter estimates and 85% CIs so that CIs of any width can be readily calculated.

Detection frequency

Although occupancy estimates provide information about distribution of both squirrel species along the gradient, it is based on daily presence/absence data and does not provide an accurate representation of activity levels or abundance. To understand relative activity levels, we determined annual and seasonal daily detection frequencies for both species by compiling timestamp data for each sampling period and calculating mean daily detection (MDD) frequencies. To tally the number of detections, we counted the number of unique squirrels in each image for each calendar day, which approximated daylight hours because we excluded infrared (black and white) images from our analysis. MDD was then calculated by dividing the tally by the total number of days in the sampling season for each site. We then conducted a two-way ANOVA for each species to investigate the effects of landscape category (urban, suburban, rural) and season (winter, spring, summer, fall) as well as the interaction of landscape and season on MDD. We transformed data [ln(x + 1.5)] prior to analyses. All analyses were conducted in R version 4.2.1 (R Development Core Team 2022).

Results

We photo-tagged 12,357 gray squirrel images across all 34 camera sites, with the exception of a suburban golf course, and 314 fox squirrel images at 11 camera sites from an average of 110 (±

1.1) camera trap surveys (~28 days/season) along our 40 km transect. Fox squirrels were only detected at suburban and rural sites, and never at urban sites. Encounter histories and timestamp reports for camera trap surveys are provided as Supplementary Files.

Occupancy modeling

The model that included the urban intensity site covariate was the only supported model for both fox and gray squirrels (Table 1). On average, fox squirrel occupancy (0.28, 85% CI = 0.18, 0.42) was roughly 3.3 times lower than gray squirrel occupancy (0.93, 85% CI = 0.88, 0.96). Despite fox squirrel being less common than gray squirrel, temporal dependence in occupancy from one sampling period to the next was roughly 4.2 times greater for fox squirrel ($\theta_{fox} = 2.72$, SE = 0.59, 85% CI = 1.87, 3.56) than gray squirrel ($\theta_{gray} = 0.65$, SE = 0.60, 85% CI = −0.21, 1.51; Table 2). Furthermore, fox and gray squirrel had contrasting associations to urban intensity such that fox squirrel negatively covaried with this gradient ($\beta_{urban\ intensity,\ fox} = -0.32$, SE = 0.17, 85% CI = −0.56, −0.07) while gray squirrel positively covaried (Fig. 3; $\beta_{urban\ intensity,\ gray} = 0.56$, SE = 0.20, 85% CI = 0.27, 0.85; Table 2). This urban intensity relationship resulted in gray squirrel being far more common in more urban parts of St. Louis whereas the two species had similar occupancy in less urban parts (Fig. 3).

Average daily detection probabilities were roughly 3.7 times lower for fox squirrel (0.15, 85% CI = 0.13, 0.18) than gray squirrel (0.56, 85% CI = 0.55, 0.58). Regardless, given 28 days of sampling the probability fox and gray squirrel were detected at least once if they were present at an average site was 0.99 and 1.00. As with occupancy, fox and gray squirrel detection probability covaried with urban intensity in opposite directions such that fox squirrel had a negative association while gray squirrel was positive (Table 1). For example, given a one unit increase in our urban intensity metric from an average site (i.e. urban intensity increased from a value of 0 to 1), fox squirrel detection probability decreased by roughly 13% from 0.15 (85% CI = 0.13, 0.18) to 0.13 (85% CI = 0.10, 0.16) while gray squirrel detection probability increased by ~16% from 0.56 (85% CI = 0.55, 0.58) to 0.65 (85% CI = 0.64, 0.66).

Detection frequency

Annual estimates of mean daily detection (MDD, ± SE) were higher for gray squirrel (GS) than fox squirrel (FS) in urban (GS = 6.25 ± 1.61, FS = 0) and suburban sites (GS = 3.14 ± 0.74, FS = 0.08 ± 0.05), but more similar between the two species in rural sites (GS = 0.77 ± 0.21, FS = 0.18 ± 0.07). Fox and gray squirrel MDD rates varied across the landscape categories as well as season (Table 3, Figs 1–5). Post-hoc comparisons using the Tukey HSD test revealed that MDD rates for gray squirrel were higher in

Table 1. AIC rankings for the autologistic occupancy analysis for fox squirrel and eastern gray squirrel surveyed during four, 28-day seasons (fall 2018–summer 2019) across an urbanization gradient in St. Louis, MO, USA.[a]

| Species	Model	K	AIC	ΔAIC	AIC weight
Fox squirrel	Urban	5	994.26	0	0.99
	Intercept only	3	1005.65	11.39	0.01
Gray squirrel	Urban	5	4341.67	0	1.00
	Intercept only	3	4563.37	221.70	0.00

[a] For each species and season, we fit two models: an intercept only model and a model using the urban intensity covariate on both occupancy and detection. K represents the number of parameters in the model.

Table 2. Logit-scale coefficient estimates, standard errors, and 85% confidence intervals (CIs) for occupancy (Ψ) and detection (p) of fox squirrel and eastern gray squirrel surveyed during four, 28-day seasons (fall 2018–summer 2019) across an urbanization gradient in St. Louis, MO, USA.[a]

Species	Process	Parameter	Estimate	Standard error	85% CI
Fox squirrel	Ψ	Intercept	−1.96	0.31	−2.41, −1.52
		Urban Intensity (PC1)	−0.32	0.17	−0.56, −0.07
		θ	2.72	0.59	1.87, 3.56
	p	Intercept	−1.70	0.12	−1.87, −1.53
		Urban Intensity (PC1)	−0.21	0.07	−0.31, −0.12
Gray squirrel	Ψ	Intercept	2.03	0.49	1.32, 2.73
		Urban Intensity (PC1)	0.56	0.20	0.27, 0.85
		Θ	0.65	0.60	−0.21, 1.51
	p	Intercept	0.25	0.04	0.20, 0.31
		Urban Intensity (PC1)	0.37	0.03	0.33, 0.40

[a] Estimates are reported for the top models for fox squirrel and gray squirrel.
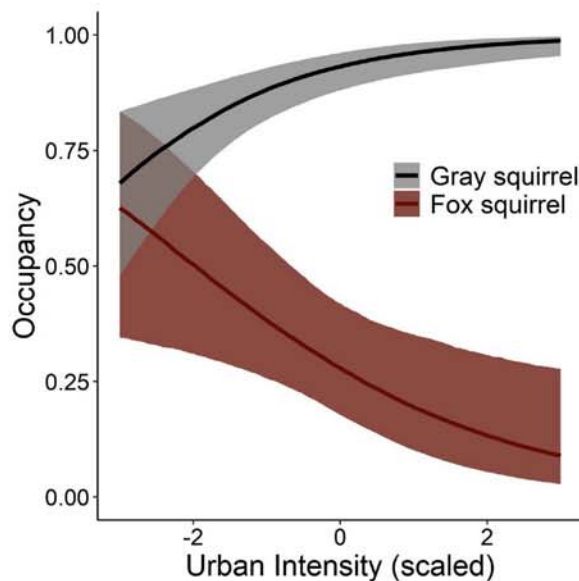
Figure 3. Expected occupancy estimates for fox squirrel (*Sciurus niger*) and eastern gray squirrel (*Sciurus carolinensis*) across a gradient of urban intensity. The camera trap data used to generate these predictions was collected between fall 2018 and summer 2019 and came from 33 green spaces throughout St. Louis, Missouri.

Table 3. Results from two-way ANOVA tests comparing seasonal mean daily detection (MDD) rates for fox squirrel and gray squirrel at camera traps placed at sites in St. Louis, MO, USA among three landscape categories: urban ($n = 8$), suburban ($n = 16$), and rural ($n = 9$).

	Source	df	F	P
Fox squirrel	Season	3	2.758	**0.045**[a]
	Category	2	5.425	**0.006**
	Season: Category	6	1.016	0.419
	Error	121		
Gray squirrel	Season	3	11.574	**<0.001**
	Category	2	20.933	**<0.001**
	Season: Category	6	1.443	0.204
	Error	121		

[a] Bold text indicates significant values.

urban sites compared to suburban ($P < .001$) and rural sites ($P < .001$), and MDD rates were higher in suburban compared to rural sites ($P = .002$; Table 4; Fig. 4). In contrast, MDD rates for fox squirrel were higher in rural than urban ($P = .005$) and suburban sites ($P = .056$; Table 4; Fig. 4). Seasonal comparisons showed that

MDD rates for gray squirrel were significantly higher in the fall compared to the winter ($P < .001$) and summer ($P < .001$), and spring was higher compared to summer ($P = .006$; Table 4; Fig. 5). Fox squirrel MDD rates were higher in the fall compared to the summer ($P = .038$; Table 4; Fig. 5). No other pairwise comparisons were statistically significant. For both species, we failed to detect a significant effect in the landscape category*season interaction term (Table 3).

Discussion

We found interspecific differences in the distributions of gray squirrel and fox squirrel along an urban-to-rural gradient in St. Louis. Urban landscape variables (% impervious surface, human population density and vegetation structure) reliably predicted occupancy of fox squirrels in green spaces along an urban-to-rural gradient in the greater St. Louis metro area, with fox squirrels being absent from areas with high urban intensity. In contrast, gray squirrels were observed more frequently than fox squirrels and though were detected throughout the transect, exhibited a positive correlation between occupancy and urban intensity. Our investigation also revealed that the number of daily detections of gray squirrels was significantly higher in urban areas, whereas daily detections of fox squirrels were higher in rural green spaces suggesting that levels of human modification influences behavior or abundance along the gradient. Our results provide insight into the mechanisms that influence distribution of urban species and lead to additional hypotheses about factors that shape species interactions, which are important for understanding broader impacts of urbanization in human-modified landscapes.

Urbanization results in changes in the availability and quality of resources and may alter abundance and of co-distributed and ecologically similar squirrel species (Sovie et al. 2021, Larson et al. 2024). For example, some species decline with the disappearance of native forest habitats, whereas others experience positive relationships with urban environments (Glennon and Porter 2007, Gonzales et al. 2008). Human-modified environments can also change competitive interactions between species, such as gray and fox squirrels (Sovie et al. 2021). Previous studies have shown that fox squirrels have a high tolerance to human disturbance (McCleery et al. 2007, McCleery 2009). However, though fox squirrels do occur in high densities in metropolitan areas outside of their native range (King et al. 2010), gray squirrels tend to predominate in highly urbanized areas (Sexton 1990, Van Der Merwe et al. 2005). Gray squirrels are considered generalists and will occupy the same habitats as fox squirrels, yet gray squirrels will use a greater variety of trees for nesting and will

Table 4. Tukeys post hoc test results from comparing seasonal (fall, winter, spring, summer) mean daily detection (MDD) rates for gray squirrel and fox squirrel detected at camera traps placed at sites in St. Louis, MO, USA among three landscape categories: urban (n = 8), suburban (n = 16), and rural (n = 9).[a]

	Fox squirrel					Gray squirrel			
Season	diff	lwr	upr	P	Season	diff	lwr	upr	P
Spring–Fall	−0.54	−0.61	−0.46	0.525	Spring–Fall	−0.79	−1.02	−0.44	0.118
Summer–Fall	**−0.58**	**−0.65**	**−0.50**	**0.038**	**Summer–Fall**	**−1.07**	**−1.21**	**−0.86**	**<0.001**
Winter–Fall	−0.56	−0.64	−0.49	0.145	**Winter–Fall**	**−0.96**	**−1.14**	**−0.70**	**<0.001**
Summer–Spring	−0.54	−0.61	−0.46	0.524	**Summer–Spring**	**−0.90**	**−1.09**	**−0.61**	**0.006**
Winter–Spring	−0.52	−0.60	−0.44	0.855	Winter–Spring	−0.74	−0.99	−0.38	0.249
Winter–Summer	−0.48	−0.56	−0.40	0.943	Winter–Summer	−0.25	−0.66	0.36	0.445
Landscape category					Landscape category				
Suburban–rural	**−0.56**	**−0.62**	**−0.50**	**0.056**	**Suburban–rural**	**0.08**	**−0.33**	**0.65**	**0.002**
Urban–rural	**−0.59**	**−0.65**	**−0.53**	**0.005**	**Urban–rural**	**1.09**	**0.33**	**2.18**	**<0.001**
Urban–suburban	−0.54	−0.59	−0.47	0.374	**Urban–suburban**	**0.14**	**−0.30**	**0.74**	**<0.001**

[a] Reported are the mean differences (diff), the lower bound of the 95% CI (lwr), and the upper bound of the 95% CI (upr) of each post hoc comparison. Values have been backtransformed to their original data scale. Bold text indicates significant values.
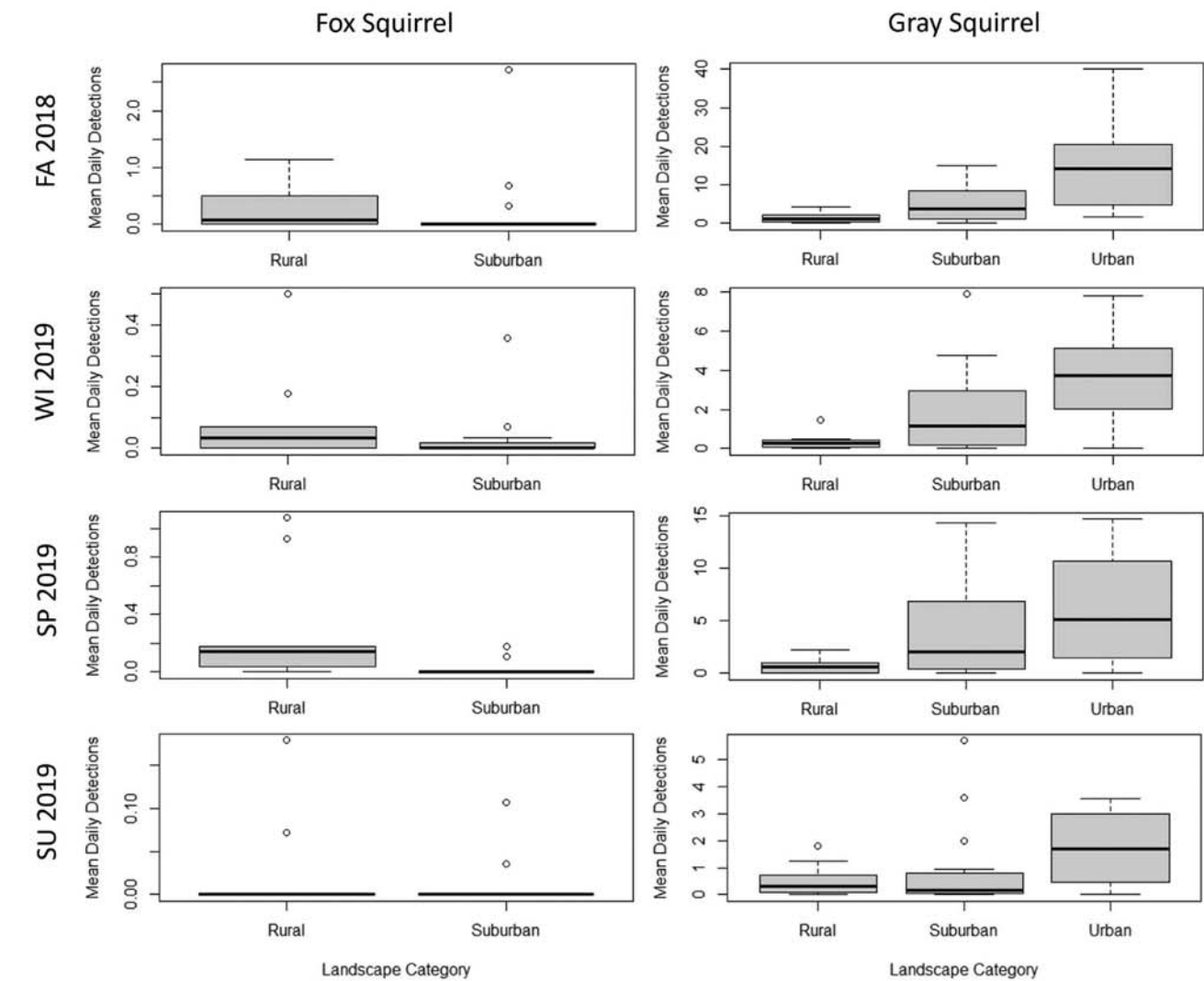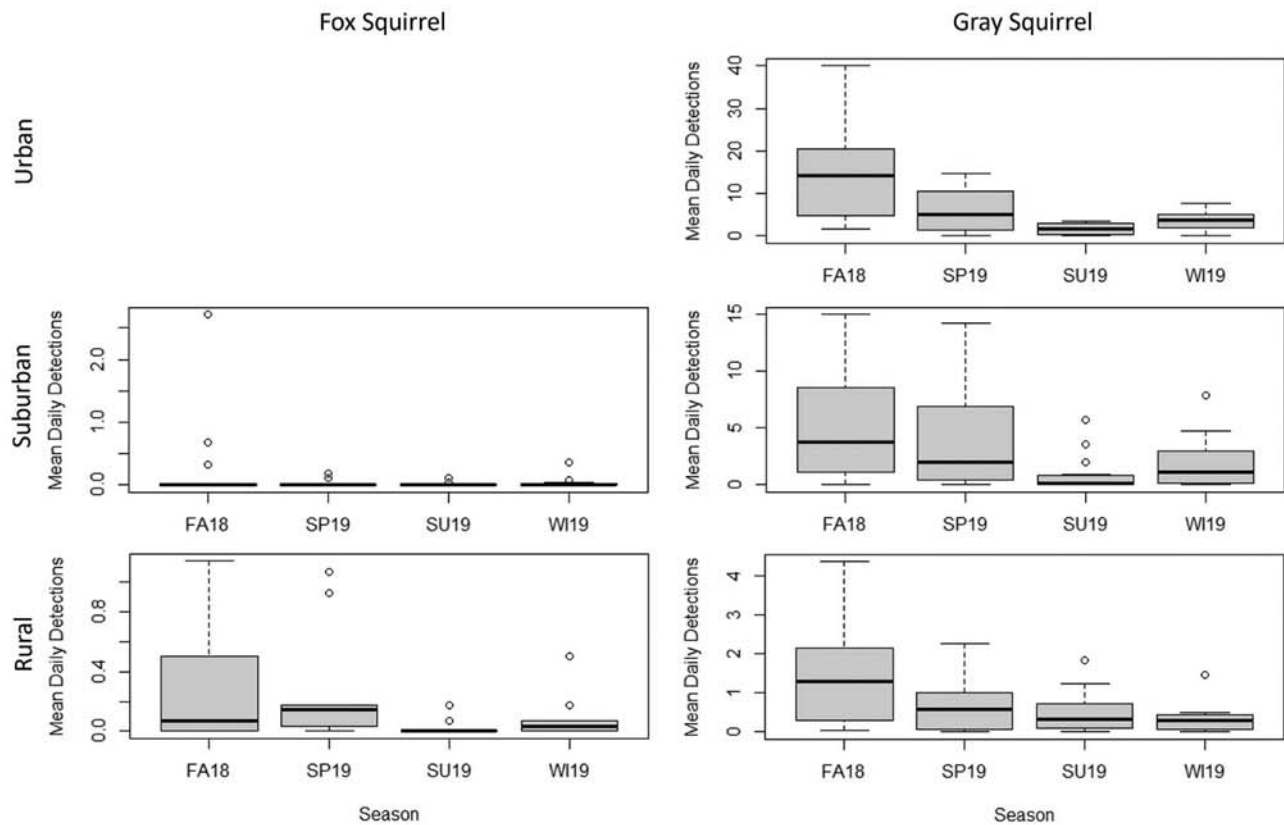

Figure 4. Boxplots of mean daily detection (MDD) estimates for fox squirrel (*Sciurus niger*) and eastern gray squirrel (*Sciurus carolinensis*) for rural (n = 9), suburban (n = 16) and urban (n = 9) green spaces along an urbanization gradient in St. Louis, Missouri. Estimates are shown for four sampling sessions: fall 2018, winter 2019, spring 2019, and summer 2019. Fox squirrels were not detected in urban green spaces during this study.

use habitats with more structure than fox squirrels (Edwards et al. 1998). In our study, higher temporal dependence in site occupancy for fox squirrels could be explained by stricter habitat

associations than found in the more generalist gray squirrels. Factors that influence interspecific dynamics can also vary or interact differently across spatial scales along gradients (Sovie

Figure 5. Boxplots of mean daily detection (MDD) estimates for fox squirrel (*Sciurus niger*) and eastern gray squirrel (*Sciurus carolinensis*) for fall 2018 (FA18), spring 2019 (SP19), summer 2019 (SU19) and winter 2019 (WI19) at green spaces along an urbanization gradient in St. Louis, Missouri. Estimates are shown for three landscape categories: urban ($n = 9$), suburban ($n = 16$), and rural ($n = 9$). Fox squirrels were not detected in urban green spaces during this study.

et al. 2020, Fardell et al. 2022). Localized, urban green spaces may offer opportunities for increased foraging efficiency and density dependent interactions that favor the more gregarious gray squirrel (Sovie et al. 2020), whereas at broader and more heterogeneous landscape scales, fox squirrels may benefit from greater dispersal ability and lower predation risk afforded by larger body size (Goheen et al. 2003).

Although there is a lack of evidence for strong interspecific competition between gray and fox squirrels (Armitage and Harris 1982, Brown and Batzli 1985, Larson and Sander 2022), antagonistic interactions may occur over nesting locations or food resources in human-modified landscapes (Sexton 1990). Empirical data from experimental manipulations also support that a combination of human-altered landscapes and competition may be a driving force behind the replacement of fox squirrel by gray squirrel (Sovie et al. 2021). Sovie et al. (2021) observed that fox squirrels increased their activity after experimental removal of gray squirrels in closed-canopy patches. In addition, competitive exclusion of native red squirrels by introduced populations of gray squirrels have been documented in Europe (Bertolino et al. 2014, Wauters et al. 2023) and western gray squirrels are at risk of being displaced by introduced fox and eastern gray squirrels in human-modified landscapes in North America (Tran et al. 2022). Though we did not test for interspecific dependence between fox and gray squirrels, the skewed distribution of fox squirrels along the urbanization gradient found in our study and anecdotal evidence for displacement of fox squirrels by gray squirrels in our study region (Sexton 1990), presents opportunities for future hypothesis testing in our system. Understanding how urbanization

affects interspecific interactions will be important for maintaining fox squirrel populations in the metro area and protecting local biodiversity.

In addition to occupancy, urban intensity may also influence behavior or abundance along our urbanization gradient. For gray squirrels, the mean number of daily detections were significantly greater in urban sites compared to suburban and rural sites. Similarly, a previous observational study in St. Louis reported that gray squirrel density increased with man-induced habitat changes (Engel et al. 2020). Gray squirrels may spend more time foraging at urban sites because they are more tolerant of human disturbance than squirrels in less urban sites. Prey animals display plasticity in vigilance or anti-predator behavior along urbanization gradients, with those in urban environments more tolerant of human and predator stressors (Bowers and Breland 1996, McCleery 2009, Engel et al. 2020, Fardell et al. 2022). Alternatively, gray squirrels may occur in higher densities in urban green spaces, where availability of resources, such as nut-producing trees, are more concentrated (Engel et al. 2020). Augmentation of food resources (i.e. bird feeders) and plantings of woody vegetation in urban green spaces may produce favorable habitat conditions for gray squirrels (Sexton 1990, Bonnington et al. 2014, Hansen et al. 2020). Conversely, fox squirrels were never detected in urban green spaces and had significantly higher mean daily detection estimates in rural sites compared to suburban sites. This result is consistent with the negative correlation between fox squirrel occupancy and urban intensity that we observed in this study. Although we cannot directly measure abundance using our camera trap dataset, MDD

could represent a metric of relative abundance across landscape categories. In any case, juxtaposing our estimates of occupancy and mean daily detection rates expands our understanding of squirrel distribution and behavior and is an important reminder that species' response to urbanization is complex and may vary across scale of disturbance (Sovie et al. 2020, Larson et al. 2024).

Despite interspecific differences in occupancy and detection rates across the urbanization gradient, seasonal trends in mean daily detections were similar between the species with numbers of daily detections highest during the fall and lowest during the summer. Foraging and nesting behavior are likely drivers of our observed activity patterns. For example, activity likely peaks in the fall during foraging and caching of tree nuts (Koprowski 1994a,b). Conversely, activity is lowest in the summer months when individuals remain close to nesting sites and activity is concentrated in the tree canopy (Armitage and Harris 1982). Our occupancy modeling approach precluded us from estimating seasonal occupancy and detection, thus it is possible that these estimates may also vary seasonally. Although we were not able to directly address competition in our study, it is possible that interspecific resource partitioning or competition may shift with seasonal resource availability along the urbanization gradient (Sovie et al. 2019, Larson and Sander 2022).

Protecting and maintaining biodiversity in urban regions requires understanding how human modification of the landscape affects distributions and interactions of living things in these ever increasing, novel environments (McKinney 2002, Gallo et al. 2017). Our work indicates that eastern gray squirrels thrive in urban environments whereas fox squirrel occupancy and detection may be constrained by stricter habitat associations found in more rural green spaces, but more fine-scale approaches are needed to adequately test for spatial and temporal partitioning of resources. For example, sampling grid arrays at sites where both species occur would better evaluate interspecific interactions at fine spatial and temporal scales (Sovie et al. 2020). Long-term monitoring may reveal shifts in occupancy estimates and detection rates over time (Sexton 1990). Measurement of local habitat characteristics such as abundance and size of tree species that provide nesting and food resources could also help test habitat partitioning hypotheses as interactions between fox and gray squirrel are shaped by fine-scale vegetation cover (Sovie et al. 2020). In addition, predation pressure and plasticity in anthropogenic tolerance may interact along the urbanization gradient and play a role in occupancy and detection frequency along our transect. In Chicago, fox squirrels were observed more than gray squirrels in an area with a higher abundance of cats, suggesting a difference in predation pressure (Van Der Merwe et al. 2005). We were not able to include presence of predators because of the limited time frame of our study but approaches that can also account for the effects of the presence of important predator or prey species will aid in understanding how species coexist in urban ecosystems. As more people live in urban environments and more land is converted to support humans, it is important to understand how organisms adapt and behave in these novel environments and how we can leverage this information to support biodiversity.

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Author contributions

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Supplementary data

Supplementary data are available at *JUECOL* online.

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Data availability

Detection history, photo-tagging summary statistics, and timestamp data are provided as supplementary data files in .xlsx format.

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