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Abstract - Behavioral responses to urbanization may differ with environmental variation across metropolitan areas. We compared relative abundance and escape behavior of *Sciurus carolinensis* (Eastern Gray Squirrels) in common urban habitats in St. Louis, Missouri, USA. We found that squirrels were abundant in urban park, forest, and neighborhood habitats and nearly absent in cemeteries and golf courses. Across all sites, we found abundance was positively associated with anthropogenic habitat modification: more people, impervious surface cover, roads, high intensity developed land use, and less canopy cover. Escape responses also varied across the urban landscape. Flight initiation distance, a metric of risk perception, was least in neighborhood and forest habitats and greatest in park and cemetery habitats. Most squirrels fled by sprinting a short distance and stopping in all habitat types, and those that ran quickly to a refuge tended to have greater flight initiation distances. Squirrels more readily fled in habitats with fewer roads and more residential land use. These findings suggest that responses to urbanization in Eastern Gray Squirrels are heterogeneous within the metropolitan region.

Introduction

Urban development rapidly transforms landscapes through increased impervious surface cover, changes in vegetation type, novel landscape features, and decreased green space (Grimm et al. 2008). Consequently, urbanization poses a threat to biodiversity by fragmenting populations, reshaping predation pressures, and changing food availability (Ditchkoff et al. 2006, McKinney 2008). Yet some species tolerate or even thrive in cities, exploiting urban resources and, in some cases, adapting to urban environments (Ditchkoff et al. 2006, Johnson and Munshi-South 2017). Clear morphological, behavioral, and physiological differences exist between urban and non-urban populations of many species (reviewed in Johnson and Munshi-South 2017). Yet, the extent to which variation in environmental features, such as human presence and habitat structure, relate to variation within metropolitan regions has been relatively understudied.

A wide variety of behavioral modifications have been documented in urban animals compared to rural conspecifics (reviewed in Ditchkoff et al. 2006, Lowry et al. 2013). *Tamias striatus* (Eastern Chipmunks) from urban habitats, for example, are more sedentary and have lower fecal cortisol concentrations compared to those from non-urban habitats (Lyons et al. 2017). Many urban behavioral shifts are related to risk assessment, escape strategy, and boldness, likely in response to shifts in predation pressures and habituation (Fischer et al. 2012, Lowry et al. 2013). Modification of risk-taking behaviors may allow additional time and energy for other behaviors, such as foraging, and thereby may increase fitness where predation risk is reduced (Lima and Dill 1990, Sparkman et al. 2018). Urban-associated behavioral traits, such as increased boldness, decreased neophobia, and decreased fear of humans, have been documented in urban populations of lizard species (*Intellagama lesueurii* [Australian Water Dragons], Baxter-Gilbert et al. 2019; *Anolis sagrei* [Brown Anoles],

¹Department of Biology, Washington University, St. Louis, MO 63130, USA. ²Department of Biology, Fordham University, Bronx, NY 10458, USA. *Corresponding author: kmwinchell@wustl.edu.

Lapiedra et al. 2016). Similarly, in many taxa, particularly birds, urban individuals are less wary of humans than non-urban conspecifics (reviewed in Lowry et al. 2013).

Behavioral responses to predation risk, such as fear responses and boldness, can provide valuable insight into the decision-making processes of wildlife (Ydenberg and Dill 1986), as well as how specific environments shape behavior (Lowry et al. 2013). Flight initiation distance (FID) is a commonly used metric for measuring perceived predation risk (Stankowich and Blumstein 2005). FID measures how close a potential threat (commonly a human or model predator) can approach a focal individual before eliciting a flight response (Cooper et al. 2015), and is often used in studies examining optimal escape theory—which predicts that animals flee when the risk of staying outweighs the cost of leaving (Ydenberg and Dill 1986). Animals that appropriately assess and respond to the risks posed by potential urban threats, in particular by humans, should be more likely to succeed in urban environments (Samia et al. 2015). FID is, therefore, a particularly relevant metric for advancing our understanding of which species are likely to tolerate increasing human presence and exploit urban spaces where they will be exposed to novel selective pressures (Winchell et al. 2020).

Decreased FID does not necessarily correspond to decreased vigilance or fear in urban animals. For example, escape distance in Brown Anoles decreased with urbanization, but cautiousness increased (measured by latency to explore a novel environment), which was attributed to increased ground predation (Lapiedra et al. 2016). Factors driving variable FID may also differ between populations because of habituation, where a decreased behavioral response to a repeated stimulus can influence the time and energy spent on anti-predator and foraging behaviors (Chapman et al. 2012). Animals routinely exposed to human presence may be less disturbed by them—allowing for closer approaches. Following this logic, researchers have found a consistent pattern of decreasing FID with increasing human exposure in multiple species of sciurids (Chapman et al. 2012, Cooper et al. 2008, Engelhardt and Weladji 2011, Uchida et al. 2016) as well as birds (Carrete and Tella 2010, Ducatez et al. 2016).

Sciurus carolinensis (Eastern Gray Squirrels, Gmelin, 1788) are a particularly good focal species for urban behavioral studies due to their synanthropic distribution and abundance in both urban and non-urban habitats. This species is successful in urban environments and is commonly habituated to human presence (Bateman and Fleming 2014, Cooper et al. 2008, Engelhardt and Weladji 2011). Previous behavioral studies have examined relationships between risk assessment behavior, such as FID, and a variety of ecological and environmental factors. This body of research has established that squirrels flee at shorter distances (e.g., are less wary of human approach) in sites with higher levels of human activity (Cooper et al. 2008), greater squirrel density (Parker and Nilon 2012), and distance to refuge (Dill and Houtman 1989, but see Engelhardt and Weladji 2011). Furthermore, human behavior has also been correlated with altered FID, with squirrels fleeing more readily when humans approach while looking directly at them (Bateman and Fleming 2014). Modified behavioral responses in urban habitats depend on the interaction of perceived risk versus reward, which may vary on fine scales with habitat features. For example, Bowers and Breland (1996) found that squirrels were willing to forage longer (estimated by giving-up density, another metric of risk assessment) at urban and suburban sites and in locations where the distances to human structures were low, densities of squirrels were high, and trees were abundant.

In this study, we investigated the abundance and behavior of Eastern Gray Squirrels across the St. Louis metropolitan area (Missouri, USA) to understand how behavioral responses vary across distinct urban habitat types. We sampled 17 sites representing common urban habitat types (parks, cemeteries, golf courses, residential neighborhoods, and urban forest) that also varied in key habitat characteristics (number of people, canopy cover, per-

cent impervious surface cover, roads, and land use). We addressed three main questions. We first asked if squirrel abundance differs across the urban landscape. We predicted squirrels would be more abundant in habitats such as forested areas and parks, which are more similar to their natural habitat. We next asked how squirrel escape behavior varies across the urban landscape. We predicted that squirrels in neighborhoods would have lower FID compared to individuals from other habitat types, due to an increased exposure to humans. Finally, we asked if differences in local and landscape-scale features were relevant to squirrel abundance and escape behavior. We predicted that patterns of abundance and flight behavior would be correlated with key ecological and environmental features across habitat types. Specifically, we expected that abundances would be greatest and that squirrels would be most wary (flee more readily and flee to refuge) in habitats with greater canopy cover, less impervious surface, less developed land cover, and fewer people.

Field Site Description

St. Louis is a metropolitan region located along the Mississippi River in the states of Missouri and Illinois in the United States (Fig. 1). The metropolitan region (metropolitan statistical area) is a large, developed, and populous region with an estimated population of 2.8 million people in 2018, with over 300,00 residents in the central city of St. Louis, Missouri (U.S. Census Bureau 2019). We sampled 17 sites distributed across approximately 70 km² in the core metropolitan area in St. Louis City and County in eastern Missouri (Fig. 1).

We focused our sampling on five urban habitat types: golf courses, residential neighborhoods, parks, cemeteries, and an urban forest. We chose these habitat types to capture variation in both intensity of habitat modification (i.e., extent of impervious surface versus tree cover and presence of anthropogenic structures) and human presence. The most heavily modified sites were residential neighborhoods, which had many trees but discontinuous tree canopy, with houses, impervious surfaces (streets, sidewalks), landscaped vegetation, and a consistent presence of humans. Parks, golf courses, and cemeteries were intermediate in disturbance, representing highly modified urban green-spaces that still had substantial vegetation and tree cover but differed in human presence and activity. We sampled only a single urban forest fragment (most urban forest fragments within our sample region resembled park habitat more than forest), located in Forest Park. Forest Park is a large (>500 ha) urban green space with mixed land uses including golf courses, recreation areas, a zoo, museums, and native forest fragments. The forest portion of the park sampled, located in the south-west corner, had minimal disturbance (some paved walking paths), nearly continuous tree canopy cover, and very few people.

Methods

Study Organism

The Eastern Gray Squirrel is a small arboreal mammal (38.0–52.5 cm average body length, including tail; Koprowski 1994) that occurs natively throughout eastern North America and has been introduced in Ireland, Italy, South Africa, and the United Kingdom (IUCN ISSG 2018). Eastern Gray Squirrels are found in mature woodlands with tree species that produce winter-storable seeds as well as anthropogenic environments, including residential areas and urban parks (Baker 1959, Nixon and Hansen 1987). In forest habitats, Eastern Gray Squirrel densities have been reported as <1/ha (Healy and Welsh 1992, Uhlig 1957) and by the mid 20th century, dwindling numbers outside of urban environments caused concern for the species'

persistence (Baker 1959). Conversely, squirrel densities in urban habitats are often greater (Hein 1997). In urban parks, densities have been reported to range between 2–51.5/ha (Manski et al. 1980, Parker and Nilon 2008), with densities on an urban university campus reported at 5/ha (Hein 1997). Estimates of home ranges of Eastern Gray Squirrels vary from 0.5–20.2 ha, although territorial exclusion is unlikely and overlap in home ranges is common (Doebel and McGinnes 1974, Don 1983, Thompson 1978). Specifically within urban parks, home ranges have been reported between 1.90–4.52 ha (Tounzen et al. 2012). The species descends to the ground frequently to forage and cache food. Peak activity is in summer and autumn. In autumn, activity peaks approximately 2 hours after sunrise and 2–5 hours before sunset (Bakken 1959, Thompson 1977).

Field Methods

We conducted surveys in the autumn of 2018 (19 September – 1 December), alternating habitat types so that all land-use types were sampled throughout the entire season. To account for minor seasonal variation throughout the sampling period, we noted the weather condi-

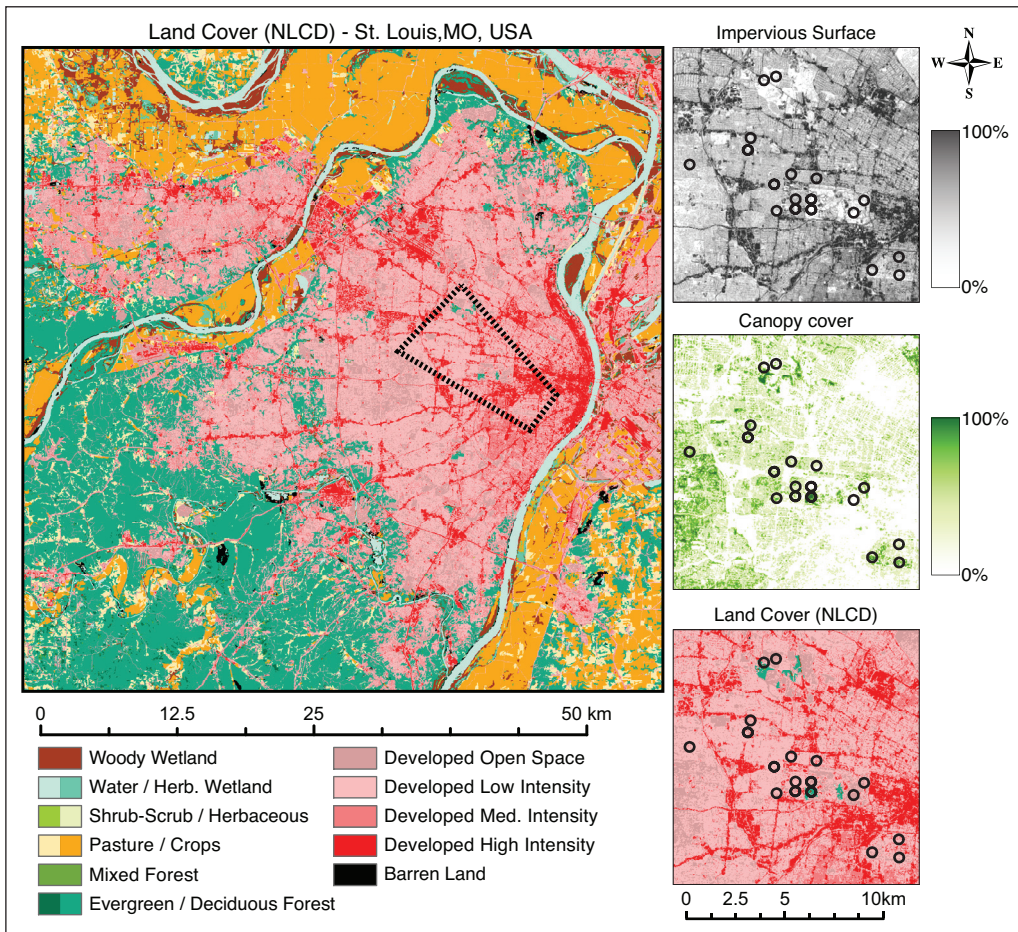


Figure 1. The St. Louis, Missouri metropolitan region and associated land cover. Left: St. Louis city, county, and surrounding areas with sampled area outlined (dotted rectangle) and NLCD land cover (NLCD v.2011; Homer et al. 2015). Right: impervious surface cover (top), tree canopy cover (middle), and NLCD land cover (bottom) for the sampled region with sample locations indicated by small black circles. NLCD land cover classes for both land cover images are on the lower left.

tions at each site and obtained the average air temperature for St. Louis for the date and time sampled at each site from the National Weather Service (NOAA 2019). The same researcher (LDE) performed all field surveys and FID tests. We conducted habitat surveys on days with typical land use and human presence for each site type (e.g., no major landscaping activity or public events).

We surveyed each site once, for approximately 1.5 hours, recording distance covered (using Gaia GPS, Trailbehind Inc. 2009–2019), elapsed time, and number of people seen. We followed established walking paths or sidewalks at each site where possible, walking along a single linear path without revisiting any portions of the habitat. Although we did not mark squirrels sampled, it is unlikely that we encountered the same squirrel more than once during our single sampling period per site. We counted all squirrels we observed and noted whether they were on the ground or on a structure, as well as if the structure was natural (e.g., vegetation, trees) or anthropogenic (e.g., buildings, fences).

When we spotted a squirrel on the ground, we measured the distance between the squirrel and the researcher (sight distance) because the distance at which a researcher begins approaching has been shown to influence FID in Eastern Gray Squirrels (Engelhardt and Weladji 2011). The researcher then walked toward the squirrel in a standardized approach (arms raised above head at a slow and constant pace) at an angle where the researcher was clearly visible to the squirrel. We measured the distance between the squirrel's starting location and the researcher when the squirrel began to move away from the observer (FID). Sight distance and FID were both measured using a laser distance meter (GLM 20, Bosch). After the squirrel fled, we measured the distance from the squirrel's starting location to the nearest vegetation the squirrel could use for escape (i.e., large enough to support the weight of a squirrel) and noted the escape strategy used by the squirrel ("sprint and stop" versus "run to refuge"). In addition, we recorded the number of people and estimated the percentage of impervious surface within a 10 m radius from the squirrel's starting location.

Landscape Analysis

We processed the following layers in ArcMap 10.6.1 (ESRI): National Land Cover Database (NLCD) land cover, canopy cover, and impervious surface (NLCD v.2011; Homer et al. 2015), roads (US Census Bureau 2017), squirrel locations, and linear path sampled. We projected all data to a common coordinate system (NAD 1983 UTM Zone 15N). We buffered each sampling path by a 40 m radius based on the minimum reported adult home range size for Eastern Gray Squirrels of 0.5 ha (Doebel and McGinnes 1974). We resampled NLCD rasters (land cover, canopy, and impervious surface) from 30 m² cell size to 5 m² using bilinear resampling for canopy cover and impervious surface and nearest neighbor for land cover classes. For each site (defined by the buffered sample path), we obtained the range, mean, and standard deviation of the continuous raster variables and percentage of land cover types for the NLCD land cover. We also determined the linear distance of roads within each buffer and standardized this metric by the linear distance travelled in each site.

We quantified a total of nine landscape variables that capture key differences in the five habitat types: impervious surface and canopy cover, number of people observed, road extent, and NLCD land cover categorizations of developed open space (NLCD 21), high intensity residential (NLCD 22), commercial and industrial (NLCD 23), developed high intensity (NLCD 24), and forest (NLCD 41–43, 90). We used linear discriminant analysis (implemented with the "lda" function in R package *MASS*; Venables and Ripley 2002) of the nine scaled landscape variables using habitat type (neighborhood, park, forest, golf course, cemetery) as the grouping factor. We validated the accuracy of the analysis in discriminating

habitat types using the function “confusionMatrix” in the R package *caret* (Kuhn 2019). We used ANOVA to determine if each linear discriminant (LD) differed by habitat type with marginal means pairwise comparisons implemented with the *emmeans* R package to evaluate which habitat levels differed from each other (Lenth 2017). We use linear discriminants that differed by habitat type in subsequent analyses.

Abundance Analyses

We estimated relative abundance as the total number of squirrels observed per site divided by the total area sampled (linear distance travelled with a buffer of 10 m, an estimate of how far we could consistently observe squirrels from a sampling path). We analyzed abundance as the total number of squirrels observed per site. We first verified that sites did not significantly differ in average temperature or sampling effort (time elapsed or distance travelled) with ANOVA. We then conducted a generalized linear model (GLM) with Poisson error distribution for the number of squirrels by significant linear discriminants from the landscape analysis. Sampling effort (ln-transformed distance travelled and amount of time spent sampling at a site) were significantly correlated with abundance and so we included them as covariates. We also conducted a generalized linear model with binomial error distribution for the fraction of squirrels on trees versus the ground by significant linear discriminants from the landscape analysis, with ln-transformed distance sampled as a covariate (temperature and sampling time were not significantly related to this response and so were not included).

We next analyzed a generalized linear model of abundance by landscape features per site: impervious surface and canopy cover, number of people, road extent, and NLCD land cover categories developed open space, high intensity residential, commercial and industrial, and developed high intensity. We did not include forest cover in the model because only two sites had non-zero values for this variable. We again used a Poisson error distribution and included average temperature and time spent sampling each site as covariates. We used bidirectional model selection by Akaike’s information criterion (AIC) to reduce the model, implemented with the function “step” in R base *stats*. We evaluated the significance of terms in all three models with a likelihood ratio test (LRT) implemented with the “drop1” function in R base *stats*.

Behavior Analyses

We used a generalized linear model with binomial error distribution to analyze escape strategies (“sprint and stop” versus “run to refuge”) with respect to the significant landscape LDs and including sight distance as a covariate. We used a linear model of ln-transformed FID by significant landscape LDs with average temperature and ln-transformed sight distance as covariates.

We used a second binomial GLM to examine escape strategy (with ln-transformed sight distance as a covariate) including the same seven landscape variables used in the abundance models, as well as three on-the-ground measurements taken for each focal squirrel (number of people and estimated impervious surface within 10 m of the squirrel, and distance from the squirrel to the nearest tree). We did not include number of people observed per site but instead included the number of people observed within 10 m of the squirrel. We also ran a second linear model of ln-transformed FID (with ln-transformed sight distance and temperature as covariates) with respect to these same 10 variables. For each model, we used bidirectional model selection by AIC to reduce the model and type III ANOVA implemented with the “drop1” function in R base *stats* to evaluate the significance of terms.

We completed all statistical analyses in R (R Core Team 2019). We used the following R packages in our analyses and visualizations of results: *ggplot2* (Wickham 2016), *reshape2*

(Wickham 2007), *emmeans* (Lenth 2017), *Rmisc* (Hope 2013), *gridExtra* (Baptiste 2017) and *dplyr* (Wickham et al. 2019).

Results

Habitat Variation

We sampled 17 sites: five residential neighborhoods, five parks, three cemeteries, three golf courses, and one urban forest. Sites varied in number of people, road extent, impervious surface cover, canopy cover, and NLCD land cover classes. Our linear discriminant analysis (LDA) had an overall accuracy of 1 (indicating complete discrimination based on habitat type, with 95% CI of 0.805–1). The first three LDs significantly differed by habitat type and together explained 99% of between-class variance (Table 1). These three axes were thus included in subsequent analyses. LD1 clearly separated golf course, park, and cemetery habitats (pairwise marginal means t-tests with $\alpha < 0.05$; Fig. 2A). LD2 separated

Table 1. Linear Discriminant Analysis (LDA) of habitat types (cemetery “C”, forest “F”, golf course “GC”, neighborhood “N”, park “P”) based on nine landscape variables (see methods for details). Between-class variance explained by each linear discriminant (LD), results of ANOVA by habitat type for each LD, number of groups discriminated and identity of groups based on pairwise marginal means t-tests with $\alpha=0.05$ (habitat types within parentheses do not differ at $\alpha=0.05$).

	Variance	ANOVA ~ habitat	N Groups	Marginal Mean Groups
LD1	0.56	$F_{4,12} = 51.425, p < 0.001$	4	(GC), (P), (C), (N, F)
LD2	0.29	$F_{4,12} = 26.802, p < 0.001$	3	(N), (P, GC, C), (F)
LD3	0.14	$F_{4,12} = 12.689, p = 0.003$	2	(GC, C, N), (P)
LD4	0.01	$F_{4,12} = 1.090, p = 0.405$	1	(C, P, N, GC, F)

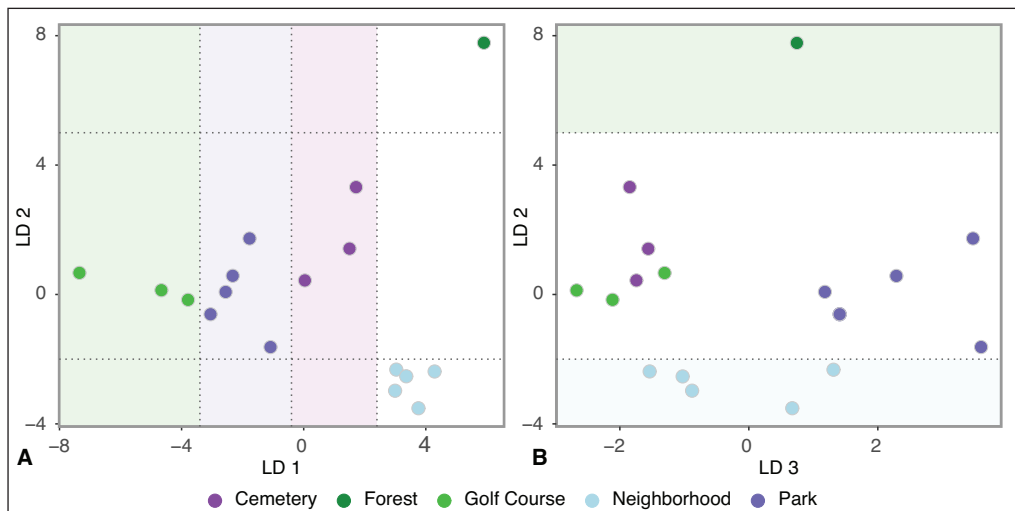


Figure 2. Linear Discriminant Analysis (LDA) of landscape variables by habitat type (Cemetery, Forest, Golf Course, Neighborhood, and Park). Each habitat type is uniquely distinguished by a combination of LD1 and LD2. Sites are plotted with respect to (A) LD1 and LD2, and (B) LD2 and LD3, with colors corresponding to habitat type. Shaded boxes and dashed lines indicate which habitats are significantly distinguished by LD1 and LD2 in A and B, respectively (see Table 1).

sites into three groups: neighborhood and forest habitats were at the extremes with a single group formed by golf course, cemetery, and park habitats (Fig. 2B). LD3 divided sites into two groups, with golf course, cemetery, and park habitats forming one group, park habitats forming another, and forest habitat intermediate between the two groups (Fig. 2B).

Abundance

We observed 337 squirrels across all sites. Parks had the highest estimated average abundance across all sites (32 squirrels/ha, range: 13–75 squirrels/ha), followed by the urban forest site (6 squirrels/ha), residential neighborhoods (5 squirrels/ha, range: 6–25 squirrels/ha), cemeteries (4 squirrels/ha, range: 1–9 squirrels/ha), and golf courses (<1 squirrels/ha, range: 0–1 squirrels/ha). We observed only three squirrels in neighborhoods and one in a cemetery using anthropogenic structures.

Time spent, distance covered, and average air temperature while sampling squirrel abundance at each site did not differ between sites (ANOVA, time: $F_{4,12} = 1.030$, $p = 0.431$; distance: $F_{4,12} = 1.118$, $p = 0.393$; temperature: $F_{4,12} = 0.514$, $p = 0.727$). Total number of squirrels observed was positively associated with sampling effort: time spent at each site (Poisson GLM, $z = 8.179$, $p < 0.001$) and ln-transformed distance travelled (Poisson GLM, $z = 7.891$, $p < 0.001$). Fraction of squirrels observed on trees versus on the ground was also correlated with sampling effort (ln-transformed distance; Binomial GLM, $z = -3.916$, $p < 0.001$).

Accounting for these covariates, we found that squirrel abundance (number of squirrels observed per site) and habitat use (observed on ground or tree) varied significantly across the urban landscape (Fig. 3). Abundance was positively correlated with LD1 and LD3, and negatively correlated with LD2 (likelihood-ratio test; LD1: $\chi = 4.197$, $p = 0.041$; LD2: $\chi = 5.953$, $p = 0.015$; LD3: $\chi = 25.609$, $p < 0.001$). This corresponds to higher abundances in neighborhood, forest, and park habitats compared to cemetery and golf course habitats. Fraction of squirrels observed on trees versus on the ground was negatively correlated (i.e., more squirrels were found in trees) with LD1 only (likelihood-ratio test; $\chi = -2.141$, $p = 0.032$). The abundance by landscape features model revealed multiple significant

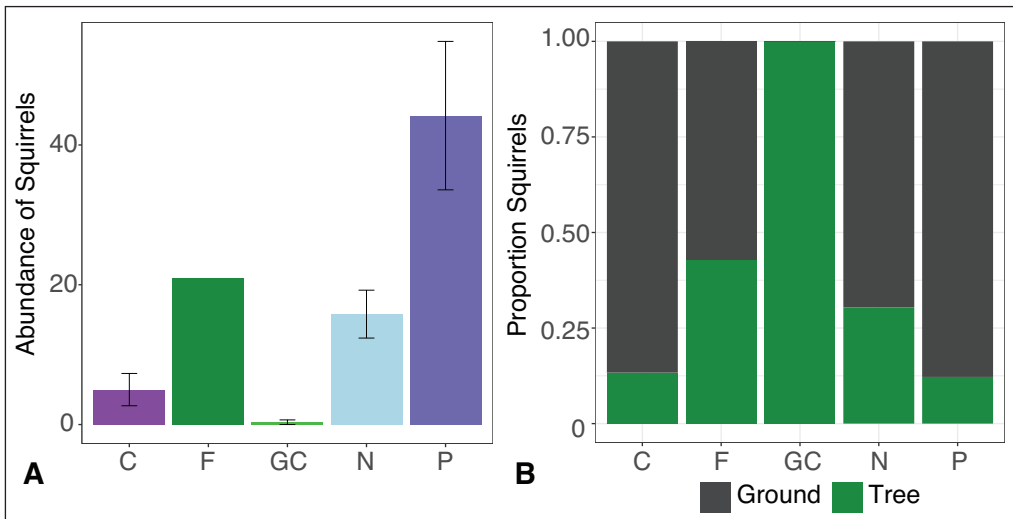


Figure 3. Relative abundance of squirrels by habitat type across all habitat types. (A) The mean abundance of squirrels observed plus and minus standard error per site for each habitat type (Cemetery: “C”, Forest: “F”, Golf Course: “GC”, Neighborhood: “N”, and Park: “P”). (B) The fraction of squirrels across all sites within a habitat type found on trees (or anthropogenic structures) vs. on the ground.

positive associations between squirrel abundance and landscape features (Table 2). Higher abundances were associated with more: people, impervious surface cover, roads, and high intensity developed land. Higher abundances were also associated with less: canopy cover, developed open space, residential land use, and commercial/industrial land use.

Escape Behavior

We measured escape behavior (escape strategy and FID) for 136 squirrels in park ($n = 76$), neighborhood ($n = 41$), forest ($n = 10$), and cemetery ($n = 9$) habitats. We were unable to obtain any behavioral measurements on squirrels on golf courses because we observed only a single squirrel across the three golf course sites sampled. Escape strategies and FID were both correlated with ln-transformed sight distance (escape strategy: Binomial GLM, $z = 2.338$, $p = 0.019$; FID: t-test, $t = 11.423$, $df = 134$, $p < 0.001$). Additionally, average air temperature during sampling was also associated with FID (t-test, $t = 3.897$, $df = 134$, $p < 0.001$). We therefore included ln-transformed sight distance in both models and temperature in the FID model.

Escape strategies were correlated with FID, but not with landscape LDs (likelihood-ratio test; FID: $\chi = 6.917$, $df = 1$, $p = 0.009$). Across all habitat types, most squirrels sprinted a short distance and stopped and 29% ran quickly to a tree or other refuge; sprinting quickly to refuge was associated with greater FID (Fig. 4A). Escape by running quickly to a refuge was associated with lesser road extent (likelihood-ratio test; $\chi = 9.932$, $df = 135$, $p = 0.002$) and higher proportions of residential (likelihood-ratio test; $\chi = 11.228$, $df = 135$, $p < 0.001$) and high intensity developed land (likelihood-ratio test; $\chi = 15.535$, $df = 135$, $p < 0.001$; Table 3). FID was negatively correlated with landscape LD1 only, indicating squirrels in cemetery and park habitats had longer FIDs compared to those in neighborhood and forest habitats (Type III ANOVA, $F_{1,130} = 7.077$, $p = 0.009$; Fig. 4B). FID across all sites was negatively correlated with impervious surface cover (Type III ANOVA, $F_{1,127} = 4.028$, $p = 0.047$) and road extent (Type III ANOVA, $F_{1,127} = 8.693$, $p = 0.004$), and positively correlated with greater amounts of residential land use (Type III ANOVA, $F_{1,127} = 4.767$, $p = 0.031$; Table 3).

Table 2. Full model for abundance by habitat characteristics for squirrels across all sites. Estimate (Est.) and standard error (SE) are given with χ test statistic and significance (p-value). Significant terms ($p < 0.05$) are shaded. The full model contained all significant terms and could not be reduced further.

Abundance	Full Model (AIC: 119.48)			
	Est.	SE	χ	p
Time sampled	2.74	0.32	92.010	<0.001
Distance sampled	-2.14	0.27	79.673	<0.001
Number people	0.06	0.01	60.919	<0.001
Impervious	21.09	10.73	3.946	0.047
Canopy	-2.68	1.27	4.586	0.032
Road extent	1.86	5.16	13.810	<0.001
Developed open	-1.98	0.86	5.488	0.019
Residential	-8.68	2.65	11.457	0.001
Commercial	-33.37	9.09	14.183	<0.001
Developed high intensity	33.13	10.39	10.111	0.001

Discussion

Although behavioral shifts in response to urbanization are well documented in many taxa, few studies have examined how these responses differ across various urban landscapes. Here we analyzed abundance and escape behavior of a common urban mammal across 17 sites and five different urban habitat types. We analyzed these responses with respect to continuous linear discriminants that clearly separate habitat types based on multiple landscape variables. In doing so, we are able to better understand how abundance and behavior varies in distinct urban habitat spaces that differ along a continuum of co-varying habitat features. We also analyze these responses with respect to habitat features to understand how specific landscape characteristics relate to abundance and behavior across the urban region regardless of habitat type.

Abundance

We expected squirrels to be most abundant in areas with extensive canopy cover, as found in previous studies (Bonnington et al. 2013, Williamson 1983). Greater canopy cover provides increased protection and refuges from urban predators and seed-bearing tree species are important food sources (Powell 1982, Williamson 1983). Moreover, a radiotracking study of Eastern Gray Squirrels in an urban forest found that squirrels consistently avoided developed and open grassy portions of the habitat (Tounzen et al. 2012). To some extent, our results support our prediction: we observed abundant squirrels in our forest site, albeit fewer than in parks. However, cemeteries and golf courses, which were minimally impacted by urbanization and had abundant tree canopy cover, had the lowest relative abundances of squirrels. Our linear discriminant analysis supports this observation: abundance was correlated with all three linear discriminants indicating the lowest abundances in golf course and cemetery habitat types (Table 2).

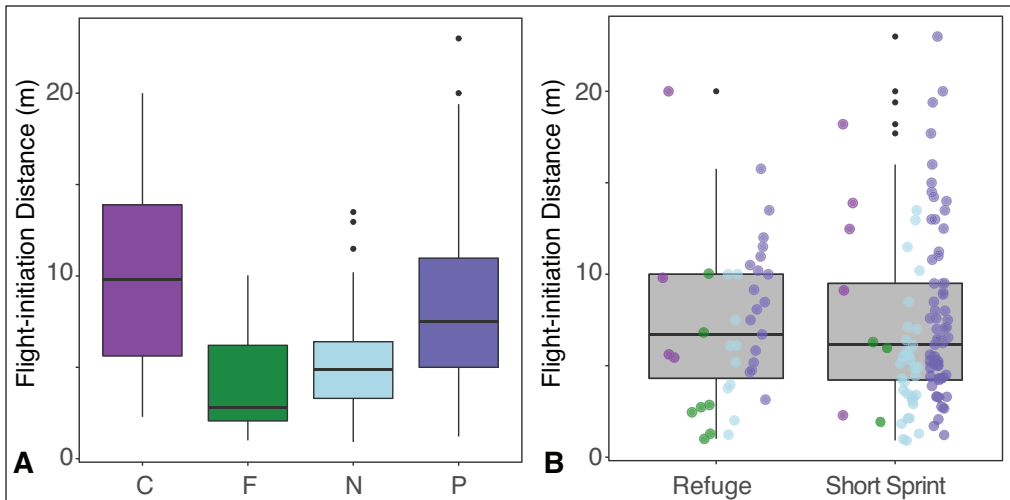


Figure 4. Flight initiation distance by discrete habitat type and by escape strategy. Boxes show mean and 1st and 3rd quantiles, with whiskers extending 1.5 times the inter-quartile range and black dots representing outliers. (A) Flight initiation distance (FID) differed across habitats sampled. Note that although presented as discrete categories here, we analyzed FID with respect to the linear discriminants (Table 1, Fig. 2). (B) FID was associated with escape strategy: squirrels that ran to refuge had greater FID than squirrels that sprinted a short distance and stopped in all habitat types (dots represent samples from each habitat type, colored as in A).

Golf courses are important habitats for many urban taxa, supporting high abundances, stable populations, and diverse communities (Colding and Folke 2008, Hodgkison et al. 2007, Winchell and Gibbs 2016). A related species, the *Sciurus niger avicennia* (Big Cypress Fox Squirrel), is common in golf course habitats in other urban regions, and cemeteries are known to support high abundances of Eastern Gray Squirrels (Ditgen et al. 2007, Thompson 1978). Eastern Gray Squirrels in St. Louis may not extensively use golf course or cemetery habitats because of factors not measured here. For example, landscaping activity may discourage squirrel presence by interfering with anti-predator behavior because of decreased auditory cues or may decrease forage effectiveness by disturbing food resources on the ground (Barber et al. 2010). Additional anthropogenic activities may also be a factor

Table 3. Full and reduced models for escape behavior and FID by habitat characteristics for squirrels across all sites. Estimate (Est.) and standard error (SE) for each model term are given. We evaluated significance of terms in the escape strategy model with a likelihood ratio test and in the FID model with type III ANOVA, and report the relevant statistics, χ and F, and p-values. Significant terms ($p < 0.05$) are shaded.

Escape Strategy	Full Model (AIC: 155.53)				Reduced Model (AIC: 147.27)			
	Est.	SE	χ	P	Est.	SE	χ	P
Sight distance	0.64	0.41	2.49	0.115	0.70	0.33	4.64	0.031
Impervious	9.35	54.19	0.03	0.864				
Canopy	4.75	4.18	1.46	0.227				
Road extent	-2.23	2.14	1.16	0.282	-3.24	1.16	9.93	0.002
Dev. Open	2.37	3.15	0.56	0.456				
Residential	4.00	12.91	0.10	0.754	5.70	1.87	11.23	0.001
Commercial	-4.51	43.25	0.01	0.917				
Dev. high intensity	92.58	52.45	4.74	0.030	109.05	50.17	15.54	0.001
People <10m	-0.42	0.35	2.85	0.091	-0.34	0.26	2.65	0.104
Imperv. <10m	1.26	1.78	0.52	0.471				
Nearest tree	-0.06	0.07	0.64	0.423				

FID	Full Model (AIC: 192.95)				Reduced Model (AIC: 188.57)			
	Est.	SE	F	P	Est.	SE	F	P
Sight distance	0.81	0.09	84.05	<0.001	0.79	0.08	88.96	0.001
Temperature	0.01	0.01	1.02	0.314	0.01	0.00	2.61	0.109
Impervious	-19.43	10.07	3.73	0.056	-17.79	8.87	4.03	0.047
Canopy	-0.99	6.25	2.49	0.117	-1.02	0.60	2.88	0.092
Road extent	-1.13	3.92	8.32	0.005	-1.10	3.73	8.69	0.004
Dev. Open	-0.83	0.54	2.35	0.128	-0.72	0.50	2.08	0.151
Residential	5.12	2.31	4.92	0.028	4.65	2.13	4.77	0.031
Commercial	15.38	7.54	4.16	0.044	13.67	7.07	3.75	0.055
Dev. high intensity	-1.46	8.97	0.03	0.871				
People <10m	-0.07	0.04	2.51	0.116	-0.07	0.04	2.92	0.090
Imperv. <10m	-0.14	0.32	0.19	0.660				
Nearest tree	-0.02	0.01	1.26	0.263				

across specific urban habitat types, such as the active culling of squirrels or the use of herbicides and pesticides that could lead to accidental poisoning—although these possibilities are purely speculative and require further investigation.

We observed the greatest abundances of squirrels in sites with the highest values of linear discriminants LD1 (forest and neighborhood habitats) and LD3 (park habitats), and lowest values of LD2 (forest habitat). Parks, neighborhoods, and forests drastically differ in their landscape composition and human activity levels. Park and forest habitats have many features that should promote large populations of squirrels (e.g., abundant tree cover), but neighborhood habitats have features that should disfavor abundant populations (e.g., extensive roads, impervious surface cover, and developed land). We interpret our result that forest and neighborhood habitats support similarly high abundances with caution. Observed abundance in the forest site may be underestimated if we failed to detect squirrels or may simply be a peculiarity of the single site we sampled. The other habitat types we sampled were significantly more open and detection was not likely an issue.

Neighborhoods and other urban environments commonly have readily available anthropogenic food resources, such as bird feeders and anthropogenic waste, which often support increased abundances of urban animals (Ditchkoff et al. 2006). We detected a significant positive association between anthropogenic landscape features and abundance across all sites suggesting greater abundances with greater human disturbance. Higher abundances were associated with more people at a site, greater impervious surface, lower canopy cover, more roads, and more high intensity land use (Table 2). Lower abundances were associated with sites that had greater proportions of developed open space (i.e., recreational space), and residential and commercial land uses. Although Williamson (1983) documented lower abundances of Eastern Gray Squirrels in areas with extensive impervious surface and building cover, Hein (1997) noted a pattern of greater densities of Eastern Gray Squirrels in urban habitats. Abundances of urban species of birds and reptiles have also been shown to increase with low to moderate levels of human density and decline only at very high levels of human presence (de Andrade 2019, Tratalos et al. 2007). Despite the overall positive relationship between observed numbers of squirrels and anthropogenic disturbance that we detected, we also found a negative relationship with increased commercial/industrial land use. These relationships suggest the intriguing possibility that there may be a degree of moderate anthropogenic disturbance that supports elevated abundances of Eastern Gray Squirrels.

Escape Behavior

We found that escape behavior significantly differed across the urban landscape with respect to our landscape linear discriminants as well as with specific habitat features. FID was positively correlated with linear discriminant LD1, with squirrels in park habitats fleeing at the greatest distance and squirrels in forests and neighborhoods allowing closer approach before fleeing. We also found that squirrels allowed closer approach (decreased FID) in habitats that had greater impervious surface coverage and road extent and less residential land use (Table 3). Our results thus add to the growing number of studies finding decreased FID in sciurids with increasing anthropogenic habitat modification (Chapman et al. 2012, Cooper et al. 2008, Engelhardt and Weladji 2011, Uchida et al. 2016). Notably, the habitats that had the highest abundances were the same in which squirrels had the shortest FID, a finding similar to Parker and Nilon (2008), who found decreased wariness in squirrels at higher densities.

Although escape strategy (fleeing to refuge versus short sprint and stop) did not differ across the urban landscape, escape strategy was correlated with specific landscape attributes. Squirrels were more likely to flee towards a refuge in habitats that had fewer roads and greater

proportions of residential and high intensity urban land use (Table 3). Cooper et al. (2008) similarly found that squirrels reacted to an approaching human at a closer distance in more heavily disturbed and open environments. In more open environments such as these, where the distance to refuge is likely greater, squirrels may be less likely to flee and more likely to remain immobile. However, there is no clear consensus on the relationship between FID and distance to refuge in the Eastern Gray Squirrel: some studies have found an increased FID with greater distance to refuge (Dill and Houtman 1989), yet others found no effect (Engelhardt and Weladji 2011). In this study, we find no effect of distance to nearest tree on FID nor on escape strategy across all sites. The relationship between urban land cover features and escape strategy is one avenue of future study in this system.

Variation in flight responses may be attributable to personality differences among squirrels related to boldness and fear. We found that squirrels that ran a short distance then stopped were also more likely to allow a closer approach (shorter FID) compared to those that ran towards a refuge. In other words, bolder squirrels may allow closer approach and not run as far when they flee. Squirrels that have a low propensity to flee may also occupy more urbanized landscapes if bolder animals are more likely to occur in more anthropogenically disturbed habitats as suggested by Lowry et al. (2013). If use of such habitat leads to increased interaction with humans, fear and startle responses may be increasingly dampened through habituation (Batabyal et al. 2017, Engelhardt and Weladji 2011, Fernández-Juricic et al. 2009). Future studies may investigate this topic further by examining how innate behavioral traits influence variation in flight responses with repeated exposure to anthropogenic stimuli.

Overall, we found that both abundance and behavioral responses related to urbanization are heterogeneous across a large portion of the core St. Louis urban landscape and may reflect variation in habituation and other behaviors at local scales. Our results highlight the importance of sampling multiple urban land-use types to understand nuanced differences in species responses across complex urban landscapes. Failure to do so may impact the magnitude of behavioral differences observed in simplified urban-rural comparisons. Local habitat features appear to affect urban squirrel behavior, suggesting that FID and habituation may vary in predictable ways among individuals inhabiting different types of urban habitats and even different portions of a habitat. Behavioral modifications in response to human presence can alter immune responses, stress levels, and reproductive success in urban animals, with implications for their persistence and well-being (Atwell et al. 2012, French et al. 2008, Gotanda et al. 2009, Lyons et al. 2017). Individuals that properly assess the risk of humans as a threat and respond appropriately with decreased FID will likely have increased fitness in these populations, especially as urbanization intensifies and human population increases.

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