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Cover Photograph: An Eastern gray squirrel (black morph) perches in a birch tree in Syracuse. Photo by: Dr. Jason Luscier.

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Nest Tree Selection by Eastern Gray Squirrels (*Sciurus carolinensis*) in an Urban Center

Jack F. McGovern^{1,*} and Jason D. Luscier¹

Abstract - Urbanization is a rapidly accelerating global phenomenon that exposes wildlife to a host of novel habitat pressures. Despite these challenges, many species are able to survive and even thrive via adaptations to the urban environment. The Eastern Gray Squirrel (*Sciurus carolinensis*; hereafter gray squirrel) is abundant in city landscapes across North America and Europe. Leaf nests constructed by gray squirrels (dreys) are an indicator of habitat use; understanding how certain urban habitat variables influence where dreys are constructed can therefore help to anticipate geospatial distributions of squirrel populations across a city landscape. Our main objective was to assess the potential effect of 2 different measures of noise pollution (roadway proximity and max dB) on nest tree selection by the gray squirrel in combination with already well-established nest tree selection variables (DBH and canopy connectivity). To do this, we systematically surveyed the city center of Syracuse, NY to locate trees hosting dreys as well as viable but unoccupied nearby trees for comparison. Predictor variables were used to draft candidate explanatory models *a priori* to evaluate any relationship between the variables and the probability of a drey occurring in a given tree. Candidate models were then ranked according to Akaike's Information Criterion (AIC_c). Model ranking indicated canopy connectivity and DBH were the strongest predictors of drey presence, while noise pollution had negligible effects on the probability of drey presence in a given tree.

Introduction

As the number of humans living on this planet soars, major population centers are expanding and exposing increasing numbers of species to the ecological pressures associated with urbanization. Species that are to succeed in urban centers must contend with the urban terrain and its associated challenges such as pollution, limited resource availability, and an intense alteration of naturally available habitat. A number of species have proven to be well adapted to city landscapes and demonstrate the capacity to survive and proliferate despite these challenges. The Eastern Gray Squirrel (*Sciurus carolinensis*; hereafter gray squirrel) is one such mammal capable of maintaining dense populations even in intensely developed areas (Williams 2011, Engel et al. 2020). While the presence of urban populations of gray squirrels can be ecologically and aesthetically beneficial (Benson 2013), overpopulation has the potential to increase the likelihood of certain nuisance behaviors associated with gray squirrels. Power outages, for instance, are frequently attributed to gray squirrel nesting activity (Hamilton et al. 1989).

McPherson and Nilon (1987) drafted a habitat suitability index (HSI) in an attempt to predict gray squirrel population densities based on characteristics of a given site, including canopy cover, availability of winter food and supplemental food sources, and size of available trees for nesting. A later study, however, demonstrated that this HSI was not fully able to account for different abundances observed in urban parks in Baltimore, MD and Washington, D.C. (Parker and Nilon 2008), emphasizing a need to further discern habitat features that could have an effect on squirrel population distributions in urban areas. Noise pollution, a prominent characteristic of urban habitats, can interfere with the acoustic environment which

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is used by gray squirrels to detect predators (Lilly 2019) and has also been observed to have an effect on the foraging behavior of gray squirrels (Thompson and Dall 2025). Therefore, noise pollution could be a potential variable of interest affecting squirrel populations on a given site.

The gray squirrel as an arboreal rodent relies heavily on the overstory for spatial navigation, both to forage and to escape predators (Koprowski 1994). Leaf nests (dreys) are constructed in tree canopies and are an important aspect of gray squirrel ecology, providing protection from predators and a shelter in which to overwinter and raise young (Steele and Koprowski 2001). Population densities of gray squirrels can also be approximated via determination of drey density on a given site (Don 1985). The general characteristics of preferred nesting trees are well understood: dreys tend to be constructed in trees that possess a larger DBH with multiple adjacent tree crowns (Sanderson 1975, Williams 2011). While studies have been conducted that identified a physiological tolerance by the gray squirrel to urban stressors (Rimbach et al. 2022), none have yet been conducted that explicitly assess the effect noise pollution may have on nest tree selection. Our study aims to model drey presence using the novel predictor variables of maximum decibel level recorded at a tree (MdB) and distance to the nearest roadway (D_road) in combination with the previously established predictor variables of DBH and connectivity in the city center in an effort to build on the existing understanding of squirrel behaviors in urban areas.

Methods

Study area

The city of Syracuse has a population of 145,560 spread across ~65 km², with the downtown area covering only about 1.5 km² (U.S. Census Bureau 2023). It is situated in a temperate deciduous forest biome with local average temperatures ranging between 15 °C and 27 °C in the summer and between -6 °C and 2.5 °C during the winter (US Climate Data 2025). Survey efforts were focused mainly within the delineated downtown sector (Tomorrow's Neighborhoods Today 2022; Fig. 1), but also extended to parks and roadways directly adjacent to the edge of the zone. This area is characterized by ~9% tree coverage (City of Syracuse 2016) consisting of *Juglans nigra* L. (Black Walnut), *Platanus occidentalis* L. (Sycamore), and various species of *Acer* spp. L. (Maple), *Prunus* spp. L. (Cherry), *Quercus* spp. (Oak) and *Carya* spp. Nutt. (Hickory; U.S. Department of Agriculture 2022). Green space is distributed throughout the area via several small parks and trees planted alongside roadways. Building cover is roughly homogenous; primarily consisting of offices, apartment complexes, and commercial buildings.

Identification of drey trees

We identified drey trees on foot via a systematic survey of the study area from August through October 2022. The systematic survey involved walking and visually searching along each street within the delineated area. A small number of dreys were seen in trees located in hazardous areas or on inaccessible private property; these were not included on account of safety and legal concerns. Additional dreys not encountered during the initial systematic survey were located during habitat measurements and included in our study. To ensure consistency, surveying was conducted by the same observer for the duration of the study. Dreys that were visible directly outside of the delineated study area were included in the survey in order to maximize sample size. Active status of dreys was not used as a qualification for use in the study. All nests and measurements were recorded before leaf fall in late October so that seasonal variation would be minimal.

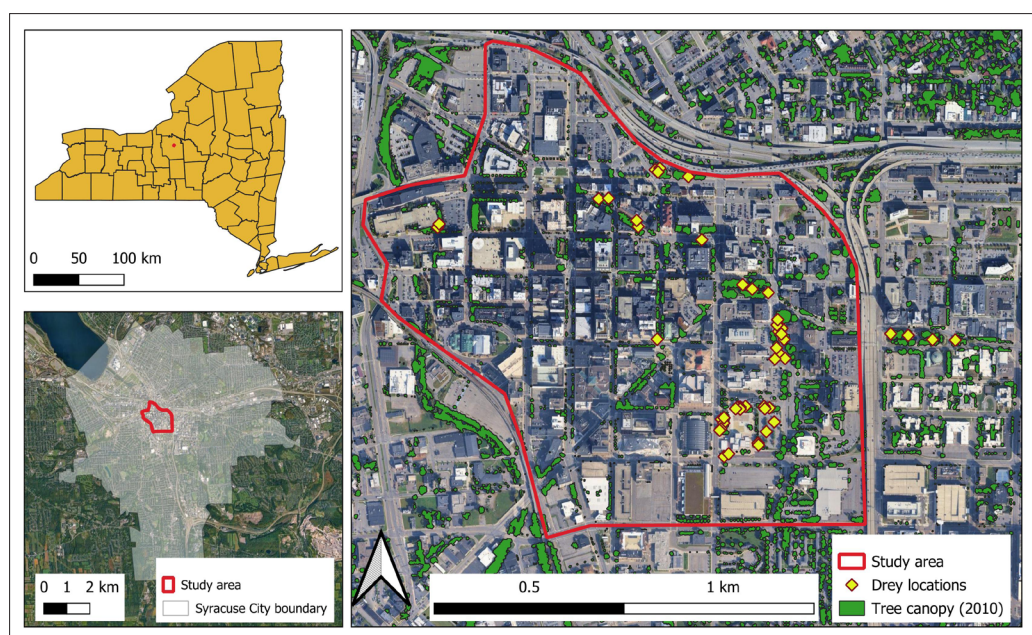


Figure 1. Map of the study area (downtown Syracuse), along with its location in the state of New York, denoting the locations of dreys identified in the study as well as an approximation of canopy coverage within the area.

Selection of unoccupied trees

We used a matched pair design to select 1 unoccupied but available tree adjacent to each of our drey trees. This approach allowed us to pair trees occupied by dreys with available unoccupied trees nearby (Manly et al. 2002, Duchesne et al. 2010). Candidate vacant trees were classified as those with a DBH of >12.7 cm (US Forest Service 1967) and nearest to a point 30 m from the tree in a random direction. Direction was chosen by randomly generating a number (0–360) and correlating it directly with an azimuth. By selecting trees within a relatively close distance to each other, we aimed to capture more subtle differences between trees that might cause one to be selected for nesting in favor of another. For example, noise pollution in particular can be highly variable across a cityscape as sound is tunneled, focused, and absorbed by buildings and other architecture (Balderrama et al. 2022).

Measuring predictor variables

We measured five habitat variables at each occupied and unoccupied tree (Table 1). Proximity to the nearest roadway from each drey site was measured using a tape measure for distances <6 m, a Nikon ForestryPro rangefinder for distances >6 m, and satellite imagery via Google Earth for distances that were not manually measurable. Tree height (H) was measured using the Nikon ForestryPro rangefinder. Diameter at breast height (DBH) of each tree was measured using Forestry Supplier's forestry tape. Canopy connectivity was measured by counting the number of tree crowns interlocking or directly adjacent to a selected tree (Gregory et al. 2010).

Noise pollution was measured using a Reed R8050 A-weighted decibel meter held at a height of 1.5 m on the side of the trunk facing the most apparent source of noise pollution (e.g. streets and building fans). At each site we recorded the maximum decibel level (MdB) detected over a period of 7 minutes (maximum continuous reading period of the instrument)

Table 1. List of explanatory variables that were used to generate Eastern gray squirrel nest site probability models for downtown Syracuse, NY.

Abbreviation	Variable	Description
DBH	DBH	Diameter at breast height (cm)
Con	Canopy connectivity	Count (number of tree crowns overlapping that of the tree of interest)
D_road	Distance to road	Distance (m) to the nearest road
MbD	Max decibel reading	Maximum dB recorded at a focal tree over a 7-minute interval

with readings collected during peak evening traffic hours (16:00–18:30) Monday through Thursday, to minimize day-to-day variability. Trees for which we were unable to obtain a decibel reading by the end of October were dropped from analysis in order to reduce potential seasonal variation in the acoustic environment.

Statistical analysis

All statistical analyses were conducted in RStudio version 4.2.2 (R Core Team 2025). To assess the potential issue of co-linearity, which could produce regression models with misleadingly high fits and inflated standard errors (Dorman et al. 2013), Pearson’s correlation coefficients were generated for related predictor variables. DBH and H, for instance, are both measures of tree size, while D_road and MbD both provide a rough measure of noise pollution at a given tree. This approach allowed us to narrow down the number of variables used in drafting a set of explanatory models and avoid including models that would be marred by high degrees of multicollinearity.

We drafted a set of candidate logistic regression models designed to evaluate relationships among our habitat variables with drey trees versus unoccupied trees. Candidate models drafted *a priori* were ranked according to Akaike’s information criterion corrected for small sample sizes (AIC_c). All models yielding ΔAIC_c values of ≤ 2.0 were considered equally plausible in explaining patterns in drey tree selection (Burnham and Anderson 2004). AIC_c weights (AIC_w), as well as the respective evidence ratio for each model, were included alongside model rankings to provide a more complete picture of the relative strengths of AIC_c rankings. Lastly, model-averaged parameter estimates were generated for all predictor variables to illustrate the direction and magnitude of effect that each parameter of interest had on the probability of a drey being present.

Results

In total, we identified 42 nest trees and 42 respective unoccupied but viable trees across the study area (Table 1). Of the 42 trees hosting nests, 12 species were identified, with black walnut being the most common (Table 2). Occupied trees had a significantly greater DBH and degree of canopy connectivity when compared with unoccupied trees (Table 3). Neither measure of noise pollution (MbD nor D_road) exhibited a significant difference between occupied and unoccupied trees.

Correlation coefficients indicated a high degree of correlation between DBH and H ($r = 0.511$), as well as between MbD and D_road ($r = -0.544$). Height was therefore omitted from

Table 2. Summary of tree species included in the survey with their respective quantities. Species names taken from USDA 2022.

Species name	Common name	Occupied	Unoccupied
<i>Juglans</i> spp. L.	Walnut	19	14
<i>Acer</i> spp. L.	Maple	8	7
<i>Prunus</i> spp. L.	Cherry	7	9
<i>Tilia</i> spp. L.	Linden	3	3
<i>Robinia</i> spp. L.	Locust	2	0
<i>Quercus</i> spp. L.	Oak	1	1
<i>Carya</i> spp. Nutt.	Hickory	1	2
<i>Platanus</i> spp. L.	Sycamore	1	2
<i>Fagus</i> spp. L.	Beech	0	1
<i>Carpinus</i> spp. L.	Hornbeam	0	1
<i>Pinus</i> spp. L.	Pine	0	1
<i>Picea</i> spp. A. Dietr.	Spruce	0	1

Table 3. Summary statistics of measured variables of trees hosting Eastern gray squirrel nests versus nearby unoccupied trees in downtown Syracuse, NY.

Variable	Occupied trees		Unoccupied trees		P value
	Mean	SE	Mean	SE	
DBH (cm)*	44.0	1.89	36.2	2.97	0.0299
Con*	2.76	0.233	1.40	1.15	0.00001
D_road (m)	23.2	3.63	21.5	4.42	0.7626
MdB	71.9	1.10	72.0	1.08	0.9581

*denotes significant difference between occupied and unoccupied groups at the 95% confidence level

use in drafting explanatory models, with DBH being used exclusively to represent tree size. Since the effects of MdB and D_road on drey tree selection have not been previously established and could capture unanticipated selection preferences (e.g., the threat of cars), both were kept as predictor variables, albeit in separate models to avoid the issue of collinearity with the exception of the global model.

Three models were determined to be plausible according to AIC_c rankings. Canopy connectivity was present in all 3 and by itself represented the strongest model, while DBH was present in models ranked 2nd and 3rd (Table 4). D_road was present in the 3rd strongest model; however, the magnitude of the associated beta estimate (Table 5) suggests that its presence is likely spurious. Our data yielded very little support for the null model. Model-averaged parameters associated with connectivity and DBH indicate a positive correlation with drey presence (i.e., probability of a drey increases with canopy connectivity and DBH). Parameter estimates for these 2 variables indicate that connectivity is a much stronger predictor variable than DBH.

Discussion

The probability of a drey being present in a given tree was most strongly influenced by tree DBH and canopy connectivity, with canopy connectivity appearing to be the overall

Table 4. Ranking of *a priori* drafted explanatory models for the probability of a drey being present in a given tree. Models considered to be plausible ($AIC_2 \leq 2$) are bolded. Rankings are based on a model's ability to parsimoniously fit the data set.

Model name	ΔAIC	AIC_w	Ev. ratio
Con	0.00	0.42522	1.000
DBH + Con	1.33	0.21915	0.515
U.S. Census Bureau. + Con + D_road	1.80	0.17276	0.406
DBH + Con + MdB	2.5	0.12196	0.287
Global	3.90	0.06049	0.142
DBH	14.65	0.00028	<0.001
Null	17.38	0.00007	<0.001
D_road	19.43	0.00003	<0.001
MdB	19.52	0.00002	<0.001

*minimum AIC_c value = 108.70

Table 5. Model-averaged beta estimates from candidate models evaluating effects of predictor variables on the probability of a drey being present in a given tree in downtown Syracuse.

Parameter	β	SE	LCL	UCL
DBH	<0.01	<0.01	<0.01	0.01
Con	0.15	0.04	0.08	0.23
D_road	<0.01	<0.01	-0.01	<0.01
MdB	0.01	0.01	-0.01	0.02

strongest predictor variable. Model rankings indicate that a combination of both a relatively large DBH and canopy connectivity will increase the probability of a tree being selected for drey construction. However, canopy connectivity on its own has a substantial influence on drey tree selection. Trees possessing a larger DBH are likely attractive for nesting due to the fact that they provide a larger space within which to construct dreys. Canopy connectivity enhances maneuverability from a nest which facilitates foraging and escape from predators (Steele and Koprowski 2001). Higher canopy connectivity at a given tree also signifies that the tree is located on a site with a higher degree of canopy coverage which has been demonstrated to be conducive to a site hosting larger gray squirrel population (McPherson and Nilon 1987). The role that canopy connectivity plays in drey tree selection by the gray squirrel is likely a combination of these 2 considerations.

Although we did not explicitly examine the effect that species had on drey tree selection, we did observe most dreys to be located in black walnut which is a popular food source for the gray squirrel (Barber 1975). This in itself is not sufficient evidence to suggest a preference for hard mast trees for nest construction, but it does coincide with previous observations of a preference for food trees like walnuts as nesting sites (Williams 2011). Our primary aim with recording tree species encountered in the study was to provide a more complete picture of the arboreal community within the direct study area. Black walnuts are the most frequently encountered trees in downtown Syracuse, so it follows that they would host a higher frequency of nests.

Neither measure of noise pollution had an apparent influence on the probability of a tree being selected for drey construction. Despite being present in 1 of the top 3 models, D_road

yielded a near-zero beta estimate. Hypothesis testing also did not detect a significant difference for this variable between occupied and unoccupied sample groups. MdB was absent from all plausible models, possessed a weak beta estimate, and was also not significantly different between both groups of trees. These findings coincide with those made by previous studies, namely that gray squirrels in urban areas have been observed to have heightened physiological tolerance to urban stressors (Rimbach et al. 2022) and a reduced perceived threat of predation in the presence of human development (Parker and Nilon 2008, Thompson and Dall 2025).

While noise pollution was not determined to be a factor guiding nest tree selection by gray squirrels in urban areas, this could be different in less urbanized habitats as other behaviors of gray squirrels have been noted to change with an increasing degree of urbanization. For instance, gray squirrels living in an urban habitat have been observed to display decreased wariness (Parker and Nilon 2008, Engel et al. 2020), potentially as a result of the reduced threat of predation that exists in cities. Since squirrels use the acoustic environment to detect predators (Lilly 2019), noise pollution interfering with that environment could potentially have a greater impact on squirrels living in habitats with a lesser degree of urbanization and a higher perceived threat of predation. A study assessing the response of squirrels to noise pollution in undeveloped habitats could further advance understanding of how nesting behavior of the gray squirrel is affected by urbanization.

The findings of this study might have yielded stronger results if not for a few limitations. First, sample size was limited on account of the relatively small area in which the drey survey was conducted (about 1.5 km²), as well as the previously mentioned concerns with private property and accessibility hazards—some trees spotted hosting dreys were either in fenced off areas or steep ditches. Additionally, by not ensuring that exclusively active dreys were included in the study, we ran the risk of inadvertently including inactive dreys. Dreys constructed in previous years might have been located in trees that were selected for nesting for reasons other than when they were actually spotted.

Our findings build upon previous research demonstrating an insensitivity of the gray squirrel to habitat pressures associated with urban development, particularly regarding nesting behavior and stress tolerance (Williams 2011, Rimbach et al. 2022). Considering the importance of tree canopies to gray squirrel ecology, it is unsurprising that canopy connectivity was determined to be the single most important predictor of drey occurrence. Canopy connectivity for the gray squirrel acts as a habitat corridor and facilitates navigation of the urban matrix. Generally, urban green spaces provide important wildlife habitat, and habitat corridors allow safe movement of wildlife across cities and are important for the survival of healthy populations of urban wildlife (Bennett 1999). As a prevalent component of urban ecosystems, monitoring and managing healthy gray squirrel populations can help ecologists to better understand urban wildlife dynamics. However, urban squirrels can also represent a nuisance (Hamilton 1989). Based on the results from our study, wildlife damage management programs could consider controlling canopy connectivity as a means for deterring gray squirrels from occurring in target areas.

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