Distribution Patterns of *Sciurus niger* (Eastern Fox Squirrel) Leaf Nests Within Woodlots Across a Suburban/Urban Landscape

Carmen M. Salsbury*

Abstract - To determine habitat characteristics that influence *Sciurus niger* (Eastern Fox Squirrel) abundance and distribution within a suburban/urban landscape in the midwestern United States, I documented the density and placement of fox squirrel leaf nests in 20 woodlots in the Indianapolis metropolitan area, Marion County, IN. The woodlots varied in size (0.94 to 19.5 ha), approximate age, shape, and degree of isolation from other woodlots and suitable squirrel habitat in the surrounding area. Only 8.0% of nests were located in a tree with another nest, and nests were randomly distributed in all but one woodlot, where they were uniformly dispersed. Nest density was not significantly related to woodlot size, approximate age, shape, or degree of isolation. Fox squirrel leaf nests were not found in greater densities along the edge of each woodlot, contrary to previous reports. My results suggest that the distribution patterns of fox squirrels within suburban/urban landscapes are similar to patterns within landscapes fragmented by agriculture.

Introduction

Habitat selection and space-use patterns of animals have long been of interest to ecologists. For many terrestrial mammals facing habitat loss, fragmentation, and degradation due to human activities, the details of habitat selection and space use are of great importance to the persistence and abundance of populations. In the agriculturally dominated Midwest, a substantial effort has been made to examine the sensitivity of mammal populations inhabiting landscapes fragmented by agriculture (Fitzgibbon 1993, Goheen et al. 2003, Nupp and Swihart 2000, Swihart and Nupp 1998). Less attention has focused on mammal populations living within suburban/urban habitats. As urbanization continues to encroach upon and further modify both agricultural and natural areas, there is a pressing need to examine the habitat selection and space-use patterns of species living within suburban/urban landscapes, in addition to examining the ultimate effects of habitat loss and fragmentation on persistence and abundance of populations.

North American tree squirrels, such as *Sciurus niger* Linnaeus (Eastern Fox Squirrel), are prime subjects for research examining the effects of habitat fragmentation due to urbanization (Koprowski 2005). This species readily adapts to and lives in and around suburban and urban centers (Steele and Koprowski 2001). However, the majority of what is known about the sensitivity and response to habitat fragmentation of fox squirrels is the result

*Department of Biological Sciences, Butler University, Indianapolis, IN 46208; csalsbur@butler.edu.

of studies conducted in agriculturally fragmented landscapes as opposed to landscapes fragmented by urban sprawl (McCleery et al. 2007, Salsbury et al. 2004). The frequency of Eastern Fox Squirrel colonization was positively affected by woodlot size in one study conducted within an agriculturally fragmented landscape in west-central Indiana (Goheen et al. 2003). Yet in a review by Koprowski (2005), density was negatively related to woodlot size for *S. niger*. Further, the degree of isolation of woodlots across agricultural landscapes in west-central Indiana and east-central Illinois appeared to have little effect on fox squirrel distributions (Goheen et al. 2003, Nupp and Swihart 2000, Rosenblatt et al. 1999, Swihart and Nupp 1998). The movements of Eastern Fox Squirrels between woodlots isolated by agricultural fields in west-central Indiana were, however, restricted to hedgerows, and movement across the open agricultural matrix was rare (Sheperd and Swihart 1995).

Suburban/urban landscapes may pose unique challenges to sciurids inhabiting forest fragments therein. Common elements of many suburban/urban landscapes, such as parking lots, major roadways, and retention ponds, are uninhabitable by sciurids. These suburban/urban areas contain little to no food and may pose an increased threat to survival due to exposure to predators and motorized vehicles (Williamson 1983). In one of the few studies focused on urban fox squirrel populations, fox squirrels were found to avoid paved areas within the urban landscape (McCleery et al. 2007). Other suburban/urban areas may serve as favorable microhabitats for fox squirrels as they contain bird feeders, horticultural plantings, or mast-producing trees (Jodice and Humphrey 1992, McComb 1984, Sexton 1990). Further, while many suburban/urban areas are likely devoid of many natural predators of sciurids, such as some hawks, owls, snakes, fox, and mustelids, other threats to survivorship, such as domestic pets and automobiles, may be substantial within suburban/urban landscapes (Bowers and Breland 1996, Faeth et al. 2005, Shochat 2004). Previous work indicates that squirrels minimize foraging activity in areas with high densities of domestic cats and dogs (Bowers and Breland 1996). Given the unique nature of suburban/urban landscapes, it is unclear whether the effects of forest fragmentation within an agricultural landscape are applicable to sciurids living in suburban/urban areas.

The objective of this study was to examine how the size, approximate age, shape, and degree of isolation of woodlots influence the relative abundance of fox squirrels living within a suburban/urban landscape. It is unclear whether the matrix of the suburban/urban landscape is more inhospitable than the matrix of an agricultural landscape. I assumed that some aspects of the suburban/urban landscape, such as parking lots and major roadways, would serve as barriers to squirrel movement; therefore, the abundance of Eastern Fox Squirrels would be negatively related to woodlot isolation. This prediction is contrary to observations within agricultural landscapes (Goheen et al. 2003, Rosenblatt et al. 1999). I also predicted that fox squirrel abundance would be negatively correlated to woodlot size. Because suburban/urban woodlots are often adjacent to habitats unsuitable to fox squirrels, such as parking lots and major roadways, I further predicted that fox squirrels would not prefer to nest near the edge of the suburban/urban woodlots.

Field-site Description

My study was conducted in 20 woodlots located throughout Marion County, IN from November 2003 to April 2005. Marion County encompasses the metropolitan area of Indianapolis, IN. The woodlots I surveyed ranged in size from 0.94 to 19.5 ha, and they varied with regard to appoximate age, shape, and degree of isolation. Using a 1941 aerial photo of Marion County, I determined that 7 of the surveyed woodlots were fully intact in 1941, 7 were non-existent, and 6 were composed of partially wooded areas mixed with open farmland.

Many of the woodlots surveyed were surrounded, in part, by a variety of different habitats known to be suitable for fox squirrels, such as park woods and wooded residential areas. Likewise, a number of the woodlots were surrounded, in part, by habitats unsuitable for Eastern Fox Squirrels, such as major roads (4 or more traffic lanes) and highways and large commercial areas (buildings and parking lots; Fig. 1). Although I did not characterize vegetative characteristics in detail for this study, the woodlots resembled disturbed woodlots characterized in a previous study (Salsbury et al. 2004) conducted in the same area. The woodlots in this study consisted of disturbed secondary growth stands comprised of deciduous trees, most notably *Quercus rubra* L. (Northern Red Oak), *Q. alba* L. (White Oak), *Acer saccharum* Marshall (Sugar Maple), *A. rubrum* L. (Red Maple), *Fraxinus* spp. (ash), *Ulmus* spp. (elm), *Carya* spp. (hickory), and *Celtis occidentalis* L. (Hackberry). Levels of disturbance within the woodlots varied from the presence of human footpaths to piles of trash and yard waste to felled trees. The density and composition of the understory and herbaceous layer also varied among the woodlots. The understory, when present, generally consisted of

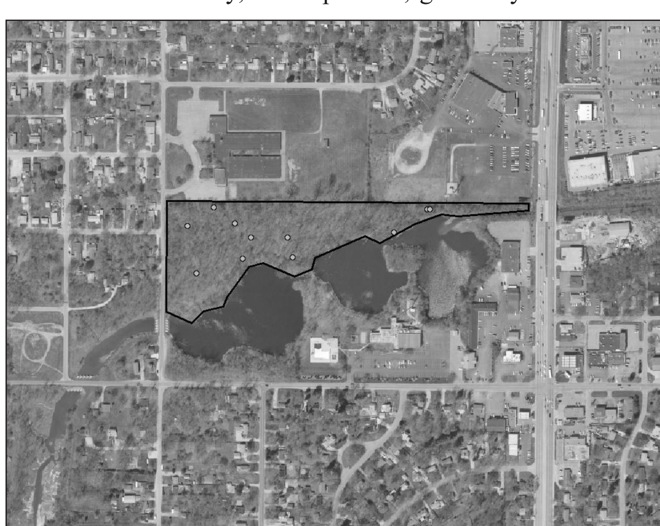

Figure 1. Aerial photo (2004) of one of the 20 suburban/urban woodlots in Marion County, IN surveyed for this study. The woodlot is bounded by a polygon and the leaf nests by circles therein. Photo scale 1: 3500.

invasive *Lonicera maackii* (Rupr.) Herder (Amur Honeysuckle) and canopy tree seedlings. The herbaceous layer often consisted of many native grasses and ephemeral spring wildflowers as well as invasive species such as *Alliaria petiolata* (Bieb.) Carvara and Grande (Garlic Mustard), *Euonymous fortunei* (Turcz.) Hand. - Maz. (Winter Creeper), and *Rosa multiflora* Thunb. ex Murr. (Multiflora Rose).

Methods

Leaf nest surveys

I estimated the presence and relative abundance of fox squirrels in each woodlot by counting the number of leaf nests present between November 2003 and April 2005. Previous studies showed that leaf-nest abundance may be used to estimate tree squirrel population density in an area (Don 1985, Wauters and Dhondt 1988). I did not attempt to estimate actual densities of fox squirrels in each woodlot, but instead used nest densities as an indicator of relative squirrel densities among woodlots. With the help of assistants, I surveyed each woodlot once during the course of the study to record the number and location of the fox squirrel leaf nests. We surveyed all woodlots after leaf fall, when nests were most visible. We located the nests by walking straight-line transects through each of the woodlots and identifying each nest with the use of binoculars from the ground level. Once a nest was found, we geo-referenced the exact location to within 6 m using a handheld GPS unit (Garmin V), and we marked each nest tree with a dot of flour. I walked behind each assistant through each woodlot to ensure that we recorded the location of every active fox squirrel leaf nest. We included only active nests in this study. We considered a nest to be inactive if we could see daylight through the nest when viewing it from below or if nest material was hanging from the central body of the nest.

I was confident that all nests included in this study were Eastern Fox Squirrel nests, as Eastern Fox Squirrels are the dominant tree squirrel in central Indiana (Mumford and Whitaker 1982), and I observed many fox squirrels within the woodlots surveyed. *Sciurus carolinensis* Gmelin (Eastern Gray Squirrel), *Tamiasciurus hudsonicus* Erxleben (Red Squirrel), and *Glaucomys volans* L. (Southern Flying Squirrel) are also found throughout Indiana, and all are known to build or occasionally inhabit leaf nests for shelter (Edwards et al. 2003, Mumford and Whitaker 1982, Yahner 2003). However, no individuals of these species were observed within the woodlots surveyed. Further, Eastern Gray Squirrels are rare in Marion County and thought to be decreasing in number in the northern half of the state (Goheen et al. 2003, Mumford and Whitaker 1982). The leaf nests of Red Squirrels tend to be smaller and more compact than those of *Sciurus* spp. (Mumford and Whitaker 1982), and Red Squirrels tend to prefer to nest in conifers (Yahner 2003), which were not present in the woodlots surveyed. Southern Flying Squirrels are almost exclusively cavity nesters (Mumford and Whitaker 1982) that are rarely found in small (<4.6 ha) isolated woodlots (Nupp and Swihart 2000). Further, I could find no accounts of Southern Flying Squirrels in Marion County, IN (Mumford and Whitaker 1982).

Analysis

All nest locations were plotted on 2004 geo-referenced aerial photographs of Marion County, IN using ArcGIS software (ESRI version 9.1). A polygon outlining the boundaries of each woodlot was created in ArcGIS and this delineation allowed me to calculate the total area of each woodlot. I also set a 10-m wide internal-edge buffer for each woodlot. Wales (1972) found that major vegetative changes caused by the edge generally extend 10 to 20 m into forests depending on exposure, and 10 m appeared to be sufficient to capture the edge vegetation for woodlots in this study (C.M. Salsbury, pers. observ.). I calculated the area of each edge-buffer and subtracted this value from the total area to determine the interior area of each woodlot. Nest densities were calculated for the total area, the edge buffer, and the interior of each woodlot. A ratio of edge buffer area to total area (hereafter the "buffer ratio") was calculated for each woodlot to serve as a measure of the relative amount of edge present for each woodlot. I also estimated the fractal dimension (FD; McGarigal and Marks 1995) of each woodlot as another estimator of woodlot shape. The FD of each woodlot was calculated as 2 times the logarithm of the woodlot perimeter (m) divided by the logarithm of the woodlot area (m^2).

I estimated the isolation of each woodlot surveyed in the suburban/urban landscape in two ways. First, I determined the distance between the woodlot of interest and the nearest woodlot ≥1.0 ha in area. I chose 1.0 ha as the minimum size, as this area was roughly equivalent to the area of the smallest woodlot surveyed in this study. I recorded the Euclidian distance (m) in most cases, unless there were barriers or unsuitable habitats, such as retaining ponds, large expanses of parking lot, or commercial buildings, across which squirrels could not move along the straight-line route. Where barriers occurred, I measured the shortest passable route between the woodlots. Second, I generated an "isolation index" for each woodlot that incorporated the suitability of the habitats surrounding each woodlot as potential fox squirrel habitat. I assigned values to habitat types ranging from 5 (impassable or unsuitable) to 1 (optimal or ideal habitats) (Table 1). I measured the

Table 1. Habitat suitability scores used in the calculation of isolation indices for 20 urban woodlots surveyed in Marion County, IN from 2003 to 2005. Scores represent the suitability of habitats adjacent to surveyed woodlots to support fox squirrel populations. The habitat scores range from 5 for unsuitable habitats to 1 for optimal habitats.

Score	Habitat type
5	Bodies of water, commercial buildings and parking lots lacking trees, major highways
4	Commercial areas with few trees, streets with >2 lanes
3	Open green areas lacking trees
2	Tree-lined streets with 2 lanes
1.5	Wooded residential areas
1	Woodlots, wooded parks

length (m) of each woodlot perimeter and calculated a weighted average habitat score using the length of the perimeter corresponding to each of the adjacent habitat types. This weighted average served as the isolation index. I calculated the average distance between nests in each woodlot using the nearest-neighbor-distance spatial analysis tool in ArcGIS Toolbox. I used the nearest-neighbor index to test whether the nests were clustered, random, or uniformly distributed within each woodlot.

I calculated coefficients of variation corrected for bias (CV; Sokal and Rohlf 1981) for woodlot size, shape as represented by buffer ratio, and degree of isolation as represented by the isolation index and distance to the nearest woodlot. The effects of woodlot size, shape, and isolation were examined using a stepwise linear regression analysis. I assigned woodlot area, buffer ratio (arcsine transformed), FD, isolation index, and nearest-woodlot distance as independent predictors of total nest density. I set conditions to enter and exit the model to $\alpha = 0.15$ and 0.20, respectively. I also compared nest density in the edge buffer to nest density in the interior for each woodlot using a paired t-test.

Fox squirrels are known to nest in tree cavities (Baumgartner 1939, Koprowski 1994) and the abundance of tree cavities within woodlots increases with woodlot age (Newton 1994). I was unable to document the abundance of tree cavities in the woodlots surveyed in this study. Thus, to rule out the possibility that leaf nest densities were lower in some woodlots due to higher tree-cavity availability, I compared the nest densities of the 7 "old" woodlots (those intact in 1941) with the nest densities of the 7 "young" woodlots (those non-existent in 1941) using a one-tailed t-test. I tested the a priori assumption that leaf nest densities would be lower in the older woodlots. I used Minitab statistical software (Release 13 for Windows) to perform all statistical analyses, and I assumed statistical significance at $\alpha = 0.05$.

Results

I located 498 leaf nests in 20 woodlots throughout Marion County, IN. Among all woodlots combined, I observed 19 trees with more than one nest; the most nests observed in one tree were 3. Of the 498 nests, only 40 (8.0%) were found in trees with at least one other nest.

Woodlot characteristics varied among the woodlots surveyed (Table 2). Of the four variables for which I calculated the coefficient of variation, distance to the nearest woodlot (CV = 112.32) displayed the most variation, followed by woodlot size (CV = 81.45), shape as represented by buffer ratio (CV = 40.98), and degree of isolation as represented by the isolation index (CV = 31.35). The greatest distance to the nearest woodlot ≥1 ha was 1135 m and the shortest distance was 10 m. The isolation index of the woodlots varied from 4.93 for the most-isolated woodlot, which was surrounded by retention ponds, commercial areas, and a six-lane highway, to 1.0 for the least-isolated woodlot, which was adjacent to another wooded area and surrounded by wooded residential areas. Most woodlots, however, were only moderately isolated, and nearly all were adjacent, in some degree, to wooded residential areas.

Nest density also varied among woodlots (Table 2); however, stepwise regression analysis indicated that woodlot area, buffer ratio, FD, distance to nearest woodlot, and isolation index did not significantly explain the variation in nest density among woodlots. Nest density was negatively related to woodlot area, and woodlot area was the only variable to enter the stepwise model; however, the model was not statistically significant (Fig. 2). Nest density was not significantly higher within the 10-m internal-edge buffer compared to the interior of each woodlot (paired t = - 0.38, df = 19, P = 0.710; Table 2). The distribution of the nests varied significantly from random in only one woodlot and, in this case, the nests were uniformly dispersed. Nest density also did not differ between "old" and "young" woodlots (one-tailed t = -1.52, d.f. = 10, P = 0.920).

Discussion

Forest fragmentation within a suburban/urban landscape in the midwestern United States does not appear to negatively affect Eastern Fox Squirrel presence or abundance as indicated by leaf-nest density. The leaf-nest density within woodlots was not influenced by woodlot size, approximate age, shape, or degree of isolation. This result agrees, in part, with observations of fox squirrel colonization patterns in forest fragments across agricultural landscapes. As in the current study, Eastern Fox Squirrel presence within forest fragments was unaffected by the distance to the nearest forest patch (Goheen et al. 2003, Nupp and Swihart 2000, Rosenblatt et al. 1999, Swihart and Nupp 1998). The well-developed dispersal ability of Eastern Fox Squirrels and their willingness to move across the landscape were suggested to explain the colonization patterns within an agricultural landscape (Mech and Zollner 2002, Swihart and Nupp 1998,

Table 2. Descriptive statistics of urban woodlot characteristics and fox squirrel leaf-nest densities. The results are for 20 woodlots surveyed in Marion County, IN from 2003 to 2005.

Factor	Mean	Range	SD
Woodlot area (ha)	5.83	0.94–19.50	4.690
Buffer area (ha)	1.27	0.53–2.90	0.771
Interior area (ha)	4.53	0.34–16.77	4.071
Buffer ratio	0.27	0.11–0.64	0.111
Fractal dimension	1.32	1.24–1.41	0.045
Isolation index	2.63	1.00–4.93	0.813
Distance to nearest woodlot ≥1 ha (m)	279.90	10.00–1135.00	310.500
Total number of nests	24.90	5.00–71.00	18.220
Number of nests in buffer	5.70	1.00–19.00	4.219
Number of nests in interior	19.20	2.00–60.00	16.340
Total nest density (per ha)	5.09	1.30–12.37	3.093
Buffer nest density (per ha)	4.83	0.49–12.00	2.889
Interior nest density (per ha)	5.15	0.63–15.11	3.759
Nearest neighbor distance among nests (m)	26.31	13.90–49.17	9.570

Zollner 2000). These factors may also explain the current findings. I did not track individual movements in the current study, but I did observe fox squirrels frequently moving from woodlots into surrounding park or residential areas. Further, I observed leaf nests in trees neighboring woodlots and occasionally observed dead fox squirrels on roadways separating woodlots from surrounding habitats. These observations, along with the lack of a relationship between leaf-nest density and woodlot isolation, suggest that fox squirrels are frequenting wooded parks and residential areas between woodlots and that these areas may serve as permanent habitats or dispersal corridors. The fact that fox squirrels were present within even the most isolated woodlots in this study, at relative densities similar to non-isolated woodlots, suggests that even restricted access to wooded residential areas is sufficient to support colonization. These findings are consistent with results from a previous study of fox squirrel movement patterns within an urban landscape (McCleery et al. 2007). Although McCleery et al. found that fox squirrels avoided paved areas, these areas, ultimately, did not restrict their movements across the landscape. Whether wooded residential habitats serve as sources or sinks (Pulliam 1988) for fox squirrel populations is unknown. Further investigation of the population dynamics of fox squirrels living in wooded residential areas is necessary to gain a complete understanding of the effects of habitat fragmentation on fox squirrels within suburban/urban landscapes.

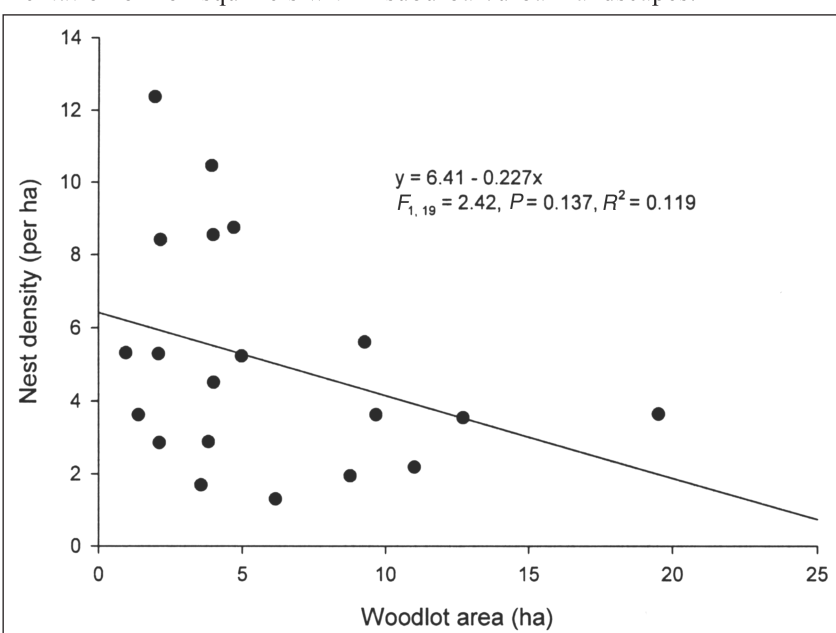

Figure 2. Relationship between woodlot area and density of leaf nests constructed by Eastern Fox Squirrels in 20 suburban/urban woodlots surveyed in Marion County, IN. Regression line and statistics depict the results of a simple linear regression.

Although not significant, the tendency for leaf-nest density to be negatively related to woodlot size is in agreement with previous findings that show a negative relationship between density and woodlot size (Koprowski 2005, but see Goheen et al. 2003). Nest densities in small woodlots were either similar to or greater than those in large woodlots in the current study (Fig. 2). This finding, along with the presence of leaf nests in all woodlots surveyed, suggests that home-range compaction may have occurred in the smaller woodlots. A positive relationship between home-range size and woodlot area has been observed for Eastern Fox Squirrels in previous studies (Baumgartner 1943, Koprowski 2005, Shepard and Swihart 1995). Further, the similar nest densities between "old" and "young" woodlots suggests that woodlot age and, in turn, tree-cavity availability have little influence on leaf-nest densities within the suburban/urban landscape.

Leaf-nest distribution within suburban/urban woodlots rarely differed from random. Salsbury et al. (2004) found that Eastern Fox Squirrels preferred to nest in trees with diameters at breast height larger than average in fragmented suburban/urban woodlots, but they showed no consistent preference for tree species. If Eastern Fox Squirrels observed in this study placed nests in trees with a larger than average diameter at breast height, the random nest distribution suggests that these large trees must have been randomly distributed or highly abundant in all but one woodlot observed. Further, leaf nests were not more likely to be located near the woodlot edge than in the woodlot interior. Previous examination of habitat use by fox squirrels inhabiting agricultural landscapes in Pennsylvania indicates that they prefer forest edges to the forest interior (Derge and Yahner 2000, Drake and Brenner 1995). Fox squirrels living within agricultural landscapes may prefer forest edges because of their close proximity to nearby agricultural fields where they occasionally feed (Korschgen 1981, Nixon and Hansen 1987). With the exception of neighboring park woods and residential areas, the matrix surrounding the suburban/urban woodlots surveyed in this study was most likely devoid of food. However, greater utilization of forest edges by fox squirrels may be better indicated by activity patterns not observed in this study rather than by leaf-nest placement.

The results of this study suggest that Eastern Fox Squirrels in the midwestern United States have adjusted well to the unique nature of the suburban/urban landscape and the current level of habitat fragmentation. Eastern Fox Squirrels appear to readily use and move through residential areas, and paved areas and major roadways seem to pose little deterrent to squirrel movement. Future research is needed, however, to determine the importance of residential areas to Eastern Fox Squirrel persistence and abundance, as squirrel presence in these areas may not be a good indicator of habitat quality (Van Horne 1983). Further, dispersers move more slowly through matrix areas devoid of quality food, shelter, and protection from predation, which in turn reduces dispersal success (Bakker and Van Vuren 2004, Zollner and Lima 2005). Thus, as matrix areas expand across suburban/urban landscapes, the persistence and abundance of Eastern Fox Squirrels may be negatively affected by fragmentation, as has been observed for other tree squirrel species (Swihart and Nupp 1998). Future studies of fox squirrel metapopulations living within suburban/urban landscapes are necessary to determine at what point fragmentation begins to negatively influence persistence and abundance.

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Literature Cited

Bakker, V.J., and D. Van Vuren. 2004. Gap-crossing decisions by the Red Squirrel, a forest-dependent small mammal. Conservation Biology 18:689–697.

Baumgartner, L.L. 1939. Fox Squirrel dens. Journal of Mammalogy 20:456–465.

Baumgartner, L.L. 1943. Fox Squirrels of Ohio. Journal of Wildlife Management 7: 193–202.

Bowers, M.A., and B. Breland. 1996. Foraging of Gray Squirrels on an urban-rural gradient: Use of the GUD to assess anthropogenic impact. Ecological Applications 6:1135–1142.

Derge, K.L., and R.H. Yahner. 2000. Ecology of sympatric Fox Squirrels (*Sciurus niger*) and Gray Squirrels (*S. carolinensis*) at forest-farmland interfaces in Pennsylvania. American Midland Naturalist 143:355–369.

Don, B.A.C. 1985. The use of drey counts to estimate Grey Squirrel populations. Journal of Zoology, London 206:282–286.

Drake, J.C., and F.J. Brenner. 1995. Comparison of habitat preferences of Gray and Fox Squirrels in Northwestern Pennsylvania. Journal of the Pennsylvania Academy of Science 69:73–76.

Edwards, J., M. Ford, and D. Guynn. 2003. Fox and Gray Squirrels (*Sciurus niger* and *S. carolinensis*). Pp. 248–267, *In* G.A. Feldhamer, B.C. Thompson, and J.A. Chapman (Eds.). Wild Mammals of North America: Biology, Management, and Conservation. The Johns Hopkins University Press, Baltimore, MD. 1216 pp.

Faeth, S.H., P.S. Warren, E. Shochat, and W.A. Marussich. 2005. Trophic dynamics in urban communities. BioScience 55:399–407.

Fitzgibbon, C.D. 1993. The distribution of Gray Squirrel dreys in farm woodland: The influence of wood area, isolation, and management. Journal of Applied Ecology 30:736–742.

Goheen, J.R., R.K. Swihart, T.M. Gehring, and M.S. Miller. 2003. Forces structuring tree squirrel communities in landscapes fragmented by agriculture: Species differences in perceptions of forest connectivity and carrying capacity. Oikos 102:95–103.

Jodice, P.G.R., and S.R. Humphrey. 1992. Activity and diet of an urban population of Big Cypress Fox Squirrels. Journal of Wildlife Management 56:685–692.

Koprowski, J.L. 1994. *Sciurus niger*. Mammalian Species 479:1–9.

Koprowski, J.L. 2005. The response of tree squirrels to fragmentation: A review and synthesis. Animal Conservation 8:369–376.

Korschgen, L.J. 1981. Foods of Fox and Gray Squirrels in Missouri. Journal of Wildlife Management 45:260–266.

McCleery, R.A., R.R. Lopez, N.J. Silvy, and S.N. Kahlick. 2007. Habitat use of fox squirrels in an urban environment. Journal of Wildlife Management 71: 1149–1157.

McComb, W.C. 1984. Managing urban forests to increase or decrease Gray Squirrel populations. Southern Journal of Applied Forestry 8:31–34.

McGarigal, K., and B.J. Marks. 1995. FRAGSTATS: Spatial pattern analysis program for quantifying landscape structure. United States Forest Service, Pacific Northwest Research Station, Portland, OR. General Technical Report PNW-GTR-351.

Mech, S.G., and P.A. Zollner. 2002. Using body size to predict perceptual range. Oikos 98:47–52.

Mumford, R.E., and J.O. Whitaker, Jr. 1982. Mammals of Indiana. Indiana University Press, Bloomington, IN. 537 pp.

Newton, I. 1994. The role of nest sites in limiting the numbers of hole-nesting birds: A review. Biological Conservation 70:265–276.

Nixon, C.M., and L.P. Hansen. 1987. Managing forests to maintain populations of gray and fox squirrels (Technical Bulletin 5). Illinois Department of Conservation.

Nupp, T.E., and R.K. Swihart. 2000. Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. Journal of Mammalogy 81: 512–526.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

Rosenblatt, D.L., E.J. Heske, S.L. Nelson, D.M. Barber, M.A. Miller, and B. MacAllister. 1999. Forest fragments in east-central Illinois: Islands or habitat patches for mammals? American Midland Naturalist 141:115–123.

Salsbury, C.M., R.W. Dolan, and E.B. Pentzer. 2004. The distribution of Fox Squirrel (*Sciurus niger*) leaf nests within forest fragments in Central Indiana. American Midland Naturalist 151:369–377.

Sexton, O.J. 1990. Replacement of Fox Squirrels by Gray Squirrels in a suburban habitat. American Midland Naturalist 124:198–205.

Sheperd, B.F., and R.K. Swihart. 1995. Spatial dynamics of Fox Squirrels (*Sciurus niger*) in fragmented landscapes. Canadian Journal of Zoology 73:2098–2105.

Shochat, E. 2004. Credit or debit? Resource input changes population dynamics of city slicker birds. Oikos 106:622–626.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry. W.H. Freeman and Company, New York, NY. 859 pp.

Steele, M.A., and J.L. Koprowski. 2001. North American Tree Squirrels. Smithsonian Institution Press, Washington, DC. 201 pp.

Swihart, R.K., and T.E. Nupp. 1998. Modeling population responses of North American tree squirrels to agriculturally induced fragmentation of forests. Pp. 1–19, *In* M.A. Steele, J.F. Merritt, and D.A. Zegers (Eds.). Ecology and Evolutionary Biology of Tree Squirrels. Special Publication 6, Virginia Museum of Natural History, Martinsville, VA. 320 pp.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

Wales, B.A. 1972. Vegetation analysis of north and south edges in a mature oak-hickory forest. Ecological Monographs 42:451–471.

Wauters, L.A., and A.A. Dhondt. 1988. The use of Red Squirrel (*Sciurus vulgaris*) dreys to estimate population density. Journal of Zoology, London 214:179–187.

Williamson, R.D. 1983. Identification of urban habitat components which affect Eastern Gray Squirrel abundance. Urban Ecology 7:345–356.

Yahner, R.H. 2003. Pine squirrels (*Tamiasciurus hudsonicus* and *T. douglasii*). Pp. 268–275, *In* G.A. Feldhamer, B.C. Thompson, and J.A. Chapman (Eds.). Wild Mammals of North America: Biology, Management, and Conservation. The Johns Hopkins University Press, Baltimore, MD. 1216 pp.

Zollner, P.A. 2000. Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. Landscape Ecology 15:523–533.

Zollner, P.A., and S.L. Lima. 2005. Behavioral tradeoffs when dispersing across a patchy landscape. Oikos 408:219–230.