Spatial dynamics of fox squirrels (*Sciurus niger*) in fragmented landscapes

B. Forrest Sheperd and Robert K. Swihart

Abstract: We examined the spatial dynamics of fox squirrels (*Sciurus niger*) occupying 12 woodland sites in a predominantly agricultural landscape of west-central Indiana. The 12 sites represented woodlands of varying degrees of isolation and size. Forty-nine adult fox squirrels were fitted with radio collars and monitored from May 1993 through September 1994. No movements of collared adults were observed between wooded sites during the study, although squirrels traveled 200–500 m from woodlots along hedgerows, and 2.6% of observations occurred in agricultural fields. Multiple regression revealed a positive linear relationship between home-range size and woodland size, with larger home ranges in the growing season. Home-range size was not related to woodland isolation, squirrel density, or sex. We found no evidence of spatial interactions between pairs of squirrels (i.e., male–male, male–female, female–female) at resolutions of 20, 40, or 100 m. Excursions beyond a core area were of relatively greater magnitude for squirrels occupying continuous forest. Agriculturally induced fragmentation of forests appears to restrict movements of adult fox squirrels, despite the well-documented ability of the species to persist in such a landscape.

Résumé : Nous avons étudié la dynamique spatiale de l’Écureuil fauve (*Sciurus niger*) dans 12 boisés situés dans une zone surtout agricole du centre ouest de l’Indiana. Les 12 boisés variaient par leur taille et leur degré d’isolation. Quarante-neuf écureuils ont été munis de colliers émetteurs et suivis de mai 1993 à septembre 1994. Aucun déplacement d’un boisé à un autre n’a été enregistré au cours de l’étude et pourtant les écureuils se déplaçaient beaucoup puisqu’ils ont enregistré des trajets de 200–500 m. Les excursions au-delà d’une zone centrale étaient d’amplitude relativement plus grande chez les écureuils habitant des forêts continues. La fragmentation des zones boisées par le développement de terres agricoles semble restreindre les déplacements des écureuils adultes, même si l’espèce est reconnue pour sa capacité de survivre dans un tel milieu.

[Traduit par la Rédaction]

Introduction

Agriculturally induced fragmentation of forests has dramatically altered the landscape of the midwestern United States. Clearing of land for agriculture has permanently removed extensive tracts of forest, yielding landscapes characterized by predominantly small isolated woodlots, a series of interconnecting hedgerows, and large unbroken riparian woodland systems embedded within a matrix of cropland. For example, nearly 80% of the original forested area of Illinois was lost between 1820 and 1980 (Iverson 1988).

Species vary in their sensitivities to fragmentation. Area-sensitive species whose home ranges may be larger than available habitat (Wilson and Willis 1975; Noss 1983; Meffe and Carroll 1994), or species reliant upon forest interiors, are often adversely affected by reductions in forest area (Ambuel and Temple 1983; Temple and Cary 1988; Lord and Norton 1990; Blake 1991; Meffe and Carroll 1994). Additionally, the relative amount of edge habitat increases as forest area declines. Increased edge can lead to environmental alterations in forests (Saunders et al. 1991) and can reduce nest success for some species of birds through increased nest parasitism and increased predation (Temple and Cary 1988). As isolation of forested sites increases, dispersal ability also may be hindered. For some rodents and birds, travel corridors between wooded sites may become important avenues of dispersal (Wegner and Merriam 1979; Middleton and Merriam 1981; Henderson et al. 1985).

Presumably, species with broad habitat tolerances, good mobility, and adaptations to large edge areas are well adapted to landscapes dominated by agriculture (Saunders et al. 1991; Meffe and Carroll 1994). The fox squirrel (*Sciurus niger*) seems to fit this characterization. Fox squirrels frequent woodlots of intermediate size with abundant edge...
(Mumford and Whitaker 1982; Nixon and Hansen 1987). Allen (1943) and Nixon et al. (1978) concluded that excellent habitat was created for fox squirrels as virgin forest was removed for agriculture. Although principally reliant upon naturally occurring mast for winter food, fox squirrels also use agricultural crops as a winter food source (Baumgartner 1943; Nixon and Hansen 1987).

We examined the effects of agriculturally induced forest fragmentation on the spatial dynamics of the fox squirrel. Although available evidence suggests that fragmentation should not negatively impact fox squirrels, previous research has not examined the spatial aspects of fox squirrel ecology from a landscape perspective. In addition, previous research on spatial dynamics of fox squirrels has been restricted to one or two study sites (Hawera and Nixon 1978; Benson 1980; Hansen and Nixon 1985; Koprowski 1991), has been limited in terms of numbers of observations per animal because of constraints imposed by trapping and field observations, or has dealt with a small number of squirrels (Adams 1973, 1976; Benson 1980; Armitage and Harris 1982). Moreover, analysis of spatial interactions has focused principally on interspecific interactions of fox squirrels and gray squirrels (Sciurus carolinensis); we are unaware of any studies examining intraspecific changes in spatial interactions associated with fragmentation in an agricultural landscape. We used radiotelemetry to test whether inter-woodlot movements, home-range sizes, or intensity of spatial interactions of fox squirrels were related to attributes of wooded sites within an agricultural landscape. Specifically, we determined whether these factors were related to woodland size and degree of isolation, after accounting for possible effects due to sex, season, and an index of squirrel density.

**Study area**

We conducted our study from December 1992 to September 1994 in Tippecanoe and Warren counties in west-central Indiana, U.S.A. Forested sites were chosen in and adjacent to the watersheds of Indian Creek and Little Pine Creek. An additional site approximately 14 km south of these watersheds but representing a comparable landscape was chosen in 1994. Based on 1986 Thematic Mapper data, the landscape within the study area was primarily agricultural (82%), planted principally to corn and soybeans, with some winter wheat. Forest comprised 16% of the area. Of the forested land 11% occurred in a continuous riparian zone, whereas the remaining 89% occurred primarily as scattered woodlots. The forested area was dominated by an oak (Quercus spp.), hickory (Carya spp.), and black walnut (Juglans nigra) overstory, with maple (Acer spp.), hackberry (Celtis occidentalis), black cherry (Prunus serotina), and sycamore (Platanus occidentalis) also present in the canopy and subcanopy. Brushy hedgerows traversed portions of the landscape and connected some of the woodlots.

We selected 12 wooded sites for study. Wooded tracts were chosen to span a range of sizes and degrees of isolation (Fig. 1). Ten of the sites were woodlots, ranging in size from 0.8 to 32.2 ha. The remaining two sites occurred within a 842-ha continuous forest on the north bank of the Wabash River and were separated by a distance (5.7 km) sufficient to restrict squirrel movement between the sites. These two sites represented two different topological conditions. One site was within the floodplain of the Wabash River and exhibited considerable topographical relief. The second site was an upland area with a sparser understory. Wooded sites were generally similar in successional stage, although two of the woodlots exhibited canopies that were substantially more open than the other sites.

**Methods**

**Capturing squirrels**

Trapping was conducted at irregular intervals throughout the study. We captured fox squirrels using Tomahawk live traps (15 × 15 × 60 cm) baited with corn, English walnuts, or a mixture of sunflower, oats, and peanut butter. Traps were positioned at the bases of trees containing leaf nests and cavities to maximize capture success. Upon capture we recorded the sex, mass, reproductive condition, and capture locations of squirrels. The ears of squirrels also were fitted with numbered fingerling tags.

**Radiotelemetry**

Selected adult squirrels from each wooded site were equipped with radio collars (Wildlife Materials, Carbondale, Illinois, U.S.A.). We obtained bearings on squirrels from stations scattered throughout a site that were mapped with respect to a reference location obtained via a global positioning system. At one forested site, topographic relief required that five reference locations be used. Each squirrel was located 2–5 times weekly during the period over which it was monitored, and we varied the time of day that readings were taken. The number of readings taken per squirrel varied because squirrels were followed for varying periods of time and because we did not attempt to locate all squirrels on a given day. We selected stations from which readings were taken such that vectors crossed at approximately 90° angles, subject to the constraint that the stations selected did not disrupt the squirrel’s behavior. Thirty percent of the paired readings were obtained simultaneously using two observers, whereas the remaining readings were obtained by a single observer, with readings at a pair of stations separated by <5 min. Angular error resulted in a mean error polygon of 162 m² for readings taken at a distance of 60 m from a target transmitter. If we failed to locate a squirrel, the farmland and woods within a 2- to 3-km radius of the site were searched systematically by truck while using an elevated antenna. We also made regular checks for missing squirrels at greater distances. Properly functioning transmitters had a range of >0.5 km; thus, if we failed to locate a squirrel after an expanded search, we concluded that the transmitter was functioning improperly.

**Analysis of home-range size**

We used area-observation plots (Odum and Kuenzler 1955) to identify squirrels with readings adequate to describe the full home range. Home range area was calculated using the minimum convex polygon estimator for 3, 3 + k, 3 + 2k, \ldots, n, where n is the number of observations for a squirrel and k was chosen such that the total number of areas calculated for an individual animal averaged 10 (range 6–17). Home-range size was then regressed against sample size, and a significant asymptotic component was necessary for inclu-
Fig. 1. Pixel-based map of the study area in west-central Indiana, depicting woodlot (W) and continuous forest (F) sites at which fox squirrels were studied using radiotelemetry. One of the woodlots used in the study was located 14 km to the south and is not shown.

Quantifying spatial interaction between squirrels

We used the methods of Doncaster (1990) to test for interactions between neighboring pairs of squirrels. Preliminary to this analysis, kernel 100% isopleths were used to calculate the percentage of overlap between each pair of squirrels. Any pair that showed less than 5% overlap was omitted from analysis of interactions.

Static interaction is the degree of overlap between two home ranges and congruence in at least part of their corresponding utilization distributions; that is, static interaction is a measure of the correlation in frequency of use of an area by 2 animals with overlapping home ranges (Doncaster 1990). We assessed static interaction by calculating Spearman's coefficient of rank correlation, r, of the frequency of use of 20 × 20 m grid cells visited by 1 or both squirrels in a pair. Values of r can range from −1 to +1. Increasingly negative values represent an increasingly stronger component of repulsion in home-range use, whereas increasingly positive values represent an increasingly greater component of attraction. Doncaster (1990) demonstrated theoretically that r could vary over a wide range for a given level of home-range overlap. In our study, though, r covaried positively and significantly (p < 0.05) with home-range overlap; thus, we regressed r against percent overlap in grid-cell use and used the resulting residuals as our measure of static interaction. These residuals were used in regression models to examine
static interaction as it was affected by a wooded site’s characteristics (area, isolation), season, and squirrel pair type (male–male, male–female, female–female).

Dynamic interaction occurs when 1 animal’s position within its home range is dependent upon the movements of another. Under conditions of avoidance, simultaneous positions of a pair are likely to be farther apart than non-simultaneous positions. Conversely, conspecific attraction would lead to shorter distances between simultaneous observations than between simultaneous observations (Doncaster 1990). Dynamic interaction was also examined using a nonparametric approach. We calculated distances between pairs of animals sampled simultaneously (<15 min apart). The frequency distribution of these observed distances (n) was then compared with the frequency distribution of distances expected under the null hypothesis that movements by pair members occurred without regard to the location of the other squirrel. This null distribution was generated using all n² distances for a pair of squirrels. A binomial test was used to determine whether the frequency of observations less than or equal to a specified distance differed from the frequency expected if no interaction occurred. Because of the arbitrary nature of specifying a critical distance, we chose to conduct the test at distances of ≤20, ≤40, and ≤100 m. As a test of whether the frequency distributions of observed distances differed from the null distribution, we also conducted a two-sample Kolmogorov–Smirnov test (Conover 1980).

Explanatory variables

Woodlot area
The area of wooded sites was calculated for nine woodlots from a digitized 2.54 cm = 201 m outline traced from United States Soil Conservation Service (SCS) 1986 National High Altitude Program aerial photographs and converted to raster (pixel) data at 1 m resolution. Thematic Mapper data were used in Geographic Resources Analysis Support System (GRASS, version 4.1, 1993, developed by the U.S. Army Construction Engineering Research Laboratory) for two continuous forest sites and one large woodlot (1 ha resolution).

Isolation of wooded sites
Previous measures of isolation either were sensitive to the size of the focal patch (Gustafson and Parker 1992) or did not permit comparison among landscapes (Swihart and Nupp 1996). For a focal patch in a landscape consisting of k forested patches, we defined an index of isolation as

\[ I = \sum_{i=1}^{k} (d_i a_i / (A - a_i))/P \]

where \( d_i \) is the mean distance from focal patch \( j \) to patch \( i \), \( a_i \) and \( a_j \) represent the areas of patch \( i \), and \( j \), respectively, \( A \) denotes the total forested area, and \( P \) is the proportion of the landscape that is forested, independent of the focal patch. For nine woodlot study sites, we defined the landscapes as 9 × 9 km areas centered on an individual study site. Values used in the equation were derived from a grid of 1-ha cells overlaid on SCS 1986 aerial photographs. Cells containing only hedgerows were each assigned weights of 0.1 ha. For the remaining three sites, an area of 25 km² was centered on the area in which squirrels were radio-tracked. The larger landscape was used because of the extent of the forested area of these three sites. I thus becomes an index that is independent of the area of the local study site (focal patch). Larger I values can result from either greater mean distances to patches in a landscape, smaller sizes of adjacent patches, or proportionately smaller amounts of forested habitat in a landscape. Values of log₁₀(I) for our woodlands ranged from 3.66 to 5.43 (\( \bar{X} = 4.31 \)).

Index of squirrel density
Our trapping effort was sporadic and designed with the principal intent of capturing squirrels for telemetry. Thus, traditional mark–release–recapture estimation of abundance (Seber 1973; Otis et al. 1978) was not possible. To obtain an index of relative abundance, we used information compiled from three sources. Based on trapping results, we calculated captures per 100 trap-days (CAP) for each study site. These data were supplemented with modified time–area counts (CNT) at feeding stations. From January to March 1994, feeding platforms (24 × 60 cm) were erected, baited with corn, and placed within a study site at densities of approximately one per 1.5 ha. At each site, a count was made of squirrels using platforms during a 5- to 10-min period each afternoon for 3–4 consecutive days. Finally, the abundance of leaf nests (LN) was determined for each site during February and March 1994 by walking parallel transects separated by 15 m.

These three indexes were significantly correlated with each other (\( p < 0.05 \) for all pairs), with correlation coefficients of 0.59 for CNT and LN, 0.94 for CNT and CAP, and 0.64 for LN and CAP. Because of these correlations, we conducted a principal component analysis to collapse our three univariate indexes into a single index of density expressed as a linear combination of the original variables. The first principal component (PC1) of the three indexes represented 82% of the variation in the original variables, and each variable contributed similarly (dominant eigenvector for (CNT, LN, CAP) = \((-0.6, -0.5, -0.6)\)). Thus, PC1 is a general index of squirrel density (cf. Swihart 1992), greater values being indicative of lower relative density.

Season
We defined growing and nongrowing seasons as commencing on 1 May and 1 October, respectively. These seasons coincided reasonably well with the planting and harvesting of crops as well as the budding and mast-fall regime of our study area.

Regression analysis
Measures of home-range size and static interaction were regressed against the five explanatory variables (woodland area, index of woodland isolation, index of squirrel density, sex, and season). Area and isolation were subjected to log₁₀ transformations before multiple regressions were conducted. No significant correlation occurred between independent variables (\( p > 0.05 \)).

Results
Home-range analysis
We caught 144 fox squirrels during 2105 trap-days. Sixty-eight of those were fitted with radio collars and 49 adults
Table 1. Results of multiple regressions relating woodland characteristics to various measures of home-range size of adult fox squirrels.

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Area(a)</th>
<th>Isolation(a)</th>
<th>Season</th>
<th>Sex</th>
<th>Density</th>
<th>(R^2)</th>
<th>(p)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>All woodlands</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MCP 100%</td>
<td>4.68***</td>
<td>-1.36</td>
<td>-3.59***</td>
<td>-0.22</td>
<td>0.37</td>
<td>0.42</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>MCP 50%</td>
<td>2.01**</td>
<td>-0.49</td>
<td>-3.43**</td>
<td>0.08</td>
<td>0.53</td>
<td>0.23</td>
<td>0.003</td>
</tr>
<tr>
<td>Kernel 100%</td>
<td>4.57***</td>
<td>-0.63</td>
<td>-3.71***</td>
<td>0.00</td>
<td>0.45</td>
<td>0.45</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Kernel 50%</td>
<td>2.73**</td>
<td>-0.42</td>
<td>-2.96**</td>
<td>-0.20</td>
<td>0.48</td>
<td>0.24</td>
<td>0.002</td>
</tr>
<tr>
<td><strong>Woodlots only</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MCP 100%</td>
<td>4.20***</td>
<td>-1.20</td>
<td>3.90***</td>
<td>-2.45</td>
<td>0.24</td>
<td>0.50</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>MCP 50%</td>
<td>3.33**</td>
<td>0.74</td>
<td>-3.77***</td>
<td>-0.76</td>
<td>0.01</td>
<td>0.44</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Kernel 100%</td>
<td>4.06***</td>
<td>-0.36</td>
<td>-3.39**</td>
<td>-1.34</td>
<td>0.19</td>
<td>0.45</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Kernel 50%</td>
<td>3.91***</td>
<td>0.16</td>
<td>-2.94**</td>
<td>-1.70</td>
<td>0.15</td>
<td>0.44</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td><strong>Percent change</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MCP, all woodlands</td>
<td>2.82**</td>
<td>-1.02</td>
<td>-0.11</td>
<td>-1.09</td>
<td>-0.15</td>
<td>0.07</td>
<td>0.14</td>
</tr>
<tr>
<td>MCP, woodlots only</td>
<td>-0.77</td>
<td>-0.65</td>
<td>1.11</td>
<td>-0.53</td>
<td>0.41</td>
<td>0.06</td>
<td>0.72</td>
</tr>
<tr>
<td>Kernel, all woodlands</td>
<td>3.90***</td>
<td>-0.96</td>
<td>-0.07</td>
<td>0.21</td>
<td>0.22</td>
<td>0.22</td>
<td>0.003</td>
</tr>
<tr>
<td>Kernel, woodlots only</td>
<td>0.73</td>
<td>-0.69</td>
<td>-1.00</td>
<td>0.56</td>
<td>0.40</td>
<td>0.07</td>
<td>0.60</td>
</tr>
<tr>
<td><strong>Maximum distance</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All woodlands</td>
<td>3.58***</td>
<td>-1.07</td>
<td>-2.44*</td>
<td>0.13</td>
<td>0.87</td>
<td>0.30</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Woodlots only</td>
<td>1.89*</td>
<td>-0.69</td>
<td>-2.15*</td>
<td>-1.29</td>
<td>0.98</td>
<td>0.18</td>
<td>0.04</td>
</tr>
</tbody>
</table>

Note: Values in columns are \(t\) values; *, \(p < 0.05\); **, \(p < 0.01\); ***, \(p < 0.001\). The adjusted coefficients of multiple determination (\(R^2\)) and overall significance levels for regressions are also given.

\(a\) Subjected to \(\log_{10}\) transformation.

(26 male, 23 female) had at least seven telemetry readings taken (a maximum of 56 in an individual season; \(\bar{x} = 36\)). Of the 19 squirrels with <7 readings, we were able to document that 7 were fitted with collars that failed to function properly and 4 others died. We recovered five additional collars that were shed by squirrels during the first 3 months of the study. Recovered transmitters typically had been gnawed, and this was especially true of collars worn by lactating females. We could not account for the fate of the remaining squirrels in the group with <7 readings, but we suspect that they either shed their collars or disabled them by gnawing.

A total of 1111 telemetry readings were used in analysis. Of the 49 squirrels, 8 (4 males, 4 females) were removed from home-range analysis because they either had <10 usable readings or failed to exhibit an asymptotic component to their home range for any given season. Data were collected on 1 squirrel for all three definable tracking seasons, and 9 squirrels yielded usable readings in two distinct seasons. We observed no movement between woodlots during the course of the study.

Mean (±1 SE) 100% MCP home ranges for males (2.95 ± 0.04 ha) and females (3.74 ± 1.04 ha) were not significantly different (\(t = 0.88, 52 df, p = 0.38\)). Females exhibited a larger range of home-range sizes (0.38–14.1 ha) than did males (0.26–7.36). The kernel estimator of home-range size produced larger estimates of home-range area at both the 100% (total) and 50% (core) levels than did the MCP estimator. The MCP and kernel estimators were significantly (\(p < 0.0001\)) and positively correlated with each other at both the 100% (\(r = 0.918\)) and 50% (\(r = 0.952\)) levels.

Home-range size was related significantly to season and forested area, but there was no significant relationship for woodland isolation, sex, or squirrel density. Squirrels displayed larger home ranges in larger wooded sites, and home ranges were larger in the growing season than in the nongrowing season (Table 1). A comparable analysis for woodlots only indicated a significant correlation between home-range size and woodlot size (\(p < 0.05\); Table 1). These relationships were consistent for both the MCP and the kernel estimators of home range at the total and core levels.

The percent change (\((\text{total} – \text{core/core}) \times 100\)) in home-range size between the core and total home-range estimates was positively correlated (\(p < 0.05\)) with woodland size, although \(R^2\) values were low (0.07 and 0.22) (Table 1). The percent change between core and total home-range size versus woodlot size was not significant (\(p > 0.05\); Table 1). There was a positive linear relationship between woodland size and the reading farthest from the arithmetic center of a given home range (\(p < 0.05\); Table 1). In addition, distances were greater during the growing season (\(p < 0.05\)).

**Interaction analysis**

Seventy-two pairs of squirrels were used for interaction analysis. There were 20 male–male pairs, 36 male–female pairs, and 16 female–female pairs. The binomial test for dynamic interaction (after Doncaster 1990) at critical distances of 20 and 100 m was not significant. Seventy-one of the 72 pairs at a critical distance of 40 m likewise produced no significant interactions. A Kolmogorov–Smirnov test between the observed cumulative distance curve and the expected cumulative distance curve was not significant for any of the 72 pairs. There was a significant relationship between the measure of static interaction, Spearman’s \(r\), and
woodland size \( (r = -0.6, 5 \text{ df, } p < 0.001) \). However, after correcting for differences due to overlap, no significant relationship remained \( (p = 0.887) \).

**Discussion**

**Long-range movements from and between woodlots**

We observed no inter-woodlot movement of adult fox squirrels monitored in our study. We cannot rule out large-scale movements by 3 squirrels whose fates were unknown, but the intensity of our monitoring and searching programs led us to conclude that such movements were unlikely to have occurred. Although adult squirrels are capable of moving > 1 km on occasion (Baumgartner 1943; Adams 1976), most dispersal involves juveniles and subadults (Nixon et al. 1974, 1986; Delong 1986). Adams (1976) found that subadults exhibited the largest home ranges, and he attributed this to investigative behavior, possibly in preparation for dispersal. Nonetheless, he noted that most dispersal was within a woodlot.

Despite a lack of observed inter-woodlot movements, our data also indicate the potential for long-range movement of fox squirrels. For example, 1 male (No. 850) traveled > 500 m through a system of hedgerows to retrieve cached walnuts from a soybean field (Shepherd 1994). Another male (No. 815) consistently traveled 200 m down a hedgerow to use corn and soybean fields. One of our woodlot study sites was surrounded by agricultural fields, the nearest tree being approximately 800 m away. During the fall of 1993 an adult female colonized the site. Before April 1994 at least 2 males also colonized the site. The female had disappeared by June 1994, but not before she had, presumably, weaned at least 2 offspring that we captured as juveniles in August 1994. Additionally, it was not unusual to find fox squirrels using roadside ditches hundreds of metres from any woodlots, nor to find squirrels using agricultural fields for retrieval of crop residue or caching of mast.

**Home range**

Home-range size did not vary with population density, degree of woodland isolation, or the sex of the squirrels. Mean home-range size was 3.3 ha (MCP; SD = 3.2 ha) for both seasons and all study sites, which was well within the range of values reported from previous studies. McCloskey (1975) reported average home-range sizes of 2.7 ha for male fox squirrels and 2.4 ha for females. Benson (1980) reported mean home-range sizes of 1.5 ha for males and 0.8 ha for females. Adams (1976) reported average home-range sizes of 7.6 ha for males and 3.6 ha for females.

Home ranges were significantly smaller in the non-growing season than in the growing season. Constriction of the home range may be a function of energy conservation when ambient temperatures are low, a strategy adopted by many mammalian species (e.g., Slade and Swihart 1983). For instance, gray squirrels move less when temperatures are low and wind speed is high (Doebel and McGinnies 1974). Increased reliance on stored food also may result in smaller home ranges during winter, as more scatter-hoarded nuts are placed near the core of a home range (see Stapanian and Smith 1978).

On average, home-range size increased with increases in woodland area (Table 1). Baumgartner (1943) suggested a connection between woodland size and home-range size but offered no empirical evidence. Adams (1973) noted a possible relationship between woodland size and home-range size for the four woodlots in his study. We suggest that interspecific competition for existing food resources may produce the observed variation in home-range size. Competition with other granivorous species in larger woodlands may require fox squirrels to travel more extensively, and on a regular basis, to fulfill their energetic requirements. Larger forested tracts contain more species of granivorous rodents, and species such as the gray squirrel and southern flying squirrel (Glaucomys volans) are found only in large woodlots and continuous forests of our study area (Nupp and Swihart 1993). The presence of these species may reduce resource density below levels found in smaller woodlots, where these species are absent. In addition, small woodlots invariably abut ≥ 1 agricultural field, and fox squirrels occupying these woodlots commonly use the residual crops as food (Baumgartner 1943; Shepherd 1994). In fact, Yeager (1959) noted that grains made up a significant portion of the fox squirrel’s diet in marginal habitat where no hard mast was available. Agricultural crops such as corn and soybeans provide a reliable supplemental food to buffer variation in mast crops for fox squirrels in woodlots, yet crops are less readily available to fox squirrels in continuous forest habitats.

In addition to differences in quality of woodlots and forest sites, fox squirrels in larger wooded areas may have larger home ranges because the risks associated with more extensive movements are reduced. Adams (1976) suggested that fox squirrels moving extensively over large open areas may suffer increased risks of predation, and Stapanian and Smith (1978, 1984, 1986) concluded that a foraging squirrel will restrict its movements to minimize the risk of predation when cover is lacking. The availability of wooded cover may allow individuals to explore and use greater portions of contiguous habitat in larger wooded sites, as indicated by the regressions for the percent change in core and total home-range area and by the regressions for maximum radial distance moved from the arithmetic center (Table 1). Fox squirrels hardly viewed the agricultural matrix as an impermeable barrier to movement. We commonly observed squirrels outside of woodlots caching mast or foraging on waste grain, and 2.6% of all telemetry readings were outside of the woodland canopy. However, these behaviors were limited to ≤ 60 m from a woodlot edge. All extensive movements of our collared woodland squirrels involved travel along hedgerows.

Fragmentation affects many different species, at many different spatial scales, and in many different life stages. Although the fox squirrel is presumably well adapted to fragmented landscapes, we found that movements in fragmented areas were restricted relative to those in unfragmented areas, at least for adults. We suggest that in our study area, exploration for resources by adults is more limited in woodlots. In addition, breeding opportunities for males, and mate choices by females, may be limited for squirrels occupying woodlots in fragmented landscapes (Sheperd 1994). Finally, extinction of local fox squirrel populations in woodlots is likely, and may be caused by chance demographic events, mast crop failures, or hunting. Similar dynamics were noted for other mammalian species occupying fragmented landscapes (Smith 1974; Nixon et al. 1991).
Acknowledgments

We thank H.P. Weeks, Jr., G.R. Parker, and two anonymous reviewers for their comments and assistance during the preparation of this manuscript. We also thank S. Hollingshead, T. Tholen, D. Sillings, and T. Nupp for aid in data collection. We gratefully acknowledge the National Rifle Association for financial support (Grand-in-Aid 93-21). This is manuscript No. 14528 of the Purdue University Agricultural Research Programs.

References


