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LANDSCAPE-LEVEL CORRELATES OF SMALL-MAMMAL ASSEMBLAGES IN FOREST FRAGMENTS OF FARMLAND

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We studied effects of forest fragmentation on 15 species of small mammals, including 6 species of forest-dwelling granivorous rodents, in the Indian Pine watershed of west-central Indiana. Presence–absence and population densities of small mammals were assessed in spring in 35 woodlots of various sizes (0.1–150 ha) and 2 continuous forest sites (>1,000 ha) using live traps in 1992–1996. Presence–absence and population density were related to landscape attributes using logistic and multiple linear regression models, respectively. Species richness of forest-dwelling small mammals increased with area and was highest in continuous forest sites. Nested subsets of the full complement of species were found in smaller woodlots. White-footed mice (Peromyscus leucopus) were ubiquitous, and eastern chipmunks (Tamias striatus) were nearly ubiquitous across the landscape; densities of both species were related inversely to forested area. Fox squirrels (Sciurus niger) were found at 84% of study sites, and they did not respond negatively to isolation of forest patches. Red squirrels (Tamiasciurus hudsonicus) were unevenly distributed across the landscape and were found most often in woodlots with large core areas and simple shapes, possibly indicating sensitivity to edge. Southern flying squirrels (Glaucymys volans) and gray squirrels (S. carolinensis) were restricted to continuous forest sites and >4.6-ha woodlots adjacent to other wooded habitat. Species of small mammals differ appreciably in their sensitivities to agriculturally induced fragmentation of forests. Interspecific differences within this assemblage were not due solely, or even primarily, to body size. Rather, differential responses of species to fragmentation likely resulted from variation in habitat breadth and ability to move through an agricultural matrix.

Key words: agriculture, forest, fragmentation, Glaucymys volans, Indiana, Peromyscus leucopus, Sciurus carolinensis, Sciurus niger, Tamias striatus, Tamiasciurus hudsonicus

As human-dominated landscapes become more prevalent, an understanding of the effects of habitat fragmentation on communities and populations of organisms takes on increasing importance for conservation and management of biotas (Collinge 1996). Concerns over effects of human-induced fragmentation of native habitats often focus on effects of fragmentation on structure and function of native communities and species most sensitive to fragmentation. Many studies have focused on the relationship between habitat (or island) area and number of species (Brown 1971; MacArthur and Wilson 1967; Ronesnweig 1995), and some have focused on effects of fragmentation on individual species (Beier 1993; Collins and Barrett 1997; Lindenmayer and Possingham 1996; Pulliam et al. 1992). However, fewer studies have examined effects of fragmentation on an assemblage of potentially competing species whose members may be influenced differentially by fragmentation (Dunstan and Fox 1996; Lima et al. 1996).

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We report on effects of agriculturally induced fragmentation of forest habitat on 6 species of granivorous rodents occurring syntopically in Indiana’s forests: white-footed mice (Peromyscus leucopus), southern flying squirrels (Glaucomys volans), eastern chipmunks (Tamias striatus), red squirrels (Tamiasciurus hudsonicus), gray squirrels (Sciurus carolinensis), and fox squirrels (S. niger). These species vary widely in size and natural history (Table 1), but all are largely dependent on hard mast as winter food.

The landscape of the midwestern United States has been altered drastically by humans, largely due to conversion of native habitats to row-crop agriculture (Andersen et al. 1996; Iverson 1988). For example, during the past 150 years Indiana’s forests have been reduced to 22% of their original area (Hartman 1994; Miller 1993). Remaining forest patches vary widely in size and degree of isolation from other patches (Spetich et al. 1997). Such extensive fragmentation and combined effects of patch size and isolation likely have caused changes in the local biota beyond what would be expected from habitat loss alone (Andrén 1994).

Main effects of habitat fragmentation are thought to be exerted on species principally in terms of their sensitivities to changes in habitat area, isolation of habitat patches, and proportion of edge habitat. We examined effects of landscape fragmentation on an assemblage of small mammals, focusing primarily on the 6 species of granivorous rodents listed above. Based on their ecological characteristics, we predicted the following main effects of fragmentation. Area requirements and local density scale allometrically in mammals (Damuth 1981; Harstad and Bunnell 1979; Swihart et al. 1988); thus, we hypothesized that sensitivity to forest patch area should vary inversely with body size for these 6 species, such that the greatest sensitivity should be demonstrated by fox squirrels and the least sensitivity by white-footed mice (Table 1). Vigilance and body size also can be related positively, and isolation of forest patches should exert its greatest impact on species that, by virtue of their small size or intolerance of the agricultural matrix, experience difficulty dispersing among isolated habitat fragments. Species that are less likely to be affected by isolation, or may even derive benefits from it, include those with affinities for savannalike habitats or possibly those that benefit from absence of isolation-sensitive competitors. Thus, we predicted that the gliding locomotion of southern flying squirrels would hamper their movements through an agricultural matrix and thereby increase their sensitivity to isolation of patches. Conversely, we predicted that the subspecies of fox squirrel (S. n. rufiventris), which is adapted to life in oak savanna (Koprowski 1994a; Nixon et al. 1978; Sheperd and Swihart 1995), and white-footed mice, which appear to respond to competitive release (Nupp and Swihart 1996, 1998), should show little sensitivity or even be associated positively isolation of forest patches. We also assumed that habitat and dietary generalists would be affected less adversely by shifts in amount and type of edge habitat created by agriculture, especially those with affinities for edge habitats or contact with agricultural crops. Thus, we predicted that fox squirrels, white-footed mice, and red squirrels would be least affected by increases in edge habitat.

As a complement to analyses of individual species, we also examined the manner in which species composition varied among forest patches in an agricultural landscape. Smaller, more isolated patches of habitat usually contain fewer species than do larger, less isolated patches because of increased extinction rates or decreased colonization rates (MacArthur and Wilson 1967; Rosenzweig 1995). Species-specific population responses to fragmentation can lead to extinction or colonization rates that vary predictably among species. Consequently, small or isolated patches may contain a nested subset of the biota found on larger

<table>
<thead>
<tr>
<th>Trait</th>
<th>White-footed mouse</th>
<th>Eastern chipmunk</th>
<th>Southern flying</th>
<th>Tree squirrels</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Red</td>
</tr>
<tr>
<td>Body size (g)</td>
<td>21</td>
<td>110</td>
<td>65</td>
<td>200</td>
</tr>
<tr>
<td>Home range (ha)</td>
<td>0.1</td>
<td>0.2</td>
<td>0.4–16</td>
<td>1.4</td>
</tr>
<tr>
<td>Food habits*</td>
<td>S &gt; I &gt; V</td>
<td>S &gt; I, F</td>
<td>S, I</td>
<td>S &gt; I, F</td>
</tr>
<tr>
<td>Habitat preference</td>
<td>Woods</td>
<td>Woods, brush</td>
<td>Woods</td>
<td>Woods</td>
</tr>
<tr>
<td>Habitat breadth</td>
<td>Broad</td>
<td>Medium</td>
<td>Narrow</td>
<td>Medium broad</td>
</tr>
<tr>
<td>Hoarding strategy*</td>
<td>L</td>
<td>L &gt; S</td>
<td>L, S</td>
<td>L, S</td>
</tr>
<tr>
<td>Activity period*</td>
<td>N</td>
<td>D, H</td>
<td>N</td>
<td>D</td>
</tr>
<tr>
<td>Nest sites*</td>
<td>A, G, U</td>
<td>U</td>
<td>A&lt;sub&gt;TC&lt;/sub&gt;</td>
<td>A&lt;sub&gt;LN&lt;/sub&gt; &gt; A&lt;sub&gt;TC&lt;/sub&gt; &gt; U</td>
</tr>
</tbody>
</table>

* S = seeds; I = invertebrates; V = vegetation; F = fungus.
* Fox squirrels also feed upon corn and soybeans.
* L = larder hoard (single food cache); S = scatter hoard (multiple food caches).
* N = nocturnal; D = diurnal; H = hibernator.
* A = arboreal; A<sub>TC</sub> = tree cavity; A<sub>LN</sub> = leaf nest; G = ground; U = underground.
or less isolated patches (Atmar and Patterson 1993; Patterson and Atmar 1986). Patterson and Atmar (1986) introduced the "nested-subset hypothesis" to explain patterns of species assemblages that they observed in the distribution of small mammals on remnants of high-elevation forests in the southern Rocky Mountains. They found that large "islands" of mountaintop habitat contained more species than small islands and, moreover, that the small islands contained specific nonrandom subsets (nested subsets) of the species found on large islands. The term "nestedness" describes the degree to which a suite of biotas approximates nested subsets. Thus, a measure of nestedness quantifies the extent to which species extinction or colonization processes have structured species assemblages among islands of habitat (cf. Cutler 1994). We tested whether assemblages of small mammals occupying forest patches in farmland exhibit significant levels of nestedness. Such analyses are important 1st steps in predicting species-specific population responses to agriculturally induced fragmentation of midwestern landscapes. They also provide the basis for devising management strategies to ameliorate negative effects of habitat fragmentation.

**Materials and Methods**

Our study was conducted on the Indian Pine Natural Resources Area in west-central Indiana. That 259-km² area encompasses 2 major watersheds in Tippecanoe and Warren counties; 82% of the landscape was subjected to cultivation, principally for production of corn and soybeans. Within the agricultural landscape, woodlands comprised 16% of the area and consisted of small, more or less isolated, farmland woodlots and larger wooded riparian strips (Sheperd and Swihart 1995). Thirty-five woodlots (0.1–150 ha) and 2 sites representative of more extensive wooded areas (~1,500 ha) were selected for study based on the criteria of relatively mature woody vegetation. These study sites were 30–870 m from their nearest neighboring forest patch. Sites typically lacked fencerow connections with other forested patches.

Study sites were sampled at least once in spring (1992–1996) by live trapping, and captured animals were marked and released. Eighteen sites were sampled in multiple years, and 1 site was sampled in all years. Individual Sherman live traps (7.5 by 9.0 by 30 cm) were placed at 15-m intervals, and these were paired with Tomahawk live traps (15 by 15 by 60 cm) at 30-m intervals on sampling grids established at each study site. All traps were prebaited for 2 nights followed by 5 nights of trapping. Sherman traps were baited with a mixture of rolled oats, sunflower seeds, and peanut butter, and Tomahawk traps were baited with English walnuts.

Abundance estimates of adult mice (>18 g—Cummings and Vessey 1994) were calculated using the program CAPTURE (Otis et al. 1978), and abundance of other adult small mammals (southern flying squirrels >50 g, eastern chipmunks >80 g, red squirrels >200 g, gray squirrels >400 g, and fox squirrels >600 g) was estimated using minimum number known alive (MNKA—Krebs 1966). Density estimates were calculated using either the entire area of woodlots (when the entire area was trapped) or the area of the trapping grid plus a 7.5-m buffer on all sides for areas that were too large to cover completely, in which case a grid of about 2 ha was used. Biomass (g/ha) of granivores was calculated as MNKA × average adult mass/trapping grid area.

The nestedness temperature calculator (Patterson and Atmar 1995) was used to evaluate degree of nestedness exhibited among the study sites for granivores only and for all small-mammal species. For example, consider an array of isolated fragments that before fragmentation had been occupied by a common assemblage of species. If extinction of species occurred in an identical, entirely predictable fashion on each isolate, then each smaller isolate eventually would contain only an included (i.e., nested) subset of the species found on larger isolates, and an array of these isolates would constitute a nested series. To quantify the degree of nestedness, the computer program used the analogy of "temperature" to measure the deviation of a suite of biotas from perfectly nested subsets. Perfectly nested biotas have a temperature of 0°, and if the processes leading to the current conditions could be repeated, extinction or colonization events would follow a predictable order with
complete certainty. Higher temperatures indicate more randomness in the composition of biotas and less predictability of extinction or colonization order. Monte Carlo trials were used to estimate the probability of randomly generating the observed species distribution among study sites.

Forest patches within the landscape at Indian Pine were digitized from aerial photographs (1:15,000), and the digital map was analyzed using the program FRAGSTATS (McGarigal and Marks 1995). That program produced numerous statistics describing patch attributes and spatial structure of patches. We chose 5 landscape statistics for our analysis: area (A), proximity (PROX), nearest-neighbor distance (NN), core-area index (CAI), and fractal dimension (FD). PROX was a measure of isolation and was the sum of patch area (m²) divided by the nearest squared edge-to-edge distance (m²) between the patch and the focal patch for all patches whose edges were within a specified radius of the focal patch (1,000 m was used in our analysis). The NN was measured as the nearest edge-to-edge distance (m) between the focal woodlot and the nearest woodlot. The CAI was a measure of the ratio of interior to edge habitat and was calculated as the percentage of the total woodlot area that was >50 m from the woodlot’s edge. The FD was a measure of shape complexity and was equal to 2 times the logarithm of patch perimeter (m) divided by the logarithm of patch area (m²). Landscape variables A, PROX, and NN for the study sites ranged over several orders of magnitude and therefore were log₁₀ transformed for all analyses. The CAI values were 0–62% and were square-root transformed. The transformed landscape variables and the squares of log₁₀A (log₁₀A²), CAI (CAI), and log₁₀PROX (log₁₀PROX²), as well as fractal dimension, were used in “best possible subsets” models of multiple regression to predict densities of granivorous rodents, biomass of granivorous rodents per hectare, and species richness of granivores and all small-mammal species. To account for the effect of year of trapping, we 1st conducted a regression for each dependent variable in which year was the sole independent variable. For regressions in which a significant association with year was demonstrated, we constructed subsequent best-possible-subsets models based on the residual variation remaining after controlling for year. We also used landscape statistics to predict presence–absence of selected small-mammal species using logistic regression and a stepwise selection algorithm with an alpha of 0.3 to enter the model and an alpha of 0.1 to stay in the model (SAS Institute, 1994). Although our samples were somewhat small for use with logistic regression (Lomolino et al. 1995), the binary nature of the response variable made that approach preferable to alternatives in terms of its biological realism (Rita and Ranta 1995). Moreover, jackknife validation of those and comparable models indicated that use of logistic regression resulted in models that were reasonably robust (Nupp 1997). We examined species–area relationships of the 2 continuous forests by subsampling data from those study sites and plotting the species-accumulation curve (Rosenzweig 1995).

RESULTS

We captured 1,669 white-footed mice at 37 sites, 264 eastern chipmunks at 32 sites, 207 fox squirrels at 31 sites, 31 red squirrels at 10 sites, 78 gray squirrels at 7 sites, and 58 southern flying squirrels at 5 sites in 33,790 trap days/nights. Other species captured included 322 short-tailed shrews (Blarina brevicauda) at 24 sites, 24 Sorex at 11 sites, 5 deer mice (Peromyscus maniculatus) at 4 sites, 18 meadow jumping mice (Zapus hudsonius) at 3 sites, 6 prairie voles (Microtus ochrogaster) at 3 sites, 4 house mice (Mus musculus) at 3 sites, 8 pine voles (Microtus pinitorum) at 2 sites, 6 southern bog lemmings (Synaptomys cooperi) at 2 sites, and 1 meadow vole (M. pennsylvanicus). We measured cumulative capture frequency for each study site to ascertain if the 5-day trapping period adequately represented all the small-mammal species that were present (Fig. 1). One day of trapping yielded on average 75% of all species captured during the 5-day session, and 93% were obtained by the 3rd day of trapping.

Nestedness.—Assemblages of granivores and all small mammals exhibited a highly ordered and nested distribution among the study sites. The nestedness temperature calculator calculated temperatures of 8.11° (P < 0.0001) for the group of granivores and 11.02° (P < 0.0001) for all small mammals.
Fig. 1.—Mean (± SE) of the cumulative fraction of all small mammals captured at a forest patch, expressed as a function of the number of days of trapping effort.

For comparison, the mean temperature of 100 random assortments of the richness data was 48.13° ± 5.95 SD for granivores only and 58.41° ± 5.35° for all small mammals.

Species richness.—Species richness of granivores was related positively to log_{10}A, log_{10}NN, and log_{10}PROX and related negatively to FD (F = 20.79; d.f. = 4, 32; P = 0.0001; Table 2; Fig. 2a). Species richness of all species was positively related to log_{10}A and log_{10}NN and negatively related to FD (F = 27.78; d.f. = 3, 33; P = 0.0001; Table 2; Fig. 2b).

Biomass and local density.—Biomass per hectare of granivorous rodents was related negatively to log_{10}A and related positively to √CAI and log_{10}A^2, indicating a curvilinear relationship with patch area (F = 17.06; d.f. = 3, 57; P = 0.0001; Table 2; Fig. 3). Significant multiple regression models were developed for predicting the densities of white-footed mice, eastern chipmunks, southern flying squirrels, red squirrels, and gray squirrels but not for fox squirrels (Table 3). Over the range of patch sizes we examined, densities of white-footed mice
Fig. 2.—Species richness of a) granivores and b) all small-mammal species in woodlot (solid circles) and forest sites (open triangles and circles) in west-central Indiana; open triangles represent subsampling within forest sites.

Fig. 3.—Biomass of granivores for 37 study sites livetrapped during spring 1992–1996 in west-central Indiana.

Table 3.—Predictive models of granivore density (no. animals/ha) in an agricultural landscape of west-central Indiana.

<table>
<thead>
<tr>
<th>Species</th>
<th>Coefficients</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>White-footed mice</td>
<td>$b_0 = +15.82, b_1 = -25.79 \log_{10}(A)$</td>
<td>0.37</td>
</tr>
<tr>
<td>Southern flying squirrels</td>
<td>$b_0 = +7.68, b_1 = +6.83 \log_{10}(A)$</td>
<td>0.31</td>
</tr>
<tr>
<td>Eastern chipmunks</td>
<td>$b_0 = +3.14, b_1 = +0.38 \log_{10}(A)$</td>
<td>0.30</td>
</tr>
<tr>
<td>Red squirrels</td>
<td>$b_0 = +20.65, b_1 = +0.86 \log_{10}(A)$</td>
<td>0.35</td>
</tr>
<tr>
<td>Gray squirrels</td>
<td>$b_0 = -0.14, b_1 = -0.19 \log_{10}(A)$</td>
<td>0.40</td>
</tr>
</tbody>
</table>

*No model for fox squirrels.

Regression models determined after removing variation due to year of trapping.
and eastern chipmunks declined with log_{10} A, whereas densities of southern flying squirrels and gray squirrels tended to increase (Table 3; Fig. 4). Red squirrels attained their greatest densities in woodlots of intermediate size with relatively large core areas (Table 3).

Models of presence–absence.—Significant logistic regression models were developed predicting presence of southern flying squirrels, red squirrels, gray squirrels, and fox squirrels (Table 4; Fig. 5). White-footed mice were present at all trapping sites, and no significant model could be developed for predicting presence of eastern chipmunks. Probability of occurrence of southern flying squirrels, gray squirrels, and fox squirrels increased with log_{10} A. Gray squirrels were associated negatively with log_{10} PROX, whereas fox squirrels were associated positively with log_{10} PROX. Red squirrel presence was related positively to CAI.

**DISCUSSION**

**Nestedness.**—Distributions of all small mammals and the 6 species of granivorous forest rodents sampled in this study exhibited a highly ordered pattern of nested subsets among study woodlots. This pattern was likely a consequence of differential extinction or colonization probabilities among species as a result of habitat fragmentation.

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**TABLE 4.** Predictive models of small-mammal presence (logistic models) in an agricultural landscape of west-central Indiana.

<table>
<thead>
<tr>
<th>Species</th>
<th>b₀</th>
<th>b₁</th>
<th>b₂</th>
<th>% concordant</th>
<th>Somers’ D</th>
</tr>
</thead>
<tbody>
<tr>
<td>White-footed mice</td>
<td>−3.77</td>
<td>+0.99</td>
<td>+1.84 (year)</td>
<td>91.9</td>
<td>0.838</td>
</tr>
<tr>
<td>Southern flying squirrels</td>
<td>−3.96</td>
<td>−1.51 (log_{10} A)</td>
<td>90.7</td>
<td>0.819</td>
<td></td>
</tr>
<tr>
<td>Red squirrels</td>
<td>−3.68</td>
<td>+2.11 (log_{10} A)</td>
<td>91.9</td>
<td>0.843</td>
<td></td>
</tr>
<tr>
<td>Gray squirrels</td>
<td>+0.75</td>
<td>−3.78 (log_{10} PROX)</td>
<td>88.2</td>
<td>0.785</td>
<td></td>
</tr>
<tr>
<td>Fox squirrels</td>
<td>−3.04</td>
<td>−23.99 (FD)</td>
<td>96.5</td>
<td>0.93</td>
<td></td>
</tr>
<tr>
<td>Short-tailed shrews</td>
<td>+0.01</td>
<td>+31.13 (log_{10} A)</td>
<td>84.5</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*No model for eastern chipmunks.
Fig. 5.—Isoclines of probability of occurrence for a) southern flying squirrel, b) gray squirrel, and c) fox squirrel at 4 levels of patch proximity in west-central Indiana.

(Patterson 1990) and is consistent with results of studies of some taxa occupying fragmented habitats, which were often found to be strongly nested (Wright et al. 1998). A high degree of nestedness among study woodlots indicates that changes in the study landscape should have produced predictable changes in the spatial distribution of small mammals. For the 6 granivores that we considered, the predicted order of loss of species from forest patches was southern flying squirrels lost 1st, followed by gray squirrels, red squirrels, fox squirrels, and eastern chipmunks. These findings correspond with predictions derived by Swihart and Nupp (1998) from spatially explicit demographic models of the squirrel species, except that the order of red and fox squirrels was reversed. This information, in combination with the information that relates a species’ occurrence or abundance with ecological and life-history traits, should be useful in land-use planning to ameliorate or under some circumstances accentuate effects of forest fragmentation (Kenward et al. 1988b; Laurance and Gascon 1997; White et al. 1997).

Species richness.—Species richness increased as a function of woodlot area for granivores and all small-mammal species (Fig. 2). The granivore species–accumulation curve derived from subsampled parts of continuous forest sites rose more sharply than the species–area curve from study woodlots. This indicates that the 6 species of granivores can coexist within a relatively small area, provided that the area is part of a larger continuous forest. The comparative slopes of the species–area curve for woodlots and continuous forests and the high degree of nestedness in species distribution indicate that some species are sensitive to habitat area, isolation, or edge effects. Our results indicate that species in an assemblage may respond to ≥1 of these factors in different ways that are determined by morphology, habitat requirements, and life-history characteristics (cf. Rosenblatt et al. 1999).

The wide range in body mass among species (25–750 g; Table 1) could result in differential responses to habitat fragmentation and nestedness among fragments due to species differences in minimum area requirements or vagility (Patterson 1984; Patterson and Atmar 1986). However, unlike the studies of mammals on mountaintops (Brown 1971; Patterson 1984) our results failed to reveal interspecific differences in sensitivity to patch area that covaried with body mass. For example, local densities of white-footed mice and gray squirrels re-
sponded to changes in area in qualitatively similar ways (Table 3), as did probabilities of occurrence of flying squirrels and fox squirrels (Table 4).

Andrén (1994) indicated that in landscapes with highly fragmented habitats, patch size and isolation complement the effect of habitat loss and result in changes in species distribution or abundance greater than would be expected by loss of habitat alone. Species with low vagility should have been the most sensitive to effects of isolation. The relation between local density of flying squirrels and degree of patch isolation was consistent with this prediction (Table 3).

Numerous authors have shown that species vary considerably in their responses to habitat fragmentation, with some species actually benefiting from increase in edge habitat or the loss of competitors or predators (George 1987; Laurance 1990, 1991; Murcia 1995; Nixon et al. 1991; Nupp and Swihart 1996; Robinson et al. 1992; Sekgororane and Dilworth 1995; Sheperd and Swihart 1995). Our results indicate that eastern chipmunks have responded positively to increased edge created by habitat fragmentation, whereas species such as red squirrels may be affected negatively (Tables 3 and 4).

Species responses to fragmentation.—Landscape-level statistics were not good predictors of fox squirrel abundance, indicating that this species is insensitive to levels of forest fragmentation found within our study area. Fox squirrels were the largest granivorous rodents in this study and might have been expected to show greater sensitivity than smaller granivores to forest fragmentation. Sheperd and Swihart (1995) reported reduced home ranges of fox squirrels in smaller woodlots but noted that fox squirrels traveled and foraged in agricultural fields surrounding woodlots. Thus, mobility of fox squirrels and their use of agricultural crops surrounding forest patches may ameliorate negative effects of small patch areas or high levels of isolation and could have been responsible for our inability to develop significant models of abundance based on landscape statistics (Swihart and Nupp 1998). Consistent with our predictions (Table 1), our logistic model of presence-absence of fox squirrels indicated that they were more likely to occur in larger, more isolated woodlots (Table 4; Fig. 5a). These findings were further reinforced by the larger than expected idiosyncratic scores for fox squirrels in the nestedness analysis. Larger than expected idiosyncratic scores may be explained by greater than expected recolonization probabilities (Patterson and Atmar 1995), which reinforces the notion of the fox squirrel as a species requiring moderate to large woodlots but quite capable of traversing the intervening cropland matrix.

Whereas fox squirrels were found in 84% of study sites, the next largest granivore, the gray squirrel, was found in only 14% of the woodlots (all of which were >4.86 ha) and the 2 continuous forest sites (1,500 ha). A logistic model of presence-absence of gray squirrels showed a positive relationship with woodlot area and a negative relationship with woodlot isolation (Table 4; Fig. 5b). Using demographic data from other populations, simulation models of gray squirrels at Indian Pine have yielded comparable results (Swihart and Nupp 1998). Our results also were consistent with research from Great Britain, where the gray squirrel is considered a pest species and a competitor with native red squirrels (S. vulgaris—Fitzgibbon 1993; Kenward et al. 1988a, 1988b). Fitzgibbon (1993) indicated that gray squirrels were less likely to be found in isolated woodlots with few hedge-row connections and in those >500 m from the nearest woodlot of ≥5 ha. Similar observations by Kenward et al. (1988b) led to recommendations that new farm woodlots should be isolated as much as possible from other woodlots to reduce tree damage caused by gray squirrels. In the midwestern United States, where the gray squirrel is considered an important game species, Nix-
on et al. (1978) estimated that they require \( \geq 20\% \) of the land area to be forested to remain abundant. It also may be beneficial to retain fencerow connections and riparian corridors between woodlands to maintain populations of gray squirrel (Nixon et al. 1978).

The red squirrel is distributed primarily in boreal forests and arrived in the hardwood forests of Indiana only in about the last 100 years (Mumford and Whitaker 1982). We found red squirrels in 27% of the study sites; all areas were \( >4.0 \) ha. Abundance of red squirrels show a positive curvilinear relationship with woodlot area and CAI, which measured percentage of interior habitat. Logistic regressions of presence-absence of red squirrels showed similar relationships. These findings suggest that red squirrels may be affected adversely by large amounts of edge habitat, in contrast to our prediction (Table 1). However, red squirrels seem capable of adapting to a highly fragmented landscape, and their current distribution may reflect the relatively short period of time during which they have occupied the study area. After the completion of our study, a red squirrel was documented (Page 1998) at a 0.81-ha isolated (PROX = 0.02) woodlot that had been sampled repeatedly by us. Moreover, in stochastic simulation models of populations inhabiting fragmented agricultural landscapes of west-central Indiana, red squirrels attained the greatest abundance and had the longest persistence of the 4 species of tree squirrels (Swihart and Nupp 1998). An important caveat of the simulation was that demographic data were obtained from populations in localities other than Indiana (Swihart and Nupp 1998). Nevertheless, red squirrels appear to be capable of moving across an agricultural matrix. They also may be capable of expanding their numbers and distribution in a highly fragmented agricultural landscape, although additional ecological and demographic data from such regions are needed to test this hypothesis.

In the current study, eastern chipmunks were trapped in 86% of the study sites, and their densities were related inversely to woodlot area. Henein et al. (1998) and Nupp and Swihart (1998) have compared sensitivity of eastern chipmunks and white-footed mice to agriculturally induced fragmentation of forest habitat. Eastern chipmunks are larger, have more specialized habitat requirements, and are intolerant of nonforested habitats (Bennett et al. 1994; Nupp and Swihart 1998; Table 1). Thus, eastern chipmunks should be more negatively affected by landscape changes induced by agricultural fragmentation of forest habitat. Henein et al. (1998) supported this prediction. They constructed a landscape model parameterized using previously collected data and concluded that connectivity was the most important factor determining persistence of eastern chipmunks in agricultural landscapes. In our study area, populations of chipmunks in woodlots exhibited lower survival rates than those occupying large expanses of forest (Nupp and Swihart 1998).

Southern flying squirrels are the only nocturnal gliding granivorous rodent in Indiana. Southern flying squirrels also were the most spottily distributed granivores in our study area, occurring at only 9% of the woodlots (\( >4.6 \) ha) and the 2 continuous forest sites. Local density of southern flying squirrels was related positively to woodlot area and negatively to isolation. A logistic model indicated a positive relationship between woodlot area and probability of presence of southern flying squirrels (Table 4; Fig. 5c). Similar area and isolation effects were predicted for flying squirrels in the simulation models of Swihart and Nupp (1998). Woodworth et al. (in press) found southern flying squirrels absent from the most isolated woodlots in southern Illinois, but these authors did not detect an area effect, although all of their study sites were \( >6 \) ha. Although southern flying squirrels are mobile in continuous habitats (Fridell and Litvaitis 1991), their gliding locomotion presumably is poorly suited to moving
across large expanses of unforest ed habitat. Thus, small woodlots in agricultural landscapes likely would not be recolonized following periodic extinctions (Rosenblatt et al. 1999). Additionally, southern flying squirrels are communal nesters for thermoregulatory reasons, at least in winter (Stapp et al. 1991). Stapp et al. (1991) estimated that nesting groups of 6 southern flying squirrels reduced their winter energy expenditures by 36% over individual non-huddling squirrels. This life-history strategy may make southern flying squirrels particularly vulnerable to local extinction in small woodlots with few individuals, especially at northern latitudes.

White-footed mice were ubiquitous in the study area, and their densities were related inversely to woodlot area (Nupp and Swihart 1996, 1998; Fig. 4). White-footed mice have small area requirements, are generalists, are tolerant of marginal habitats, and thus might be expected to thrive in fragmented landscapes (Table 1). Henein et al. (1998) concluded that the ability of mice to use nonforested habitat was important to their success. Absence of larger competitors also is likely to have benefited mice (Nupp and Swihart 1996, 1998).

Biomass per hectare of granivores was greatest at the smallest and the largest study sites (Fig. 3). This relationship resulted from the high densities of white-footed mice and eastern chipmunks at the smallest woodlots combined with the lack of southern flying squirrels, red squirrels, and gray squirrels in woodlots <4.0 ha. The largest study sites had populations of most of the full complement of granivores and thus high biomass per hectare. If resource availability is similar among different sizes of woodlots (Nupp and Swihart 1998) “density compensation” may explain patterns in the smaller woodlots because populations of white-footed mice and eastern chipmunks increased in the absence of other potential competitors (Williamson 1981).

**Conclusions**

Our study has demonstrated that populations of small mammals in forests exhibit a highly nested distribution in fragmented agricultural landscapes. Additionally, each species of granivorous rodent was unique in its response to fragmentation, with positive and negative impacts. Two of the species, gray squirrels and southern flying squirrels, were particularly sensitive to area and isolation effects. Responses of granivores were not predicted well by body mass, indicating the necessity of examining the life-history, vagility, and minimum-area requirements of each species to understand or predict effects of fragmentation. Similarly, Laurance (1991) found that only abundance in a matrix of 7 ecological traits including body size, longevity, fecundity, trophic level, dietary specialization, natural abundance in rain forest, and abundance in the surrounding habitat matrix was a good predictor of extinction vulnerability in Australian mammals. Density compensation may occur in populations of white-footed mice and eastern chipmunks in woodlots with lower species richness. It also is possible that abnormally high densities of these 2 species influence the community structure of granivorous rodents by inhibiting recolonization of woodlots or limiting seed resources available to other species. Further research into direct and indirect effects (sensu Strauss 1991; Wootton 1994) of small-mammal abundance on other species would be helpful in understanding the long-term ecological impacts of habitat fragmentation.

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