MODELING POPULATION RESPONSES OF NORTH AMERICAN TREE SQUIRRELS TO AGRICULTURALLY INDUCED FRAGMENTATION OF FORESTS

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ABSTRACT.—Agriculturally induced fragmentation of forests has been extensive in the midwestern United States, resulting in a landscape characterized by fewer and more isolated tracts of woodland. Much of this region is occupied by four species of tree squirrels: Sciurus niger, S. carolinensis, Tamiasciurus hudsonicus, and Glaucomys volans. Differences in morphology, ecology, and life history among these species are suggestive of differential sensitivities to forest fragmentation. Qualitative information from Indiana suggests that S. niger and T. hudsonicus have expanded their ranges in conjunction with increasing fragmentation, whereas S. carolinensis and G. volans have been negatively affected. Does fragmentation of forests affect species of squirrels differently? Is fragmentation capable of molding community structure at the patch or landscape level? To address these questions, we constructed spatially explicit models of metapopulations for each species of squirrel using demographic data derived from the literature. Model results were qualitatively consistent with data collected via livetrapping in a fragmented landscape in northwestern Indiana. In terms of population size and persistence in fragmented landscapes, the order of performance was T. hudsonicus > S. niger > S. carolinensis > G. volans. Isolation and size of fragments were important determinants of occupancy, especially for S. carolinensis and G. volans. In highly fragmented landscapes, metapopulation dynamics rather than interspecific competition appear primarily responsible for structuring communities of squirrels.

INTRODUCTION

Agriculture has caused extensive modification of native vegetation on every continent except Antarctica, and these modifications have had important repercussions for native plants and animals (Saunders et al., 1991). One consequence of extensive conversion of land for production of crops is that the remaining native vegetation often occurs in fragmented patches within a predominantly agricultural landscape. Conversion of forest land has been widespread in the midwestern United States. For instance, nearly 80% of forests in Illinois in 1820 had been converted to agricultural use by 1980 (Iverson, 1988).

Theoretical studies generally have concluded that a species is more likely to survive in a continuous tract of habitat than in a habitat that has been fragmented (Burkey, 1989). Fragmentation results in local populations that may be linked by movements of individuals, producing metapopulations (Gilpin, 1987). Most models and field studies of vertebrate metapopulations have focused on birds (e.g., Temple, 1986; Temple and Cary, 1988; Rolsstad, 1991; Pulliam et al., 1992), although work with small mammals has been conducted occasionally (e.g., Henderson et al., 1985; Lefkovitch and Fahrig, 1985; Lorenz and Barrett, 1990). Our objective was to model the impact of fragmentation on tree squirrels in the midwestern U.S., to explore interspecific differences in responses to fragmentation, and to assess the potential importance of fragmentation in shaping communities of squirrels at the local and landscape level.

Four species of tree squirrels occur syntopically within the agricultural landscape of the Midwest. In Indiana, historical records suggest that changes
In land use have had differential impacts on the species within this guild (Mumford and Whitaker, 1982). Fox squirrels (Sciurus niger) and red squirrels (Tamiasciurus hudsonicus) have expanded their ranges in conjunction with increasing fragmentation, whereas gray squirrels (Sciurus carolinensis) and southern flying squirrels (Glaucomys volans) presumably have been negatively affected. Two likely explanations exist for these phenomena, the first related to competitive interactions and the second related principally to species demography. If competition among species is intense and fragmentation has a greater negative impact on gray and southern flying squirrels, it is possible that the observed responses of fox and red squirrels could be a consequence of competitive release induced by fragmentation, or at least changes in competition coefficients favoring fox and red squirrels over gray and southern flying squirrels. Alternatively, structural or vegetative changes in woodlands and the surrounding landscape caused by agriculturally induced fragmentation could combine with interspecific differences in behavior and demography to elicit the observed responses.

Competition seems likely among species exhibiting considerable overlap in habitat requirements and food habits; yet little documentation of competition exists for the species of tree squirrels considered. Manipulation of densities of female fox squirrels by Brown and Batzli (1985b) had little effect on abundance of gray squirrels, although some negative interactions were suggested by altered dispersion patterns of gray squirrels. Red squirrels are reputed to behave agonistically toward other sciurids (Flyger and Gates, 1982), and reports exist of red squirrels chasing gray and southern flying squirrels (Klugh, 1927; Preston, 1948). The relationship between red squirrels and gray squirrels is unclear at best, because additional observations of nonterritorial red squirrels suggest that interspecific aggression is minimal (Layne, 1954; Ackerman and Weigl, 1970).

Considerably more evidence can be gathered in support of the hypothesis that differential responses to fragmentation are engendered by interspecific differences in behavior and life history attributes. For instance, fox squirrels exhibit evolutionary affinities to open woods and bur oak (Quercus macrocarpa) savannahs at the interface of the eastern deciduous forest and the tall grass prairie (Jones and Birney, 1988; Hoffmeister, 1989). Fox squirrels commonly travel away from woodlots along brushy fencerows (Sheperd, 1994), and they are capable of relying upon agricultural crops to a considerable extent (Korschgen, 1981; Hansen et al., 1986). In contrast, gray squirrels make limited use of agricultural crops as a supplemental source of food (Korschgen, 1981) and are more apt to occupy large tracts of mature forest with a well-developed understory (Nixon et al., 1978). Although typically inhabiting coniferous forests, red squirrels appear capable of functioning as habitat generalists. They exhibit phenotypic flexibility in tailoring behavioral traits to specific environments, including presence or absence of territoriality (Layne, 1954; C. C. Smith, 1968; Rusch and Reeder, 1978), larder or scatter hoarding of seeds (Layne, 1954; C. C. Smith, 1968), and use of cavities, leaf nests, or burrows as nest sites (Yahner, 1980). Demographically, the potential for population increase apparently is better developed in red squirrels than in the other three species (Table 1). Southern flying squirrels inhabit mature hardwood forests in the Midwest (Jones and Birney, 1988), where they move by gliding from tree to tree. Although less is known about southern flying squirrels, agricultural landscapes lacking wooded corridors between forest fragments presumably restrict their interpatch movements.

In general, species with broad habitat tolerances, good mobility, and adaptations to disturbance (and the resulting edge habitat) are well adapted to landscapes dominated by agriculture (Saunders et al., 1991; Meffe and Carroll, 1994). Assuming that these generalities hold for tree squirrels, we predict that fox and red squirrels should be least affected by agriculturally induced fragmentation, with greater negative impacts on populations of gray and southern flying squirrels. To examine our predictions in more detail, we developed spatially explicit population models (Dunning et al., 1995) for each of the four species of squirrels. Each model was constructed with the intent of mimicking as nearly as possible the behavioral and demographic characteristics of the species. No competitive interactions were included in the models; the fate of each species was determined solely by its behavioral and demographic characteristics. Consequently, if model results are similar to changes in composition and abundance documented in the field, the most parsimonious explanation is that the observed changes occurred because of behavioral and demographic differences rather than shifts in competitive interactions.
Table 1. Parameters used in constructing population projection matrices for tree squirrels, as well as resulting stable age distributions and growth rates. Probability of mortality during dispersal also is given, expressed per 100 m.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Age1</th>
<th>Gray</th>
<th>Fox</th>
<th>Red</th>
<th>Flying</th>
</tr>
</thead>
<tbody>
<tr>
<td>Survival2</td>
<td>Juvenile</td>
<td>0.67</td>
<td>0.47</td>
<td>0.52</td>
<td>0.81</td>
</tr>
<tr>
<td></td>
<td>Subadult1</td>
<td>0.79</td>
<td>0.74</td>
<td>0.65</td>
<td>0.44</td>
</tr>
<tr>
<td></td>
<td>Subadult2</td>
<td>0.77</td>
<td>0.83</td>
<td>0.83</td>
<td>0.72</td>
</tr>
<tr>
<td></td>
<td>Yearling</td>
<td>0.77</td>
<td>0.88</td>
<td>0.83</td>
<td>0.68</td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>0.77</td>
<td>0.90</td>
<td>0.83</td>
<td>0.78</td>
</tr>
<tr>
<td>Proportion of Females</td>
<td>Subadult2</td>
<td>0.02</td>
<td>0.00</td>
<td>0.02</td>
<td>0.94</td>
</tr>
<tr>
<td></td>
<td>Yearling</td>
<td>0.56</td>
<td>0.23</td>
<td>0.52</td>
<td>0.80</td>
</tr>
<tr>
<td></td>
<td>Adult</td>
<td>0.64</td>
<td>0.54</td>
<td>0.82</td>
<td>0.71</td>
</tr>
<tr>
<td>Litter Size3</td>
<td>Subadult2</td>
<td>2.43</td>
<td>0.00</td>
<td>3.50</td>
<td>2.66</td>
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<td>2.50</td>
<td>3.85</td>
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<tr>
<td></td>
<td>Adult</td>
<td>3.00</td>
<td>2.93</td>
<td>5.03</td>
<td>3.56</td>
</tr>
<tr>
<td>Stable age distribution</td>
<td>Juvenile</td>
<td>0.33</td>
<td>0.41</td>
<td>0.55</td>
<td>0.55</td>
</tr>
<tr>
<td></td>
<td>Subadult2</td>
<td>0.25</td>
<td>0.09</td>
<td>0.15</td>
<td>0.15</td>
</tr>
<tr>
<td>after spring</td>
<td>Yearling</td>
<td>0.13</td>
<td>0.11</td>
<td>0.11</td>
<td>0.14</td>
</tr>
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<td>birth pulse</td>
<td>Adult</td>
<td>0.29</td>
<td>0.39</td>
<td>0.19</td>
<td>0.16</td>
</tr>
<tr>
<td>Growth rate, ( \lambda ):</td>
<td></td>
<td>1.07</td>
<td>1.08</td>
<td>1.35</td>
<td>1.07</td>
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<td>Dispersal mortality:</td>
<td></td>
<td>0.025</td>
<td>0.010</td>
<td>0.040</td>
<td>0.350</td>
</tr>
</tbody>
</table>

1Pre-adult age classes represent 4-month intervals; thus subadult, squirrels are 4-8 months old, subadult, squirrels are 8-12 months old, etc.

2Probability of surviving a 4-month interval.

3If values differed between the first and second birth pulse within an age class, the mean is given.


DERIVATION OF SPATIALLY EXPLICIT DEMOGRAPHIC MODELS

We constructed age-specific models of population growth for each species of squirrel in fragmented landscapes consisting of patches of suitable forested habitat. Local populations in fragments were linked by dispersal between patches. Stochastic variation in births and deaths was incorporated into the models, along with stochastic variation in production of mast. Mast determined carrying capacity of local patches and influenced rates of reproduction, dispersal, and survival of juveniles, as well as litter size. The following sections detail the models’ components.

Reproduction and survival.—For each species, we compiled information on age-specific rates of survival and fertility from the literature (Table 1). Demographic data for gray and fox squirrels were relatively plentiful, whereas data for red and southern flying squirrels were scarce. Thus, we place more confidence in the models constructed for the former species than for the latter. Demographic data were used to construct population projection matrices for the purpose of calculating annual rates of growth, \( \lambda \), and stable age distributions (Caswell, 1989). Because two pulses of births, separated by about 4 months, are common for all four species in the Midwest, we constructed four 4-month projection matrices. These matrices were multiplied together to yield an annual projection matrix. A \( \lambda \) value of 1.07-1.08 was shared by gray, fox, and southern flying squirrels. For red squirrels \( \lambda = 1.35 \), indicating a much higher propensity for increase.
Environmental variation in production of mast.—Each of the tree squirrels in our study relies upon mast as their principal source of food, and variation in the production of mast can influence survival and reproduction (Nixon and McClain, 1969; Nixon et al., 1975; Koprowski, 1991). To enhance realism of the models, we incorporated annual variation in production of soft and hard mast. Cumulative distribution functions (Fig. 1) were constructed from 9 years of data collected for production of hard mast in Ohio (Nixon et al., 1975) and 25 years of data on production of soft mast in Wisconsin (Godman and Mattson, 1976). A mast-yield category was selected randomly using the cumulative distribution function for soft mast, and a particular value within the category was determined by assuming that each value within the interval had an equal probability of occurrence. Selection of hard-mast yield was complicated by the fact that conditions affecting soft-mast yield in spring may affect hard-mast yield in autumn. Thus, yields of soft and hard mast within a year are not necessarily independent. Reports of correlations between production of hard and soft mast within a year varied widely; we used a moderate correlation ($r = 0.47$) in our simulations. No correlation in yield was assumed between years.

Fragmented landscapes.—Populations occupied a square, 25 km$^2$ landscape, of which 5% (125 ha) was forest. Non-forested portions of the landscape were presumed to be homogenous and unsuitable for permanent occupancy by tree squirrels. For simplicity, the landscape was constructed using hexagonal cells measuring 1 ha (Pulliam et al., 1992). A patch was defined as a collection of forested hexagons that shared at least one side.

All forested hexagons within a landscape were assumed to be equal in quality, on average. Although spatial variation in, for example, precipitation and temperature precludes a perfectly correlated environment with respect to production of mast, we suspected that patches within a landscape of the size we studied should exhibit a high degree of covariation in production of mast. In other words, if conditions favored a bumper year in one portion of the landscape, chances are that similar conditions occurred elsewhere in the landscape. Accordingly, in our simulations we used a fairly large inter-patch correlation in production of mast within a season ($r = 0.77$). This correlation was achieved by randomly selecting a yield value for the first patch and then restricting the range of values from which yields were randomly selected for subsequent patches to 45% of the possible range, centered on the initial value.
Thus, autocorrelation in production of mast was evident on a temporal (seasonal) scale as well as on a spatial scale. Although Hanski (1991) termed correlated environmental variation among patches "regional stochasticity," we use the term environmental stochasticity to refer to both temporal and spatial variation in production of mast.

We simulated population dynamics for landscapes (Fig. 2) varying in dispersion of patches (uniform, clumped) and number of patches (4, 25, and 125). Growth of each species was monitored in each landscape, with 10 replications, yielding a 4 x 2 x 3 factorial design. Although viability analysis for a population generally requires a substantially

Fig. 2.—Hexagonal landscapes in which dynamics of squirrel populations were simulated. Each hexagon represents 1 ha. Solid circles represent hexagons of forested habitat suitable for use by squirrels, and contiguous forested hexagons are considered forest patches. Note that in the landscapes with four patches, the patch in the upper left is 32 ha, whereas the other three patches are 31 ha.
greater number of replicates (Harris et al., 1987), our principal intent was not to conduct a viability analysis, but rather to compare responses of species to fragmentation, as well as factors influencing responses. Small samples tend to reduce the likelihood of detecting subtle differences, thus our results should be viewed as conservative.

To establish baseline levels of performance by populations, we also simulated growth of populations occupying a single 125-ha patch. Habitat heterogeneity within these relatively large expanses of forest was modeled by treating 5-ha blocks of forest as individual patches from the standpoint of production of mast within a season. A 5-ha block size was chosen because it approximates the average size of a patch in the area in which we conduct our fieldwork (see below). This simulation sheds light on the performance of each species in a continuous, albeit somewhat small, habitat as opposed to a landscape consisting of an equal amount of forest scattered among fragments.

Finally, growth of each species was simulated on a landscape in Tippecanoe County, Indiana (Fig. 3). The landscape includes 17 forest patches and is representative of agricultural landscapes throughout much of the upper Midwest. Results of the simulation were compared to the continuous-forest simulation and to data derived from live trapping during 1991-1993 in and immediately adjacent to the area in question.

Dispersal.—Few data exist on dispersal abilities of tree squirrels, and no data exist on distributions of dispersal distances in fragmented landscapes. We chose to model dispersal in the following manner: a disperser originating from a randomly selected hexagon within a patch was assumed to be capable of detecting any other forested patches within 1 km. Although our choice of detection radius was arbitrary, sensitivity analysis for southern flying squirrels, the least-mobile species, indicated that model results were affected only slightly by changes in the detection radius (see below).

A dispersing squirrel had no prior knowledge of whether any unvisited patches were saturated. If a patch occurred <1 km away, the squirrel moved directly toward the patch (if >1 patch was involved, a random selection was made). Otherwise, the disperser moved in one of six possible directions determined by the midpoints of the sides of the hexagon (Pulliam et al., 1992). If a disperser reached an unsaturated patch, it settled there. Otherwise, it continued searching for a new patch. Squirrels were assumed to have memories adequate to avoid revisiting saturated patches.

Each step in the dispersal process was associated with a certain probability of mortality (Table 1). Values were chosen partly based on allometric considerations of running costs (Taylor et al., 1970) and daily energetic requirements (Nagy, 1987); greater proportional costs (and presumably greater risk of mortality) are incurred by smaller species. The principal rationale for our choice of values relied upon differences in morphology and modes of locomotion, as well as frequency of use of open, non-forested habitat. Fox squirrels are highly mobile animals with documented dispersal distances of several kilometers; they also commonly venture out into the agricultural matrix (Sheperd, 1994).

Gray squirrels also are capable of long-distance dispersal in continuous forest, but they rarely are seen crossing agricultural areas. Southern flying squirrels are fairly mobile in continuous forests, but we were unable to find any documentation of movements across agricultural areas. Because of their gliding mode of locomotion, cropland undoubtedly presents a formidable barrier to their movement. We could find no information on dispersal of red squirrels in deciduous forests; hence our value for this species is highly speculative. Based on body size and home-range size, we assigned red squirrels an expected dispersal distance
slightly less than that used for gray squirrels. The expected distances at which mortality would occur if dispersal were across non-forested habitat were 10 km for fox squirrels, 4 km for gray squirrels, 2.5 km for red squirrels, and 0.3 km for southern flying squirrels. Expected dispersal distances through forested habitat were arbitrarily set in a lower end of magnitude greater for each species.

Dispersal of squirrels in autumn was dictated by hard-mast yield. A linear relationship was assumed between carrying capacity in autumn ($k$) and production of hard mast ($m_n$). A median carrying capacity in autumn ($k'$; all subsequent symbols with an asterisk superscript refer to median values) of 1/ha was used for fox (Koprowski, 1994), gray (Uhlilg, 1957; Barkalow et al., 1970), and red (Baumgartner, 1938; Linduska, 1950, in Layne, 1954) squirrels, whereas a value of 4/ha was used for southern flying squirrels (Layne, 1954; Sonenshine et al., 1979). For all species except fox squirrels, failure of a mast crop was assumed to make the habitat unsuitable (i.e., carrying capacity in autumn = 0). Thus, the relationship was of the form $k_n = (k'/m_n)m_n$. Based upon studies of nutrition and food habits (Havera and Smith 1979, Korschgen 1981), we concluded that agricultural crops could support about 15% of the median population of fox squirrels in the absence of hard mast. Thus, for $m_n < m_n^*$, $k_n = 0.15 + (k' - 0.15k')/m_n^*$. Production of mast above median values influenced carrying capacity for fox squirrels in the same manner as for the other species.

If the abundance of squirrels in a patch exceeded carrying capacity for the patch in autumn, excess individuals were forced to disperse. Dispersal was hierarchical with respect to age; subadults dispersed first, followed by yearlings, and finally by adults if necessary. We randomized the order in which patches were selected for processing of dispersers.

Dispersal in spring differed from dispersal in autumn in that only subadults born in the previous summer dispersed this time. Thompson (1978) noted that about 10-20% of subadult gray squirrels dispersed during spring. In models for all four species, we assigned each subadult a dispersal probability of 0.1.

**Modeling the annual cycle.**—A simulation began immediately after the first birth pulse (Fig. 4). Initially, all patches in a landscape received $k'$ individuals in each 1-ha cell. Sex ratios were assumed to be 1:1, and individuals were assigned to age classes approximately in accordance with values for stable age distributions (Table 1). Production of soft mast ($m_s$) was then determined using the data of Godman and Mattson (1976). Survival of juveniles can be reduced by failure of soft mast (Koprowski, 1991); for the 4-month interval between birth pulses, we set our lower limits to juvenile survival as 0.30 for fox, gray, and red squirrels (Barkalow et al., 1970; Koprowski, 1991) and 0.64 for southern flying squirrels. The higher value for flying squirrels reflects the more carnivorous habits of this species (Dolan and Carter, 1977) while maintaining a reduction of the probability of survival equal to that used for fox squirrels (Table 1). Survival of individuals to the second birth pulse was then determined stochastically.

**ANNUAL CYCLE**

- **March**
  - Spring dispersal
  - Birth Pulse 1
- **April**
  - Soft Mast Production
  - Adjustment of Juvenile Survival
- **July**
  - Birth Pulse 2
- **November**
  - Hard Mast Production
  - Fall Dispersal

**Fig. 4**—Schematic representation of the annual cycle used in modeling dynamics of populations of tree squirrels in fragmented landscapes. Details of the simulation procedure are provided in the text.
Surviving females reproduced with a probability \( P_2 \) dependent upon the soft-mast yield; namely \( P_2 = P_2' / m_s' \), where \( 0 \leq P_2 \leq 1 \). Two exceptions to this relationship were assumed: when \( m_s < m_s' \), we used a linear relationship between \( p_3 \) and \( m_s' \) for southern flying squirrels and gray squirrels with intercepts of \( P_2 = 0.15 \) and 0.10, respectively. In essence, these alterations reflect a slightly reduced reliance by these species on soft mast as the sole factor governing summer reproduction and seem justified based on our review of the literature (Dolan and Carter, 1977; Kropinski, 1994b).

After production of young in the second birth pulse, we simulated survival to autumn. Hard-mast yield and \( k_s \) were then computed, and autumn dispersal was initiated. After computing overwinter survival, we simulated spring dispersal, followed by reproduction in the first birth pulse (Fig. 4). For the first birth pulse, \( p_1 = (p_1' / m_s')m_s \) for all species. For both birth pulses, the number of young per female \( (y) \) was computed using minimal and maximal mean litter sizes of the form \( y_{\text{min}} = 2y'/3 \) and \( y_{\text{max}} = 11y'/3 \). These values correspond to ranges reported in the literature and were used in conjunction with production of mast \( (m) \) to estimate \( y \) using the linear function:

\[
y = bm_s' + y_{\text{max}}, \text{ where } b = (y' - y_{\text{min}}) / m_s' \text{ and } y_{\text{min}} \leq y \leq y_{\text{max}}
\]

**METHODS OF ANALYSIS**

**Statistical analysis.**—Each simulation lasted 100 years or until extinction of the metapopulation occurred (i.e., no individuals remaining). For each run in which a metapopulation persisted, we computed the mean number of squirrels in the landscape during the last 90 years of the simulation, as well as the mean proportion of squirrels dispersing each year and the mean mortality rate of dispersers. We also calculated the mean isolation and size of occupied and vacant patches in a landscape. We computed an index of isolation for a focal patch \( (I) \) as the sum of distances to all other \( k-1 \) patches in the landscape, weighted by the fraction of the total forested area comprised, exclusive of the focal patch. Mathematically,

\[
I = \Sigma d_{ij}(a_i / (A-a_i)),
\]

where \( d_{ij} \) = distance from the focal patch to patch \( i \) (center to center), \( a_i \) = area of patch \( i \), and \( A = (a_i) - a_i \). Thus, large values of \( I \) indicate that the majority of remaining forest habitat in the landscape is far away. We prefer \( I \) to other measures of isolation because, for any given landscape, the use of \( A \) ensures that \( I \) is not dependent upon the size of the focal patch (Gustafson and Parker, 1992).

For the factorial design (species by patch dispersion by patch number and size), mean sizes of population were compared using a three-way analysis of variance, with Student-Newman-Keuls a posteriori comparisons of means. To permit interspecific comparisons of abundance with different values of \( k' \), we computed the fractional change in abundance relative to the initial size of the metapopulation \( (N_0 = 125k') \) and used this as our dependent variable. Because some cells had missing data, the three-way interaction term and the species-by-number-of-patches interaction were omitted from the analysis. Probabilities of landscape-level extinction by year 100 were compared using logistic regression (Fienberg, 1980; Hintze, 1992), with species, patch dispersion, and patch number as the explanatory variables. For simulations with the Tippecanoe County landscape (Fig. 3), we recorded presence or absence of species in each patch annually, as well as mean abundance and number of successful immigrants and emigrants in each patch. Presence-absence data were used to calculate probabilities of extinction of local patches. The difference in successful immigrants and emigrants at a patch was used as an index of a patch’s relative contribution to metapopulation growth. A positive value for this index indicates that a patch served principally as a sink, because immigrants exceeded emigrants. In contrast, a negative value indicates a net contribution to the growth of a metapopulation by virtue of production of emigrants in excess of immigrants. We used each of these dependent variables (mean abundance, probability of patch extinction, and the sink index) to develop multiple-regression models for each species, using area, \( I \), and the interaction term area by \( I \) as explanatory variables. If the interaction term was not significant, it was removed when calculating the final regression model. Mean values of abundance derived from the Tippecanoe County landscape also were compared with values from the 125-ha continuous forest using a two-way ANOVA (species by extent of fragmentation).

**Sensitivity analysis.**—Because input parameters for our models rely upon data from various sources (e.g., Table 1) as well as educated guesses (especially with respect to dispersal mortality), we evaluated the sensitivity of our simulation results to changes in the values of specific parameters. Sensitivity of population size at year 50, \( S_A \), was measured as

\[
S_A = (\Delta N / N) / (\Delta P / P),
\]

where \( \Delta N / N \) is the fractional change in \( N \) resulting from a fractional change in the parameter of interest, \( P \) (Jorgensen, 1994). In general, \( S_A < 1 \) indicates that
the model results are insensitive to changes in the parameter value, whereas larger values of $S_a$ indicate increasing sensitivity. For each species, we calculated sensitivity to changes in the probability of dispersal mortality, $DM$, expressed as the expected dispersal distance in kilometers, i.e., $0.1/DM$. We also examined sensitivity of our results for southern flying squirrel, the species with the most limited mobility (Table 1), to changes in the detection radius.

To determine which rates of age-specific survival and fertility had the greatest effect on population growth, we conducted sensitivity analyses on periodic transition matrices as described by Caswell and Trevisan (1994). Briefly, we divided the annual life cycle of each species into three stages distinguished by the birth pulse in spring, the birth pulse in summer, and dispersal in autumn (Fig. 4). For each stage we constructed a Leslie transition matrix, labelled $B^{[1]}$, $B^{[2]}$, and $B^{[3]}$, respectively. A sensitivity matrix was then calculated for each $B^{[i]}$. For example, $S_{[2]} = [B^{[2]} B^{[3]}]^{-1}$, where the superscript $T$ represents matrix transposition and $S_{[2]}$ is the matrix whose elements $s_{ij}$ are the sensitivities of $S_{ij}$ to changes in the corresponding entries for $A^{[2]} = B^{[2]} B^{[3]} B^{[2]}$, the product matrix used to project the matrix through a 1-year interval from stage 2. The elements $a_{ij}$ of $S^{[2]}$ are obtained as $\delta a_{ij} / \delta a_{ij} = \gamma a_{ij} / \langle w, v \rangle$ (Caswell, 1989), where $\gamma$ and $\langle w, v \rangle$ are the stable age distribution and vector of age-specific reproductive values of $A^{[2]}$, respectively, and the denominator denotes the vector inner product of $w$ and $v$. The proportional sensitivities of $\lambda$ to each element of $B^{[2]}$ are termed elasticities (De Kroon et al., 1986) and are computed as $e_{ij} = \partial \lambda / \partial a_{ij} \delta a_{ij} / \delta a_{ij}$. The elasticities measure the proportional contribution of the matrix entries to population growth (De Kroon et al., 1986). After computing elasticity values for $B^{[1]}$, $B^{[2]}$, and $B^{[3]}$, we determined the proportional contribution of each element to annual growth by summing the matrices and dividing by three. For each species, the element contributing the most to annual population growth was then selected for sensitivity analysis in the full stochastic model using the procedures described above for dispersal mortality.

**COMPARISON WITH FIELD DATA**

We compared results from our simulation models with data on presence-absence of squirrels collected in Tippecanoe County and adjoining sites during 1991-1993. Livetrapping was conducted in 18 forested areas of differing sizes and levels of isolation. At each site trapping was conducted for a minimum of 5 days during spring, and some sites also were trapped in summer and autumn. Grids were established at all sites, with 30 m between adjacent traps. In forested areas <10 ha, the entire area was trapped, whereas grids of 2-3 ha were established in larger forested sites.

**RESULTS**

Effects of differences in species and landscapes.—For the six fragmented landscapes used in the factorial design, species differed significantly in the mean fractional deviation from $N_{eq}$ (Table 2). Red squirrels exhibited the greatest relative density, increasing 80.3% above their initial density, followed by fox squirrels with an increase of 35.8%. Gray squirrels declined an average of 33.2% from $N_{eq}$, and southern flying squirrels declined 55.3%. Values for all species differed significantly ($P<0.05$).

For all species, both the number and dispersion of patches influenced relative density, but a significant interaction effect (Table 2) precluded interpretation beyond noting that relative density dropped below the initial density only for the four-patch landscape in which patches were uniformly distributed.

Isolation values for occupied and vacant patches varied as a function of species, dispersion, and number of patches (Table 2). Southern flying squirrels differed from the other three species in that vacant patches were more isolated than occupied patches in uniform landscapes rather than in landscapes with a clumped distribution of patches (Table 2, Sp by Pp interaction). In landscapes with 125 1-ha patches, a clumped distribution of patches resulted in a few, highly isolated patches being vacant, whereas vacant patches on average were less isolated than occupied patches when patches were uniformly distributed (Table 2, Pp by Np interaction).

Based on results of logistic regression, probability of extinction of a metapopulation was significantly related to the species involved ($\chi^2 = 32.1$, $P<0.001$), with a rank order (probability of extinction in parentheses) of southern flying (0.77) > gray (0.65) > red (0). When all species were considered together, no effects of patch dispersion or patch number and size were evident ($P>0.15$ for both variables). Logistic regressions for each species revealed a significantly elevated probability of extinction for southern flying squirrels occupying landscapes with 125 1-ha patches relative to landscapes with fewer, larger patches ($\chi^2 = 9.1$, $P=0.002$). No significant effects of dispersion or patch size were evident for the other species.
Table 2.—Results of analyses of variance for relative density (expressed as a fraction of $K'$) and difference in isolation of vacant and occupied patches as a function of squirrel species (fox, gray, red, southern flying), spatial pattern of forest patches (uniform or clumped), and number of patches (4, 25, 125).

<table>
<thead>
<tr>
<th>Response Variable</th>
<th>Source</th>
<th>Degrees of Freedom</th>
<th>Mean Square</th>
<th>$F$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density</td>
<td>Sp</td>
<td>3</td>
<td>10.462</td>
<td>695.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Pp</td>
<td>1</td>
<td>0.085</td>
<td>5.6</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td>Np</td>
<td>2</td>
<td>0.728</td>
<td>48.4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Sp x Pp</td>
<td>3</td>
<td>0.027</td>
<td>1.8</td>
<td>0.15</td>
</tr>
<tr>
<td></td>
<td>Pp x Np</td>
<td>2</td>
<td>0.220</td>
<td>14.6</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>143</td>
<td>0.015</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Patch</td>
<td>Sp</td>
<td>3</td>
<td>1.489</td>
<td>2.5</td>
<td>0.06</td>
</tr>
<tr>
<td>Isolation</td>
<td>Pp</td>
<td>1</td>
<td>1.892</td>
<td>3.2</td>
<td>0.08</td>
</tr>
<tr>
<td></td>
<td>Np</td>
<td>2</td>
<td>2.581</td>
<td>4.4</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>Sp x Pp</td>
<td>3</td>
<td>1.715</td>
<td>2.9</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>Pp x Np</td>
<td>2</td>
<td>16.470</td>
<td>27.9</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Error</td>
<td>117</td>
<td>0.590</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

'Sp = species, Pp = pattern of patches, Np = number of patches.

Fig. 5.—Population trajectories simulated for four species of tree squirrels over 100 years in a 25-km² landscape. The continuous forest consisted of one 125-ha patch, whereas the Tippecanoe County, Indiana, landscape consisted of 17 patches, ranging in size from 1-69 ha, and totaling 125 ha. Vertical bars at 10-year intervals represent ±1 standard error, with n = 10 replicates. Note that the scale of the ordinates differ for each species.
Table 3.—Coefficients of multiple regression equations for simulated squirrel populations in a Tippecanoe County, Indiana, landscape. The symbol NS indicates that a regression was not significant ($p > 0.05$).

<table>
<thead>
<tr>
<th>Dependent Variable</th>
<th>Species</th>
<th>$R^2$</th>
<th>Coeff (A)</th>
<th>P</th>
<th>Coeff (I)</th>
<th>P</th>
<th>Coeff (A x I)</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>N²</td>
<td>Gray</td>
<td>0.80</td>
<td>0.001</td>
<td>0.942</td>
<td>-0.014</td>
<td>0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fox</td>
<td>0.43</td>
<td>-0.045</td>
<td>0.029</td>
<td>-0.005</td>
<td>0.029</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Red</td>
<td>0.63</td>
<td>-0.102</td>
<td>0.0004</td>
<td>-0.005</td>
<td>0.044</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Flying</td>
<td>0.38</td>
<td>0.001</td>
<td>0.931</td>
<td>-0.005</td>
<td>0.012</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pₜ</td>
<td>Gray</td>
<td>0.92</td>
<td>-9.903</td>
<td>0.0001</td>
<td>1.155</td>
<td>0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fox</td>
<td>0.78</td>
<td>5.077</td>
<td>0.246</td>
<td>0.715</td>
<td>0.003</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Red</td>
<td>0.69</td>
<td>10.347</td>
<td>0.050</td>
<td>0.753</td>
<td>0.005</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Flying</td>
<td>0.69</td>
<td>-7.526</td>
<td>0.0006</td>
<td>0.555</td>
<td>0.010</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sink²</td>
<td>Gray</td>
<td>0.52</td>
<td>3.348</td>
<td>0.009</td>
<td>0.343</td>
<td>0.015</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fox</td>
<td>0.13</td>
<td>NS</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Red</td>
<td>0.44</td>
<td>10.499</td>
<td>0.018</td>
<td>0.970</td>
<td>0.039</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Flying</td>
<td>0.57</td>
<td>-9.383</td>
<td>0.001</td>
<td>-0.413</td>
<td>0.118</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1. Area was subjected to log$_e$ transformation before regression.
2. Fractional change in abundance relative to $N_0$.
3. Probability of extinction at a patch, $x 100$.
4. Difference in successful immigrants to a patch and successful emigrants emanating from the patch.

Species differences in "real" landscapes.—Differences in relative density occurred among species ($F_{3.81} = 243.8$, $P < 0.001$) and between the simulated Tippecanoe County landscape and the simulated 125-ha continuous forest ($F_{3.81} = 47.2$, $P < 0.001$). The interaction term was not significant ($F_{3.81} = 0.1$, $P = 0.96$).

Red squirrels achieved the greatest increase in density (86% above $N_0$), followed by fox squirrels (36% above $N_0$). Declines in relative density were registered by gray squirrels (18% below $N_0$) and southern flying squirrels (50% below $N_0$). All interspecific differences were significant (a posteriori tests, $P < 0.05$).

The fragmented landscape of Tippecanoe County significantly reduced the relative abundance of all species compared with the continuous forest (Fig. 5, $P < 0.05$ for all a posteriori tests), and gray and southern flying squirrels seemed to be particularly susceptible. For instance, persistence of flying squirrels for 100 years dropped from 90 to 50%, and the mean relative density of gray squirrels dropped from near stability (4.5% below $N_0$) in the continuous forest to a considerably lower level (32.3% below $N_0$) in the fragmented, Tippecanoe County, landscape (Fig. 5).

Attributes of local populations.—For the Tippecanoe County landscape, isolation (I) values were 15.3-38.7, and patch areas were 1-69 ha; correlation between the two variables was small ($r = -0.07$). Using I, area, and the interaction term I, by area as explanatory variables, multiple regression revealed that increasing area of a patch did not influence relative abundance in a patch for gray and southern flying squirrels but resulted in lower relative abundance for fox squirrels and especially for red squirrels (Table 3).

As isolation of a patch increased, relative abundance within the patch declined for all species, with the greatest negative impact on relative abundance of gray squirrels, followed by flying squirrels, fox squirrels, and red squirrels (Table 3). The probability of local extinction was negatively related to the area of a patch and positively related to isolation for gray and southern flying squirrels. The area-by-isolation interaction was a significant predictor of extinction probability for fox and red squirrels (Table 3), with a marked tendency for local populations in small, highly isolated woodlots to exhibit the greatest probabilities of extinction, whereas populations in the largest and least-isolated tracts exhibited the lowest rates of extinction.

Source-sink dynamics differed greatly among the species. For gray and red squirrels, increased isolation and patch size were associated with an increased influx of individuals, whereas for
Table 4.—Sensitivity, $S_y$, of population size at year 50 to changes in parameter values for the expected dispersal distance travelled before mortality ($E(\text{Dist})$), detection radius ($\text{Radius}$), and survival rates of juvenile ($S_j$), yearling ($S_y$), and adult ($S_a$) squirrels. Results were obtained for metapopulations simulated on a Tippecanoe County, Indiana, landscape. Initial values of parameters are described in the text, and $n$ represents the number of replicates.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Species</th>
<th>in Parameter</th>
<th>Sensitivity</th>
<th>$n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$E(\text{Dist})$</td>
<td>Fox</td>
<td>2</td>
<td>0.0</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.025</td>
<td>0.4</td>
</tr>
<tr>
<td></td>
<td>Gray</td>
<td>5</td>
<td>0.0</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.0625</td>
<td>0.7</td>
</tr>
<tr>
<td></td>
<td>Red</td>
<td>8</td>
<td>0.0</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.1</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>Flying</td>
<td>70</td>
<td>0.0</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.875</td>
<td>0.1</td>
</tr>
<tr>
<td>$\text{Radius}$</td>
<td>Flying</td>
<td>0.5</td>
<td>0.5</td>
<td>20</td>
</tr>
<tr>
<td>$S_a$</td>
<td>Fox</td>
<td>1.2</td>
<td>1.9</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Gray</td>
<td>1.2</td>
<td>8.7</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Red</td>
<td>1.2</td>
<td>1.9</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Flying</td>
<td>1.2</td>
<td>9.8</td>
<td>10</td>
</tr>
<tr>
<td>$S_j$</td>
<td>Flying</td>
<td>1.2</td>
<td>3.3</td>
<td>10</td>
</tr>
<tr>
<td>$S_y$</td>
<td>Flying</td>
<td>1.2</td>
<td>2.0</td>
<td>10</td>
</tr>
</tbody>
</table>

Fig. 6.—Elasticity, the proportional contribution to population growth rate, of age-specific fertility coefficients and probabilities of survival. Filled symbols represent probabilities of survival, whereas hollow symbols represent fertility coefficients.
Table 5.—Presence of tree squirrels in forested sites in and adjacent to Tippecanoe County, Indiana, classified by area and isolation, and expressed as the number of sites containing squirrels divided by the total number examined within a particular classification. Example: 1/3 indicates presence in one of three sites.

<table>
<thead>
<tr>
<th>Degree of Isolation</th>
<th>Species</th>
<th>Small</th>
<th>Medium</th>
<th>Large</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fox</td>
<td>1/1</td>
<td>2/2</td>
<td>2/2</td>
<td></td>
</tr>
<tr>
<td>Red</td>
<td>0/1</td>
<td>2/2</td>
<td>1/2</td>
<td></td>
</tr>
<tr>
<td>Gray</td>
<td>0/1</td>
<td>1/2</td>
<td>2/2</td>
<td></td>
</tr>
<tr>
<td>Flying</td>
<td>0/1</td>
<td>1/2</td>
<td>2/2</td>
<td></td>
</tr>
<tr>
<td>Fox</td>
<td>4/4</td>
<td>4/4</td>
<td>1/1</td>
<td></td>
</tr>
<tr>
<td>Red</td>
<td>0/4</td>
<td>2/4</td>
<td>0/1</td>
<td></td>
</tr>
<tr>
<td>Gray</td>
<td>0/4</td>
<td>1/4</td>
<td>0/1</td>
<td></td>
</tr>
<tr>
<td>Flying</td>
<td>0/4</td>
<td>0/4</td>
<td>1/1</td>
<td></td>
</tr>
<tr>
<td>Fox</td>
<td>3/3</td>
<td>1/1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Red</td>
<td>0/3</td>
<td>1/1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gray</td>
<td>0/3</td>
<td>0/1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Flying</td>
<td>0/3</td>
<td>0/1</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

southern flying squirrels the opposite was true. Attributes of patches had no effect on source-sink dynamics of fox squirrels (Table 3).

**Sensitivity analysis.**—Population size was relatively unaffected by changes in the probability of dispersal mortality for all species, with $S_n$ values of 0-0.70 (Table 4). Changes in the radius of detection had little effect on model results for southern flying squirrels ($S_n = 0.46$).

In contrast, rates of population growth were sensitive to various aspects of survival and fertility, and interspecific differences were apparent. Rates of population growth were most affected by survivorship of adults for all species (Fig. 6). Among species, survival of adults was relatively more important in influencing growth rates of fox squirrels, whereas survival of juveniles had less of an effect on this species (Fig. 6). Elasticity values of fertility coefficients were greatest for adults of all species, with fox squirrels exhibiting the smallest value (Fig. 6).

Values of $S_n$ derived from alteration of parameter values in the full stochastic model confirmed that population size was sensitive to changes in survival of adults, with changes having the greatest impact on gray and southern flying squirrels (Table 4). The reduced sensitivities of fox and red squirrels reflect their superior ability to cope with fragmentation. Because fox and red squirrels exist in simulated fragmented landscapes at densities closer to carrying capacity than either gray or southern flying squirrels (Fig. 5), density dependence limits their ability to respond to changes in survival rates of adults relative to the latter two species.

**Livetrapping data.**—To permit qualitative comparison with simulation results, data on presence-absence of species at each of the 18 forested areas was cross-classified according to size of woodlot and isolation (Table 5). Fox squirrels were in all forested sites. Red squirrels were less common but occurred in sites irrespective of their degree of
isolation or size. Gray squirrels and southern flying squirrels never occurred in small or isolated woodlots.

DISCUSSION

Interspecific differences.—Populations of all four species of tree squirrels were affected negatively by fragmentation of forests in our simulations (Fig. 5), but to varying degrees. In general, populations of red squirrels were least affected. The effects of fragmentation on red squirrels undoubtedly are buffered by the large growth potential of the species ($\lambda_r = 1.35$), which permits rapid repopulation of vacant patches.

Fragmentation also seemed to have less of an effect on fox squirrels. Growth potential of fox squirrels ($\lambda_f = 1.08$) was lower than red squirrels, making their success all the more remarkable. As a consequence of their well-developed ability to disperse (Table 1), dispersal mortality of fox squirrels typically was low relative to the other species. Because of their use of agricultural crops, fox squirrels also were affected less by variation in production of mast.

Gray squirrels and southern flying squirrels fared poorly in the fragmented landscapes that we modeled. Although flying squirrels are quite mobile in continuous tracts of mature forest, we were unable to find documentation of extensive movements over open ground. If an agricultural matrix is a major impediment to movements of flying squirrels, then clumps of forest patches in close proximity presumably would provide the most innocuous form of fragmentation. Consistent with this prediction, our factorial simulations revealed that populations of flying squirrel fared better in clumped landscapes, due to a reduction in dispersal mortality.

Fragmentation of midwestern forests coincided with declines in abundance of gray squirrels (Nixon et al., 1978), and our model yielded results consistent with these observations. The potential rate of growth of gray squirrels is comparable to that of fox squirrels, and their dispersal ability is seemingly well developed. Our simulations suggest two factors that may contribute to the poorer performance of gray squirrels. First, the stable age distribution of gray squirrels contains proportionately fewer adults than for fox squirrels (Table 1). This discrepancy is even more pronounced after winter and before the first birth pulse, when only 43% of the gray squirrel population consists of adults, whereas 39% are subadults. By comparison, adults and subadults comprise 66 and 14% of fox squirrel populations at this stage of the annual cycle. Following a year in which populations were reduced by a poor mast crop, populations of gray squirrels would recover more slowly because of a relative dearth of adult females. In addition, the stable age structure suggests that because of the relative abundance of subadult gray squirrels, dispersal rates in spring should be higher for gray squirrels than for fox squirrels, and this expectation was borne out by our simulations. Second, gray squirrels are more severely affected by poor production of mast than fox squirrels because they make limited use of agricultural crops as a supplemental source of food (Korschgen, 1981).

Influence of patch size and isolation.—Simulations with the Tippecanoe County landscape indicated that isolation of a patch had the greatest impact on gray squirrels; more-isolated patches exhibited lower relative densities and larger probabilities of annual extinction (Table 3). These results are consistent with data on regional trends in abundance and distribution of gray squirrels. Gray squirrels declined throughout the Midwest in the 1800s as settlers cleared land for increasingly intensive agricultural uses, indicating that loss and fragmentation of extensive tracts of mature forest precipitated the reduction in populations (Nixon et al., 1978). Area of a woodlot dictated occupancy most strongly for gray squirrels (Table 3), with larger woodlots being more likely to contain gray squirrels. Brown and Batzli (1984) examined selection of habitat by gray squirrels and concluded that the size of a forest patch may be an important determinant of occupancy for the species, relative to fox squirrels.

The source-sink dynamics of patches apparently were governed by dispersal ability in our fragmented landscapes (Table 3). Species with poor ability to disperse (i.e., flying squirrels) produced more colonists in large and, to a marginal degree, more isolated patches. Presumably, the size of these patches buffered them against local extinctions, yet their isolation made them relatively inaccessible to potential immigrants. Conversely, species with well-developed dispersal ability (i.e., gray and red squirrels) produced fewer colonists in large, isolated patches. For a given shape and orientation, large patches are easier for a disperser to locate than small patches (Gutzwiller and Anderson, 1992). Thus, dispersers operating with a fixed radius of detection, as in our simulations, would have a greater probability of locating a larger patch, creating an area-dependent “oasis effect.” An oasis effect would not occur for southern flying squirrels due to their limited mobility. For fox squirrels, neither isolation nor area of patches correlated with frequency of colonization, indicating that inter-patch movements of fox squirrels were not constrained by these characteristics.

Comparison of simulations with field data.—Our
simulations were consistent not only with findings of previous researchers, but also with our field data. Gray squirrels and southern flying squirrels were captured only in reasonably large forest patches in close proximity to other wooded sites (Table 5). As indicated by our simulations, field data suggest that these species are sensitive to area and isolation effects imposed by fragmentation. Fox squirrels, conversely, were ubiquitous, indicating that the size and isolation of patches have little impact on their distribution in a fragmented landscape such as that encountered in Tippecanoe County. Again, this result was consistent with predictions from our simulations. Red squirrels apparently were not affected by degree of woodlot isolation (Table 5), but they were not distributed as widely across the landscape as predicted by our simulations. This disparity could stem from the relatively recent appearance of red squirrels into the area in conjunction with plantings of Pinus (Mumford and Whitaker 1982), although we cannot rule out alternative explanations (see below).

Determinants of guild structure.—Our results suggest that fragmentation of forests strongly influences the structure of this guild of squirrels, and that interspecific differences in demography and behavior are more likely to determine guild structure than interspecific competition. Here, we generate hypotheses, formulated as questions, regarding the effect of biotic and abiotic factors on guild organization at local and landscape levels. We hope that these hypotheses, as well as our tentative predictions, will stimulate further research on this or other guilds in fragmented environments.

To what extent do differences in demography and mobility influence the structure and dynamics of a guild? Our simulations suggest that growth potential can be an important determinant of a species’ success in a fragmented landscape. Based on a simulation model, Fahrig and Palowhelmo (1988) concluded that species with an enhanced ability to disperse are less affected by fragmentation, and that high local rates of dispersal reduce abundance in the affected patch. Thus, vagile species with good growth potential should fare well in fragmented landscapes, all else being equal. In our models, however, changes in mobility had little effect on population size (Table 4). Pulliam et al. (1992) also found that population size of Bachman’s sparrow (Atmophila aestiva) was affected much less by changes in dispersal ability relative to changes in survival of adults. Closer inspection of this prediction will require better demographic data, particularly for survival of adults (Fig. 6). In particular, data on age-specific fertility and survival are scarce for southern flying squirrels and virtually nonexistent for red squirrels in deciduous forests. Moreover, movements of squirrels in fragmented landscapes have not been examined in detail, and no information presently exists on the ability of squirrels to detect distant patches of suitable habitat. Factors influencing movements also are poorly understood.

How does environmental variation in food supply influence population dynamics at local and landscape levels? Guild structure in our model was predicated on interspecific differences in demography and dispersal, within the context of a varying food supply. Spatio-temporal variation in production of mast potentially exerts considerable influence over guild dynamics, and may prevent saturation of local patches. The importance of such variation is determined by several factors, including: 1) the diet breadth of a species, 2) its ability to escape poor conditions via dispersal, and 3) demographic characteristics that govern its ability to rebound locally after poor mast years. In all of these respects, fox squirrels apparently are superior to gray squirrels, resulting in a greater degree of buffering from environmental stochasticity. A poor mast year may spell trouble for local populations of southern flying squirrels in a fragmented landscape, because they are characterized by a slow rate of growth, and their poor ability to disperse limits recruitment from outside the patch. Populations of red squirrels can be decimated by mast failures (M. C. Smith, 1968), but they exhibit a greater propensity for in situ recovery following a decline than the other three species.

The role of competition?—Many of the woodlots we trapped contained less than the full complement of species, and it would be tempting to invoke interspecific competition in a fragmented and variable environment as an explanation for this pattern (Cornell and Lawton, 1992). However, our simulation model assumed that each species functioned entirely independently of other species; i.e., we modeled a non-interactive community (sensu Cornell and Lawton, 1992) with no local biotic interactions. Environmental stochasticity can influence community patterns by reducing the relative importance of competition (Drake, 1990), and our simulation findings for this guild, generated in the absence of competition, reasonably mimic patterns observed in the field. Thus, community patterns in this group of species likely arise from interspecific differences in vital rates and susceptibility to random disturbances (i.e., variation in mast). In fact, environmental stochasticity may be of paramount importance in determining the structure of guilds in a fragmented landscape.
In a constant environment, the niche overlap exhibited by these squirrels suggests that strong competitive interactions would ensue (Preston, 1948; Brown and Batzli, 1985a, 1985b), and these interactions might determine whether a species absent from a patch could successfully colonize that patch (Case, 1991). However, in the world of granivorous rodents environmental variation in availability of food is the norm (Nixon et al., 1975 Munger and Brown, 1981). Consequently, it is more appropriate to speak in terms of the relative effects of environmental variation on a species. We hypothesize that among species of similar size, richness in local patches is mediated by the triad of demography, dispersal, and breadth of diet. That is, this triad imposes constraints upon responses of a species to local variation in food supply, and fragmentation exaggerates the importance of these constraints for persistence and mean abundance. When constraints imposed by dispersal are relaxed, as in continuous forests, persistence of species should improve, but with a concomitant increase in interspecific interactions. Thus, we predict that fragments should exhibit lower species richness than continuous forests, with local extinctions of gray and southern flying squirrels occurring most frequently. For species that are better able to tolerate fragmentation, such as fox and red squirrels, we predict greater mean population densities in fragments than in continuous forests. In fact, competitive release induced by fragmentation should extend to other granivores occurring in the landscape, such as white-footed mice (Peromyscus leucopus) and eastern chipmunks (Tamias striatus). Allometric constraints imposed by fragmentation may also become important as the body-size range of the species pool under consideration expands. Small species may achieve release from larger competitors in patches with insufficient areas to support viable populations of the larger species (Nupp and Swihart, 1996). At any rate, we suggest that interspecific interactions are functions of the landscape in which the species occur and are not solely due to intrinsic properties of the species (Danielson, 1991). For the guild considered here, effects of interspecific competition apparently are of lesser importance than intraspecific demographic and ecological responses to environmental stochasticity in determining the structure of local communities.

CONCLUDING COMMENTS

Our metapopulation models for tree squirrels can be improved by refinement of parameters and assumptions, as well as by inclusion of additional biologically relevant information that enables us to view landscapes from a squirrel’s perspective (Boyce, 1992; Lima and Zollner, 1996; Milne, 1992). For instance, species composition of patches undoubtedly is influenced by local habitat features in addition to features of the surrounding landscape, and future attempts to predict guild structure should incorporate variables representing each of these scales (Harris and Kangas, 1988; Van Horne and Wiens, 1991). Moreover, patches undergo succession; hence, changes in their suitability over time also must be considered (Holt et al., 1995). Likewise, the landscape matrix in which patches occur is not uniform; in agricultural areas variation in matrix form, and presumably permeability, is manifested spatially as fields with differing crops and temporally as changes in phenology and rotation of crops. Finally, we know little about the spatial correlation of mast production, yet correlated environments can exact a severe toll on the persistence time of metapopulations (Harrison and Quinn, 1989). Given the importance of variation in production of mast to tree squirrels occupying fragmented landscapes, information on the extent of spatial covariation in production is needed.

Anthropogenic influences on the central hardwoods region have had far-reaching impacts on tree squirrels. As we have shown, forest fragmentation can negatively impact all four species, but greatest impacts are on gray and southern flying squirrels. Although the structure of local patches presumably is influenced primarily by demography, dispersal, and breadth of diet (and perhaps by body size; Nupp and Swihart, 1996), the current guild structure at the landscape level reflects historical effects of large-scale disturbances and biogeographic distributions of species (Cornell and Lawton, 1992; Drake et al., 1993). The guild’s future structure is less clear. Can corridors mitigate the effects of fragmentation for isolation-sensitive species, such as gray and southern flying squirrels? Will the distribution of red squirrels continue to expand, as predicted by our model? Will an increasing emphasis on conservation tillage ameliorate the effects of agriculturally induced fragmentation? It is becoming increasingly clear that aspects of a species’ biology and interactions with other species can be influenced by landscape context. Improving our understanding of landscape-level effects, then, is a necessary step toward improving our ability to predict the consequences of changing landscapes for species and to min-
mize any negative consequences associated with such change.

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