

## Forces structuring tree squirrel communities in landscapes fragmented by agriculture: species differences in perceptions of forest connectivity and carrying capacity

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The North American red squirrel (*Tamiasciurus hudsonicus*) has expanded its range into the central hardwoods of the United States in conjunction with increasing forest fragmentation and declining gray squirrel (*Sciurus carolinensis*) populations. We used translocation experiments and patch occupancy data to test for interspecific differences in mobility and sensitivity to habitat loss and modification by agriculture. We released squirrels in fencerows to test the hypothesis that gray squirrels display inferior mobility relative to red and fox (*S. niger*) squirrels. Elapsed time to movement from fencerows for 76 individuals increased with distance to forest patches and harvesting of crops. Gray and red squirrels took longer to move from fencerows than fox squirrels, and gray squirrels were less successful at moving from fencerows than red and fox squirrels. Ecologically scaled landscape indices revealed the degree to which interspecific differences in mobility and individual area requirements accounted for the occurrence of these species across landscapes. Gray squirrel distribution was constrained both by individual area requirements and dispersal ability. Occurrence of red and fox squirrels was related to patch size but was unaffected by landscape connectivity.

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The boundary of a species' geographic range is determined by numerous factors, including geographic barriers, interspecific interactions, or properties of the physical environment (MacArthur 1972). Range expansion often occurs in response to the alteration of one or more of these factors (Elton 1958), such that historical barriers (physical or biological) to dispersal are removed or modified. Range expansions are facilitated by a species' mobility and dispersal ability (Elton 1958). This is especially true for species exhibiting natural range expansion (i.e. not mediated directly by humans), or following an initial colonization episode (i.e. diffusion dispersal; Davis and Thompson 2000).

The North American red squirrel (*Tamiasciurus hudsonicus*; hereafter red squirrel) is a relatively recent colonist of the central hardwoods region of the central United States. Range expansion of red squirrels in Indiana is ongoing, with the first records of the species occurring more than 60 years after the state was settled by people of European descent (Mumford and Whitaker 1982). Since the early 1900s, this species has gradually expanded its range, and currently it is present in all but the most heavily forested areas in the southwestern portion of the state (Mumford and Whitaker 1982, Goheen and Swihart, unpubl.). Row-crop agriculture is widespread throughout the central United States

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and, in the northern half of Indiana, remaining forest patches of varying sizes and degrees of isolation occur within agricultural landscapes. In contrast, larger, more continuous tracts of forest typify the southern portion of the state. Thus, at a regional scale, red squirrels appear to be insensitive to isolation of forest patches, a hypothesis consistent with research conducted at a landscape scale in west-central Indiana (Nupp and Swihart 2000).

Range expansion of red squirrels has coincided with a reduction in numbers of more fragmentation-sensitive granivores, specifically gray squirrels (*Sciurus carolinensis*). Gray squirrels in the central United States have been affected adversely by agriculturally induced fragmentation of forests, and currently they are restricted to the largest, most continuous forested sites (Rosenblatt et al. 1999, Nupp and Swihart 2000). Further, gray squirrels share a high degree of resource overlap with red squirrels where they co-occur in Indiana (Ivan and Swihart 2000), and significant competitive interactions can occur between these two species (Nupp and Swihart 2001). Thus, range expansion of red squirrels in the central hardwoods potentially has been facilitated by an indirect effect of habitat fragmentation, namely declines in abundance of a fragmentation-sensitive competitor.

A species' ability to traverse an inhospitable matrix is important in determining its presence and abundance in fragmented landscapes (Fahrig and Merriam 1994, Tilman et al. 1994). Species that move greater distances or disperse at greater rates are less likely to be negatively affected by fragmentation (Dunning et al. 1992) in that, for a given probability of mortality during dispersal, higher dispersal rates will lead to reduced effects of fragmentation. Patch isolation (i.e. the distance separating discrete habitat patches) is a key predictor influencing dispersal and interpatch movements, with lower rates of movement occurring between patches separated by greater distances (MacArthur and Wilson 1967, Turchin and Theony 1993, Haddad 1999). Mobility and individual area requirements can influence the degree to which species are affected by habitat fragmentation, and these characteristics interact with physical features of landscapes in determining the fraction of patches occupied by a species across a region (Vos et al. 2001).

Recent models of patchy populations have highlighted the importance of varying levels of matrix quality in predicting species distributions and abundances across fragmented landscapes (Gustafson and Gardner 1996, Moilanen and Hanski 1998, Vandermeer and Carvajal 2001). Empirical support for these matrix-sensitive models has begun to accrue, albeit slowly (Ricketts 2001, Vandermeer et al. 2001). The agricultural fields of the central United States, in which forest patches are embedded, vary in the amount of cover provided as crops grow, senesce, and are harvested

seasonally. The effects of changes in the quality of this agricultural matrix upon movement decisions and subsequent success of individuals likely is influenced by 2 factors: 1) the actual or perceived risk of predation an individual experiences as it moves across the matrix and 2) the degree to which individuals can perceive remote patches of habitat (perceptual range; sensu Lima and Zollner 1996). Behavioral responses to the presence or absence of cover influence an individual's perceived risk of predation (reviewed by Lima and Dill 1990), and increased cover in the matrix may trigger a decision to move between habitat patches. Therefore, we predicted that increased vegetative cover in the matrix should increase the willingness of individuals to move across the landscape as a result of decreased risk of predation, but reduce the ability with which individuals could perceive and subsequently move into the most proximal forest patches.

We conducted an experiment to compare the mobility of red and gray squirrels in a landscape dominated by row-crop agriculture in west-central Indiana. We hypothesized that red squirrels would display superior mobility relative to gray squirrels, given their recent range expansion and greater tolerance of isolation of forest patches. In addition, we assessed the mobility of a second native species, the fox squirrel (*Sciurus niger*), as a baseline for comparison. Fox squirrels are affected much less than other sciurids by isolation of forest patches, and are nearly ubiquitous throughout landscapes in the central United States (Rosenblatt et al. 1999, Nupp and Swihart 2000). We hypothesized that fox squirrels should exhibit superior mobility compared to both red and gray squirrels, providing a test of the assumption that the ability to move through an agricultural landscape is responsible for the current distribution of these species. We also tested the degree to which species-specific differences in dispersal ability account for differential patterns of patch occupancy by examining the ability of ecologically scaled landscape indices (Vos et al. 2001) to predict local occurrences of these species across landscapes in northern Indiana.

## Materials and methods

### Study site

To test hypotheses regarding mobility in relation to squirrel species, distance, matrix permeability, and connectivity, we translocated and radio-tracked squirrels within the Indian Pine Study Area in west-central Indiana. This 812-km<sup>2</sup> area is comprised of a mosaic of isolated forest patches and wooded riparian strips (ca 10% of the total area) embedded within an agricultural matrix subjected primarily to the cultivation of corn and soybeans (ca 70% of the total area). We accessed a geographic information system (GIS) with 1-m resolu-

tion in ArcView (ESRI, Redlands, California) consisting of 7 habitat types: forest, fencerow (woody vegetation), drainage ditch (herbaceous vegetation), wetland, grassland, agricultural field, and human homestead development (Gehring 2000). Forested lands consisted largely of nut-producing trees, e.g. oak (*Quercus* spp.), hickory (*Carya* spp.), black walnut (*Juglans nigra*) and maple (*Acer* spp.), whereas wooded fencerows were comprised largely of hackberry (*Celtis occidentalis*), mulberry (*Morus rubra*), and black cherry (*Prunus serotina*).

We used the GIS as an aid in selecting 13 wooded fencerows at which to translocate squirrels. Each fencerow was paired with a forest patch (0.94–8.05 ha), 28–954 m distant. This range of distances was selected because it encompasses the natural range of dispersal, colonization, and interpatch movements of red, gray, and fox squirrels reported in the literature (Larsen and Boutin 1994, Sheperd and Swihart 1995, Berteaux and Boutin 2000; but see Rosenblatt 1999). Of the 13 fencerows used in our study, 8 were isolated from their paired forest patches (hereafter termed isolated fencerows and patches). Squirrels released into isolated fencerows thus were forced to cross the agricultural matrix before moving into the most proximate forest patch with which the fencerow was paired (Table 1), as in Rosenblatt (1999). The remaining 5 fencerows were extensions of their paired forest patches (hereafter termed connected fencerows and patches). Squirrels departing from a connected fencerow did not have to cross the agricultural matrix before moving into a forest patch (Table 1).

To test the role of dispersal in determining patterns of patch occupancy, we collected data on species occurrence by sampling 60 forest patches (0.5–340 ha) across 5 landscapes in northern Indiana from May through August 2001. The landscapes each were square cells of 23 km<sup>2</sup>. Cells were selected using a stratified random sampling design based on partitioning of 14-digit hydrologic unit codes into clusters of land-use/land-cover. All sites were predominantly agricultural, although 2 sites were somewhat more forested (26.2% and 14.9%) than the other sites (7.0%, 8.0%, and 9.7%). We supplemented data from these sites with species occurrences from 32 forest patches in the Indian Pine Study Area collected from 1992 through 1996 (Nupp 1997). Forest patches across all 6 landscapes varied in distance from their nearest neighboring forest patch by 30–870 m, and forest patches typically lacked fencerow connections with other forested patches.

### Experimental study of mobility

Experimental translocations were conducted from 17 September through 27 November 2000 and from 9 August through 19 November 2001, corresponding with

Table 1. Distance between 13 tree-lined fencerows and associated forest patches. For each distance we report numbers of individuals of each species released in pre-harvest/fallow seasons.

Distance class (m)	Isolated distance (m)	Connected distance (m)
25–75	28	60
red	1/1	0/1
gray	1/1	0/1
fox	1/1	na
76–125	81	na
red	1/1	
gray	1/1	
fox	1/1	
126–200	150	130
red	1/1	0/1
gray	1/1	0/1
fox	1/1	na
201–275	Na	229
red		0/1
gray		0/1
fox		na
276–350	335	300
red	1/3	0/1
gray	1/2	0/1
fox	1/1	na
351–425	367	na
red	1/3	
gray	1/3	
fox	1/1	
500–575	525	544
red	2/1	0/1
gray	2/2	0/1
fox	1/2	na
675–750	703	Na
red	2/1	
gray	1/2	
fox	1/2	
> 850	954	Na
red	2/1	
gray	1/2	
fox	2/2	

the timing of natural dispersal in all three focal species in deciduous forests of North America (Baumgartner 1943, Thompson 1978, Goheen and Swihart, unpubl.). Because of crop harvest, this time period also enabled us to examine whether changes in vegetative cover influenced willingness to move and movement success. The agricultural matrix was characterized by tall, dense vegetation (corn or soybeans; 1–3 m) in the pre-harvest season, but largely was devoid of vegetation following harvest (i.e. the fallow season).

We captured squirrels in Tomahawk™ live traps baited with english walnuts and a peanut butter/oats mixture. Squirrels were trapped in forest patches at least 20 km away from the study area, thus minimizing the chance that individuals were familiar with the surroundings into which they were released. Following capture, squirrels were fitted with a 6.5 g radio collar (Wildlife Materials, Inc., Carbondale, Illinois) and

maintained individually in holding pens (61.0 × 40.6 × 35.6 cm) constructed of stainless steel and hardware cloth. To reduce stress on squirrels, each pen contained a wooden nest box with polyfiber bedding. Squirrels were maintained at a constant temperature (21°C ± 3°) and a 12L:12D photoperiod. A sunflower seed/corn mixture and water were provided *ad lib* prior to translocation. All squirrels were held for 1–7 days before translocation to ensure that they were healthy. To translocate squirrels, we transported nest boxes containing squirrels to fencerows between 0700 and 1100 hours on clear days. Nest boxes remained at the release site and were available to squirrels for 7 days.

Natal dispersal occurs in summer and early autumn months for all three species, and adults undergo spatial reorganization and dispersal in late summer and autumn months (Baumgartner 1943, Thompson 1978, Koprowski 1985, Price et al. 1986, Boutin et al. 1993, Berteaux and Boutin 2000, Goheen and Swihart, unpubl.). Only adult males and females (non-gravid, non-lactating) were used in this experiment, because we suspected that juveniles would incur a greater risk of predation and move shorter distances as compared to adults (Lin and Batzli 1995, Rohner and Krebs 1996). Thus, our results should be conservative and, if anything, underestimate the effects of forest fragmentation. At least one individual from each species was released at each isolated fencerow in both pre-harvest and fallow seasons (Table 1). Releases in connected fencerows were restricted to red and gray squirrels during the fallow season (Table 1), because fox squirrels routinely travel 200–500 m along wooded corridors (Sheperd and Swihart 1995); thus, we were most interested in documenting patterns between red and gray squirrels. In 2001, three individuals of each species were released at selected fencerows in both seasons, with the first of these three being based on the maximum distance at which movement from fencerows was noted for previous releases in 2000. The subsequent release distances were contingent on whether the first individual moved from its respective fencerow, and the final release distance was contingent on whether the second individual moved from its respective fencerow. If an individual moved from the fencerow in which it was released, the subsequent individual was released in the fencerow associated with the next longest distance to a forest patch. If an individual did not move from a fencerow (i.e. remained at the fencerow for 7 days), the subsequent individual was released at the same fencerow.

Following release, squirrels were relocated daily to identify the landscape element (forest patch, fencerow, agricultural matrix) in which they occurred. Squirrels were located between 0700 and 1100 hours using a vehicle-mounted 3-element Yagi antenna. We allowed squirrels to remain in fencerows for a maximum of 7 days following release, after which time individuals that had not been noted away from fencerows were recap-

tured and their radio collars were removed. This time period was selected because Rosenblatt (1999) reported means of  $2.25 \pm 3.86$  and  $3.75 \pm 2.75$  days prior to movement from an experimental release site of fox and gray squirrels, respectively. Squirrels attempting to move from fencerows in which they were released within the 7-day period were radio tracked for a minimum of 14 days (range: 14–22) to document movement events and mortality. Squirrels surviving the duration of the tracking period were recaptured, their radio collars were removed, and they were released at their original capture sites.

### Patch occupancy

Occupancy of forest patches was determined by live-trapping during spring and summer. Tomahawk™ live traps were spaced at 30-m intervals and Sherman™ live traps at 15-m intervals in either grid or web arrays, pre-baited for 1–2 days with english walnuts, pecans, or sunflower seeds, and then checked for 4–5 days. Sampling for 4–5 days was necessary to reduce to <0.15 the probability of falsely concluding that a species was absent from a patch (Gu and Swihart, unpubl.). Further details of handling and trapping are provided by Nupp and Swihart (2000).

### Statistical analyses

We modeled mobility as a two-step process. First, we used multiple regression to assess the impact of six predictor variables (squirrel species, proximity, connection between fencerows and paired forest patches, pre-harvest versus fallow season, sex, and area of paired forest patch) and a covariate (area of fencerow) upon willingness to move, as measured by the elapsed time (days) until movement from a fencerow.

For individuals that moved from fencerows into which they had been released, we conducted a logistic regression to assess the effect of the predictor variables upon success, which we defined as movement into a forest patch within the allotted 7-day time period and subsequent survival to the end of the tracking period. Consequently, failure was defined as either mortality (due to predation or exposure) following attempted movement, or a terminal movement into a landscape element other than a forest patch (e.g. another fencerow). If movements into a landscape element other than a forest patch were defined as success, the fit of our regression model increased by 0.10 but did not alter other results. We documented the cause of failure for all individuals except a male red squirrel released in the fallow season in a connected fencerow 130 m from its associated forest patch that subsequently moved into the associated forest patch then vanished. The squirrel

either shed its radio collar or died. We treated this as a failure event in the analyses, although the individual may have been alive. Treating this event as a success or omitting it from the analysis increased the fit of our regression model by 0.06, but did not alter other results. A stepwise selection algorithm was used, with  $\alpha = 0.20$  to enter the model and  $\alpha = 0.10$  to stay in the model. Squirrel species were represented as two indicator variables (SPSS Inc., 1997).

We used Fisher's exact test to determine if season affected whether squirrels leaving fencerows moved into paired forest patches (i.e. those patches nearest to the release sites). For those squirrels not moving into paired forest patches, we subtracted the area of the paired forest patch from the patch into which they moved, then used a Kruskal–Wallis test to compare the effects of squirrel species, proximity, and sex on the difference in area between the selected patch and the nearest patch. Results from the test were used to infer whether individuals of a particular sex or season were more likely to move into larger forest patches. Individuals released in fencerows connected to a paired forest patch were not included in this analysis.

Ecologically scaled landscape indices (ESLI; Vos et al. 2001) were used to assess the impact of mobility and patch area upon occurrence of each species across landscapes for the 92 forest patches sampled in our study. ESLIs are advantageous as compared to neutral landscape indices in that they link ecological characteristics of species with physical features of landscapes. Consequently, ESLIs account for scale-dependent responses of different species to habitat fragmentation. Following Vos et al. (2001), we constructed two ESLIs as indicators of species sensitivity to habitat fragmentation. In the first, the area requirement for a single reproductive unit (individual area requirement; e.g. a pregnant female) was used to account for species-specific extinction risk as a function of patch size:

$$K_{si} = A_i / IAR_{si}$$

where  $K_{si}$  is the number of individuals of species  $s$  that can occupy patch  $i$ ,  $A_i$  is the area of patch  $i$  and  $IAR_{si}$  is the individual area requirement of species  $s$  in patch  $i$ .

The second ESLI was a patch-specific measure of connectivity. Landscape connectivity varies between species as a function of mobility; thus, following the logic and terminology of Vos et al. (2001),

$$C_{si} = \sum_{j \neq i}^n A_j \exp(-\alpha_s D_{ij})$$

where  $C_{si}$  is the connectivity of species  $s$  in patch  $i$ , which is the sum of all contributions of neighboring patches  $j$  weighted both by their area ( $A_j$ ) and distance to focal patch  $i$  ( $D_{ij}$ ). The contribution of a patch at

distance  $D_{ij}$  declines exponentially with the species-specific parameter  $\alpha_s$ , such that  $1/\alpha_s$  represents the mean dispersal distance of species for a particular season. Using our mobility data from experimental releases, we estimated the maximum dispersal distance of each species as the 95<sup>th</sup> percentile of a negative exponential distribution using  $1/\alpha_s$  as the parameter (i.e. mean distance moved) for the distribution for both pre-harvest and fallow seasons. Although dispersal distance can depend upon landscape structure (With 1994), the landscape composition and physiognomy within the Indian Pine Study Area is representative of that in the five other landscapes in northern Indiana. In calculating mean dispersal distances, squirrels that did not move from fencerows were assigned a distance of 0 m in the analysis. Because depredated individuals were not consumed by avian predators at the kill sites, we omitted squirrels from the analysis that moved from fencerows but failed. Values of  $C_{si}$  in both seasons were averaged together to create a single  $C_{si}$  for connectivity for each species in each forest patch.

We used logistic regression analyses to assess relationships between the ecologically scaled landscape indices,  $K_{si}$  and  $C_{si}$ , and occurrence of each species in sampled patches. Landscapes were coded as a series of five dummy variables in the analyses. We conducted one analysis for each species, using a stepwise selection algorithm as described previously.

## Results

### Experimental study of mobility

We trapped, released, and radio tracked 28 (13 male, 15 female) red squirrels, 28 (12 male, 16 female) gray squirrels, and 20 (11 male, 9 female) fox squirrels. Of these, a male red squirrel and a male fox squirrel could not be detected 2 days after release, and a male gray squirrel and a male fox squirrel were depredated at the release site. These individuals were excluded from the analyses.

Stepwise multiple regression revealed several significant predictors of willingness of individuals to move across the agricultural matrix (full model:  $R^2 = 0.46$ ;  $d.f. = 4, 70$ ;  $P = < 0.0001$ ). Specifically, the elapsed time (days) until movement from a fencerow increased with distance to associated forest patches ( $t = 6.54$ ,  $d.f. = 1$ ,  $P < 0.0001$ ), fallow-season releases ( $t = 4.45$ ,  $d.f. = 1$ ,  $P < 0.0001$ ), and declining area of associated forest patches ( $t = 2.55$ ,  $d.f. = 1$ ,  $P < 0.01$ ). Elapsed time to movement from fencerows was not affected by sex ( $P = 0.58$ ), fencerow connectedness ( $P = 0.18$ ), or the area of fencerows into which squirrels were released ( $P = 0.32$ ). A shorter mean elapsed time to movement was exhibited by fox squirrels as compared to red and gray squirrels ( $t = 2.21$ ,  $d.f. = 1$ ,  $P = 0.03$ ). Because fox

squirrels differed from gray and red squirrels in their willingness to move from fencerows, we constructed regression models for individual species in both seasons using only those individuals released in isolated fencerows (Fig. 1). For all species, latency to movement increased with increasing distance to associated forest

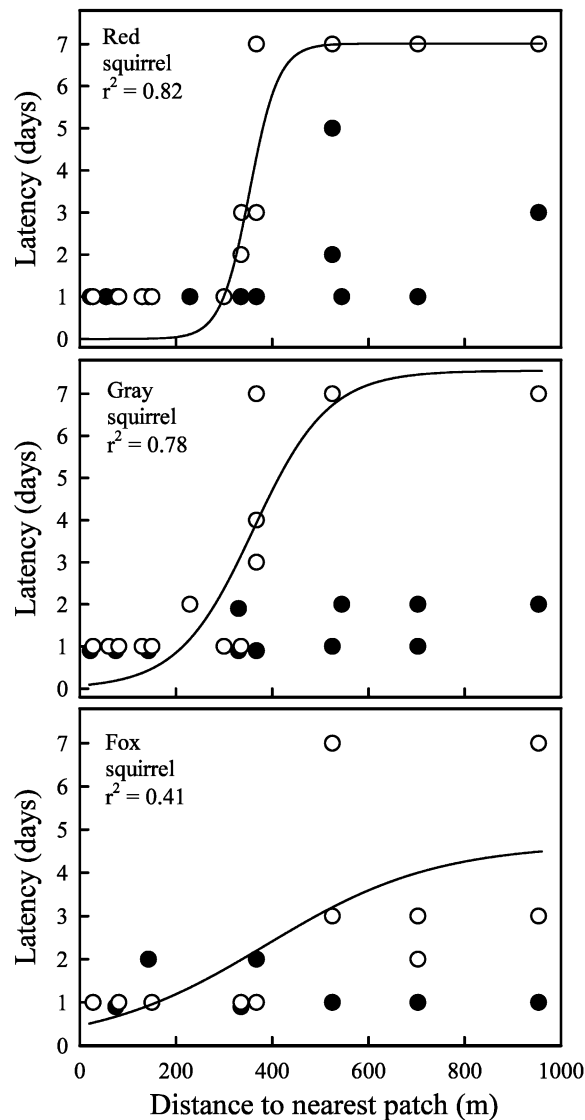


Fig. 1. Willingness of tree squirrels to move from fencerows under pre-harvest (solid circles) and fallow (open circles) field conditions as a function of distance to associated patches. Individuals that did not move from fencerows were assigned a latency of 7 days. For clarity, only equations regression lines for fallow season releases are presented. Three-parameter logistic models provided the best fit for gray and red squirrel fallow-season data. No difference in fit was noted for linear or logistic models for fox squirrel data, so the logistic model is provided for consistency. Fox squirrel model: elapsed time =  $4.67/(1 + 9.13\exp(-0.006 \times \text{distance}))$ ; gray squirrel model: elapsed time =  $7.55/(1 + 102.29\exp(0.013 \times \text{distance}))$ ; red squirrel model: elapsed time =  $7.01/(1 + 130209\exp(-0.033 \times \text{distance}))$ .  $P < 0.05$  for all models.

patches in both seasons ( $P < 0.05$  for all regressions). At distances  $> 400$  m, latency to movement increased dramatically for red and gray squirrels in a sigmoidal fashion, whereas latency to movement was more linearly related to distance for fox squirrels (Fig. 1).

Of the 76 squirrels released in our experiment, 21 red squirrels, 21 gray squirrels, and 16 fox squirrels moved from fencerows. Of these, 19, 14, and 15 were successful, with one red squirrel and six gray squirrels being depredated by avian predators (presumably red-tailed hawks, *Buteo jamaicensis* or great horned owls *Bubo virginianus*). Gray squirrels were less likely to succeed after attempting movement from fencerows than the other 2 species ( $R^2 = 0.14$ ,  $d.f. = 1$ ,  $P = 0.03$ ). Distance to associated forest patch, season, sex, connectivity, and area of associated forest patch were not significant predictors of movement success ( $P > 0.20$  for all variables).

Squirrels were less likely to move from fencerows to the nearest forest patch during the pre-harvest season when crop cover still existed (Fisher's exact test,  $P < 0.01$ ). A Kruskal-Wallis test revealed that the likelihood of moving to forest patches larger than those paired with fencerows did not vary as a function of sex, season, distance, or a sex by season interaction ( $P > 0.10$  for all variables).

### Patch occupancy

Ecologically scaled landscape indices were significant predictors of occurrence in patches for gray, fox, and red squirrels across Indiana landscapes (Table 2). Presence of all 3 species was positively related to  $K_{st}$ , and presence of gray squirrels also was positively related to  $C_{st}$ . Probability of occurrence for gray and red squirrels was unrelated to landscape identifier as measured by indicator variables, but was a significant predictor for fox squirrels.

### Discussion

Although both gray and red squirrels were similar in their willingness to move from fencerows, gray squirrels were less likely to succeed in moving into forest patches. The overall survival of gray squirrels moving from fencerows was  $71.4 \pm 9.2\%$ , whereas survival of red and fox squirrels was  $95.2 \pm 2.3\%$  and  $100\%$ , respectively. Fox squirrels were more willing than red and gray squirrels to move from fencerows following translocation, but red squirrels did not differ significantly from fox squirrels in success.

Although not predicted, these results support the notion that recent range expansion of red squirrels into Indiana, concurrent with declining gray squirrel populations throughout the central United States, may be

Table 2. Predictive models of squirrel presence in 6 fragmented landscapes of northern Indiana. Landscapes were scaled ecologically for individual area requirements ( $K_{st}$ ) and dispersal ability of species ( $C_{st}$ ). See text for further details.

Species	coefficients			% concordant*	$R^2$	$P$
	$b_0$	$b_1$	$b_2$			
Gray squirrel	-12.60	+0.010( $K_{st}$ )	+0.049( $C_{st}$ )	92.4	0.31	<0.001
Fox squirrel	-0.02	+0.015( $K_{st}$ )		75.8	0.44	<0.001
Red squirrel	-9.35	+0.001( $K_{st}$ )		76.9	0.18	<0.001

\* Percentage of cases in which the occurrence of species was correctly predicted by the model.

partly a result of species-specific differences in the risk of predation incurred during and immediately following movement events across an agricultural matrix. Litvaitis and Litvaitis (1996) documented a similar situation, whereby the eastern cottontail (*Sylvilagus floridanus*) has expanded its range in conjunction with declining New England cottontail (*S. transitionalis*) populations in fragmented portions of New England. Elevated rates of predation upon New England cottontails in fragmented landscapes were a likely mechanism driving this range expansion (Smith and Litvaitis 2000). More generally, species colonization in response to the extirpation, removal, or reduction of competitors is predicted from theory (Karieva and Wennergren 1995) and has been documented for birds (Diamond and Veitch 1981) and mammals (Ernest and Brown 2001).

In accord with our prediction, squirrels were more likely to move from fencerows across the landscape during the pre-harvest season, when vegetative cover was present in the matrix. We attribute the observed increase in likelihood of moving to a decrease in perceived risk of predation. An increased risk of predation during and immediately following dispersal and other movements has been documented in a number of mammalian species (Anderson 1989, Van Vuren and Armitage 1994, Olupot and Waser 2001), and reduced mobility, dispersal, or interpatch movements are probably a result of this (Wauters et al. 1994).

Squirrels in the pre-harvest season also were less likely to move to the most proximal forest patches as compared to those in the fallow season, irrespective of distance to the closest forest patch. Moreover, we detected no differences in size between those forest patches not paired with fencerows into which individuals moved and forest patches paired with fencerows. These results contrast with predictions of the target-area hypothesis, which states that individuals moving in a random fashion (i.e. similar to that if perceptual range were impaired) from release sites have a greater chance of encountering larger, more proximal habitat patches (Lomolino 1990, Goodwin et al. 1999). We interpret this result as selection for particular patches in the landscape during the pre-harvest season.

Willingness to move across the landscape also was negatively related to the degree of isolation of associated forest patches from their release sites. Although

intuitive, there are few empirical examples among mammals documenting higher levels of dispersal and interpatch movements as a result of lower levels of isolation (Andreassen and Ims 1998). The increased willingness of fox squirrels to move across the landscape may result from its habitat affinities and evolutionary history; fox squirrels prefer forest patches < 40 ha and evolved under savannah-like conditions at the interface of the central hardwoods and tallgrass prairie (Koprowski 1994).

Fox squirrels differed from red and gray squirrels in willingness to move from fencerows as a function of distance to the nearest forest patch. A sigmoidal curve characterized this relationship for red and gray squirrels, indicating a threshold distance at ca 400 m beyond which animals were unwilling to leave a fencerow. Thus, forest patches isolated from potential sources > 400 m may not be recolonized by these species following local extinction. Given that translocated individuals presumably were under an abnormally high degree of pressure to leave fencerows, it is possible that the threshold distance beyond which colonization does not occur naturally is much lower.

When northern Indiana landscapes were scaled ecologically to account for interspecific differences in dispersal ability and individual area requirements of squirrels, two general themes emerged. First, ecologically scaled landscape indices were significant predictors of patch occupancy, supporting the findings of Vos et al. (2001) that ESLIs can be useful tools for evaluating effects of landscape fragmentation. Second, only the occurrence of gray squirrels was affected by both isolation and area of forest patches, which suggests that gray squirrel distribution in fragmented landscapes is constrained both by colonization ability and individual area requirements. In contrast, red and fox squirrels appeared sensitive only to area of forest patches, suggesting that abandonment of small patches or constraints imposed by individual area requirements are responsible for local extinction and are driving the distribution of these species across northern Indiana. Indeed, dispersal ability generally appears to be less important in determining the occurrence of more mobile species, except for those species occurring in very isolated patches of habitat (Lomolino 1984).

The sensitivity of gray squirrels to both area and distance effects highlights the importance of habitat arrangement in landscapes subjected to a high degree of fragmentation. In a recent study, Flather and Bevers (2002) investigated the relative effects of habitat amount versus habitat arrangement upon population responses in a series of simulated landscapes. They found that the amount of habitat within a landscape accounted for >96% of the variation in population size. However, in examining only those landscapes below the persistence threshold (i.e., the amount of habitat required within a landscape for population persistence; in their study, between 30% and 50%), habitat arrangement explained ca 36% of the variation in population size. Our landscapes range between 7% and 26% forested habitat. Thus, given its sensitivity to both area and isolation of forest patches, we suspect that the majority of landscapes in northern Indiana occur below the persistence threshold for gray squirrels.

Our study provides support for differential dispersal ability as a mechanism underlying patterns of red, gray, and fox squirrel occurrence across fragmented landscapes. Nupp and Swihart (2000) found that distributions of these species and three other granivorous rodents exhibited a highly ordered pattern of nestedness across 37 woodlots in west-central Indiana. The “nested-subset hypothesis” (Patterson and Atmar 1986) was first introduced to explain patterns in the distribution of species in insular habitats. Across a series of mountaintops in the southern Rocky Mountains, assemblages of small mammals on smaller mountaintops contained nonrandom (i.e. nested) subsets of a larger species pool. Thus, the “nestedness” exhibited by a series of habitat islands quantifies the degree to which species composition on these islands is shaped by the forces of colonization and extinction.

Although nested patterns within insular communities have been noted for an array of taxa (Kodric-Brown and Brown 1993, Hecnar and M'Closkey 1997, Millien-Parra and Jaeger 1999), few experimental tests of mechanisms promoting nestedness exist. By using ecologically scaled landscape indices to account for variation in species-specific responses to habitat fragmentation, we have documented the relative importance of colonization and extinction in determining the local occurrence of red, gray, and fox squirrels in northern Indiana. Superior mobility of red squirrels appears to be an important factor facilitating their range expansion into fragmented landscapes of the central hardwoods, in which gray squirrel populations have declined.

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