

RESOURCE SELECTION AND PREDATION OF NORTH AMERICAN RED SQUIRRELS IN DECIDUOUS FOREST FRAGMENTS

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The North American red squirrel (*Tamiasciurus hudsonicus*) typically is regarded as having strong affinities for coniferous forests throughout its geographic range. In the state of Indiana, the red squirrel has expanded its geographic range concurrent with fragmentation of deciduous forests and widespread plantings of conifers. We undertook a radiotelemetry study to assess resource selection and survival of this species in 2 woodlots dominated by deciduous trees in west-central Indiana. Squirrels selected habitats with a high proportion of black walnut (*Juglans nigra*), avoided other hard mast-producing species, and avoided conifers. Squirrels exhibited overlapping home ranges, consistent with other studies on eastern populations. Individuals whose core areas contained conifers experienced higher survival rates than those individuals whose core areas did not contain conifers. We conclude that the increased safety conferred by conifers, as well as the presence of black walnut in these forests, are likely to contribute strongly to this species' persistence in Indiana.

Key words: deciduous forest, habitat, home range, red squirrel, resource selection, survival, *Tamiasciurus hudsonicus*

The North American red squirrel (*Tamiasciurus hudsonicus*; hereafter red squirrel) has expanded its geographic range into the state of Indiana concurrent with anthropogenic fragmentation of forests since the mid-1800s (Mumford and Whitaker 1982). Range expansion of the red squirrel is ongoing (R. K. Swihart, T. E. Nupp, J. R. Goheen, and S. Schnellker, in litt.) and probably has been facilitated by its superior dispersal ability relative to a fragmentation-sensitive competitor, the gray squirrel (*Sciurus carolinensis*—Goheen et al. 2003a; Nupp and Swihart 2001). In addition, range expansion of the red squirrel has coincided with the widespread propagation of conifer plantations in Indiana (Mumford and Whitaker 1982).

Red squirrels have strong coevolutionary ties with coniferous trees throughout the boreal forests of northern and western North America (Benkman 1995; Smith 1970), where they maintain and aggressively defend conifer cones from conspecifics in a central cache or larder (Steele 1998 and references therein). In eastern North America, dependence on conifer seeds is not as pronounced as in western populations, but eastern red squirrels display affinities for coniferous habitats nonetheless (Dempsey and Keppie 1993; Layne 1954; Riege 1991). Thus,

range expansion of red squirrels also might be due in part to the availability of a resource that was absent historically.

Two aspects of coniferous habitats might facilitate persistence and further range expansion of red squirrel populations in Indiana. First, conifers might provide a resource preferred over other foods (e.g., hard mast) or habitats (e.g., deciduous trees), or a resource used as a “buffer” when preferred foods are scarce or unavailable (e.g., mast failure). In other regions of their geographic range, red squirrel populations are limited by food availability (Klenner and Krebs 1991; Sullivan 1990; but see Rusch and Reeder 1978), and survival of individuals has been correlated with food abundance (Halvorson and Engeman 1983). Second, coniferous trees might confer to squirrels some increased measure of safety from predators. Some authors have speculated that the permanent canopy cover and interlocking branches of coniferous trees afford more opportunities for squirrels to escape potential predators (Smith 1968; Vahle and Patton 1983). Rusch and Reeder (1978) suggested that predation drove differential survival rates between squirrels inhabiting coniferous and deciduous habitats in Alberta, with individuals in coniferous habitats experiencing lower mortality. Augmentation of food and decreased risk of predation are not mutually exclusive hypotheses, and they might operate synergistically with one another to promote range expansion of red squirrels into Indiana.

We conducted a radiotelemetry study of red squirrels in a highly fragmented portion of the central hardwoods region in west-central Indiana. Our primary objective was to quantify resource selection of, and determinants of home range size for,

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red squirrels at the periphery of their geographic range in the eastern United States. Previous work in our study system demonstrated a positive relationship between density of red squirrels and presence of conifers in forest patches (Nupp 1997), although the processes responsible for this are unclear. Thus, as a secondary objective, we explored underlying mechanisms through which coniferous habitats might have contributed to the persistence and range expansion of red squirrels into Indiana. Knowledge of these objectives is critical to understanding how and why populations of red squirrels have been able to expand into and persist in a region in which they were absent historically.

MATERIALS AND METHODS

Study site and radiotelemetry.—The study was conducted from February 2000 to November 2001 in 2 forest patches in Tippecanoe County, Indiana (40°14'50.62N, 86°49'50.74W and 40°30'28.06N, 86°47'26.88W). The smaller of these patches (about 15.4 ha), known as the Waser forest, was comprised almost exclusively of deciduous tree species. Approximately one-third (28.96%) of the larger patch (about 32.0 ha), known as the Cunningham forest, was a conifer plantation established in the 1930s. Conifer stands were comprised mainly of eastern white pine (*Pinus strobus*), jack pine (*P. banksiana*), and red pine (*P. resinosa*). These forest patches were embedded within an agricultural matrix subjected to cultivation primarily of corn and soybeans.

Red squirrels were trapped at irregular intervals throughout the study. We captured squirrels in Tomahawk live traps (Tomahawk Live Trap Company, Tomahawk, Wisconsin) baited with English walnuts and a peanut butter-oats mixture. Traps were positioned at the bases of trees to maximize capture success. Following capture, we fitted each adult squirrel with a 6.5 g radiocollar (Wildlife Materials, Carbondale, Illinois) and a single fingerling ear tag. We recorded sex, mass, and reproductive condition of each individual.

Squirrels were located via triangulation with a handheld 3-element Yagi antenna and compass. We obtained fixes on radiocollared squirrels from telemetry stations scattered throughout each site. The locations of these stations were recorded via a global positioning system (GPS); these recorded locations were accurate to within 2 m of actual station locations. We tried to obtain 3–6 fixes per individual within 10 min to minimize telemetry error. Only fixes with vectors forming 70°–110° angles were used to further reduce error (White and Garrott 1990). We tested the accuracy of fixes by locating radiocollars placed at geo-referenced points ($n = 50$); test collars were placed on the ground and in trees. The absolute value of angular error ($3.36 \pm 4.71^\circ$) resulted in an average error polygon of 398.0 m².

Squirrels were located at randomly predetermined times between 0600 and 2000 h. Each squirrel was located 2–4 times per week during the period over which it was monitored. In addition, we estimated individual movements over extended periods (2–3 h), obtaining 1 location per individual every 15 minutes. Most individuals were monitored until collar battery failure (generally 8–10 weeks) or mortality due to predation. When batteries failed, we attempted to retrap squirrels and remove or replace their radiocollars. All predation events among radiocollared individuals were assigned to mammalian or avian predators based upon squirrel remains. Trapping and handling of squirrels was conducted under guidelines of the American Society of Mammalogists (1998) and a protocol approved by the Purdue Animal Care and Use Committee.

Analyses of home range size and composition.—We used program Locate II to estimate locations of squirrels (Nams 2000). We calculated 90% and 50% home range contours in conjunction with

the fixed kernel density estimator using the ArcView 3.2 Animal Movement Extension (Hooge and Eichenlaub 2000; Worton 1989). Home range contours were used to estimate total home range and core sizes, respectively, and represented the 90% and 50% confidence regions of individuals' utilization distributions (i.e., the probability distribution of an individual's position in a plane of interest). All locations were used for home range and core size estimation because kernel estimators are robust to violations of independence (Swihart and Slade 1997). Kernel estimators were formulated only for those squirrels having ≥ 30 locations to maximize accuracy of home range estimates (Seaman et al. 1999). For each individual, we regressed the number of total locations per individual against estimated home range areas (ha). We checked visually to make sure home range size estimates approached an asymptote to further ensure locations were sufficient to estimate home range size.

To assess home range composition, we recorded locations of brush piles, fallen logs, snags, and trees ≥ 20 cm diameter at breast height (dbh) via GPS, resulting in locations for 3,884 and 1,726 features at Cunningham and Waser forests, respectively. The mean GPS error noted for these locations was 4.0 ± 2.7 m. For both living and dead (hereafter snags) trees, we noted the occurrence of natural cavities and cavities made by woodpeckers (*Picoides*). Next, we constructed a geographic information system (GIS) for both forest patches using a series of 22×22 m (484 m²) grid cells. This area was selected based on GPS and telemetry error. Each tree species was classified as "walnut," "other hard mast," "soft mast," "non-mast," or "conifer" (Appendix I). After recording each tree and its classification within each grid cell, we used *k*-means cluster analysis (Legendre and Legendre 1998) to assign grid cells to 1 of 6 distinct resource groups that we specified prior to conducting the analysis: walnut, other hard mast, soft mast, non-mast, conifer, and indeterminate composition. This procedure placed grid cells into 1 of the above groups by minimizing the Euclidean distance between a grid cell and its cluster centroid. Group membership was assigned based on the composition and abundance of tree species occurring within each 22×22 m cell (Appendix I). In addition, we used a 2nd *k*-means cluster analysis to assign grid cells to 1 of 5 distinct "microhabitat" groups: brush piles, cavities, fallen logs, snags, and indeterminate composition. Because this analysis failed to produce interpretable cluster centroids, we conducted a factor analysis with subsequent varimax rotation (Legendre and Legendre 1998). This produced 1 of 3 factor loadings for each cell: nest sites (cavities and snags), woody debris (brush piles and fallen logs), and indeterminate composition.

We used backward-stepping multiple regression (SAS Institute Inc. 2001) to test for the effects of walnut and conifer use (i.e., the proportion of an individual's radio locations that occurred in walnut or conifer grid cells, respectively) upon core area and home range size. In addition, we included season as a categorical predictor in each model. Availabilities of both habitats were omitted from the analyses because of strong collinearity with use ($r > 0.82$, $P < 0.001$ for all). Finally, we used a Kolmogorov-Smirnov test to examine differences in core area and home range size between individuals at Waser forest and those individuals at Cunningham forest without conifers in their core areas or home ranges.

Analyses of spatial interactions.—We used the methods of Doncaster (1990) to estimate static and dynamic interaction between pairs of squirrels. Following Sheperd and Swihart (1995), we omitted from the analyses all pairs showing less than 5% overlap in home ranges.

Static interaction was calculated by overlap of 2 home ranges, combined with concordance in some part of the utilization distributions. We estimated this latter component by ranking 22×22 m grid cells according to their use (i.e., the number of locations falling

within each) for each individual. We then calculated Spearman's r for each pair of squirrels. Spearman's r covaried significantly ($P < 0.0001$) and positively ($r = 0.70$) with home range overlap; therefore, we treated the standardized residuals resulting from this as an index of static interaction. Thus, positive standardized residuals would characterize pairs of squirrels that tended to use areas of overlap intensively. We then used a Kruskal-Wallis test to examine the effects of season and squirrel pair type (male-male, female-female, male-female) on the standardized residuals.

Dynamic interaction is defined as dependence in the simultaneous movements of individuals. If individuals are attracted to one another, distances between simultaneous observations should be shorter than those associated with nonsimultaneous observations. Conversely, if individuals avoid one another, distances between simultaneous observations should be longer than those associated with nonsimultaneous observations (Doncaster 1990). We treated individuals that we located within 20 min of each other as simultaneous observations. Following Doncaster (1990), we constructed a 4×4 variance-covariance matrix \mathbf{A} comprised of four 2×2 submatrices ($\mathbf{A}_{11}, \mathbf{A}_{12}, \mathbf{A}_{21}, \mathbf{A}_{22}$), where \mathbf{A}_{11} and \mathbf{A}_{22} represent variances and covariances from each animal, and \mathbf{A}_{12} and \mathbf{A}_{21} represent the covariances x_1x_2, x_1y_2 , etc. for both individuals. A measure of the strength of the interaction is then given by $V = |\mathbf{A}| / (|\mathbf{A}_{11}| * |\mathbf{A}_{22}|)$, and a significance test of the null hypothesis of no interaction is given by $W = (N - 4)(1 - \sqrt{V}) / (2\sqrt{V})$, where N is the number of simultaneous observations.

Analyses of resource selection.—We detected no significant spatial interactions between most pairs of squirrels (see "Results" section). Thus, we used compositional analysis (Aebischer et al. 1993) to assess habitat selection of squirrels at both Cunningham and Waser forests. Compositional analysis is unique among resource selection methodologies in that individuals, not locations, are treated as sampling units. This technique evaluates selection of habitat types and, if use of habitats is found to be nonrandom with respect to availability, assigns a ranking of preferences based on the log ratios of used to available habitat types. MANOVA models are used to evaluate whether habitat composition within home ranges differs from the availability of habitat types across the study site as a whole ("2nd-order habitat selection"). MANOVA models are then used to assess whether habitat use within home ranges, indexed by the proportion of locations within a given habitat type, is random with respect to availability of that type within the home range ("3rd-order habitat selection"). For each site in each season, we ran an analysis for 2nd and 3rd-order habitat selection (using resource groups from the cluster analysis) and 3rd-order microhabitat selection (using loadings from the factor analysis). There were a total of 6 habitat types at Cunningham forest (black walnut, other hard mast, soft mast, non-mast, conifer, indeterminate composition) and 5 habitat types at Waser forest (no conifer type; Appendix I). Microhabitat types (nest sites, woody debris, and indeterminate composition) were identical between sites. Both analyses were conducted using Program Resource Selection for Windows (Leban 1999).

Survival analyses.—We used program MICROMORT (Heisey and Fuller 1985) to estimate survival rates of squirrels as a function of the following categorical covariates: season (growing [January–June] versus mast [July–December]), sex, and conifer occurrence within home ranges and cores. In addition, we compared survival rates of all squirrels at Waser forest to those of squirrels at Cunningham forest whose core areas contained no conifer. MICROMORT requires data on the number of radiodays in an interval as well as the number of deaths in an interval. Within an interval, survival rates of individuals are assumed to be constant and independent. Program CONTRAST (Hines and Sauer 1989—www.mbrpwr.usgs.gov/software.html,

5 January 2004) was used to test for differences in survival between selected groups. Program CONTRAST allows the user to make multiple comparisons for rate data by using associated standard errors or variance and covariance estimates, and tests the null hypothesis of homogeneity of survival rates against a chi-square distribution. Results are presented as mean \pm SD .

RESULTS

Determinants of home range and core size.—We captured 84 squirrels 160 times in 3,802 trap days. Of these, 44 (17 male, 27 female) had ≥ 30 radiolocations ($\bar{X} = 43$, range = 30–98). For each of the 44 individuals, estimated home range sizes reached an asymptote, ensuring that locations were sufficient to estimate home range size. A total of 1,872 locations were used in the analyses. Mean 90% home range sizes for males (0.88 ± 0.93 ha) and females (1.03 ± 1.15 ha) were not significantly different ($t = 0.49$, $df = 42$, $P = 0.63$). Mean 50% core sizes for males (0.21 ± 0.25 ha) and females (0.19 ± 0.17 ha) were not significantly different ($t = -0.25$, $df = 42$, $P = 0.81$).

Multiple regression revealed several significant predictors of home range size ($R^2 = 0.38$, $df = 3, 40$, $P < 0.01$) and core size ($R^2 = 0.53$, $df = 3, 40$, $P < 0.01$). Specifically, 90% home range sizes increased with increasing use of conifer ($r = 0.41$, $P = 0.01$) and decreasing use of walnut ($r = -0.30$, $P = 0.06$). In addition, home ranges were larger during the season in which mast was available ($P = 0.01$). Similarly, core areas increased with increasing use of coniferous species ($r = 0.61$, $P < 0.01$) and decreasing use of walnut ($r = -0.36$, $P = 0.02$). Core areas also were larger during the season of mast availability ($P = 0.01$). No strong collinearity was detected among predictors for either analysis (tolerance > 0.90 for all predictors). Finally, individuals that did not use conifer at Cunningham forest had significantly larger core areas ($Z = 1.59$, $P = 0.01$) and home ranges ($Z = 1.56$, $P = 0.01$) than individuals at Waser forest.

Spatial interactions.—Thirty-nine pairs of squirrels (9 male-male, 11 female-female, and 19 male-female) were used in interaction analyses. Mean overlap of home ranges (± 1 SD) was $14.5 \pm 9.9\%$. After correcting for effects of home range size, static interactions between males and females did not differ. No significant trends were noted between seasons ($\chi^2 = 0.779$, $df = 1$, $P = 0.378$). With 1 exception (a male-female pair exhibiting attraction during the growing season), we failed to detect significant dynamic interactions between pairs of squirrels (all $W < 0.77$, $P > 0.10$).

Resource selection.—Habitat and microhabitat selection did not differ as a function of season, so we pooled observations between seasons. Second-order selection of habitats was nonrandom with respect to availability for squirrels at both Cunningham (Wilk's $\lambda = 0.186$, $P < 0.0001$) and Waser (Wilk's $\lambda = 0.19$, $P < 0.01$) forests. In both forest patches, individuals selected habitats with a high proportion of black walnut and soft mast and avoided habitats with a high proportion of hard mast species other than walnut (Table 1; Fig. 1). Further, individuals avoided habitats with a high proportion of coniferous species at Cunningham forest (Table

TABLE 1.—Matrices of *t*-statistics and corresponding *P*-values comparing use between pairs of habitat types for 2nd-order selection as determined by compositional analysis with pooled seasons. Low stocking was used as the reference habitat type. Preference rankings for each habitat type are given, with the most preferred habitat = 1, the 2nd most preferred habitat = 2, to least preferred = 6.

Cluster	Walnut	Other hard	Soft	Non	Conifer	Low	Rank
Cunningham forest							
Walnut	na	3.56 0.002	0.29 0.77	1.17 0.26	1.79 0.09	0.16 0.87	1
Other hard mast		na	-3.25 0.01	2.26 0.04	-1.09 0.29	-3.70 0.002	6
Soft mast			na	1.06 0.30	1.75 0.10	0.04 0.97	2
Non-mast				na	0.59 0.57	1.92 0.07	3
Conifer					na	-2.17 0.05	5
Waser forest							
Walnut	na	8.30 <0.0001	3.49 0.001	2.06 0.05		1.02 0.32	1
Other hard mast		na	-2.48 0.02	-6.47 0.004		-3.16 <0.0001	5
Soft mast			na	1.00 0.33		1.87 0.07	2
Non-mast				na		1.01 0.32	3

1; Fig. 1). Third-order selection of habitats (i.e., within home ranges) was non-random with respect to availability for squirrels at Cunningham forest (Wilk's $\lambda = 0.20$, $P < 0.0001$), with individuals selecting habitats of indeterminate composition (Figure 2). The null hypothesis of no selection could not be rejected for individuals at Waser forest (Wilk's $\lambda = 0.89$, $P = 0.53$). Within home ranges, use of microhabitats did not differ significantly from the null hypothesis of no selection for individuals at Cunningham forest (Wilk's $\lambda = 0.81$, $P = 0.16$) or Waser forest (Wilk's $\lambda = 0.85$, $P = 0.10$).

Survival.—Twenty-five of the 44 squirrels with ≥ 30 locations were monitored for the life of their radiocollars. Seventeen of the 44 squirrels with ≥ 30 locations were depredated during the course of the study. Except for 2 individuals with < 30 locations who died due to exposure to inclement weather, predation was the sole source of mortality for squirrels in this study. Of the 17 individuals depredated, 15 displayed signs characteristic of avian predation (decapitation, bones stripped of flesh) whereas 2 displayed signs characteristic of mammalian predation (disembowelment, bones broken). The remaining 2 individuals with ≥ 30 locations disappeared from Waser forest following approximately 2 months of monitoring. We searched extensively with a vehicle-mounted antenna over a 10-km radius around the site but could not find them. Treating these observations as mortality or survival events did not alter our qualitative or quantitative conclusions; these individuals were not included in the analysis.

Males and females did not differ with respect to survival rates, and survival rates of squirrels from Waser forest did not differ from those at Cunningham forest after taking the effects of

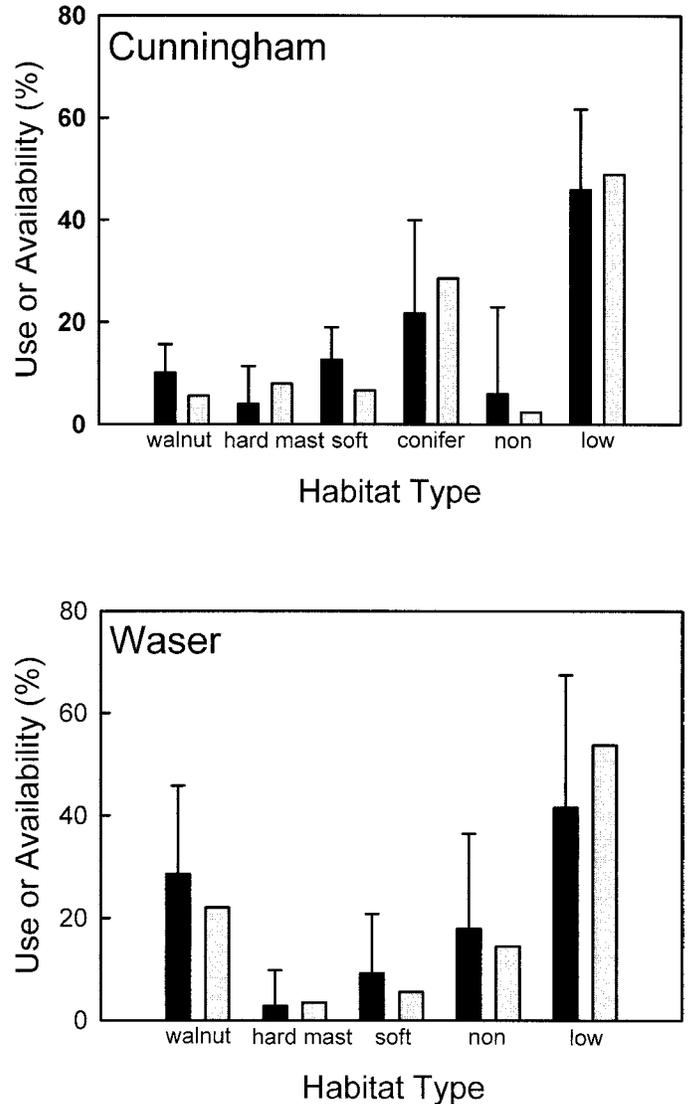


FIG. 1.—Results of 2nd-order resource selection (resource selection within study sites) using compositional analysis. Use of each resource within the forest patch (black bars) is compared with availability of that resource (gray bars). At both forest sites, red squirrels selected black walnut and avoided other species of hard mast. At Cunningham forest, red squirrels avoided conifer. Bars indicate mean \pm SD.

conifer into account ($P > 0.20$ for all tests). Thus, we pooled across sexes when testing for survival effects due to the use of conifers. Estimates of survival rates were greater for squirrels occupying conifers in all comparisons. However, survival rates were significantly greater only when core areas were considered, and only during the January–July period ($P < 0.0001$; Table 2). The annual survival rates of squirrels utilizing conifers in their core areas were substantially greater than for squirrels not utilizing conifers and approached significance ($P = 0.063$; Table 2).

DISCUSSION

At our study sites in west-central Indiana, red squirrels selected habitats with a high proportion of black walnut and soft

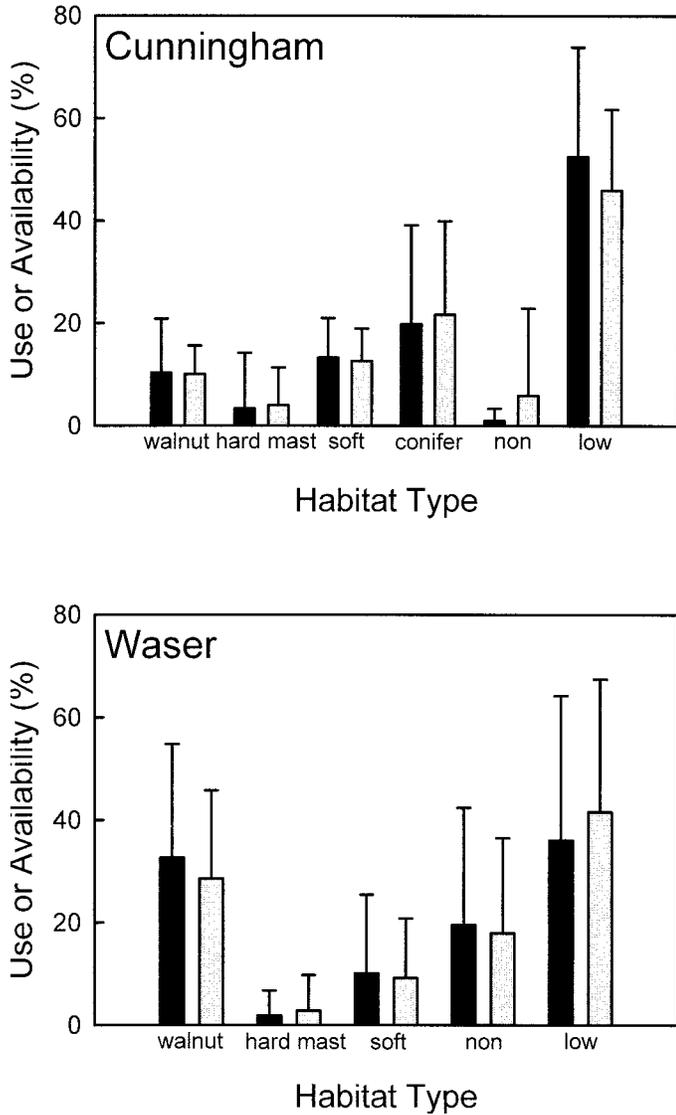


FIG. 2.—Results of 3rd-order resource selection (resource selection within home ranges) using compositional analysis. Use of each resource within the home range (black bars) is compared with availability of that resource (gray bars). At Cunningham forest, red squirrels selected areas of low tree species stocking or indeterminate composition. Bars indicate mean \pm SD.

mast and avoided habitats with high proportions of conifers and hard mast-producing species other than walnut. Home range and core sizes were inversely correlated with use of black walnut, and home range and core sizes were positively correlated with use of conifer. Space use by animals often is dictated by resource abundance and quality, as individuals tend to have smaller home ranges or defend smaller territories when resources are abundant or of high quality (reviewed in Adams 2001; Boutin 1990). In a series of field experiments, we showed previously that red squirrels avoided consumption of conifer cones and preferred instead to hoard black walnuts (Goheen and Swihart 2003; Goheen et al. 2003b). Food preferences of red squirrels in Indiana are driven largely by perishability of foods (Goheen et al. 2003b); thus, it seems likely that habitat selection by red

TABLE 2.—Results of survival analyses for squirrels whose cores and home ranges contained conifers.

Conifers present?	Estimate of survival	SE	χ^2	P
Core area, Jan–July				
No	0.450	0.127	18.74	<0.0001
Yes	1.000	0.000		
Core area, Aug–Dec				
No	0.469	0.126	0.68	0.409
Yes	0.700	0.250		
Core area, annual				
No	0.211	0.082	3.45	0.063
Yes	0.700	0.250		
Home range, Jan–July				
No	0.427	0.137	1.87	0.172
Yes	0.765	0.205		
Home range, Aug–Dec				
No	0.468	0.134	0.37	0.545
Yes	0.618	0.210		
Home range, annual				
No	0.200	0.086	1.51	0.219
Yes	0.473	0.205		

squirrels is a consequence of the reduced perishability of black walnut, relative to foods in other habitats.

Within home ranges, we noted no consistent trends in selection of habitats or microhabitats. This might have arisen for 2 reasons: selective neutrality within home ranges or methodological difficulties. Red squirrels are dietary generalists, consuming conifer seeds, hard mast, soft mast, and fungi (Steele 1998), and can build nests in trees (Fancy 1980), cavities (Layne 1954), or underground burrows (Yahner 1980). Thus, after having selected habitats with high proportions of black walnut within forest patches, squirrels might have used habitats and microhabitats equally within home ranges. Additionally, we might have experienced methodological problems in assessing availabilities of microhabitats. We only were able to make note of those cavities that were visible at ground level; thus, we might not have detected all cavities available to squirrels. Finally, our grid cell sizes were based on a combination of GPS and telemetry error, and thus were not of a sufficiently detailed resolution to detect fine scale selectivity of individual features. Others have demonstrated that habitat selection is more difficult to demonstrate with increasingly smaller scales of availability (Garshelis 2000; McClean et al 1998).

Red squirrels at our study sites exhibited overlapping home ranges. Overlapping home ranges and a reduction or absence of territoriality are characteristic of this species in eastern portions of its geographic range, particularly in deciduous habitats (Deutch 1978; Layne 1954; Pesce 1982). This has been attributed to the occurrence of other mast consumers (at our study sites, fox squirrels [*Sciurus niger*] and eastern chipmunks [*Tamias striatus*]). Because territory defense is costly to red squirrels (Stuart-Smith and Boutin 1994), the energy necessary to maintain and defend a territory in the presence of multiple mast-consuming

species might outweigh the benefits (Deutch 1978). In addition, the ability to visually detect and thus defend against intruders might be impaired in deciduous habitats (Deutch 1978).

Previous work in our system has demonstrated a positive relationship between presence of conifer and density of red squirrels (Nupp 1997) and, throughout Indiana, the occurrence of red squirrels in forest patches is strongly and positively related both to occurrence of conifer and of black walnut (J. R. Goheen and R. K. Swihart, in litt.). Because this pattern was well established prior to our study, we attempted to elucidate its causal mechanisms by conducting an intensive study within 2 forest patches differing in the occurrence and abundance of coniferous species. Although site differences partly explained variation in home range and core size, resource selection and factors influencing predation were similar between sites, lending support to our conclusions.

In nature, habitats containing high quality or quantities of food often are more risky with respect to predation (Houston et al. 1993). Although conifer was avoided within forest patches and was correlated with increased core sizes, squirrels whose core areas contained conifers had higher survival rates than those individuals having core areas in which conifers were unavailable. This was likely due to a reduction in the risk of raptor predation, either because of some increased measure of safety provided by conifers or because raptors preferred to hunt in deciduous habitats. Steury and Murray (2003) documented a decreased risk of predation with increasing territory size for red squirrels in coniferous forests in Idaho; however, this was likely due to a positive correlation between resource availability and territory size (Steury and Murray 2003).

Our study demonstrates that conifers were not a preferred resource for red squirrels, although it was not conducted long enough to assess the potential role of conifers as a buffer food source (see "Introduction"). Nonetheless, red squirrels did derive benefits from conifers. Throughout the state, the occurrence of red squirrels in forest patches is significantly related to the presence of conifer (J. R. Goheen and R. K. Swihart, in litt.). Thus, increased safety from predators derived from the presence of conifer may contribute to the range expansion and persistence of this species into Indiana.

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LITERATURE CITED

- ADAMS, E. S. 2001. Approaches to the study of territory size and shape. *Annual Review of Ecology and Systematics* 32:277–303.
- AEBISCHER, N. J., P. A. ROBERTSON, AND R. E. KENWARD. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313–1325.
- ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by The American Society of Mammalogists. *Journal of Mammalogy* 79:1416–1431.
- BENKMAN, C. W. 1995. The impact of tree squirrels (*Tamiasciurus*) on limber pine seed dispersal adaptations. *Evolution* 49:585–592.
- BOUTIN, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. *Canadian Journal of Zoology* 68:203–220.
- DEMPSEY, J. A., AND D. M. KEPPIE. 1993. Foraging patterns of eastern red squirrels. *Journal of Mammalogy* 74:1007–1013.
- DEUTCH, R. S. 1978. Seasonal activity budget of the red squirrel (*Tamiasciurus hudsonicus*) in a southern Ohio deciduous forest. M.S. thesis, University of Dayton, Dayton, Ohio.
- DONCASTER, C. P. 1990. Non-parametric estimates of interaction from radio-tracking data. *Journal of Theoretical Biology* 143:431–443.
- FANCY, S. G. 1980. Nest-tree selection by red squirrels in a boreal forest. *Canadian Field-Naturalist* 94:198.
- GARSHELIS, D. L. 2000. Delusions in habitat evaluation. Pp. 111–164 in *Research techniques in animal ecology* (L. Boitani and T. K. Fuller, eds.). Columbia University Press, New York.
- GOHEEN, J. R., AND R. K. SWIHART. 2003. Food-hoarding behavior of gray squirrels and North American red squirrels in the central hardwoods region: implications for forest regeneration. *Canadian Journal of Zoology* 81:1636–1639.
- GOHEEN, J. R., R. K. SWIHART, T. M. GEHRING, AND M. S. MILLER. 2003a. Forces structuring tree squirrel communities in fragmented landscapes: species differences in perceptions of forest connectivity and carrying capacity. *Oikos* 102:95–103.
- GOHEEN, J. R., R. K. SWIHART, AND J. H. ROBINS. 2003b. The anatomy of a range expansion: changes in cranial morphology and rates of energy extraction for North American red squirrels from different latitudes. *Oikos* 102:33–44.
- HALVORSON, C. H., AND R. M. ENGEMAN. 1983. Survival analysis for a red squirrel population. *Journal of Mammalogy* 64:332–336.
- HEISEY, D. M., AND T. K. FULLER. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. *Journal of Wildlife Management* 49:668–674.
- HOOGE, P. N., AND B. EICHENLAUB. 2000. Animal movement extension to ArcView. Version 2.0. Alaska Science Center, Biological Science Office, U.S. Geological Survey, Anchorage.
- HOUSTON, A. I., J. M. MCNAMARA, AND J. M. C. HUTCHINSON. 1993. General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society of London, B. Biological Sciences* 341:375–397.
- KLENNER, W., AND C. J. KREBS. 1991. Red squirrel population dynamics. I. The effect of supplemental food on demography. *Journal of Animal Ecology* 60:961–978.
- LAYNE, J. N. 1954. The biology of the red squirrel *Tamiasciurus hudsonicus loquax* in central New York. *Ecological Monographs* 24:227–267.
- LEBAN, F. A. 1999. Resource selection for Windows: user's guide. F. A. Leban, University of Idaho, Moscow.
- LEGENDRE, P., AND L. LEGENDRE. 1998. Numerical ecology. 2nd edition. Elsevier Science B.V., Amsterdam, The Netherlands.

- MCCLEAN, S. A., M. A. RUMBLE, R. M. KING, AND W. L. BAKER. 1998. Evaluation of resource selection methods with different definitions of availability. *Journal of Wildlife Management* 62: 793–801.
- MUMFORD, R. E., AND J. O. WHITAKER, JR. 1982. *Mammals of Indiana*. University of Indiana Press, Bloomington.
- NAMS, V. O. 2000. *Locate II user's guide*. Pacer, P.O. Box 641, Truro, Nova Scotia, Canada.
- NUPP, T. E. 1997. Population dynamics and community structure of granivorous forest rodents in a fragmented landscape. Ph.D. dissertation, Purdue University, West Lafayette, Indiana.
- NUPP, T. E., AND R. K. SWIHART. 2001. Assessing competition between forest rodents in a fragmented landscape of the Midwestern United States. *Mammalian Biology* 66:1–12.
- PESCE, A. 1982. Dynamics of a non-territorial population of red squirrels (*Tamiasciurus hudsonicus*) in southeastern Michigan. M.S. thesis, University of Michigan, Ann Arbor.
- RIEGE, D. A. 1991. Habitat specialization and social factors in distribution of red and gray squirrels. *Journal of Mammalogy* 72:152–162.
- RUSCH, D. A., AND W. G. REEDER. 1978. Population ecology of Alberta red squirrels. *Ecology* 59:400–420.
- SAS INSTITUTE INC. 2001. *SAS/STAT user's guide*. Release 8.2. SAS Institute Inc., Cary, North Carolina.
- SEAMAN, D. E., J. J. MILLSPAUGH, B. J. KERNOHAN, G. C. BRUNDIGE, K. J. RAEDEKE, AND R. A. GITZEN. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63: 739–747.
- SHEPHERD, B. F., AND R. K. SWIHART. 1995. Spatial dynamics of fox squirrels (*Sciurus niger*) in fragmented landscapes. *Canadian Journal of Zoology* 73:2098–2105.
- SMITH, C. C. 1968. The adaptive nature of social organization in the genus of tree squirrels, *Tamiasciurus*. *Ecological Monographs* 38: 31–63.
- SMITH, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. *Ecological Monographs* 40:349–371.
- STEELE, M. A. 1998. *Tamiasciurus hudsonicus*. *Mammalian Species* 586:1–9.
- STEURY, T. D., AND D. L. MURRAY. 2003. Causes and consequences of individual variation in territory size in the American red squirrel. *Oikos* 101:147–156.
- STUART-SMITH, A. K., AND S. BOUTIN. 1994. Costs of escalated territorial defense in red squirrels. *Canadian Journal of Zoology* 72: 1162–1167.
- SULLIVAN, T. P. 1990. Responses of red squirrel (*Tamiasciurus hudsonicus*) populations to supplemental food. *Journal of Mammalogy* 71:579–590.
- SWIHART, R. K., AND N. A. SLADE. 1997. On testing for independence of animal movements. *Journal of Agricultural, Biological, and Environmental Statistics* 2:48–63.
- VAHLE, J. R., AND D. R. PATTON. 1983. Red squirrel cover requirements in Arizona mixed conifer forests. *Journal of Forestry* 81: 115–127.
- WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California.
- WORTON, B. J. 1989. Kernel methods for estimating the use distribution in home-range studies. *Ecology* 70:164–168.
- YAHNER, R. H. 1980. Burrow system use by red squirrels. *American Midland Naturalist* 103:409–411.

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APPENDIX I

Composition and abundance loadings of major tree species for each of 5 distinct clusters, as determined by k-means cluster analysis.—In addition to the 5 clusters mentioned in the text, a 6th cluster was formulated to represent low abundance of all species and/or indeterminate composition. The number of grid cells for each cluster in both forest patches is reported. Walnut cluster—black walnut (*Juglans nigra*), 66 in Cunningham forest, 32 in Waser forest; other hard mast cluster—black oak (*Quercus velutina*), bur oak (*Q. macrocarpa*), chinkapin oak (*Q. muehlenbergii*), pin oak (*Q. palustris*), red oak (*Q. rubra*), shingle oak (*Q. imbricaria*), swamp white oak (*Q. bicolor*), white oak (*Q. alba*), bitternut hickory (*Carya cordiformis*), mockernut hickory (*C. tomentosa*), pignut hickory (*C. glabra*), shagbark hickory (*C. ovata*), American beech (*Fagus grandifolia*), 55 in Cunningham forest, 5 in Waser forest; soft mast cluster—black cherry (*Prunus serotina*), hackberry (*Celtis occidentalis*), honey locust (*Gleditsia triacanthos*), Kentucky coffee tree (*Gymnocladus dioica*), osage-orange (*Maclura pomifera*), red mulberry (*Morus rubra*), 50 in Cunningham forest, 8 in Waser forest; nonmast cluster—American basswood (*Tilia americana*), American elm (*Ulmus americana*), American sycamore (*Platanus occidentalis*), eastern cottonwood (*Populus deltoides*), red elm (*U. rubra*), silver maple (*Acer saccharinum*), sugar maple (*A. saccharum*), 36 in Cunningham forest, 21 in Waser forest; conifer cluster—eastern white pine (*Pinus strobus*), jack pine (*P. banksiana*), red pine (*P. resinosa*), 181 in Cunningham forest.