

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. Schnelker, 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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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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