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Resource patch array use by two squirrel species in an agricultural landscape

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Abstract

Eastern grey squirrels (*Sciurus carolinensis*) and North American red squirrels (*Tamiasciurus hudsonicus*) were studied among wooded patches within an agricultural mosaic. Fifteen sites south of Ottawa, Canada, with differing landscape and local features were censused using tracking boards placed in a woods or wooded fencerow. Regression analyses of landscape compositional and physiognomic variables within a 1-km radius isolated the best predictors of grey and red squirrel abundance and activity. Grey squirrels were found in both small woods and fencerows in farm landscapes but were not found in large woods. A polynomial regression of wooded patch size explained 79% of the variance in grey squirrel abundance. Grey squirrel activity was correlated with the percent cover of soybeans in the landscape. Red squirrels were found in fencerows, small and large woods; activity was correlated with the percent cover of both woods and corn crop in the surrounding landscape. These results indicate that distributions of both species are influenced by multiple landscape elements, but that grey squirrels may rely on fragmented agricultural landscapes whereas red squirrels make more use of both native woodland and altered landscapes.

Introduction

A heterogeneous landscape is typically viewed as a mosaic of natural habitat patches embedded in an anthropogenically-modified ‘neutral’ matrix (Bright 1993). On a finer scale, the matrix itself can be considered to be a mosaic of different patch types: vegetable crops, grain crops, pastureland, and so on (Tapper and Barnes 1986). Wooded or other natural fragments are not isolated islands of suitable habitat in a sea of impenetrable altered landscape; usually there is a degree of connectivity that allows interpatch movement for species among those fragments (Taylor et al. 1993). For some woodland species, connections are provided by wooded farm fencerows (Henein 1995). However, some woodland species are capable of moving across the landscape without the aid of fencerows, depending on patch composition (Wegner and Merriam 1990).

Organisms deal with alterations in the compositional and physiognomic patterns of their environment in different ways. The degree of flexibility in a species’ behavioural traits may allow or restrict use of a new, radically different habitat or resource type (Merriam 1991). We postulated that in a fragmented agricultural landscape, the array created by the juxtaposition of remnant wooded patches and various novel agricultural patches may make the landscape conducive to occupation by organisms not normally associated with the landscape before it was fragmented. Such a ‘mosaic species’ (sensu Bright 1993) would necessarily be able to exploit novel, ephemeral, or disturbed habitats and use elements from several different patch types. Examples of such mosaic species include *Peromyscus leucopus* (Wegner and Merriam 1990; Wegner 1995) and *Lepus europaeus* (Tapper and Barnes 1986). Conversely, some native species traditionally associated with the forest habitat react adversely to the effects of habitat loss and isolation, and hence would be found in limited numbers in a complex mosaic. These 'natural species' (sensu Bright 1993) would not be able to utilise resources in novel patch types; examples include the eastern chipmunk *Tamias striatus* (Henderson et al. 1985; Bennett et al. 1994; Henein 1995), and the Eurasian red squirrel *Sciurus vulgaris* (Andren and Delin 1994; Celada et al. 1994).

To investigate our assumptions regarding differential response to habitat fragmentation, the distribution patterns of two species: the eastern grey squirrel (*Sciurus carolinensis*), a geographically expansionist species, and the North American red squirrel (*Tamiasciurus hudsonicus*), a native species, were studied in farm landscapes in eastern Ontario. The landscape in this area is composed mainly of cultivated fields of a variety of crops, including corn, alfalfa, hay, soybean, and grains. Crops have replaced mixed transitional forest as the dominant landscape feature for over 100 years (Middleton and Merriam 1983), but tracts of mixed and coniferous forests, pure deciduous stands, residual farm woodlots (wooded fragments), and fencerows remain.

In the past the grey squirrel was rare in eastern Ontario, but has become more prevalent in the last century with range expansion (Peterson 1957; Dobbyn 1994). Carroll (1992) suggested that terrestrial species that exhibit large-scale geographic range expansions do so primarily because they flourish in fragmented habitats. We believed that this was the case for grey squirrels. Our first hypothesis was that grey squirrels would be found in highest abundance in landscapes that consisted of both wooded cover and agricultural crops. We expected lowest abundance in landscapes dominated by forested tracts that lacked agricultural patches.

In contrast, the North American red squirrel is a native of eastern Ontario's mixed transitional forests (Dobbyn 1994). It feeds primarily on pine and spruce seeds and cedar buds (Riege 1991) and dens in tree cavities, leaf nests, or ground dens (Gurnell 1987). To date little is known about North American red squirrel population dynamics in agricultural mosaics, but inferences can be drawn from studies of the Eurasian red squirrel *S. vulgaris*, a coniferous forest specialist like *T. hudsonicus* (Gurnell 1983). Wauters et al. (1994) found decreased *S. vulgaris* density in wooded fragments compared to continuous woodland. Van Apeldoorn et al. (1994) confirmed that *S. vulgaris* did use wooded fragments, but found that these were inhabited by unstable populations with high turnover rates. Negative effects of small fragment size and isolation on squirrel density were found by Celada et al. (1994). Results of these studies support the notion of detrimental effects of habitat fragmentation on forest specialists, such as *T. hudsonicus*. Our second hypothesis, therefore, was that *T. hudsonicus* would react adversely to habitat fragmentation; that they would be found in higher abundance in landscapes with larger wooded patches and little agricultural activity.

By relating the abundance of grey and red squirrels to metrics quantifying landscape composition and physiognomy, we hoped to test our hypotheses regarding the differential response of these two squirrel species to the effects of the farm landscapes that have been created.

Methods

Fifteen landscape sites were studied south and southwest of Ottawa, Ontario, Canada (N: 45°25′, W: 75°42′). A sampling point was randomly designated within a focal patch, which was either a wooded fragment ($n = 9$), a wooded fencerow ($n = 6$), or an area within a large forested tract ($n = 2$). Approximately sixty focal patches suitable for this study had been previously identified; the focal patches to be used were selected randomly from these. A wooded fragment was defined as an area covered by woody vegetation, generally less than 100 ha, that was surrounded by non-wooded patches; they included remnant mixed-coniferous lots, pine plantations, and pure deciduous stands. In contrast, a large forested tract was defined as an area covered by woody vegetation that exceeded the area covered in one landscape site (314 ha). Forested tracts in this study were greater than 350 ha, and in some cases exceeded 2000 ha. Fencerows were defined as a length of land, which at one time bordered a fence or farm road, that is now covered by trees and shrubby vegetation. Fencerows were at least 4 m wide, and had few gaps in woody vegetation, none greater than 6 m long. They could adjoin either farm woods or forest patches, but always extended into agricultural fields. The landscape site encompassed the total area within a 1-km radius from the sampling point (314 ha). Sites were a minimum of 5 km apart, to avoid pseudoreplication effects (Hurlbert 1984). The amount of land within each 314-ha site occupied by woody cover, corn, grain, alfalfa/hay crops, soybean, and pasture (including old field) was measured from 1993 air photos (Pedlar 1995). The length of edge, defined as the two-dimensional interface between wooded areas and adjacent cultivated fields, was also measured from these photos, as was the size of the focal patch, the size of the nearest adjacent woods over 1 ha, and the length of the fencerow connecting them (edge to edge) (Table 1). For focal fencerows, the distance from the midpoint of the sampling transect to the edge of the nearest woods was measured (Table 1).

Indices of squirrel abundance and activity were obtained using tracking boards (Pedlar 1995; van Apeldoorn et al. 1993). A tracking board was a 60 cm × 60 cm × 2 mm sheet of plastic or aluminum. The outer edge (10–15 cm wide) was covered with a water-resistant ink made of carbon black suspended in mineral oil. Butcher's paper was taped to the centre, then baited with peanut butter and sunflower seeds. Animals would come for the bait and step on the ink, then on the paper, thereby leaving a waterproof track that could be identified to species. Three boards were placed at each site, at least 50 m apart but not more than 100 m apart. In fencerows, a 200-m segment was chosen at random for placement of the three boards; the distance from this segment to the nearest woods differed for each sample site and was used as a predictor variable in analysis.

Tracking boards were checked weekly from October 12 1994 to November 18 1994, for a total of four to six checks; at each at check the paper was removed, replaced with a fresh piece, and rebaited. All boards remained at the same location for the entire sampling period. The percentage of boards tracked at a site over the entire sampling period (0–100%) was then square-root transformed to yield the squirrel abundance index. For example, if 2 of the 3 boards were tracked by grey squirrels in weeks one and two, 1 of 3 was tracked in week three, and 3 of 3 were tracked in week four, then the grey squirrel abundance index for that site would be $(2+2+1+3)/(3 \times 4)$ $(\times 100\%) = 67\%$. Grey and red squirrel abundance data were analysed by linear and polynomial regression (SAS Institute, 1990) for each of the independent landscape compositional and physiognomic variables. All of these variables were also included in multiple stepwise regression analyses (SAS Institute, 1990).

Track data were also used to generate an index of squirrel activity. This is simply the number of weeks (0–4) that red or grey squirrels were recorded on any of the three boards at a site. In the example above, tracks were obtained in all 4 weeks, therefore the grey squirrel activity index equals 4. In cases where the number of sample weeks exceeded four, excess samples were dropped randomly from the data set. Activity index data were log-transformed to satisfy requirements of normality, and analysed as above.

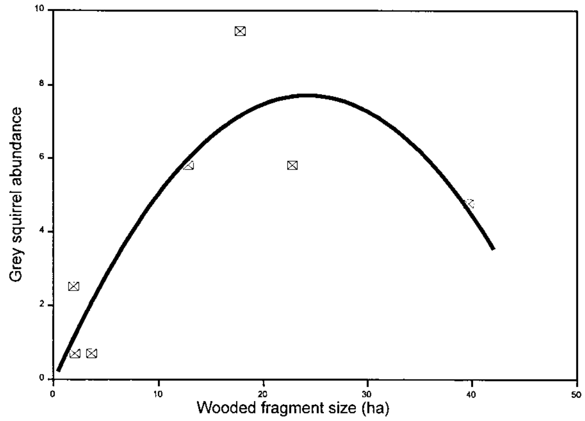

Figure 1. Second-order polynomial regression of the grey squirrel abundance index against size of wooded fragments. Actual values are shown as squares. The equation of the regression line is: square root (GREY) $= 64.03(\text{LOT}) - 131.85(\text{LOT})^2 - 0.053$.

Results

Squirrel abundance index

Grey squirrels were found at eight of the fifteen sample points; red squirrels were found at all but two wooded fragments and one fencerow. Linear, polynomial, and multiple regression analyses yielded no statistically significant variables among the landscape physiognomic or compositional data for the red squirrel abundance index. A second-order polynomial regression of the grey squirrel abundance index versus wooded fragment size, yielded the only significant predictor of that index (Table 1). Both first- and second-order terms were significant ($p < 0.05$) under Type III sums of squares. Woods size explained 79% of the variance in these data. A plot of the predictor values produced by this regression is a bell-shaped curve (Figure 1). The regression line is shown with actual data points represented by squares. Grey squirrel abundance increased with increasing wooded fragment size in a curvilinear function to approximately 23 ha, and then decreased. No grey squirrels were found in forested tracts (>350 ha, $n = 2$), or in fencerows abutting these large tracts ($n = 2$).

Table 1. Landscape compositional and physiognomic variables used in regression analyses, and their relationship to abundance or activity of two squirrel species.

Variable		Range	Mean	(Std. dev)	Relationship to squirrels	
					Signif.	% var.
Woods size (ha)		1.9–3.7	14.4	(13.8)	Grey*	79
Fencerow length (m)		109.0–1072.0	517.7	(294.4)		
Connecting fencerow length (m)		0.0–570.0	144.2	(198.5)		
Size woods adjacent (ha)		0.0–300.0	70.6	(102.3)		
Length of edge (m)		0.0–38.2	33.1	(54.6)		
% cover of	wood	7.0–88.0	41.5	(29.4)	Red**	28
	corn	0.0–18.5	6.1	(7.0)	Red**	24
	soybean	0.0–10.1	4.6	(2.9)	Grey**	40
	grain	0.0–12.8	1.7	(3.3)		
	hay	0.0–11.8	2.7	(3.2)		
	pasture	0.0–19.9	5.3	(5.9)		

**p<0.05* for 1st- and 2nd-order terms in polynomial regression on grey squirrel abundance.
** $p < 0.05$ in multiple regression analysis for grey or red squirrel activity.

Squirrel activity index

Linear and polynomial regression analyses on the squirrel activity index and landscape variables yielded no significant relationships for either species. A polynomial regression between woods size and grey squirrel activity was not significant, as it was for the grey squirrel abundance index. However, multiple stepwise regression analysis did yield significant predictors of both grey and red squirrel activity (Table 1). The only significant variable in the model for grey squirrels was the percent cover of soybeans in the landscape, which explained 40% of the variance. The model for red squirrels yielded two significant variables. The percent cover of corn in the landscape was the best predictor of red squirrel activity, explaining 28% of the variance, and the percentage of wooded cover in the landscape explained 24%, for a total of 52% of the variance explained.

Discussion

Both grey and red squirrels used wooded fragments in agricultural landscapes. Grey squirrels were most abundant in mid-size (1.9 ha–39.7 ha) woods in the agricultural mosaic (Figure 1). Caution should be observed in interpreting these data, as the downward trend is based only on two data points. However, given that no grey squirrels were found in large tracts (>350 ha) or in fencerows that abutted them (neither shown on graph), a drop in abundance can be extrapolated. Middleton and Merriam (1983) also found no grey squirrels in nearby large mixed-transitional forests (>35,000 ha) in western Quebec. This might suggest that forest fragmentation is favourable to grey squirrel occupation.

The only significant landscape predictor of grey squirrel activity was the percent cover of soybeans. Soybeans are the most rapidly increasing crop in eastern and southern Ontario, and have been a major component of the landscape in the study region for approximately 15 years. Although not directly observed in this study, the use of soybeans by grey squirrels is biologically feasible, as soybean seeds have high lipid content (Simmons and Quackenbush 1954; in Ogren and Rinne 1973) typically present in the deciduous mast (Smallwood and Peters 1986) upon which grey squirrels depend heavily for food (Koprowski 1991). Wooded fragments in this study area contained few mature deciduous masting species (Bennett et al. 1994). It should be emphasized that this study demonstrates only a correlation between soybeans and squirrel activity, not causality.

Grey squirrels' use of agricultural patch types is supported by winter snow-tracking observations, which revealed that grey squirrels did move between wooded and agricultural patches; burrowing, tunnelling, and vegetation removal from the field were observed (J. Fisher, pers. obs.). The use of non-wooded patch types in conjunction with woods and fencerows supports our hypothesis that grey squirrels in this region are relying on resource patch arrays generated by the fragmented agricultural landscape, i.e., landscape complementation (sensu Dunning et al. 1992).

Data suggest that red squirrels are using patches created from the fragmentation of woodland, as well as unmodified habitat. The percent cover of woody vegetation in the landscape was a good predictor of red squirrel activity. Since the red squirrel is purportedly a forest specialist, a large area of wooded cover in the landscape represents more available suitable habitat. However, the percent corn cover was the best predictor of red squirrel activity. Red squirrels may rely on wooded areas, probably for denning sites and predator avoidance (Gurnell 1987) and opportunistically use corn as a high quality food supplement. Although snow tracking revealed no red squirrel winter foraging in agricultural fields, red squirrels were observed gathering corn in the autumn (J. Fisher, pers. obs.). The use of multiple patch types suggests red squirrels also employ landscape complementation. Contrary to our hypothesis and the scientific literature, the red squirrel in agricultural landscapes is not a forest specialist, but has adapted to the fragmentation of its native habitat and is acting as an opportunistic mosaic species. Thus the North American red squirrel is exhibiting a behavioural plasticity, allowing it to adapt to novel landscapes (Merriam 1991), that is apparently lacking in its Eurasian counterpart (see Verboom and van Apeldoorn 1990).

None of the landscape physiognomic variables measured was significant in the multiple regression analysis for either species ($p > 0.05$). This may suggest that squirrels operate at a spatial scale different from that measured in this experiment – the landscape mosaic, at the level considered, is sufficiently fine-grained that these variables are of lesser importance. The spatial extent (sensu Kotliar and Wiens 1990) of red and grey squirrels remains obscure. Long-range movements of grey squirrels (H. Howden, pers. comm.), the high rate of individual turnover within patches (G. Merriam, unpubl. data), and tracking data, all may indicate that these squirrels are much more vagile than the literature suggests (see Gurnell 1984 and 1987). Wide-ranging organisms perceive a landscape mosaic at a given scale as more homogeneous than do less vagile organisms (Kotliar and Wiens 1990). It is possible that squirrels perceive the landscape sites studied here as fine-grained and that they are not constrained by single patches, as defined in this study.

One should note that there is a seasonal aspect to this study that makes it unrepresentative of annual squirrel dynamics. Squirrels are often more sedentary in winter (Gurnell 1987), and thus would be associated more with denning site availability than with food sources. In spring when young are born (Gurnell 1987), predator avoidance and presence of spring succulents as food may influence habitat selection. Obviously, space use varies with the seasons, and this is particularly prevalent in agricultural landscapes, given the ephemeral nature of resource patches (Szacki et al. 1993). To get a true measure of habitat selection in these two species, a future study should be expanded to include one or more years, to encompass all seasonal aspects of the squirrels' life-history cycles and resource requirements.

Many studies of the effects of habitat fragmentation deal with the consequences of loss of native habitat, the subsequent isolation and patch size reduction of remnant suitable fragments, and 'neighbourhood effects' (see Kozakiewicz 1993; Andren 1994). Few deal explicitly with matrix composition in heterogeneous environments (Szacki et al. 1993). The results of this study show that the background matrix is not 'neutral' for some woodland species. The novel resource patch array that replaces native habitats will influence the distribution of organisms in a landscape. The replacement landscape may aid the continued existence of a native species, or may facilitate introduced or geographically expanding species. This effect may be an important determinant of distribution and abundance of species in anthropogenic landscapes.

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