

The effects of habitat fragmentation by forestry and agriculture on the abundance of small mammals in the southern boreal mixedwood forest

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Abstract: To determine the effects of forest fragmentation on the abundance of small mammals, we livetrapped at edges and in the interior of forest patches in contiguous, logged, and agricultural landscapes in the southern boreal mixedwood forest of Saskatchewan. From 1994 to 1996, we captured 1548 small mammals (11 species) during 8172 trap-nights. The abundance of all small mammals combined was lower in forest patches isolated by logging than in contiguous forest or farm woodlots surrounded by agricultural land. This pattern was consistent in all years, despite significant annual fluctuations in numbers of the boreal red-backed vole (*Clethrionomys gapperi*), one of the most abundant species in our study area. Red squirrels (*Tamiasciurus hudsonicus*) and northern flying squirrels (*Glaucomys sabrinus*) were more abundant in farm woodlots. The abundance of deer mice (*Peromyscus maniculatus*) was significantly lower in forest patches surrounded by clearcuts, and we speculate that they may have used clearcuts more than forest patches. In contrast, the numbers of boreal red-backed voles were similar among landscapes. The only species showing a response to edge was the deer mouse, which was significantly more abundant at edges of farm woodlots than in interiors. We also found no significant difference in abundance of any species between small (10 ha) and large (>20 ha) farm woodlots. For most species, within-landscape attributes such as edge and patch size seemed to have little effect on their abundance. However, for a variety of reasons, small-mammal numbers seem to vary considerably among forest patches in different landscapes.

Résumé : Pour étudier les effets de la fragmentation de la forêt sur l'abondance des petits mammifères, nous avons procédé au piégeage d'animaux vivants aux abords et à l'intérieur de boisés dans des sections contiguës, coupées et agricoles de la forêt boréale mixte, dans le sud de la Saskatchewan. De 1994 à 1996, nous avons capturé 1548 petits mammifères (11 espèces) dans 8172 pièges-nuits. L'abondance de tous les petits mammifères combinés était plus faible dans les boisés isolés par la coupe que dans la forêt continue ou dans les boisés situés sur les fermes. Cette tendance s'est répétée chaque année, en dépit de fluctuations annuelles importantes chez le Campagnol à dos roux de Gapper (*Clethrionomys gapperi*), l'une des espèces les plus abondantes de la région étudiée. L'Écureuil roux (*Tamiasciurus hudsonicus*) et le Grand polatouche (*Glaucomys sabrinus*) étaient plus abondants dans les boisés situés sur les fermes. L'abondance de la Souris sylvestre (*Peromyscus maniculatus*) était significativement plus faible dans les boisés entourés de terres coupées à blanc et nous croyons que cette souris utilisait davantage les zones coupées que les boisés. Par ailleurs, l'abondance des campagnols à dos roux de Gapper était semblable d'un paysage à l'autre. La seule espèce à réagir aux bordures était la Souris sylvestre, significativement plus abondante en bordure qu'à l'intérieur des boisés situés en terre agricole. De plus, nous n'avons trouvé aucune différence significative dans l'abondance des espèces entre les petits (10 ha) et les grands (>20 ha) boisés sur les fermes. Dans la plupart des cas, les propriétés d'un paysage, comme la présence de bordures ou la taille d'une parcelle, semblent avoir peu d'effet sur l'abondance d'une espèce. Cependant, pour plusieurs raisons, le nombre de petits mammifères semble varier considérablement entre les boisés des divers types de paysages.

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Introduction

Throughout the world, forested ecosystems are being altered through a variety of human activities such as forestry, mineral extraction, road-building, and agriculture (Harris 1984; Hunter 1990; Terborgh 1992; Myers 1996). Loss of forested habitat has an obvious impact on wildlife, but the effects are often exacerbated by the fact that remnant forest patches may be small or isolated and have a high proportion of edge habitat (Soulé 1980; Harris 1984; Hunter 1990; Laurance and Yensen 1991; Saunders et al. 1991; Andrén 1994, 1995). Recent research has demonstrated that the increase in edge habitat and reduction in habitat size associated with forest fragmentation

have negative effects on many species of birds, as rates of predation, parasitism, and competition seem to increase near edges and in smaller patches (Yahner 1988; Paton 1994; Andr n 1995).

In contrast to birds, small isolated habitat patches often support higher densities of small mammals than larger contiguous habitats (reviewed by Adler and Levins 1994). However, the majority of these studies have been conducted on true islands bound by "hard" edges (e.g., water–forest) that prevent dispersal (Stamps et al. 1987). The effects of patch size and isolation on small mammals in terrestrial forest fragments with "soft" edges (e.g., field–forest) may be similar to those on true islands, but data documenting such effects are sparse (but see Gottfried 1979; van Apeldoorn et al. 1992; Nupp and Swihart 1996). Similarly, little is known about the direct effects of edge on the abundance of small mammals (Heske 1995; Mills 1995). Studies done at the interface between forest patches and clearcuts have produced ambiguous results, with species-specific responses to edge (Kirkland et al. 1985; Linzey 1989; Mills 1995; Sekgorane and Dilworth 1995). The few studies that have examined small-mammal abundance at forest–field edges in agricultural landscapes have typically shown no difference between edge and forest interior (Heske 1995; Nupp and Swihart 1996).

How small mammals respond to edge depends on both the type of edge and, at larger scales, the landscape matrix in which the edge is situated (Rudnicki and Hunter 1993; Andr n 1994; Wiens 1995). For example, at local scales, edges created by logging are often transient and possess little transition-zone vegetation, whereas edges in agricultural landscapes are more permanent and may have higher shrub densities than interior habitats (Rudnicki and Hunter 1993; Murcia 1995). At larger scales, forest patches in logged landscapes are located in a matrix that often remains dominated by forest, whereas agricultural landscapes consist of a matrix of fields, pasture, and human settlements. The shift from a forested landscape to one dominated by agriculture can result in dramatic changes in the abundance and diversity of many wildlife species (Andr n 1992, 1994; Rudnicki and Hunter 1993; Estrada et al. 1994). Separating local-scale effects (e.g., edge) from those of the surrounding landscape is an essential step in understanding how habitat fragmentation affects small mammals in forest ecosystems.

Small mammals play an important role in forest ecosystems as prey, predators, and seed dispersers (Maxson and Oring 1978; Martell 1983; Nowak 1991; Bayne et al. 1997). As forests become increasingly fragmented, knowing how small mammals respond to fragmentation attributes such as patch size, isolation, and edge will become critical to our understanding of how human changes affect forest ecosystems (Heske 1995; Mills 1995). The objective of this study was to determine whether small mammals varied in abundance among forest patches in agricultural, logged, and contiguous landscapes in the southern boreal mixedwood forest of central Saskatchewan. We also evaluated whether small-mammal abundance was influenced by within-landscape attributes such as edge and patch size.

Materials and methods

Study area

Our study was conducted in and around the Prince Albert Model

Forest (53°50'N, 105°50'W), located in the southern boreal mixed-wood zone of north-central Saskatchewan (Bouman et al. 1996). This area comprises three distinct landscapes, including 387 500 ha of contiguous forest in Prince Albert National Park (hereafter contiguous forest), 84 000 ha of commercial forest, of which approximately 25% has been logged since 1969 (hereafter leave blocks), and 135 000 ha in the rural municipality of Paddockwood, of which 70% (Bayne 1996) has been converted to grain fields, hay fields, or pasture since 1911 (hereafter farm woodlots). Study sites were mature to old (70–110 years) mixedwood forest stands of trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*) with crown closure between 55 and 100% and a stand height of 15–25 m. The shrub layer consisted of white spruce saplings, green alder (*Alnus crispa*), beaked hazelnut (*Corylus cornuta*), and red-osier dogwood (*Cornus stolonifera*). Farm woodlots were surrounded by cultivated fields planted to wheat or canola, were at least 100 m away from any other forested area, and ranged in size from 9 to 45 ha (5 were approximately 10 ha and 3 were more than 20 ha). Leave blocks covered approximately 40 ha and were isolated on three sides by regenerating clearcuts created between 1985 and 1993 or road allowances greater than 25 m wide. Contiguous forest sites were at least 100 m away from any road or permanent hiking trail. All sites were a minimum of 1 km apart.

Trapping design

We evaluated the abundance of small mammals in each landscape from July to August 1994–1996, using livetrapping. In 1994, the abundance of small mammals was determined at 2 sites in each landscape. In 1995, 6 farm woodlots and 6 leave blocks were examined, along with 3 sites in contiguous forest. In 1996, we trapped at 8 farm woodlots, 8 leave blocks, and 3 sites in contiguous forest. All study sites used in 1994 and 1995 were examined in subsequent years, except 2 leave blocks that could not be reached in 1996 because of road closures.

At each farm woodlot and leave block, one edge (hereafter farm woodlot edge and leave block edge) and two interior transects (hereafter farm woodlot interior and leave block interior) were established. Edge transects were roughly parallel to and 1–5 m from the forest edge, whereas interior transects were 50 m apart and at least 100 m from the edge of the forest patch. In contiguous forest, we established two interior transects that were 50 m apart and at least 100 m from any trail edge. At each edge transect we evaluated the abundance of small mammals, using 30 small Tomahawk™-style (30 × 8 × 8 cm) and 6 large Havahart™ Model 745 (41 × 14 × 15 cm) live traps baited with rolled oats and peanut butter. In farm woodlots and leave blocks, 18 traps were placed along each interior transect, whereas in contiguous forest there were 36 traps in each interior transect. Traps were set at 10-m intervals, with different trap types distributed in a standardized pattern. Traps were set at each site between 17:00 and 19:00 and checked between 09:00 and 11:00 daily for a period of 3 days. After a 3-day trapping period, traps were moved to new sites in a different landscape. To identify previously captured animals, numbered metal tags were attached to the ear of each animal before release.

Statistical analysis

The abundance of small mammals was measured as the number of captures per 100 trap-nights, excluding recaptures. When calculating the number of trap-nights, a correction factor of half a trap-night was arbitrarily subtracted for each trap that was closed without having caught anything, or for traps that captured a previously tagged animal (Nelson and Clark 1973). This procedure corrects for closed traps that reduce the number of animals that can be captured.

A two-factor analysis of variance (ANOVA) was used to compare the abundance of small mammals among the 3 landscapes and among years. All data were $\log(x + 1)$ -transformed prior to analysis to improve homoscedasticity (Zar 1984). Parametric tests were used only after data were tested for normality using the Kolmogorov–Smirnov test and for homoscedasticity using Bartlett's test (Zar 1984). When

the effects of landscape on the abundance of small mammals were examined, edge and interior transects were combined to calculate a total abundance of small mammals in farm woodlots and leave blocks. The data were pooled in this manner so that the numbers of trap-nights at the sites were approximately equal. Before pooling data, we used Bartlett's test to ensure that the variance between edge and interior transects was similar. A three-factor ANOVA was used to determine if edge and year influenced the abundance of small mammals in small (10 ha) and large (>20 ha) farm woodlots differently. Finally, a two-factor ANOVA was used to determine if the abundances of small mammals at leave block edge and leave block interior varied among years. Each ANOVA was performed on the abundance of all species combined and for boreal red-backed voles (*Clethrionomys gapperi*), deer mice (*Peromyscus maniculatus*), and red squirrels (*Tamiasciurus hudsonicus*) separately. Differences in the abundance of northern flying squirrels (*Glaucomys sabrinus*) were tested using a Kruskal–Wallis test, as these data were not normally distributed. In initial testing, all interactions were included in the ANOVA model. If interactions were not significant, they were removed from the model to increase power (Norusis 1993). When there were significant differences between treatments, we used Tukey's honestly significant difference test to determine which treatments differed (Zar 1984). In cases where no significant differences were observed, power analyses were used to evaluate the effectiveness of our experimental and statistical design for detecting real differences among treatments (Cohen 1988; Thomas 1997). As in Heske (1995), we calculated our standardized effect sizes, and then estimated the sample sizes that would have been required to reach a 50% probability of detecting statistical significance at $\alpha = 0.05$ (hereafter desired power).

All data are reported as mean abundance per 100 trap-nights ± 1 standard error unless otherwise stated.

Results

During 8172 trap-nights, we captured 1922 animals, for a total trapping success of 23.5%. Eleven species were captured, but 90% of captures were deer mice ($n = 868$) and boreal red-backed voles ($n = 866$). Red squirrels ($n = 131$) and northern flying squirrels ($n = 31$) were also frequently captured. The remaining 26 animals captured consisted of 4 least chipmunks (*Eutamias minimus*), 5 least weasels (*Mustela rixosa*), 4 meadow jumping mice (*Zapus hudsonius*), 3 short-tailed shrews (*Blarina brevicauda*), 6 snowshoe hares (*Lepus americanus*), 3 meadow voles (*Microtus pennsylvanicus*), and 1 unidentified shrew (*Sorex* sp.).

Landscape effects

The abundance of small mammals was significantly higher in farm woodlots and contiguous forest than in leave blocks ($F_{[2,35]} = 48.2$, $P < 0.001$; Fig. 1). The significantly lower number of small mammals in leave blocks was primarily due to a lower abundance of deer mice ($F_{[2,35]} = 48.2$, $P < 0.0001$; Fig. 2). Boreal red-backed vole abundances did not vary significantly among landscapes ($F_{[2,31]} = 1.71$, $P = 0.20$; Fig. 2), but were significantly higher in 1995 (15.9 ± 2.5) than in 1994 (5.7 ± 2.0) or 1996 (4.3 ± 0.6 ; $F_{[2,13]} = 16.9$, $P < 0.001$). Northern flying squirrels were significantly more abundant in farm woodlots than in leave blocks or contiguous forest ($H = 8.5$, $P = 0.02$; Fig. 3). Red squirrels were also significantly more abundant in farm woodlots ($F_{[2,31]} = 4.06$, $P = 0.03$; Fig. 3) than in leave blocks or contiguous forest. However, a significant interaction between year and landscape was detected for red squirrels ($F_{[4,31]} = 2.95$, $P = 0.04$), as there was

no variation in the abundance of red squirrels among landscapes in 1995. Finally, significantly fewer red squirrels were captured in 1995 (0.9 ± 0.3) than in 1994 (2.1 ± 1.1) or 1996 (2.0 ± 0.3 ; $F_{[2,31]} = 5.7$, $P < 0.01$).

Within-landscape effects

The abundances of small mammals combined did not differ between farm woodlot edge and farm woodlot interior ($F_{[1,27]} = 3.7$, $P = 0.07$; Table 1), although there was a trend towards a higher abundance at farm woodlot edge. Abundances were similar between farm woodlot edge and farm woodlot interior for boreal red-backed voles ($F_{[1,27]} = 0.5$, $P = 0.49$), northern flying squirrels ($H = 2.1$, $P = 0.15$), and red squirrels ($F_{[1,27]} = 0.7$, $P = 0.40$; Table 1). In contrast, deer mice were significantly more abundant at farm woodlot edge than in farm woodlot interior ($F_{[1,27]} = 8.4$, $P = 0.007$; Table 1). The size of the farm woodlot had no significant effect on the abundance of all small mammals combined ($F_{[1,27]} = 0.41$, $P = 0.53$), deer mice ($F_{[1,27]} = 0.03$, $P = 0.86$), red squirrels ($F_{[1,27]} = 0.09$, $P = 0.77$), northern flying squirrels ($H = 0.2$, $P = 0.65$), or boreal red-backed voles ($F_{[1,27]} = 3.6$, $P = 0.07$; Table 2). The only species in farm woodlots that varied significantly in abundance among years was the boreal red-backed vole ($F_{[2,28]} = 3.46$, $P = 0.05$), which was significantly more abundant in 1995 (12.8 ± 3.0) than in 1994 (2.9 ± 1.8) or 1996 (5.1 ± 1.0).

We did not detect a significant difference in the total numbers of small mammals caught at leave block edge relative to leave block interior ($F_{[1,28]} = 0.2$, $P = 0.65$; Table 3). However, there was significant variation among years ($F_{[2,28]} = 11.3$, $P < 0.001$), with significantly more small mammals in leave blocks in 1995 (22.5 ± 3.1) than in 1994 (8.8 ± 2.9) or 1996 (9.1 ± 1.0). As in farm woodlots, the higher abundance of small mammals in the leave blocks in 1995 was caused by an increased abundance of boreal red-backed voles in 1995 (15.7 ± 2.7) compared with 1994 (3.8 ± 2.1) and 1996 (4.6 ± 0.6 ; $F_{[2,28]} = 12.1$, $P < 0.001$). Edge in leave blocks had no effect on the abundance of boreal red-backed voles ($F_{[1,28]} = 0.52$, $P = 0.48$), deer mice ($F_{[1,28]} = 0.86$, $P = 0.36$), northern flying squirrels ($H = 0.5$, $P = 0.47$), or red squirrels ($F_{[1,28]} = 2.4$, $P = 0.13$; Table 3).

In farm woodlots, the power of the analysis comparing edge and interior for all species was 0.46 (Table 1), which indicates that we had reasonable power to detect a difference between edge and interior treatments. In contrast, the observed effect size between farm woodlot edge and interior for red squirrels and boreal red-backed voles was so low, the number of replicates required to attain desired power was logistically impossible to obtain. Similarly, our power to detect a difference between leave block edge and interior for all species combined was very low, and again, a logistically impossible number of replicates in each treatment would have been required in order to have the desired power (Table 3). Clearly, differences in the relative abundance of small mammals between edge and interior habitats, if they exist, are extremely weak in both farm woodlots and leave blocks for most species.

Discussion

Overall, small mammals were more abundant in farm woodlots and contiguous forest than in leave blocks, a pattern particularly

Fig. 1. Numbers of small mammals captured per 100 trap-nights (mean \pm 1 SE) for each landscape and year. Edge and interior transects were pooled in agricultural and logged landscapes. All species were combined. Numbers in boxes show the number of individuals of all species captured in that landscape per year.

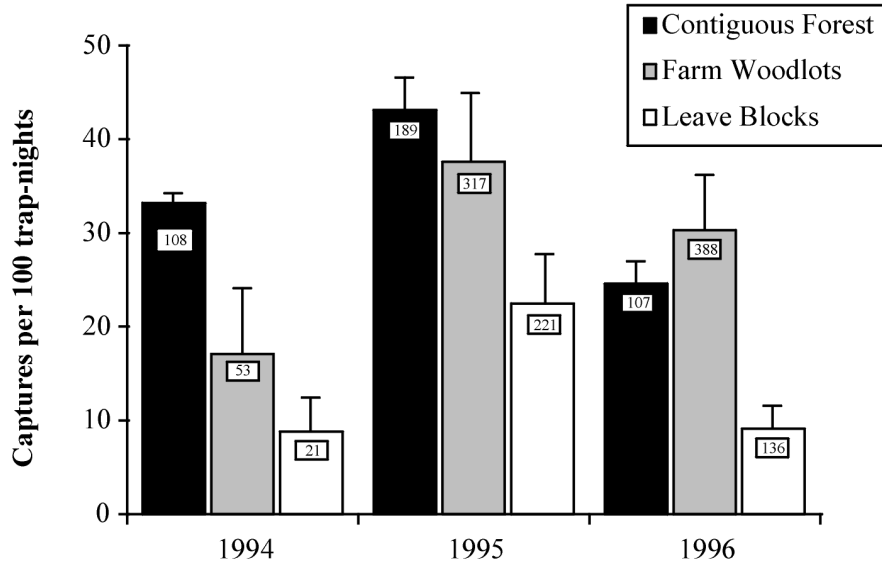
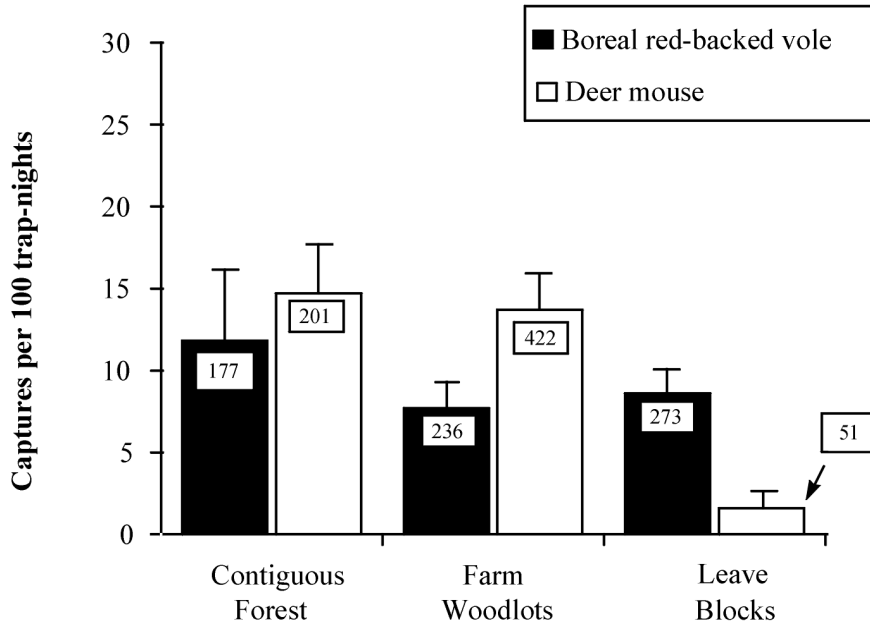


Fig. 2. Numbers of boreal red-backed voles and deer mice captured per 100 trap-nights (mean \pm 1 SE) for each species in each landscape. Edge and interior transects are pooled in agricultural and logged landscapes. Data from each year are pooled for each category. Numbers in boxes show the number of individuals of that species captured in each landscape.



evident in deer mice. Why deer mice were less abundant in leave blocks is unclear. No significant variation in vegetation among sites in different landscapes was detected (Bayne 1996), suggesting that habitat differences among landscapes were not a factor. Little annual variation in the numbers of deer mice within or among landscapes was observed, so it seems unlikely that the population cycles of this species in leave blocks differed from those in other landscapes (e.g., Probst and Rakstad 1987; Steen et al. 1996). Alternatively, deer mice often reach a higher abundance in clearcuts surrounding forest patches than in the forest patches themselves, particularly in

coniferous or mixedwood forests (reviewed by Kirkland 1990). Although we did not trap in clearcuts, deer mice in our study area are significantly more abundant in clearcuts than in forest patches adjacent to cutover areas (Jones 1978).

Deer mice and boreal red-backed voles were similar in abundance in farm woodlots and contiguous forest. This was surprising, as previous studies have shown that limited dispersal, reduced competition, and an increase in survival due to the absence of predators often lead to higher densities in small isolated forest patches (reviewed by Gliwicz 1980; Adler and Levins 1994; Nupp and Swihart 1996). However, a review of

Fig. 3. Numbers of red squirrels and northern flying squirrels captured per 100 trap-nights (mean \pm 1 SE) for each species in each landscape. Edge and interior transects are pooled in agricultural and logged landscapes. Data from each year are pooled for each category. Numbers in boxes show the number of individuals of that species captured in each landscape.

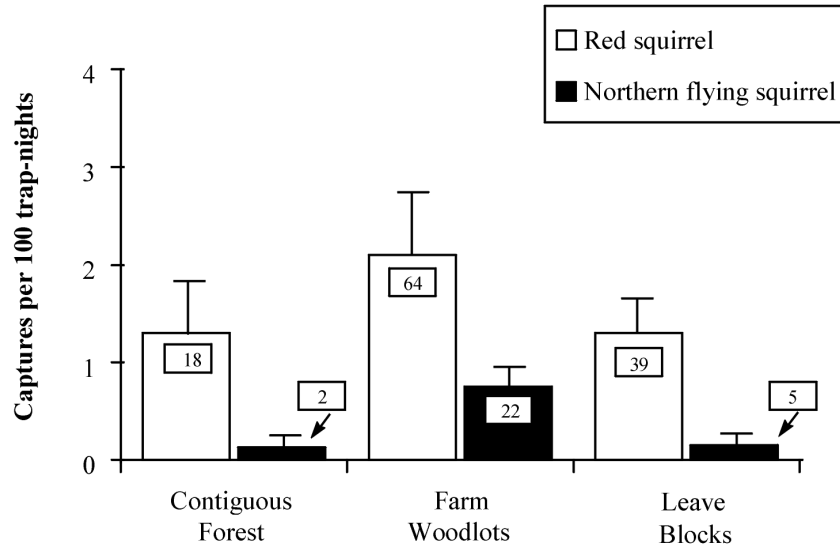


Table 1. Numbers of individuals of each species captured per 100 trap nights at edge versus interior treatments in farm woodlots (mean \pm 1 SE). Data from each year and woodlot size are pooled for each category. The statistic for each test is reported along with the resulting *P* value. The statistical power of each test is reported as well as the standardized effect size. Based on the reported standardized effect size, the number of sites per treatment that would have been required to detect statistical significance with a desirable power of 0.5 and $\alpha = 0.05$ was calculated.

	Farm woodlot		Statistic ^a	<i>P</i>	Power ^b	Standardized effect size	Required no. of sites per treatment
	Edge	Interior					
Boreal red-backed vole	8.4 \pm 2.0	7.0 \pm 2.0	0.5	0.49	0.13	0.11	489
Deer mouse	17.6 \pm 2.3	9.9 \pm 2.5	8.4	0.01	—	—	—
Red squirrel	1.6 \pm 0.4	2.6 \pm 0.9	0.7	0.40	0.16	0.15	268
Northern flying squirrel	0.4 \pm 0.2	1.0 \pm 0.3	2.1	0.15	—	—	—
Total	37.6 \pm 5.3	25.6 \pm 4.3	3.7	0.07	0.46	0.34	62

^aFor thenorthern flying squirrel the statistic reported is the *H* value of a Kruskal–Wallis test, while all others are the *F* value of an ANOVA.

^bPower analyses were not conducted on Kruskal–Wallis tests (northern flying squirrel) or in cases where the *P* value was statistically significant.

eight papers on the effects of patch size on white-footed mice (*Peromyscus leucopus*) showed that increased densities occur mainly in very small woodlots (0.1–2 ha), and that larger woodlots (5–20 ha) often have densities similar to those in contiguous forest (Nupp and Swihart 1996). As all our farm woodlots were larger than 9 ha, they may have been of sufficient size to function like contiguous forest for deer mice. However, we observed a trend towards a lower abundance of boreal red-backed voles in smaller woodlots relative to larger woodlots, suggesting that the size of the patch within a landscape may have some effect on boreal red-backed vole populations.

The abundance of northern flying squirrels and red squirrels was higher in farm woodlots than in contiguous forest or leave blocks. The higher abundance of squirrels in farm woodlots contrasts with the results of studies done in Europe, where the occurrence of the European red squirrel (*Sciurus vulgaris*) and gray squirrel (*Sciurus carolinensis*) was positively correlated

with forest patch area and negatively correlated with the level of patch isolation (Verboom and van Apeldoorn 1990; Fitzgibbon 1993; van Apeldoorn et al. 1994; Wauters et al. 1994). The higher squirrel abundance in our farm woodlots was more consistent with the results of research conducted on fox squirrels (*Sciurus niger*) in the eastern United States (Sheperd and Swihart 1995). Fox squirrels are commonly found in intermediate-sized woodlots (5–10 ha), and often reach higher densities in fragmented landscapes than in larger forest blocks (Sheperd and Swihart 1995). Unlike European squirrels, fox squirrels use waste grain in agricultural fields as a food resource (Sheperd and Swihart 1995). If the red squirrels and northern flying squirrels in our study area employ a similar strategy, the increased and more stable food supply in agricultural landscapes may allow greater numbers of squirrels to live in farm woodlots than in forested landscapes. However, there is little evidence that red squirrels or northern flying squirrels use waste grain as a food resource. Instead, squirrels in our

Table 2. Number of individuals of each species captured per 100 trap-nights in small and large farm woodlot treatments (mean ± 1 SE). Data from each year are pooled for each category. The statistic for each test is reported, along with the resulting *P* value. The statistical power of each test is reported as well as the observed standardized effect size. Based on the reported standardized effect size, the number of sites per treatment that would have been required to detect statistical significance with a power of 0.5 and $\alpha = 0.05$

	Small farm	Large farm	Statistic ^a	<i>P</i>	Power ^b	Standardized	Required no. of
	woodlots (10 ha)	woodlots (>20 ha)					
Boreal red-backed vole	7.0±2.5	9.2±2.4	3.6	0.07	0.49	0.34	62
Deer mouse	13.7±2.8	13.8±3.2	0.03	0.86	0.04	0.03	6420
Red squirrel	2.1±0.5	2.2±1.3	0.09	0.77	0.05	0.05	2319
Northern flying squirrel	0.7±0.2	0.7±0.2	0.2	0.65	—	—	—
Total	30.8±5.5	33.4±6.2	0.41	0.53	0.08	0.05	2319

^aFor the northern flying squirrel the statistic reported is the *H* value of a Kruskal–Wallis test, while all others are the *F* value of an ANOVA.

^bPower analyses were not conducted on Kruskal–Wallis tests (northern flying squirrel) or in cases where the *P* value was statistically significant

Table 3. Number of individuals of each species captured per 100 trap-nights at edge versus interior treatments in leave blocks (mean ± 1 SE). Data from each year are pooled for each category. The statistic for each test is reported, along with the resulting *P* value. The statistical power of each test is reported as well as the standardized effect size. Based on the reported standardized effect size, the number of sites per treatment that would have been required to detect statistical significance with a power of 0.5 and $\alpha = 0.05$ was calculated.

	Leave block		Statistic ^a	<i>P</i>	Power ^b	Standardized	Required no. of
	Edge	Interior					
Boreal red-backed vole	8.1±2.0	9.2±2.1	0.52	0.48	0.12	0.13	177
Deer mouse	1.7±0.4	1.5±0.6	0.86	0.36	0.16	0.17	106
Red squirrel	1.6±0.4	0.9±0.4	2.4	0.13	0.32	0.28	43
Northern flying squirrel	0.2±0.1	0.1±0.1	0.47	0.47	—	—	—
Total	14.3±2.4	13.9±2.1	0.2	0.64	0.06	0.09	362

^aFor the northern flying squirrel the statistic reported is the *H* value of a Kruskal–Wallis test, while all others are the *F* value of an ANOVA.

^bPower analyses were not conducted on Kruskal–Wallis tests (northern flying squirrel) or in cases where the *P* value was statistically significant.

farm woodlots may suffer from a “fence effect,” whereby behavioural reluctance to cross open habitats may reduce dispersal and lead to crowding (Krebs et al. 1969; Adler and Levins 1994; Sheperd and Swihart 1995). Radiotelemetry studies of European red squirrels suggest that they rarely cross open habitats such as clearcuts or fields, which may limit dispersal into and out of isolated forest patches (Andrén and Delin 1994). Additionally, squirrels may have higher survival rates in our farm woodlots because of reduced predation risk (Adler and Levins 1994; Laurance 1994), as major squirrel predators such as fishers (*Martes pennanti*) and barred owls (*Strix varia*) are typically absent from agricultural landscapes (Arthur et al. 1989; Laidig and Dobkin 1995; James et al. 1996). The absence of nocturnal predators like barred owls in farm woodlots may be particularly important for the largely nocturnal northern flying squirrel (Rosenberg and Anthony 1992).

Although northern flying squirrels are thought to be common throughout the boreal forest, relatively little is known about factors influencing their population dynamics (Wells-Gosling and Heaney 1984; McDonald 1995). Northern flying squirrels are commonly associated with large tracts of old-growth conifer or mixedwood forest (Carey 1995; Rosenberg

and Anthony 1992; McDonald 1995). Our observation that northern flying squirrels were more abundant in farm woodlots suggests some plasticity in their habitat requirements. In fact, northern flying squirrels have been observed using nest boxes along fence rows in our study area (J. Dinius, personal communication).

Edge effects

For most species in the farm woodlots, there was no difference in their relative abundance between edge and interior habitats. The absence of an edge effect in farm woodlots is consistent with the results of other studies of small mammals conducted in agricultural landscapes in Illinois and Indiana (Heske 1995; Nupp and Swihart 1996). The deer mouse was the only species whose relative abundance significantly differed between edge and interior, and then only in farm woodlots. Deer mice are omnivorous habitat generalists, although their diet is often dominated by seeds (Kirkland 1990; Nowak 1991). The higher abundance of deer mice at farm woodlot edges may indicate a focus on areas of greater seed production, which can occur along edges in agricultural landscapes (Ranney et al. 1981). Similarly, field–forest edges may provide greater access to

seed resources such as waste grain and standing crops in the agricultural matrix, while increased cover in the forested portion of an edge may reduce predation risk (Heske 1995).

In contrast to farm-field edges, recently created edges in logged landscapes contain little shrub cover and often have a lower abundance of food resources, owing to low moisture levels and high temperatures (Saunders et al. 1991). These conditions have a negative impact on many species of small mammals, particularly voles. For example, California red-backed voles (*Clethrionomys californicus*) in Oregon were six times more abundant in interiors than at edges of forest patches in a logged landscape because harsh conditions at edges reduced the abundance of mycorrhizal fungi, the main food source for this vole (Mills 1995). Similarly, Sekgororane and Dilworth (1995) found that boreal red-backed voles in New Brunswick used forest-clearcut edges, but reached their highest abundance 50 m into the forest. Based on these studies, we expected boreal red-backed voles to be susceptible to edge effects in our leave blocks. Possibly the high degree of natural fragmentation by fire and insect disturbance at both the stand and the landscape level in the boreal forest of western Canada (Eberhart and Woodard 1987) has resulted in better adaptation of boreal red-backed voles for dealing with edges in this biome than in other areas.

Conclusion

Our study showed little difference in the abundance of deer mice and boreal red-backed voles between farm woodlots and contiguous forest. In contrast, habitat fragmentation resulted in higher local densities of red squirrels and northern flying squirrels in farm woodlots. Deer mice differed significantly in abundance between contiguous forest and leave blocks and we believe that this may have resulted from the creation of an alternative habitat (clearcuts) for deer mice in the logged landscape. Although we were unable to detect a difference between edge and interior habitats or woodlots of different sizes for most of the species captured, our statistical power to detect such differences was weak. However, the sample sizes required in order to have reasonable power to detect a statistically significant difference between edge and interior were logistically impossible to obtain (also see Heske 1995), suggesting that the impact of edge on small-mammal abundance is limited for most species. The high variability in small-mammal abundance in both space and time likely limits our ability to detect more subtle influences such as those of edge and patch size in fragmented landscapes.

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