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Conservation Biology, Volume 11, Issue 6 (Dec., 1997), 1418-1429.

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Comparing the Effects of Landscape Fragmentation by Forestry and Agriculture on Predation of Artificial Nests

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Abstract: Fragmentation of forested landscapes can reduce the reproductive success of birds occupying residual forest patches. Previous studies, however, have focused primarily on how nest predation can change when landscapes become fragmented by agriculture rather than by logging. To determine if predation on artificial nests in forest patches was influenced by the surrounding landscape, we placed ground and shrub nests along the edge and interior of forest patches located in agricultural, logged, and contiguous forest landscapes within a single region of the southern boreal mixedwood forest of central Canada. Nest predators were identified using remotely triggered cameras and by marks left in plasticine eggs, whereas the relative abundance of nest predators such as corvids and small mammals was estimated by surveys and live-trapping. The percentage of ground nests destroyed at the edge and interior of patches in the logged and contiguous forest landscapes was significantly lower than at the edge or interior of patches in the agricultural landscape. No differences in predation rate were observed for shrub nests among landscapes. We attributed higher rates of predation in the agricultural landscape to higher densities of red squirrels (*Tamiasciurus hudsonicus*) in the interior and a greater diversity of predators along edges. The similarity in predation rate between logged and contiguous forest landscapes suggests that fragmentation caused by logging may result in little change in predator communities and in this respect, might be similar to fragmentation caused by natural disturbance regimes such as fire. In contrast, fragmentation by agriculture seems to have more serious consequences for nesting birds. Policy changes that limit the growth of agriculture in the southern boreal mixedwood forest are required to conserve the diverse avifauna of this region.

Comparación de los Efectos de la Fragmentación del Paisaje Causada por la Acción Forestal y Agrícola sobre la Depredación de Nidos Artificiales

Resumen: La fragmentación de paisajes forestales puede reducir el éxito reproductivo de aves que ocupan los parches residuales del bosque. Sin embargo, estudios previos se han enfocado principalmente al modo en que puede cambiar la depredación de nidos cuando los paisajes son fragmentados para agricultura en lugar de para forestería. Para determinar si el paisaje circundante influye sobre la depredación de nidos artificiales, en parches de bosque colocamos nidos sobre el suelo y en arbustos a lo largo del borde y en el interior de parches de bosque, localizados en paisajes agrícolas, talados, de bosque continuo, en una sola región del bosque boreal mixto de Canadá central. Los depredadores de nidos fueron identificados mediante cámaras disparadas remotamente y por marcas dejadas en huevos de plastilina, mientras que la abundancia relativa de depredadores de nidos como corvidos y mamíferos pequeños se estimó mediante reconocimientos y trampaos. El porcentaje de nidos sobre el suelo destruidos en el borde e interior de parches en los paisajes talados y continuos fue significativamente menor que en el borde o interior de parches en el paisaje agrícola. No se observó diferencia en las tasas de depredación de nidos en arbustos en los paisajes estudiados. Atribuimos las mayores tasas de depredación en el paisaje agrícola a la mayor densidad de ardillas rojas (*Tamiasciurus hud-*

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Paper submitted April 25, 1996; revised manuscript accepted December 2, 1996.

sonicus) en el interior y a una mayor diversidad de depredadores en los bordes. La similitud de tasas de depredación en paisajes talados y continuos sugiere que la fragmentación causada por la forestería puede producir cambios pequeños en las comunidades de depredadores y en este sentido puede ser similar a la fragmentación causada por regímenes de perturbación natural tales como fuego. En contraste, la fragmentación por agricultura parece tener consecuencias más serias para aves anidantes. Se requieren cambios políticos para limitar la expansión de la agricultura en el bosque boreal mixto para conservar la diversidad de la avifauna de esta región.

Introduction

Recently, concern has been raised over accelerated human disturbance, including mineral extraction, logging, and agricultural conversion, in the boreal forest of central Canada (Schieck et al. 1995a; Stelfox 1995). This region has one of the richest breeding bird communities anywhere in North America (Robbins et al. 1989; Pearson & Cassola 1992), and increased fragmentation of contiguous forest in this area may change the distribution and composition of avian communities because of a reduction in the quantity and quality of breeding habitat available (Saunders et al. 1991). Additionally, predators and brood parasites that are adapted to these newly fragmented landscapes may further reduce the breeding success of those forest birds that remain in residual forest patches (Gates & Gysel 1978; Yahner & DeLong 1992; Paton 1994; Robinson et al. 1995). Although forest fragmentation has been shown to be detrimental to breeding birds, the extent of this effect may differ according to the type of landscape in which forest fragments are embedded.

Previous studies investigating the influence of forest fragmentation by agriculture have shown that birds nesting in smaller, more fragmented forest patches suffer higher rates of predation than in larger blocks of forest, especially along edges (for review see Paton 1994; Andrén 1995). Fewer studies have been conducted in forested landscapes fragmented by logging, but these suggest that the consequences of such fragmentation to forest birds may be less severe than in agricultural landscapes (Ratti & Reese 1988; Storch 1991; Rudnický & Hunter 1993; Hanski et al. 1996). This difference may be associated with the fact that birds nesting in forest patches in agricultural landscapes are subjected to a predator community that has adapted to human settlement (Saunders 1990; Andrén 1995). In contrast, birds and predators in landscapes fragmented by logging are less likely to be influenced by human settlement and may be adapted to disturbance regimes that involve natural fragmentation of habitat (Hansson & Angelstam 1991; Schieck et al. 1995b). Thus, the general application of fragmentation theory may not be possible in landscapes fragmented by logging, particularly for areas such as the boreal forest where considerable natural fragmentation exists due to

fire and insect disturbance (Kabzems et al. 1986; Eberhart & Woodard 1987).

Much of the difficulty in evaluating whether the effects of fragmentation on nest predation are influenced differently by logging and agriculture, results from differences in methodology, forest type, and predator communities among studies (Paton 1994). We examined nest predation in contiguous forest, forest fragmented by logging, and forest fragmented by agriculture in the southern boreal mixedwood forest of central Canada to determine how the nature of the surrounding landscape influenced predation rates in similar forest types within a single geographic region. We chose to examine this question using artificial nests because of the difficulties in locating suitable numbers of natural nests in our study area. Numerous researchers have used artificial nests with quail eggs in order to evaluate differences in predation among landscapes (see Paton 1994 for review), but recent studies suggest that the hard shell of quail eggs may be too thick for smaller predators to penetrate, excluding them as a recognized source of predation (Haskell 1995a; DeGraaf & Maier 1996). By using quail and plasticine eggs in our nests, we were able to identify predation events by smaller predators because plasticine eggs are readily marked by small mammals during predation attempts (Haskell 1995a, 1995b). We also evaluated the relative abundance and importance of various predators based on the remains of plasticine eggs, pictures taken by remotely-triggered cameras, live-trapping of small mammals, and acoustic or visual surveys of corvids and red squirrels.

Study Area

Our study was conducted in and around the Prince Albert Model Forest of north-central Saskatchewan (53°50'N; 105°50'W), located in the mixedwood section of the southern boreal forest (Kabzems et al. 1986). Three very distinct landscapes occur in our study area: (1) 387,500 ha of protected contiguous forest in Prince Albert National Park; (2) 84,000 ha of commercial forest of which approximately 25% has been logged since 1969; and (3) 135,000 ha in the rural municipality of Paddockwood, in which 70% of the land has been converted to grain

fields, hay fields, or pasture since 1911, with about 23% of the landscape comprised of forest remnants (Fig. 1). We determined predation rates on artificial nests in each of these landscapes, for a total of five treatments: edge and interior of small forest patches embedded in an agricultural landscape (hereafter farm edge and farm interior); edge and interior of isolated forest patches surrounded by young regenerating forest caused by clearcut logging (hereafter logged edge and logged interior); and the interior of extensive contiguous forest (hereafter contiguous forest).

In 1994 artificial nests were placed at three sites in each landscape. In 1995 nests were placed at all the 1994 sites and in three new sites in both the agricultural and logged landscapes. Sites were mature to old (70–110 years) mixedwood forest of trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*) with a crown closure between 55–100% and stand height of 15–25 m. Sites in the agricultural landscape were surrounded by cultivated land, were at least 100 m from any other forested area, and were 9, 9, 10, 29, 36, and 45 ha in size. Sites in the logged landscape were surrounded on three sides by regenerating clearcuts created between 1985–1993 or road allowances greater than 25 m wide. Contiguous forest sites were at least 100 m from any road or trail. All sites were a minimum of 1 km apart, with an average distance between neighboring sites of 11 km in the agricultural landscape and 5 km in the contiguous forest. Sites in the logged land-

scape were paired, with each pair approximately 1 km apart and different pairs separated by at least 30 km.

Methods

Study Design

Wicker nest baskets (10 cm diameter and 6 cm depth), aired outside for at least 5 days prior to use and lined with dried vegetation found on site, were used as artificial nests (Rudnicki & Hunter 1993). In each artificial nest, we placed a Japanese quail (*Coturnix japonica*) egg and a plasticine egg painted to resemble a quail egg. Plasticine eggs were used to detect predation events by smaller predators such as mice, voles, and shrews that may not be detected using quail eggs alone and to provide a means of identifying predators based on dentition patterns or beak marks left in the eggs (Nour et al. 1993). Rubber boots and latex gloves were worn while handling and checking artificial nests to minimize the amount of human scent left at the nest (Small & Hunter 1988; Rudnicki & Hunter 1993; Whelan 1994).

Nests were distributed along linear transects at 20-m intervals, with nests alternated between ground and shrub (hereafter nest type). Nests were positioned randomly within 5 m of the transect line at the point of greatest cover. Although the decision to space nests at 20-m intervals was arbitrary, it is similar to the distance between nests used in many other artificial nest studies (Martin 1987; Rudnicki & Hunter 1993; Marini et al. 1995). Furthermore, in a companion study examining the temporal patterns of predation on artificial nests, we found no evidence for systematic predation by a single predator using 20-m spacing (Bayne & Hobson 1997).

Sites in the contiguous forest had two interior transects of 20 nests each. Each site in the logged landscape and each site in the agricultural landscape greater than 20 ha had one transect of 20 nests roughly parallel to and 1–5 m from the forest edge and two interior transects of 10 nests each. In order to have approximately the same density of nests across treatments, small sites in the agricultural landscape (<10 ha) had edge transects of only 12 nests and two interior transects of 6 nests. The total number of nests in each treatment and number of replicates are given in Table 1. All edge transects in the agricultural landscape ran along cultivated wheat or canola fields, whereas all edge transects in the logged landscape were along clearcuts. All interior transects were spaced approximately 50 m apart, ran parallel to each other, and were perpendicular to the edge transect. In the contiguous forest, interior transects began 100 m from maintained hiking trails and went into the forest another 400 m. In the logged and agricultural landscapes we set interior transects in the middle of the forest patch, but because of the size of our

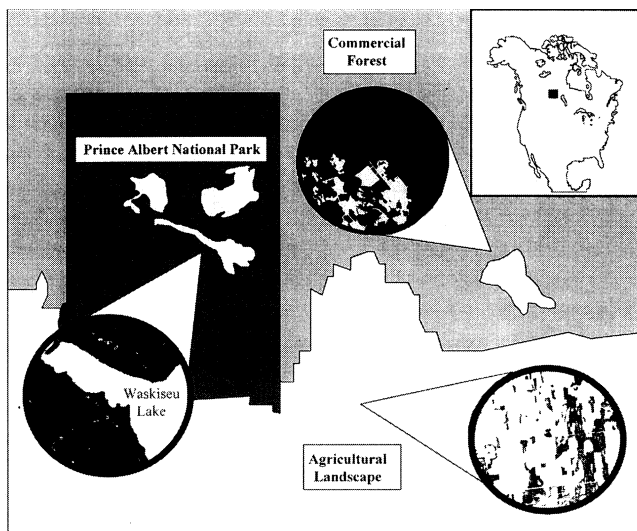


Figure 1. Location of study area. The black area within circles represents the amount of forested area within a 5-km radius of one site in each landscape. White areas represent waterbodies in the contiguous forest, clearcuts made since 1980 in the logged landscape, and fields in the agricultural landscape. Scale 1: 600,000.

Table 1. Percentage of nests destroyed at each site grouped by trial, year, nest type, and treatment.^a

Date/trial	Farm edge		Farm interior		Logged edge		Logged interior		Contiguous forest	
	Ground	Shrub	Ground	Shrub	Ground	Shrub	Ground	Shrub	Ground	Shrub
June 94										
1	100	75	100	75	50	63	0	33	40	36
2	90	100	60	100	20	60	60	80	14	11
3	50	60	70	50	20	60	40	60	25	10
Trial average	80 ± 26	73 ± 20	77 ± 21	75 ± 25	30 ± 17	61 ± 1	33 ± 31	58 ± 23	26 ± 13	19 ± 14
July 94										
1	100	100	75	50	88	100	25	63	94	44
2	70	40	100	80	90	70	50	40	45	40
3	100	60	100	80	50	50	40	70	50	20
Trial average	90 ± 17	67 ± 31	92 ± 14	70 ± 17	76 ± 22	73 ± 25	38 ± 13	58 ± 16	63 ± 27	35 ± 13
June 95										
1	83	33	100	33	22	0	30	10	45	45
2	60	80	70	70	25	40	10	30	15	30
3	100	43	100	50	40	70	50	90	70	40
4	100	100	78	82	30	20	10	0		
5	50	17	33	50	10	50	20	22		
6	70	50	60	80	40	22	40	10		
Trial average	77 ± 21	54 ± 31	74 ± 25	61 ± 19	28 ± 12	34 ± 25	27 ± 16	27 ± 33	43 ± 28	38 ± 8
July 95										
1	100	50	100	17	30	40	60	100	63	67
2	80	56	80	40	70	50	90	0	60	10
3	83	0	83	50	50	40	60	40	90	35
4	89	20	80	80	50	70	60	10		
5	33	33	50	17	70	80	50	28		
6	70	20	50	20	80	60	50	70		
Trial average	76 ± 23	30 ± 21	74 ± 20	37 ± 25	58 ± 18	57 ± 19	62 ± 15	41 ± 38	71 ± 17	37 ± 28
No. of nests ^b	148	148	148	148	180	180	180	180	240	240
Overall average	79 ± 21	52 ± 30	77 ± 21	57 ± 25	46 ± 25	53 ± 24	41 ± 23	42 ± 32	51 ± 26	32 ± 17

^aTrial average and overall average are reported as mean ± 1 SD.

^bTotal number of artificial nests placed in a particular treatment, excluding camera nests.

sites, interior transects were rarely more than 100–200 m from an edge.

Nest trials began the first week of June, a time corresponding closely to the onset of incubation for many passerines at this latitude. Nests were placed in each of the three landscapes on consecutive days. A nest was considered destroyed if any of the eggs were missing, broken, or cracked or if markings were visible on the plasticine egg. Nests were checked at 3-day intervals for 12 days. A second trial was conducted starting the last week of June in order to approximate re-nesting attempts. Where possible, interior nest transects in the second trial were moved at least 50 m from the position of the first trial transects, whereas edge transects were moved to a different side of the forest patch.

At the end of each trial, nest visibility and vegetation characteristics associated with each nest were recorded. Percentage of the nest bowl visible was estimated at a distance of 2 m from the nest at each of the four cardinal directions and where possible from 1 m above and below. Using a 1-m² quadrat centered on the nest, estimates of percent cover were calculated for deciduous trees, coniferous trees, shrubs, and dead and down woody material for four height strata (0–0.25, 0.25–1, 1–3, >3 m;

Rudnicki & Hunter 1993), whereas estimates of percent cover of grass, herbs, and moss were made for only the lowest height stratum.

Evaluation of the Predator Community

To identify predators to species, nests attached to a remote camera unit were placed in all treatments (24 in 1994 and 36 in 1995; see Bayne 1996 for design). Two to four camera nests were placed at each site for 6 days or until the nest was destroyed, after which the nest was moved to a new location at a different site. Camera nests were placed at random locations, both on the ground and in shrubs, along regular nest transects. Camera nests were at least 20 m away from any other active artificial nest and at least 50 m away from the previous location of any other camera nest. Nests with cameras attached were not used when calculating predation rate.

When nests were destroyed, all remaining quail and plasticine egg fragments were collected and we attempted to identify the predator responsible based on tooth or beak size, egg condition, or by comparisons with plasticine eggs recovered from nests with cameras. Based on measurements of museum skulls, predators

were grouped into four categories based on tooth size or beak marks: avian, mouse, squirrel, and other mammals.

Twice per year the relative abundance of corvids was estimated along a 30-km stretch of road in each landscape. At 1-km intervals all corvids heard and seen during a 3-minute stop were recorded. The total number of individuals detected per 30-km survey was then used to calculate the relative abundance of corvids in each landscape. The relative abundance of red squirrels was also estimated in each landscape by means of a combined acoustic and visual survey done twice per summer at stations located within each site. Stations were located at least 100 m from an edge and were 250 m apart, with two to five stations per site. The maximum number of squirrels recorded per station per year was used as an index of red squirrel abundance. We estimated the relative abundance of small mammals in all treatments by means of live-trapping during late July and August after the next predation experiments had finished. We chose not to conduct small mammal trapping simultaneously with the artificial nest experiments to minimize conflict between the methods (e.g., holding potential predators in traps). Traps were placed along the same transects as artificial nests from the second trial. In the agricultural and logged landscapes, 36 traps were used along the edge, whereas in the interior there were two transects of 18 traps each. In the contiguous forest, there were two transects each with 36 traps. Trapping was done for 6 nights at two sites in each landscape in 1994 and for 3 nights at every site in 1995, for a total of 4080 trap nights. Data were standardized to the total number of individuals caught per 100 trap nights, excluding recaptured animals. When calculating the number of trap nights, a correction factor of half a trap night was subtracted for each trap that was closed without catching anything or for traps that recaptured a tagged animal (Nelson & Clark 1973).

Statistical Analysis

Following arc-sine transformation, the percentages of nests destroyed per site were used as the experimental units in a four-way analysis of variance (ANOVA), with treatment, nest type, trial, and year as main effects. When significant differences were observed, multiple comparisons were made using Tukey's honestly significant difference test to determine which treatments differed (Zar 1984). Mann-Whitney U-tests were used to determine if differences in the vegetation structure around destroyed and surviving nests within each treatment and nest type were significant (Rudnicki & Hunter 1993). Two-way contingency tables using a chi-square test were used to determine if the number of plasticine eggs destroyed by a particular group of predators was significantly different among nest types and treatments. A two-way contingency table using a chi-square test was also

used to determine if the number of plasticine eggs completely removed from nests was significantly different among treatments and nest types. To determine if the abundance of corvids and red squirrels differed among landscapes and years, a two-factor Kruskal-Wallis test was used. We also used a two-factor Kruskal-Wallis test to determine if the abundance of small mammals varied among treatment and years. A non-parametric Tukey's test was used for multiple comparison of means when the Kruskal-Wallis test indicated significant effects (Zar 1984). Spearman's rank correlation was used to determine if there was a relationship between the average predation rate at a particular site (both edge and interior transects were combined when calculating predation rate) and the average number of red squirrels per station at that same site. The total number of boreal red-backed voles and deer mice (hereafter mice) captured per 100 trap nights per site was also tested against the predation rate on ground nests at a particular site (both trials were combined when calculating predation rate) using Spearman's rank correlation. Only ground nests were included in this analysis because mice do not seem to regularly destroy shrub nests. All results are reported as means \pm 1 SD unless otherwise stated.

Results

Factors Influencing Predation Rate of Artificial Nests

Artificial nests located along farm edge and farm interior suffered significantly higher rates of predation than nests in all other treatments ($F_{df=4,128} = 11.3, p < 0.001$; Table 1). The higher rate of predation at farm edge and farm interior was due to increased predation on ground nests because a significant interaction between nest type and treatment was observed ($F_{df=4,128} = 3.4, p < 0.01$). Shrub nests at farm edge and farm interior suffered intermediate rates of predation (see Table 1), but did not suffer statistically different rates of predation than any other nest type or treatment. We also could not detect any difference in predation rate between ground and shrub nests at logged edge, logged interior, or contiguous forest (Table 1). Predation was significantly higher on ground nests in July ($69 \pm 30\%$) than in June ($50 \pm 30\%$) because a significant interaction between trial and nest type was observed ($F_{df=1,128} = 5.4, p < 0.05$). Predation was also significantly higher in 1994 ($59 \pm 25\%$) than 1995 ($51 \pm 21\%$; $F_{df=1,128} = 7.2, p < 0.01$). However, when the six new sites added in 1995 were removed from the analysis, there was no year effect ($F_{df=1,68} = 2.13, p > 0.10$). All other two-way, three-way, and four-way interactions were not significant.

In 15 out of 200 possible nest type and treatment combinations, vegetation structure between surviving and destroyed nests was statistically different. However, the

patterns we observed were not consistent among treatments. Vegetation attributes that were significantly different between surviving and destroyed nests are given in Table 2.

Predator Identification and Abundance

Seventy photographs identified four different avian (16% of all photographs) and seven different mammalian (84% of all photographs) predators (Table 3). Red squirrels were the most frequently identified predator (57%). Based on photographs, predator richness was highest along farm edges where nine different predators were identified to species. Ground nests were destroyed by a wide variety of mammalian predators (96%), whereas shrub nests were destroyed by birds (38%) and red squirrels (62%).

A total of 420 plasticine eggs was recovered from destroyed nests, with the remainder completely removed from nests (53% of all nests destroyed). The predators responsible for missing eggs could not be identified, but it is unlikely they occurred in the same proportion as for destroyed eggs that were recovered. Based on camera nests where photographs identified the predator, deer mice removed plasticine eggs from the area surrounding nests less often (47% of all cases identified) than red squirrels (78%) or birds (63%). There was no significant difference in the number of plasticine eggs that were completely removed from nests among treatments and nest types ($\chi^2 = 6.7$, $p > 0.10$).

We found a significant difference in the number of plasticine eggs destroyed by different predators in each treatment when nest types were pooled ($\chi^2 = 44.3$, $df = 8$, $p < 0.001$, Fig. 2). Analysis of individual predators revealed that the number of eggs destroyed by birds and squirrels was significantly different among treatments

($\chi^2 = 23.1$, $df = 4$, $p < 0.001$; $\chi^2 = 16.4$, $df = 4$, $p < 0.01$, respectively), whereas the number destroyed by mice was not significantly different among treatments ($\chi^2 = 4.6$, $df = 4$, $p > 0.30$). By examining the residuals for each cell (Norusis 1993), we found that birds destroyed nests at logged edge and logged interior more often than expected and in contiguous forest less often than expected. The number of nests destroyed by squirrels was greater than expected at farm interior and was less than expected at logged edge and logged interior. The predators responsible for predation of ground and shrub nests (all treatments pooled) differed significantly ($\chi^2 = 126.8$, $df = 2$, $p < 0.001$, Fig. 2). Birds and squirrels destroyed more shrub nests than expected ($\chi^2 = 58.9$, $df = 2$, $p < 0.001$ and $\chi^2 = 12.2$, $df = 2$, $p < 0.001$, respectively), whereas mice were more likely to destroy ground nests ($\chi^2 = 55.5$, $df = 2$, $p < 0.001$). The other mammal category was not included because of the limited number of eggs recovered in this category.

American Crows and Black-billed Magpies were found almost exclusively in the agricultural landscape ($\chi^2 = 8.6$, $df = 2$, $p < 0.01$ and $\chi^2 = 10.5$, $df = 2$, $p < 0.01$, respectively), whereas Gray Jays were found primarily in the logged and contiguous forest ($\chi^2 = 6.3$, $df = 2$, $p < 0.05$, Table 4). The relative abundance of Common Ravens and the total number of corvids was not significantly different among landscapes ($\chi^2 = 3.7$, $df = 2$, $p > 0.10$; $\chi^2 = 4.9$, $df = 2$, $p < 0.10$, respectively, Table 4). There was no significant difference in the abundance of any species among years.

Red squirrels were present in all sites and the maximum number detected per station was significantly different among treatments and years ($\chi^2 = 20.3$, $df = 2$, $p < 0.001$ and $\chi^2 = 31.94$, $df = 1$, $p < 0.001$, respectively). Squirrel abundance was highest in the agricultural landscape (3.2 ± 1.7 squirrels detected per station) and was

Table 2. Average percent cover values for vegetation variables that were statistically different between surviving and destroyed nests for each treatment and nest type.

Nest type	Treatment	Vegetation variable	Height strata ^b	Surviving nests	Destroyed nests
Ground	Farm edge	Nest visibility ^a	NA	28.3	37.5
	Farm interior	Conifer	3	11.6	21.7
	Farm interior	Deciduous	3	7.2	3.3
	Farm interior	Herb	1	30.5	20.4
	Logged edge	Dead and downed	1	13.9	20.1
	Forest interior	Shrub	1	7.5	11.3
Shrub	Farm edge	Conifer	4	7.8	20.7
	Farm edge	Deciduous	3	22.6	13.2
	Farm edge	Moss	1	0.7	2.2
	Farm interior	Shrub	1	20.0	12.7
	Logged edge	Dead and downed	2	1.5	3.7
	Logged interior	Conifer	4	11.3	13.6
	Logged interior	Deciduous	1	1.4	0.5
	Logged interior	Deciduous	2	2.4	0.5
	Logged interior	Moss	1	15.9	31.1

^aNest visibility is the average percentage of the nest bowl visible from a distance of 2 m.

^bHeight strata at which each percent cover measure was estimated: 1, 0–0.25 m; 2, 0.25–1 m; 3, 1–3 m; and 4, >3 m.

Table 3. Number of photographs obtained for each species of predator in each treatment by remote cameras located at artificial ground and shrub nests.^a

Predator	Farm edge (283)	Farmed interior (212)	Logged edge (174)	Logged interior (210)	Contiguous forest (372)	Ground ^b (635)	Shrub ^b (616)
American Crow <i>Corvus brachyrhynchos</i>	1						1
Gray Jay <i>Perisoreus canadensis</i>	1		2	3		1	5
Black-billed Magpie <i>Pica pica</i>	2					1	1
Unknown corvid		1					1
House Wren <i>Troglodytes aedon</i>	1						1
Black bear <i>Ursus americanus</i>					1	1	
Deer mouse <i>Peromyscus maniculatus</i>	3	1		1	6	11	
Northern flying squirrel <i>Glaucomys sabrinus</i>	1					1	
Porcupine <i>Erethizon dorsatum</i>	1					1	
Red squirrel <i>Tamiasciurus hudsonicus</i>	13	12	7		8	25	15
Snowshoe hare <i>Lepus americanus</i>	1					1	
Striped skunk <i>Mephitis mephitis</i>	1			1		2	
Predator richness ^c	10	3	2	3	3	10	5

^aThe number in parentheses is the number of nights a camera unit was in a particular forest type multiplied by the number of camera units.

^bGround and shrub categories are pooled from other treatments.

^cPredator richness is the number of species identified in each treatment.

significantly higher than in the logged landscape (1.2 ± 1.2 squirrels detected per station) but not significantly different from contiguous forest (2.2 ± 1.2 squirrels detected per station). Across all landscapes significantly more

squirrels were recorded in 1994 than in 1995 (3.2 ± 1.7 and 1.7 ± 1.2 squirrels detected per station, respectively); however, no interaction was observed between year and landscape ($\chi^2 = 3.3$, $df = 2$, $p > 0.10$).

The correlation between red squirrel abundance and predation rate per site was not statistically significant when all landscape types were combined ($r = 0.39$, $p = 0.06$). When each landscape was analyzed separately, there was a significant positive correlation between predation rate and red squirrel abundance in the agricultural landscape ($r = 0.70$, $p < 0.05$), whereas there was no significant correlation in logged or contiguous forest ($r = 0.32$, $p > 0.40$; $r = -0.20$, $p > 0.70$, respectively).

Small mammal abundance was significantly greater in contiguous forest relative to the logged interior, but no other comparisons were significant ($\chi^2 = 10.89$, $df = 4$, $p < 0.05$, Table 5). Deer mice were significantly more abundant at farm edge compared with logged edge and logged interior ($\chi^2 = 16.5$, $df = 4$, $p < 0.01$), whereas the abundance of boreal red-backed voles did not differ among treatments ($\chi^2 = 3.7$, $df = 4$, $p > 0.25$). Red squirrel abundance, based on trapping data, was not significantly different among treatments ($\chi^2 = 6.0$, $df = 4$, $p > 0.10$) but was highest in farm interior (3.5 ± 4.7 captures per 100 trap nights). There was no significant difference among years for any species.

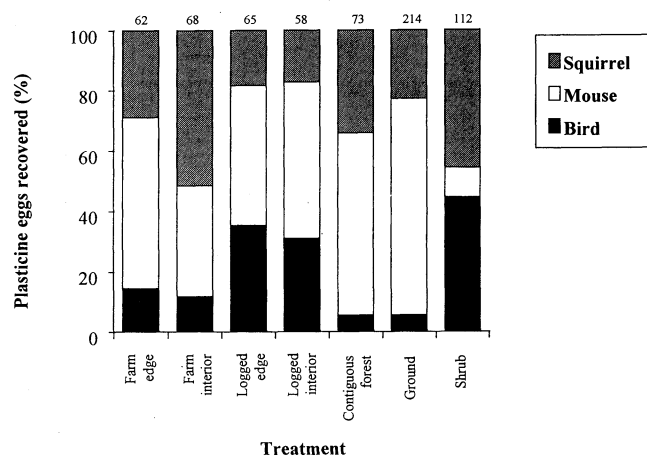


Figure 2. Percentage of plasticine eggs recovered by treatment according to predator type (ground and shrub nests pooled) and number of plasticine eggs recovered by nest type (treatments pooled) for 1994 and 1995. The number above each bar is the total number of plasticine eggs recovered in that treatment.

Table 4. Mean number of corvids by species and as a group (± 1 SD) per 30-km survey in each landscape and the results of the Kruskal-Wallis test for differences between landscapes.

Species	Farm	Logged	Contiguous forest	p
American Crow <i>Corvus brachyrhynchos</i>	32.5 \pm 17.0	0.3 \pm 0.5	1.0 \pm 0.8	<0.01
Black-billed Magpie <i>Pica pica</i>	9.5 \pm 3.7	0 \pm 0	0 \pm 0	<0.005
Gray Jay <i>Perisoreus canadensis</i>	0.3 \pm 0.5	9.0 \pm 3.7	4.5 \pm 4.7	<0.05
Common Raven <i>Corvus corax</i>	6.0 \pm 6.7	10.3 \pm 5.1	14.0 \pm 2.4	NS
Total*	48.3 \pm 18.5	20.3 \pm 8.0	20.5 \pm 7.0	NS

*Average number of individuals of all species combined in each landscape.

The abundance of mice per site was positively correlated with predation rate per site over all treatments combined ($r = 0.42$, $p < 0.01$). Furthermore, when specific treatments were analyzed, there was also a positive correlation between the abundance of mice and predation rate at farm edge ($r = 0.84$, $p < 0.01$) and farm interior ($r = 0.88$, $p < 0.01$). However, there was not significant correlation between the abundance of mice and predation rate per site for logged edge, logged interior, and contiguous forest ($r = 0.11$, $p > 0.75$; $r = -0.23$, $p > 0.50$; and $r = -0.20$, $p > 0.70$, respectively).

Discussion

Impacts of Landscape and Edge on Nest Predation

Previous research on the effects of forest fragmentation on predation of both natural and artificial nests suggests that predation tends to increase along edges of forest patches, particularly in highly fragmented agricultural landscapes (Gates & Gysel 1978; Wilcove 1985; Andr  n 1992, Paton 1994; Andr  n 1995; but see Nour et al. 1993; Marini et al. 1995). Higher nest predation at forest-field edges has previously been attributed to increases in the abundance and diversity of predators at edges, particularly generalist predators such as corvids, that invade

forest patches from the surrounding agricultural landscape (Gates & Gysel 1978; Wilcove 1985; Andr  n 1995). Our photographs indicated that nests along the edges of forest patches in the agricultural landscape were destroyed by a greater diversity of predators than in any other treatment. However, the increase in predator richness and the presence of generalist predators at edges in our agricultural landscape did not result in higher rates of predation compared to the interior of those same patches.

The absence of an edge effect in our agricultural landscape may have been caused by the relatively small size of our forest patches such that the entire patch may have constituted edge habitat. However, our photographs and remains of plasticine eggs indicated that red squirrels were the dominant predator in the interior of forest patches in the agricultural landscape. If forest patches in our agricultural landscape represented primarily edge habitat, we would have expected more evidence of generalist predators such as corvids in the interior of these patches. Furthermore, Paton (1994) suggested that any increase in predation along edges is usually limited to the first 50 m from an edge. Thus, we suspect that the high rates of predation observed in our small farm woodlots are the result of predator saturation in the agricultural landscape, both from generalist predators living in the agricultural matrix and from predators like squirrels

Table 5. Mean number of small mammals caught per 100 trap nights (± 1 SD) in each treatment and the results of the Kruskal-Wallis test for differences between treatments.^a

Species	Farm edge	Farm interior	Logged edge	Logged interior	Contiguous forest	p
Boreal red-backed vole <i>Clethrionomys gapperi</i>	13.5 \pm 9.6 (93)	8.1 \pm 10.5 (62)	12.2 \pm 7.9 (94)	12.6 \pm 9.6 (97)	16.6 \pm 9.1 (167)	>0.25
Deer mouse <i>Peromyscus maniculatus</i>	16.7 \pm 9.5 (116)	8.4 \pm 6.5 (57)	1.4 \pm 1.7 (11)	2.3 \pm 4.2 (14)	13.6 \pm 8.4 (120)	<0.01
Red squirrel <i>Tamiasciurus hudsonicus</i>	1.5 \pm 2.7 (8)	3.5 \pm 4.7 (19)	1.1 \pm 0.8 (8)	0.8 \pm 1.1 (6)	0.5 \pm 0.5 (4)	>0.10
Total ^b	32.4 \pm 16.9 (224)	21.0 \pm 14.1 (144)	15.3 \pm 8.2 (115)	16.1 \pm 7.5 (117)	32.4 \pm 3.9 (298)	<0.05

^aNumber in parentheses is the number of individuals caught.

^bAverage number of all animals caught regardless of species.

that live within the residual forest patches. Obviously, understanding factors influencing the presence or absence of edge effects and why certain landscapes suffer higher rates of predation than others requires information on the predators responsible and our study illustrates how cameras and plasticine eggs enable a more informed evaluation of these effects.

Few nest predation studies have been done in forested landscapes fragmented by logging, but most have shown no increase in predation along edges (Yahner & Wright 1985; Ratti & Reese 1988; Storch 1991; Rudnický & Hunter 1993; Hanski et al. 1996). Rudnický and Hunter (1993) argued that the absence of edge effects in landscapes fragmented by logging was due to predator communities and predator densities being typically different in landscapes fragmented by logging compared to those fragmented by agriculture. In agricultural landscapes, human activities provide a permanent change in the landscape structure and an increased food supply (e.g., crops, refuse, etc.) that may lead to higher densities of generalist predators such as corvids, particularly along edges (Angelstam 1986). In contrast, clearcuts provide little in the way of increased food and may be too short-lived to allow colonization by generalist predators adapted to more open fragmented habitats (Hanski et al. 1996). Furthermore, a "mesopredator release" (Soulé et al. 1988) may occur in agricultural landscapes because the absence of top level predators in such fragmented landscapes may allow smaller nest predators to reach higher densities than in contiguous forest. For example, the high abundance of red squirrels in our agricultural landscape may reflect the absence of major squirrel predators such as Barred Owls (*Strix varia*) and fishers (*Martes pennanti*) that occur in the contiguous and logged forest adjacent to our agricultural landscape (Arthur et al. 1989; Laidig & Dobkin 1995).

A major difference between edges in agricultural and logged landscapes is the structure of the edge vegetation. Forest-clearcut edges often possess little transition vegetation, and the lack of brushy vegetation along these edges may not attract nesting birds relative to interior habitat (Angelstam 1986; Hansson 1992), making it less rewarding for predators to forage there (Ratti & Reese 1988). In contrast, edges in agricultural landscapes may be more diverse with a higher shrub density and insect abundance (Murcia 1995) that may lead to an increase in the density of nesting passerines and a commensurate increase in predation rate as predators increase their activity in response to increased nest density (Gates & Gysel 1978; Sugden & Beyersbergen 1986; but see Reitsma 1992; Marini et al. 1995). Further studies addressing the influence of edges within both logged and agricultural landscapes are clearly required to distinguish between the effects of the landscape matrix and the structure of edges on predation rate (e.g., Small & Hunter 1988; Hawrot & Niemi 1996).

Corvids are often important nest predators in the boreal forest (Angelstam 1986; Yahner & Scott 1988; Andrén 1992). However, predation by corvids on our artificial nests was relatively low except in the logged landscape where Gray Jays were more likely to destroy nests along edges. Conversely, the importance of red squirrels and other small mammals as predators of both artificial and natural nests has only recently been recognized (Maxson & Oring 1978; Guillory 1987; Nour et al. 1993; Haskell 1995a; DeGraaf & Maier 1996; Hanski et al. 1996). Paton (1994) argued that the use of artificial nests has biased our view of predation because artificial nests are more likely to be destroyed by avian predators using visual cues, whereas natural nests are more likely to be destroyed by mammalian predators using olfactory cues. Further, recent studies have found that small predators such as chipmunks and white-footed mice are unable to break the hard shell of quail eggs that are typically used to bait artificial nests (Haskell 1995b; DeGraaf & Maier 1996). Thus, Haskell (1995a) has argued that artificial nest experiments with quail eggs do not constitute compelling evidence against the null hypothesis of no fragmentation effect because such experiments exclude common predators such as mice and chipmunks that exist in higher abundance in larger forest blocks.

Using plasticine eggs, we were able to include predation events by smaller predators such as mice yet still found predation to be highest in the agricultural landscape. We also found that the number of squirrels and small mammals was highest in the agricultural landscape, suggesting that decreased abundance of small mammals is not necessarily a consequence of fragmentation. However, although mice and other small mammalian nest predators may be able to destroy nests when no adult bird is present (e.g., artificial nests), it is unknown if mice can destroy nests when adult birds are present. In a study of the temporal distribution of predation events on artificial nests, Bayne and Hobson (submitted manuscript) found that mice were more likely to destroy nests just after sunset, a time when adult birds are commonly found incubating nests.

Effects of Nest Type and Vegetation Structure on Nest Predation

We determined that nest survivorship was dependent on nest type with ground nests generally suffering higher predation than shrub nests. The difference in predation rate between ground and shrub nests in our study is similar to findings of other studies conducted in forested ecosystems (Loiselle & Hoppes 1983; Wilcove 1985; Yahner & Scott 1988; but see Martin 1993a; Rudnický & Hunter 1993; Seitz & Zegers 1993; Marini et al. 1995). With the exception of red squirrels, we found mammals were more likely to destroy ground nests, whereas birds were more likely to destroy shrub nests.

However, we believe that generalizing the importance of nest type and its effect on nest survival may be inappropriate because the relative abundance of predators that destroy ground and shrub nests often varies among geographic areas, forest types, and landscapes (Martin 1987; Miller & Knight 1993).

Differential predation on shrub and ground nests can also be caused by the degree of nest concealment and the vegetation structure around the nest (Martin 1993a; 1994b). In general, artificial and natural nests that are more concealed and in areas of vegetation with greater structural complexity are less likely to be destroyed (Bowman & Harris 1983; Yahner & Scott 1988; Martin 1993b). However, we found little evidence that nest concealment influenced nest success. It is possible that nest concealment has little effect on nest vulnerability, particularly when the main predators are mammals that tend to use olfactory cues to find nests (Filliater et al. 1994; Howlett & Stutchbury 1996). Instead, those vegetation variables that we found to be significantly different between surviving and destroyed nests might be explained by the type of predators expected to select and use particular microhabitats (Kotliar & Wiens 1990). For example, in some treatments we found that nests with greater conifer cover were more likely to be destroyed, which may have corresponded to areas with a higher abundance of red squirrels (Wauters et al. 1992; Bayne et al. 1997). Further, destroyed ground nests at logged edges were surrounded by more dead and downed woody material than surviving nests, and these areas may have been used as travel lanes by small mammals (Planz & Kirkland 1992).

Conservation Implications

Although a number of nest predation studies have looked at the impacts of forest fragmentation on nest predation, few have been done in more than one landscape type, especially within the same geographic area. Thus, generalizing the effects of fragmentation among landscapes fragmented by different processes has been problematic. Our results suggest that forests fragmented by logging may host predator communities similar to those found in contiguous forest (e.g., Andrén 1994). However, this situation may be relevant primarily to the boreal forest where there is a relatively high degree of natural fragmentation at both the stand and landscape level to which birds and predators may have become adapted (Hunter 1992). In more homogeneous forests where the stand replacing disturbances occur less frequently, fragmentation by logging may have more dramatic impacts on the occurrence of nest predation. As well, our study area was only moderately fragmented by logging and was far less fragmented than our agricultural landscape. Areas more severely fragmented by logging and in closer proximity to human activity may show dif-

ferent results. Studies in different landscapes that share similar levels of fragmentation are required to determine if it is the degree of fragmentation or the type of fragmentation that is the more important factor influencing ecological processes. However, conversion of forest to agriculture seems to generally have more serious consequences for nesting birds. Current land-use policy and government subsidies to farmers in Saskatchewan, encourage direct conversion of forest into marginal agricultural land. Conservation of the boreal mixedwoods and the diverse avifauna of this region requires policy changes that limit the growth of agriculture in the forest fringe of Saskatchewan and other regions of central Canada.

Acknowledgments

We thank the Prince Albert Model Forest (Project #211), the Canadian-Saskatchewan Partnership Agreement in Forestry (Project CS 5006), the Canadian Wildlife Service, and the University of Saskatchewan for financial support. L. Bissett, D. Junor, and L. Blomer assisted with field work. We also thank G. Bortolotti, T. Donovan, M. Hunter, P. James, J. McConnell, D. Shutler, and an anonymous reviewer for their comments on earlier drafts of the manuscript. K. Hodge and G. Langerman assisted in preparation of the map. Personal support to EMB was supplied through a University of Saskatchewan graduate student scholarship. EMB also kindly acknowledges the help of the Canadian Wildlife Service in providing logistical support and office space at the Prairie and Northern Wildlife Research Centre in Saskatoon.

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