

NEST PREDATION IN ASPEN WOODLOTS IN AN AGRICULTURAL AREA IN ALBERTA: THE ENEMY FROM WITHIN

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ABSTRACT.—Several studies have documented elevated rates of nest predation for passerines and grouse in small forest patches and near anthropogenic edges. We examined patterns of predation on artificial nests in aspen (*Populus tremuloides*) woodlots and fencerows surrounded by agricultural land in Alberta. Nests were intended to mimic those of ground-nesting grouse and shrub-nesting passerines. We evaluated the relative importance of factors at the nest site, the forest patch, and the landscape to risk of nest predation by different predators. Total predation rates were highest in fencerows. Among woodlots, predation rates did not differ with woodlot area except in 1992, when predation on ground nests was higher in large woodlots. Most shrub nests were depredated by birds (corvids and House Wrens [*Troglodytes aedon*]). Corvid predation on shrub nests was higher in smaller woodlots and was highest on nests closest to the woodlot edge. Predation by small mammals was highest in larger woodlots and woodlots closer to farms and showed no edge effect. House Wren predation of shrub nests did not vary by any woodlot feature, nest cover, or distance to edge. We suggest that corvids forage mainly at the edges of forest patches and can fully penetrate small patches and fencerows. Small mammals are present in all woodlots, but avian predators take the eggs in small woodlots before they are detected by small mammals. Nest predators living within woodlots, such as wrens and small mammals, may be equally or more important than those living outside of woodlots in determining nest-predation risk for birds in woodlots. Received 15 January 1997, accepted 20 May 1997.

CLUTCH PREDATION can be a major influence on reproductive success for forest birds and has been linked to declines of some bird species breeding in fragmented forests (Gates and Gysel 1978, Robinson et al. 1995). In forest patches embedded in agricultural land, nest-predation rates usually are highest at forest/field edges (Paton 1994) and are highest in small forest fragments (Andrén 1995). This pattern has been detected for shrub and ground-nesting passerines (Gates and Gysel 1978, Møller 1988, Robinson et al. 1995) and for artificial nests intended to mimic nests of passerines and grouse (Wilcove 1985, Small and Hunter 1988, Andrén and Angelstam 1988, Andrén 1992, Marini et al. 1995).

Andrén (1995) stressed that the composition of local predator communities has a large influence on spatial patterns of predation within forest patches and landscapes. Thus, studies that do not identify egg predators may give misleading results on spatial patterns of predation. This was confirmed by two recent studies that found that corvid predation on eggs was higher in small woodlots and that preda-

tion by small mammals was higher in large woodlots (Nour et al. 1993, Haskell 1995b). When all predation events were combined, no effect of patch size or edge was apparent. Haskell (1995b) suggested that previous studies using artificial nests baited with quail eggs had underestimated small mammal predation. Thus, the negative relationship between patch size and predation rate based on studies using artificial nests may be spurious.

Most studies of nest predation have been conducted in eastern or central North America or in Scandinavia. Few studies have been done in western North America (Paton 1994), where predator communities may be different. In addition, few studies have evaluated the influence of vegetation of forest patches on predation rates and the proximity of patches to other forests or to areas of potential predator concentration, such as farmyards. In this paper, we examine the spatial pattern of egg predation in aspen (*Populus tremuloides*)-dominated woodlots in an agricultural area in central Alberta, Canada. We used quail and plasticine eggs placed in artificial nests to mimic shrub-nesting passerines and small chicken eggs placed on the ground to mimic Ruffed Grouse (*Bonasa*

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umbellus) nests. The study addressed three main questions: (1) Does woodlot size and distance to the woodlot/field edge affect predation rates on artificial shrub and ground nests? (2) Do the major clutch predators differ in their ability to find nests in woodlots of different size and at different distances from an edge? (3) Does vegetation of woodlots, their distance from other woodlots and from farms, and the overhead and lateral cover at nests influence nest-predation rates?

STUDY AREA AND METHODS

The study was conducted in the summers of 1991 and 1992 in a 7,000-ha agricultural area around the Meanook Biological Research Station (54°37'N, 113°20'W) near Athabasca, Alberta. The forest overstory is dominated by aspen and the understory by shrubs such as *Rosa* spp., *Cornus cornutata*, *C. stolonifera*, *Rubus* spp., *Ribes* spp., and *Viburnum edule*. The main crops in the area are alfalfa and barley, and cattle grazing is common. In the Meanook study area there are 11 farms and 12 houses on acreages plus the Meanook Biological Research Station. Forest cover in the study area is approximately 29%. Woodlots were chosen that were similar in topography and size of aspen and had minimal disturbance of the understory by cattle grazing. In 1991, we used 14 woodlots varying in size from 1.8 to 140 ha (nos. 1, 3 to 6, and 8 to 16; Fig. 1). In 1992, we used the same woodlots and added seven more small ones (1.8 to 12.5 ha; nos. 7, 19 to 24) and three fencerows (nos. 25 to 27; Fig. 1). Fencerows were 5 to 10 m wide and were 310, 850, and 900 m long. In both years, we also used a large (ca. 1,000 ha) block of forest 20 km to the west of Meanook near Narrow and Long Lakes. This forest was relatively continuous but was dissected by seismic lines and a narrow dirt road.

Predators.—The following mammalian egg predators occur in the Meanook area: red squirrels (*Tamiasciurus hudsonicus*), deer mice (*Peromyscus maniculatus*), red-backed voles (*Clethrionomys gapperi*), meadow voles (*Microtus pennsylvanicus*), least chipmunks (*Tamias minimus*), least weasels (*Mustela nivalis*; Sykes 1996), coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), and striped skunks (*Mephitis mephitis*). In addition, mink (*Mustela vison*), long-tailed weasels (*M. frenata*), and short-tailed weasels (*M. erminea*; Smith 1993) have ranges that overlap our study area. Black bears (*Ursus americanus*) are very rare in the Meanook area and occur more frequently near Narrow Lake. Cats and dogs are associated with farms in the area and occasionally are seen in the woodlots. The most commonly observed corvids in summer are American Crows (*Corvus brachyrhynchos*) followed by Black-billed Magpies (*Pica pica*), Common Ravens (*C. corax*), and Blue Jays (*Cyanocitta cristata*).

Nest-predation experiment.—Artificial nests were placed 30 m apart on transects located on the longitudinal axis through the center of each woodlot or fencerow (4 to 30 nests/woodlot). In the large forest block, two transects (nos. 17 and 18) of 30 nests each were placed 1,600 m apart on either side of Long Lake. Each transect was at least 500 m from the lake and both were >1 km from any farm buildings. Transects in woodlots started 15 m from an edge, and on all transects nests were offset from the flagged transect line by 5 to 10 m in different directions at each station. Nest locations were not flagged; a detailed description of distance, direction, and site characteristics facilitated subsequent location of nests. We placed ground nests and shrub nests at alternate stations. Ground nests were scrapes at the base of trees or shrubs and contained two brown "peewee" chicken eggs (50 × 37 mm). These nests resembled nests of Ruffed Grouse, whose eggs measure approximately 40 × 30 mm (Hannon unpubl. data). We placed a nail penetrating a 2-cm piece of orange flagging tape out of sight under the eggs to facilitate finding the nest if the eggs were taken. Shrub nests, intended to resemble those of passerines, were wicker baskets (11 cm wide, 7 cm deep) lined with dry grass and baited with two Japanese Quail (*Coturnix c. japonica*) eggs. Quail eggs (31 × 24 mm) were slightly larger than eggs of three shrub-nesting species found in the Meanook area: Rose-breasted Grosbeak (*Pheucticus ludovicianus*; 25 × 18 mm), American Robin (*Turdus migratorius*; 30 × 22 mm), and Swainson's Thrush (*Catharus ustulatus*; 23 × 17 mm; Hannon unpubl. data). In 1992, we replaced one of the quail eggs with a plasticine egg, painted to mimic a quail egg, to determine the identity of predators. Eggs were obtained a week prior to the experiment and kept refrigerated until used. Shrub nests were placed 0.6 to 1.5 m high in small trees or shrubs. We wore rubber gloves whenever we handled eggs and nests.

Nests were placed on transects between 22 and 28 May each year and were checked once a week for three weeks, a period reflecting incubation by Ruffed Grouse and the laying and incubation periods of passerines. In 1992, we switched the order of nests on each transect (i.e. a station with a shrub nest in 1991 had a ground nest in 1992). In 1992, we also set out quail/plasticine eggs on the ground on three transects (of 4, 7 and 15 nests) to determine whether predation rates were similar on quail and chicken eggs on the ground and between quail eggs on the ground and in shrubs. A predation event was considered to have occurred if at least one egg at a nest was taken, punctured, or broken.

Predator identification.—We did not identify predators in 1991 because plasticine eggs were not used. In 1992, mouse/vole and red squirrel/chipmunk depredations were identified by bite marks in plasticine eggs that matched bite marks produced by museum

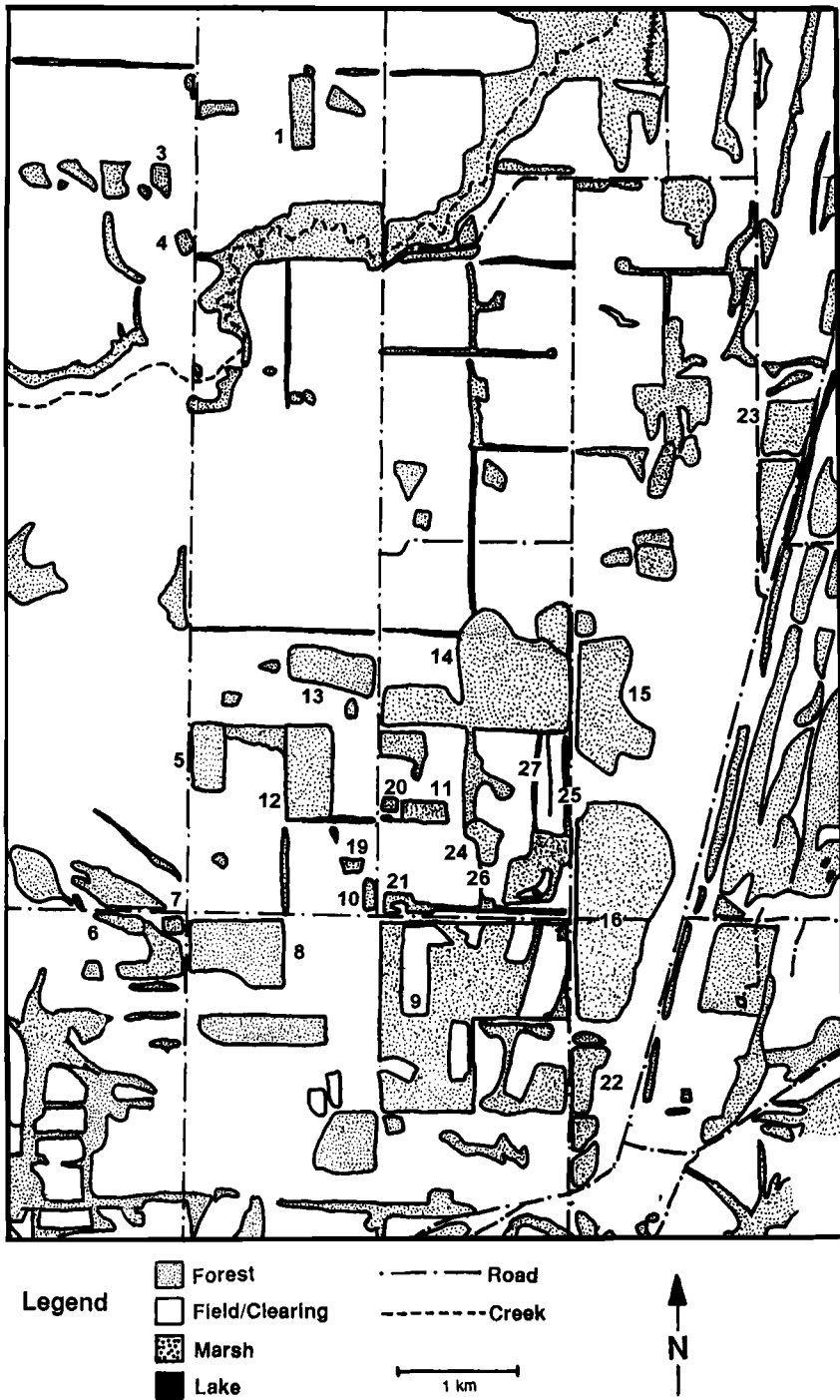


FIG. 1. Study area near the Meanook Biological Research Station, south of Athabasca, Alberta, showing woodlots and fencerows used in the study (numbered). Map does not show transects 17 and 18, which are in continuous forest 20 km to the west.

specimens. Chicken and quail eggs that were punctured and plasticine eggs with small, crescent-shaped peck marks were attributed to bird predators. We used the size of peck marks on the plasticine eggs at two nests where a Blue Jay and a House Wren (*Troglodytes aedon*) were photographed pecking eggs to distinguish wren predation from that by corvids. Scratch marks on eggs were classified as predation by rodents. Eggs taken from a nest with no sign of nest disturbance were classified as missing. Nests containing plasticine eggs with unidentifiable marks, eggs that had been moved around the nest or buried under leaf litter, and those with eggshell fragments were classified as having an unknown predator.

House Wren surveys.—House Wrens were surveyed as part of a general breeding bird survey done in 16 woodlots near Meanook and Narrow Lake (Hannon unpubl. data). Birds were surveyed using 6-min point counts over unlimited distance, from stations placed at least 500m apart, three times between 7 May and 10 July in 1991 and 1992. For this paper, we used only data from point-count stations within 300 m of a nest transect to include wrens with territories that potentially overlapped the nest transect.

Vegetation measurements.—We estimated lateral and overhead vegetative cover at each nest in 1992 only. Lateral cover was the percentage of the circumference of the nest covered by vegetation when viewed from 50 to 60 cm away. Overhead cover was the percent of a 50-cm diameter circle above the nest that was obscured by vegetation when viewed from directly above the nest. We measured the distance from each nest to the closest edge of the woodlot using aerial photographs. "Edge" was defined as the interface of forest and pasture, cropland, road, or other anthropogenic clearing.

Vegetation was measured at each nest station, at point-count stations and, in order to make sampling effort proportional to area of woodlot, at additional randomly chosen points in each woodlot. Canopy cover was measured from a photograph (4 × 6 inches) taken straight up from the sampling point using a 50-mm lens. A 4 × 6 grid of 50 evenly spaced dots was placed over the picture and the number of times a dot covered part of the canopy was recorded. This value was multiplied by two to get percent canopy cover (Freemark and Merriam 1986). Canopy height was estimated from an average tree using a clinometer at 30 m from sampling points. Tree density, dbh, shrub height, and shrub density were measured using the point-quarter method (Krebs 1989). Height of herbaceous plants and percent herbaceous cover were measured in a plot (1 × 0.2 m) centered on the sampling point.

Statistical analyses.—We tested to see whether each nest was independent of the next nest (i.e. predation events were not clumped) for ground and shrub nests separately, to satisfy assumptions of subsequent statistical tests. For each transect, we located

the first nest that was depredated (excluding all first and last nests on transects, which did not have a nest on either side) and scored whether the nests on either side were taken (i.e. both taken, one taken, neither taken). We then compared actual frequencies of predation with expected frequencies generated from a random (binomial) distribution ($p^2 + 2pq + q^2$), where p^2 is the probability that a depredated nest is between two depredated nests, q^2 is the probability that a depredated nest is between two intact nests, and $2pq$ is the probability that a depredated nest is between a depredated and an intact nest. Values of p (probability of nest being taken) and q (probability of nest being intact) were generated using the overall probability of predation for a shrub nest ($p = 0.66$, $q = 0.34$; fencerows excluded) and a ground nest ($p = 0.22$, $q = 0.78$; fencerows excluded). Expected frequencies were calculated by multiplying the terms of the model by the total number of central depredated nests in the trios of nests on the transects used above. Expected and observed frequencies were compared using a G-test with William's correction.

To determine differences in predation rates for egg type (quail vs. chicken), nest position (shrub vs. ground), and year, we used G-tests with William's correction on data combined from all woodlots. In situations where cell frequencies were less than five, we used a G randomization (G_{ran}) test with 1,000 iterations.

We examined the relationship between woodlot size and predation in two ways. First, to circumvent the potential problem of comparing proportions of nests depredated between woodlots with different numbers of nests per transect and hence different denominators, we used a Monte Carlo technique. Woodlots were classified as small (< 13 ha), medium (15 to 45 ha), and large (>100 ha). The three fencerows were placed in a separate group. Our null hypothesis was that predation rates in small and medium woodlots did not differ from those in large forest blocks. We generated a comparison group for the small and medium woodlots by creating a distribution of predation rates from the transects in large woodlots, for ground and shrub nests separately. We did this by randomly choosing small contiguous segments of nests from transects in the large woodlots that contained similar numbers of nests as those in each of the small and medium woodlots. This sequence of events was repeated three times for each woodlot (i.e. three times as many random segments were selected from the large transect as the number of woodlots or fencerows in each size class). A predation rate was then calculated for each of the randomly chosen segments from the large woodlots. The distributions of predation rates from small and medium woodlots were compared with that from large woodlots using Mann-Whitney U -tests. This first method was time consuming, and we found that correlations between woodlot area and predation rate gave the same qualitative results; consequently,

TABLE 1. Percent predation of artificial nests by year (number of nests in parentheses). Ground nests were baited with "peewee" chicken eggs; shrub nests were baited with Japanese Quail eggs.

1991	1992	G	P
Ground nests			
6.9 (145)	31.6 (177)	32.66	<0.001
	19.8 (177) ^a	11.02	<0.001
Shrub nests			
34.8 (141)	71.6 (190)	45.08	<0.001

^a Eggs with scratches coded as not depredated.

for analyses of predator type and woodlot area we used Spearman rank correlations.

We used the following variables to assess the relationship of other woodlot features on overall proportion of nests depredated within a woodlot: log (woodlot area), distance from edge of the woodlot to closest woodlot of 100 ha or larger, distance from center of woodlot to closest farm, and mean vegetation measurements for each woodlot. Because of significant correlations between some vegetation variables, we reduced them to the following: tree density, shrub density, and herbaceous cover. This was done for 1992 data only, for shrub and ground nests separately, and for each predator group separately. We used Spearman rank correlations to test relationships between percent of nests depredated in a woodlot and woodlot features because the dependent variable was not normally distributed (even after transformations).

To determine features at the nest site that might influence probability of nest predation, we performed a logistic regression of predation (yes vs. no) on lateral cover, overhead cover, and distance to the closest edge for ground and shrub nests separately, and for different predator types for shrub nests, where we had plasticine eggs and could identify predators. We excluded fencerows because all nests were less than 1 m from an edge, and we included 1992 data only for cover estimates because we did not measure cover in 1991.

Variables expressed as percentages were arcsine square-root transformed; all others were log transformed if they were not normally distributed. We used SPSS version 6.1 for the logistic regression, SYSTAT version 5.0 for correlations and Mann-Whitney *U*-tests, and our own computer programs for *G*-tests.

RESULTS

Previous studies (e.g. Willebrand and Marctöm 1988) have suggested that artificial nests are poor mimics of real nests. Our nests, however, "fooled" some of the birds in the woodlots. One shrub nest was parasitized by a

TABLE 2. Major predator types of ground and shrub nests baited with quail and plasticine eggs in 1992.

Predator type	% of total nests			
	Ground	<i>n</i>	Shrub	<i>n</i>
Mouse/vole	19.2	5	8.4	16
Red squirrel/chipmunk	7.7	2	1.6	3
Wren	0.0	0	18.4	35
Corvid	0.0	0	3.7	7
Unknown bird or mammal	0.0	0	17.4	33
Missing eggs	7.7	2	22.1	42
Total nests		26		190

Brown headed Cowbird (*Molothrus ater*), two shrub nests were incubated by female Rose-breasted Grosbeaks, and a female Ruffed Grouse laid a clutch of eggs in one of the ground nests.

Observed frequencies of predation for both shrub and ground nests did not differ from expected frequencies generated from a random distribution (shrub nests: $G = 1.08$, $P = 0.58$; ground nests: $G = 3.59$, $P = 0.17$). Thus, for further analyses we assumed that predation events were independent. Predation was higher in 1992 than 1991 for both shrub and ground nests (Table 1). In 1992, many of the chicken eggs were scratched by rodents, which may have been too small to prey on grouse nests. When scratched eggs were considered as not being depredated, predation was still higher in 1992 (Table 1). Thus, years are treated separately in all subsequent analyses.

Predator identification.—Based on marks in the plasticine and quail eggs, birds were the main predators identified at shrub nests in 1992 (Table 2). The majority of shrub nests from which eggs were missing without any sign of disturbance were probably depredated by birds. Haskell (1995b) reported that American Crows and Blue Jays removed eggs from nests before consuming them, and mice or voles probably could not remove eggs from nests. Red squirrels, which may remove eggs, accounted for only a small portion of known predation events and are not common in the area. Thus, if we attribute missing eggs to corvids, overall avian predation of shrub nests was 44.2% (18.4% by wrens and 25.8% by corvids). House Wrens were heard in 13 of 16 woodlots surveyed and were equally likely to be detected in small, medium, and large woodlots (5 of 7 in small, 5 of 8 in medium, and 7 of 12 in large woodlots; $G_{ran} = 0.33$, $P = 0.86$), and their presence was not

TABLE 3. Proportion of nests taken (\bar{x} , with SE in parentheses) by predators from small- and medium-sized woodlots and fencerows compared with proportion taken from randomly selected same-length segments from large woodlots.

Nest type	Woodlot		Proportion nests taken			
	n^a	Area	Woodlot	Random	U	P
1991						
Ground	7	Small	0.036 (0.036)	0.076 (0.035)	66.5	0.302
Shrub	7	Small	0.402 (0.153)	0.325 (0.067)	65.5	0.166
Ground	4	Medium	0.021 (0.021)	0.082 (0.039)	18.0	0.201
Shrub	4	Medium	0.301 (0.168)	0.253 (0.089)	22.0	0.431
1992						
Ground	13	Small	0.064 (0.038)	0.422 (0.051)	95.5	<0.001
Shrub	13	Small	0.692 (0.081)	0.650 (0.049)	230.5	0.311
Ground	4	Medium	0.211 (0.091)	0.355 (0.066)	13.5	0.099
Shrub	4	Medium	0.671 (0.087)	0.543 (0.063)	15.5	0.150
Ground	3	Fencerow	0.702 (0.230)	0.287 (0.083)	4.0	0.038
Shrub	3	Fencerow	1.000 (0.000)	0.603 (0.069)	1.5	0.011

^a n = number of woodlots (number of randomly chosen comparison segments is three times the number of woodlots).

restricted to edges. Seventeen of the 24 woodlots or fencerows sampled in 1992 contained nests that appeared to have been depredated by wrens.

Quail nests on the ground were taken mainly by small mammals or were missing; no bird

predation was detected (Table 2). This may not reflect predation on chicken eggs, however, because chicken eggs were taken at a lower rate than quail eggs placed on the ground (11.5% vs. 34.6%; $G_{ran} = 4.04, P = 0.045$). For the ground nests baited with chicken eggs, most of the depredated eggs either were missing or scratched by rodents. In 1991, only 10 of 145 nests were depredated; six had missing eggs, three had crushed shells, and one had a fractured egg. In 1992, 25 of 177 nests had eggs missing (one nest had a black bear scat beside it), five had crushed eggshells, four contained eggs that were moved or buried, one was pecked by a corvid, and 21 were scratched. This latter group may represent eggs unsuccessfully attacked by small rodents.

Woodlot characteristics and nest-predation rates.— In 1991, predation rates for ground and shrub nests in small and medium woodlots were not different from those in large woodlots (Table 3). In 1992, predation rates for ground nests, but not for shrub nests, were significantly higher in large woodlots than in small or medium woodlots, which was opposite to our prediction. Predation rates for ground and shrub nests in fencerows were substantially greater than those in woodlots.

For ground nests in 1992, predation was higher in larger woodlots ($r = 0.43, P = 0.05$; Fig. 2) and lower in more isolated woodlots ($r = -0.41, P = 0.07$); however, smaller woodlots tended to be more isolated ($r = -0.59, P = 0.008$). These relationships persisted when we

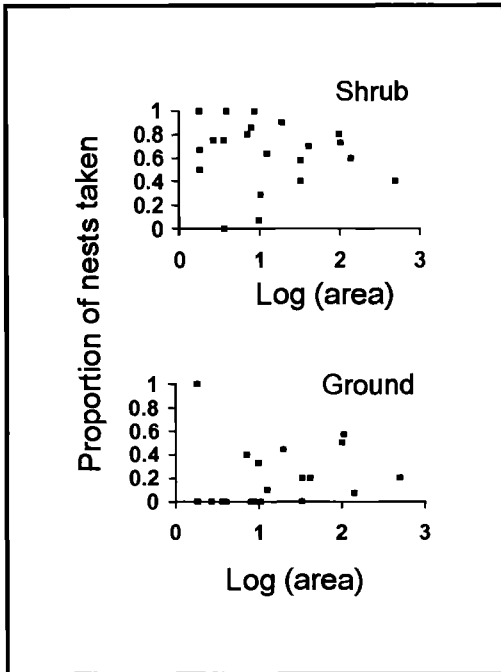


FIG. 2. Proportion of shrub and ground nests taken by predators in woodlots of different size in 1992.

TABLE 4. Percentage of shrub nests taken by different predator types over three weeks in 1992. Number of nests available per week decreases due to predation occurring in previous week.

Predator type	Week 1	Week 2	Week 3	G	P
Small mammal	3.2	4.4	11.1	5.7	0.06
Corvid	12.1	15.8	11.1	11.1	0.58
Wren	14.7	6.1	0.0	20.8	<0.001
Unknown	10.0	10.5	2.8	4.9	0.08
No. nests available	190	114	72		

omitted eggs that had been scratched by rodents, with the exception that herbaceous cover became negatively correlated with predation ($r = -0.44$, $P = 0.047$). Shrub nests in 1992 had higher total predation rates in woodlots with higher shrub density ($r = 0.61$, $P = 0.007$), but no other variables were significant, including woodlot area (Fig. 2).

For subsequent analyses of predator type and predation on shrub nests we used three groups: corvids (known cases and missing eggs), small mammals, and House Wrens. Because we did not use plasticine eggs in ground nests, we did not analyze patterns of predation by predator type for ground nests. Small mammal predation was higher in larger woodlots ($r = 0.41$, $P = 0.06$) and lower at greater distances from farms ($r = -0.39$, $P = 0.08$). Corvid predation was highest in small, more isolated woodlots ($r = -0.44$, $P = 0.05$ and $r = 0.46$, $P = 0.04$, respectively). Wren predation was not significantly correlated with any woodlot variable. Corvids were the main predators of shrub nests in fencerows (corvids 57.1%, small mammals 10.7%, wrens 7.1%, unknown 25%; $n = 28$ nests).

Small mammal predation may have been lower in small woodlots because birds took eggs before mammals could locate them. We examined temporal patterns of predation of shrub nests by predator type in 1992. Fifty-six percent of 136 nests that were depredated were taken in the first week, 30.9% in the second week, and 13.2% in the third week. Most of the wren predation occurred in the first week, whereas corvid predation occurred fairly evenly over three weeks, and small mammal predation increased over three weeks (Table 4).

Nest-site vegetation and distance from an edge.—For both years, distance from edge ranged

TABLE 5. Results of logistic regression models describing the influence of distance to an edge (DIST), vertical cover (VCOV), and lateral cover (LCOV) at nest sites on the probability of egg predation during 1991 and 1992. Model improvement by each variable is expressed as a X^2 value and associated probability level. VCOV did not enter any of the models.

Year	Nest type	n	Model improvement		
			Variable	X^2	P
1991	Ground	145		0.04	0.83
1992	Ground	154	LCOV	10.98 ^a	0.01
1991	Shrub	141		1.81	0.18
1992	Shrub	160		2.20	0.53
1992	Corvid	160	DIST	10.56	0.01
1992	Wren	160		0.49	0.92
1992	Small mammal	160		4.09	0.25

^a Data include scratched eggs; without scratched eggs $P = 0.03$.

from 15 to 370 m and did not predict whether or not a ground or shrub nest was depredated (Table 5). Ground nests with lower lateral cover were more likely to be taken, but the model had a low probability of correctly predicting depredated nests (2.8% correct for depredated and 98.3% correct for nondepredated). We repeated the analyses by predator type for shrub nests in 1992. Probability of a nest being taken by a small mammal or a wren was not related to distance to edge or nest cover; however, corvids were more likely to prey on nests close to the edge (Table 5). Again, the model had a low probability of predicting depredated nests (3% correct for depredated and 98% correct for nondepredated).

DISCUSSION

Patterns of predation on shrub nests.—Similar to Nour et al. (1993) and Haskell (1995b), we found that different predator species had different spatial patterns of nest predation. When all nest-predation events were combined, woodlot size and distance from edge had no influence on predation rates. However, corvid predation was highest in small woodlots and fencerows and at edges, small mammal predation was highest in larger woodlots, and wren predation did not vary with woodlot size or position of nests with respect to edge. The compensatory effects of corvid and small mammal predation and the large influence of wren predation on shrub nests resulted in an overall

pattern of nest predation that showed no edge or area effects. Fencerows, linear features that are all edge, appeared to be "ecological traps" (Gates and Gysel 1978) where most of the nests were depredated.

Shrub nests were taken mainly by wrens and corvids. Magpies and crows in our study area were associated mainly with pastures and farmyards and may take nests at the edges of woodlots and in fencerows opportunistically. Ravens were not common, probably because of their large home-range requirements and the low amount of forest cover in the region (see Andrén 1992). Blue Jays have been implicated as major nest predators (e.g. Yahner and Wright 1985, Yahner and Scott 1988), particularly at forest/farmland edges (Wilcove 1985 in Terborgh 1989), and have been seen taking eggs and being mobbed by songbirds in our study area.

Small mammals can be important nest predators (Maxson and Oring 1978, Guillory 1987, Martin 1988, Reitsma et al. 1990, Cotterill 1996, Hanski et al. 1996), and their influence on nests of small passerines may be underestimated in studies using large artificial eggs (Roper 1992, Haskell 1995a, b). Mice or voles (possibly deer mice, red-backed voles, or meadow voles; Sykes 1996) were the most prevalent mammal predators on shrub nests in our study. Small mammal predation was higher closer to farms, suggesting that local populations are enhanced by abundant resources associated with farmyards.

House Wrens occurred in most of the fragments, regardless of size, and did not congregate at edges. Wren predation did not vary with woodlot size or distance from edge. House Wren predation has not been reported in many other studies using artificial nests, although wrens are predators on eggs of small passerines (see Belles-Isles and Picman 1986). We noted a few tiny pecks in quail eggs in 1991, but the potential influence of wren predation became apparent in 1992 when we used plasticine eggs. Quail eggshells may be too thick for most wrens to perforate (Belles-Isles and Picman 1986); consequently, studies using only quail eggs probably will underestimate wren predation.

We explain the pattern of predation with respect to woodlot size, vegetation, and distance to edge as follows. Small mammals occur in

small forest patches (Sykes 1996), but corvids and wrens detect the nests before small mammals do. Corvids take nests near the edge and likely penetrate entire fencerows and small woodlots and take these nests early, making them unavailable to small mammals. Vegetation characteristics of woodlots do not appear to influence predation rates, except that shrub nests have higher total predation in areas with higher shrub density. This may be related to higher abundance of wrens in woodlots with more shrubs, although for wren predation alone, this was not significant ($P = 0.13$). We chose woodlots to be similar in vegetation characteristics, so it is not surprising that few vegetation variables were significant.

Patterns of predation on ground nests.—Predation on ground nests was low (6.9% in 1991 and 19.8% in 1992) compared with that recorded for Ruffed Grouse nests in New York (34% over 13 years; Bump et al. 1947). We were unable to identify predators of most ground nests because we did not use plasticine eggs. Most of the depredated nests had missing eggs or crushed eggshells. Missing eggs could be attributed to red foxes, larger corvids such as ravens, crows and magpies, or to weasels (Bump et al. 1947, Rearden 1951) and crushed eggs to skunks or mink (Rearden 1951). Red squirrels were major predators on Spruce Grouse (*Falci-pennis canadensis*) eggs in Alberta (Boag et al. 1984). Given the low numbers of red squirrels in our aspen woodlots, however, we suspect that squirrels were not important predators on grouse nests. Raccoons (*Procyon lotor*), which commonly prey on grouse nests in other areas (e.g. Bump et al. 1947), are not found in our area (Smith 1993).

Contrary to Andrén and Angelstam (1988) and Andrén (1992), we found that negative edge and area effects were not present in our agricultural landscape. Those studies were done in areas where corvids were the main predators, and they used conspicuous white chicken eggs placed on greased boards, which probably attracted these edge predators. A number of other authors have noted the ability of corvids to use visual stimuli to find nests (e.g. Picozzi 1975, Yahner and Wright 1985). The understory was quite dense in our woodlots, and ground nests had higher cover than did shrub nests and may have been hidden from visual predators such as corvids. We

found higher predation in larger woodlots in one year, suggesting that interior predators were more important than edge predators. Mammal predators that usually are associated with habitat edges, such as skunks, can be important predators within large forest blocks (Leimgruber et al. 1994). Because we could not identify predators of ground nests, we cannot confirm this result.

Use of artificial nests.—Concerns about the use of artificial nests raise a cautionary note to our interpretation of predation risk and pattern (Major and Kendal 1996). Large differences can occur between predation rates on real and artificial eggs (Martin 1987, Storaas 1988, Willebrand and Marcström 1988, O'Reilly and Hannon 1989). Moreover, the use of Japanese Quail eggs as surrogates for passerine eggs can underestimate predation by mammals that are too small to handle quail eggs (Roper 1992, Haskell 1995a). We attempted to overcome these potential biases by using fresh eggs close in size to those of birds nesting in the woodlots, not marking nest sites, using discrete flags on the transects, using rubber gloves when handling eggs, and not placing nests at high densities. Despite these precautions, we probably underestimated the actual predation rate on Ruffed Grouse nests because many mammalian predators use olfaction to detect the female or her trail (Willebrand and Marcström 1988, Storaas 1988). In contrast, our estimate of predation at shrub nests may have been too high because the wicker nests we used were more conspicuous than real nests, and there were no parent birds to defend nests against predators. Despite this, our study provides an index of spatial patterns of predation by predator type within a region, and we do not infer that our estimates of predation rates reflect those on real nests.

Conclusions.—Our study emphasizes that effects found in fragmented agricultural landscapes in eastern North American and Europe cannot be generalized to other geographical areas. Even within the same ecoregion, patterns of predation may be different depending on the type of anthropogenic disturbance (e.g. Rudnicki and Hunter 1993). For example, Cotterill (1996) completed a similar study to ours about 100 km north of Meanook in forest fragments next to recent clearcuts. She found that predation did not vary with distance from an edge

and that the major predators of shrub nests were red squirrels; corvids and House Wrens were much less common in that landscape (Hannon unpubl. data). Andrén (1995) noted differences in patterns of predation in forest fragments embedded in different matrices (e.g. agricultural vs. clearcut) and pointed out the importance of the composition of the predator community on spatial patterns of predation. The enemies from within woodlots (House Wrens and small mammals in our case) may be just as important or more important in determining predation risk to nests than the enemies from outside of woodlots.

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