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Effects of variations in micro-mammal abundance on artificial nest predation in conifer plantations and adjoining deciduous forests

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Abstract

Although conifers are extensively planted throughout the world, relatively few studies have investigated the effects these plantations might have on communities of nest predators and avian reproductive success. To address these issues, we placed artificial nests containing plasticine eggs along transects perpendicular to the edge between mature hardwood forests and adjacent spruce plantations in a managed forest landscape of northwestern New Brunswick, Canada. We used logistic regression models to assess the relative influence of habitat type, vegetation characteristics, distance from the nearest forest/plantation edge, and year on the risk of nest predation. In 1998, nest predation was significantly higher ($P < 0.0001$) in plantations (45.8%) than in forests (19.4%), and the probability of nest predation was negatively related to the density of stems 0.5–1 m high, and positively related to the density of stems 6–8 m high. In 1999, nest predation was not related to habitat type but was positively related to the density of stems 2–4 m high and negatively related to percent cover of bare ground. The distance to the nearest forest/plantation edge did not significantly contribute to either model. In 1998, black bear (*Ursus americanus*) was the most frequent nest predator (44% of depredated nests), whereas micro-mammals were in 1999 (49% of depredated nests). The high degree of temporal variability we recorded in the relative influence of various nest predators was apparently related to changes in their abundance between years, which in turn may have influenced which variables were significant predictors of the probability of nest predation each year. Conifer plantations did not appear to represent ecological traps for breeding birds, at least not consistently over time. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Conifer plantations; *Peromyscus maniculatus*; *Ursus americanus*; Artificial nest; Predation; Micro-mammals

1. Introduction

Forest harvesting and fragmentation can influence avian reproductive success directly by reducing the quantity and quality of particular habitat types (Saunders et al., 1991; Murcia, 1995) or indirectly,

through their influence on demographic processes (Robinson et al., 1995; Villard et al., 1995) and interspecific relationships (Whitcomb et al., 1981; Ambuel and Temple, 1983; Andrén et al., 1985). Numerous studies indicate that forest loss and increased fragmentation are followed by an increase in nest predation and/or brood parasitism (Robinson et al., 1995; Major and Kendal, 1996; Donovan et al., 1997), mainly near forest edges (Gates and Gysel, 1978; Wilcove, 1985; Andrén and Angelstam, 1988;

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Marini et al., 1995). Martin (1992) has shown that nest predation is the main source of nesting mortality in birds. In some cases, nest predation rates exceeding 80% have been reported (Best and Stauffer, 1980; Martin, 1992; Hanski et al., 1996). Hence, any type of disturbance or natural process that increases the abundance of nest predators would be expected to have important effects on avian reproductive success.

In a literature review, Paton (1994) concluded that edge-related increases in nest predation and brood parasitism were most significant within the first 50 m. Many experiments conducted in agricultural landscapes support this conclusion (Nour et al., 1993; Huhta et al., 1996; Hannon and Cotterill, 1998; Sargent et al., 1998). However, some authors have cautioned that results obtained in forests fragmented by agriculture may not be applicable to managed forest landscapes (Rudnicki and Hunter, 1993; Fenske-Crawford and Niemi, 1997). In fact, results are not consistent among studies conducted in the latter type of landscape: some indicate a greater risk of nest predation (1) in forest fragments near edges (Linder and Bollinger, 1995; King et al., 1996, 1998), (2) in forest fragments far from edges (Major, 1990; Storch, 1991), or (3) an absence of correlation between nest predation and distance from the nearest forest edge (Rudnicki and Hunter, 1993; Seitz and Zegers, 1993; Huhta et al., 1996; Keyser et al., 1998). Finally, studies comparing overall predation rates between landscapes fragmented by agriculture versus forestry in the same region have found higher predation rates in the former landscape type (Andr en, 1995; Huhta et al., 1996; Bayne et al., 1997). Both Donovan et al. (1997) and Hartley and Hunter (1998) attributed this phenomenon to an increase in nest predation as the amount of forest cover decreases, agricultural landscapes usually being less forested than managed forest landscapes.

Although replacing naturally-regenerated forest stands by conifer plantations is a widely-used silvicultural practice in many parts of the world, including New Brunswick, little is known about the effects of plantations on forest birds and nest predator communities. Most studies conducted in managed forest landscapes have focused on regenerating clear-cuts rather than on conifer plantations and have reported higher rates of nest predation in mature forests than in clear-cuts (Yahner and Wright, 1985; Ratti and Reese,

1988; Rudnicki and Hunter, 1993; Hanski et al., 1996). Our study should provide for a better understanding of the effects of plantations and, because of its 2-year duration, allow temporal variation in the influence of certain variables, particularly relative nest predator influence. The objectives of the present study were, thus, to compare rates of nest predation (1) between two habitat types (conifer plantations versus mature hardwood forests), (2) as a function of distance from the nearest forest/plantation edge, and (3) to identify nest predators and determine their relative influence using artificial nests and eggs.

Artificial nests are useful in this type of study as they provide flexibility in the experimental design by allowing to control of many parameters like nest height and distance from edges, and they ensure a larger sample size than studies based on natural nests (Leimgruber et al., 1994). Unfortunately, as indicated by Reitsma et al. (1990), these nests also have disadvantages: (1) there is no parental or nestling activity at or near the nest, (2) artificial nests are generally more visible than natural nests, (3) olfactory cues are different, (4) eggs used are often bigger than those of small passerines, and (5) the specific location of each nest is different. However, these shortcomings have been tolerated in artificial nest experiments since the objective is not to obtain precise estimates of predation on actual nests, but rather to obtain a measure of nesting success that can be compared among landscapes, habitat types, various distances from edges, etc. As for artificial (i.e. plasticine or clay) eggs, they are useful if one is interested in observing the influence of all potential predators, including small-mouthed predators that larger, thicker-shelled eggs fail to detect (Roper, 1992; Haskell, 1995; DeGraaf and Maier, 1996).

2. Methods

2.1. Study area

This study was conducted in the Acadian forest of northwestern New Brunswick (Canada), approximately 25 km north of Plaster Rock (47°11'N, 67°13'W) (Fig. 1). Study sites were located in areas where young (8–11 years old) conifer plantations were adjacent to patches of mature, shade-tolerant hard-

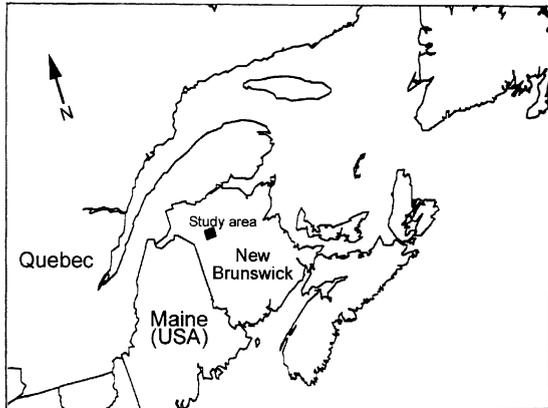


Fig. 1. Location of the study area.

woods. Landscape context varied according to the intensity of forestry (see Bourque and Villard (2001) for details). Hardwood stands were dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*). The understory was dominated by sugar maple, American beech, mountain maple (*A. spicatum*), and hobblebush (*Viburnum alnifolium*). Conifer plantations were mainly composed of black spruce (*Picea mariana*), although some white spruce (*P. glauca*) plantations were also present.

2.2. Experimental design

In 1998, we placed eight (10 in 1999), 350 m long transects containing 12 nests each ($n = 96$ in 1998 and $n = 120$ in 1999). Using aerial photographs (1:12 500) and forest inventories from Fraser Papers Nexfor, we selected sites where each transect could be placed perpendicularly to the edge between a plantation and a hardwood stand. We chose relatively abrupt edges

because nest predation rates have been shown to differ between abrupt and feathered edges (Ratti and Reese, 1988; Fenske-Crawford and Niemi, 1997; Suarez et al., 1997). All transects started 100 m into a plantation and extended 250 m into the forest because conifer plantations were too small to accommodate longer transects on many sites. Each nest was placed 5–10 m away from the transect line, alternating sides (left to right) and nest type (ground versus 50 cm high shrub nests). To allow us to detect possible edge effects more precisely (particularly in adjacent forests), nests were placed at least 25 m apart from 50 m into the plantation to 150 m into the forest, and 50 m apart elsewhere (Fig. 2). One potential caveat of this design is that closer nests could potentially lead to higher rates of nest predation due to “trapping” by individual predators. Although Bayne and Hobson (1997a) did not detect evidence of trapping for nests placed as close as 20 m apart, we followed a “scent-minimizing” protocol whenever nests and eggs were installed or visited so as to reduce the risk of trapping by predators using olfactory cues. Observers wore rubber boots at all times and rubbed their hands in leaf litter before any manipulation of experimental materials.

2.3. Artificial nests and eggs

We made cup-shaped nests out of chicken wire and filled them with straw to approximate the appearance of a white-throated sparrow (*Zonotrichia albicollis*) nest. Nests had an outer diameter of 10 cm and a depth of 4 cm and were either placed on the ground or ca. 50 cm high, mimicking two nest positions that are commonly found among songbird species nesting in our study area (Carignan, personal observation). Each nest contained two sparrow-sized (21 mm × 16 mm) plasticine eggs painted with latex to mimic the color

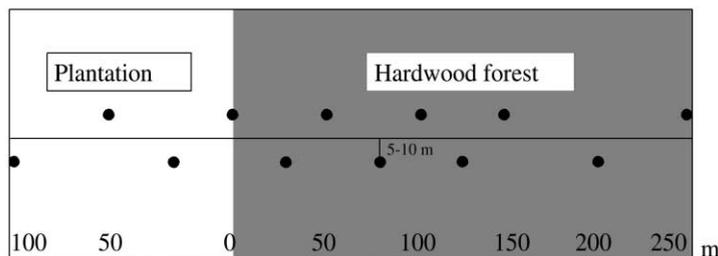


Fig. 2. Spatial arrangement of nests on each transect.

patterns of this species and dipped in transparent paraffin to cover the smell of plasticine and paint. On each transect, nests and eggs were tied to the closest woody stem with fishing wire and screws to reduce the probability of removal by nest predators like corvids (Ouellet, 1970; Sugden and Beyersbergen, 1986; Haskell, 1995), deer mouse (Bayne and Hobson, 1997b), and red squirrel (Boag et al., 1984; Sealy, 1994), that have all been observed carrying eggs or nestlings out of bird nests.

The experiment took place during the third and fourth weeks of June 1998 and 1999, a period corresponding to the peak of the breeding season of forest songbirds in our study area (Villard, unpublished data). On the seventh day of exposure, nests were visited to record predation events, but we did not manipulate the eggs to detect subtle marks left by predators. All nests were removed on the 13th day and eggs were examined with a dissecting microscope to identify marks left by predators. Our reference collection included eggs placed in live-traps containing deer mice (*Peromyscus maniculatus*) as well as eggs marked using specimens from Université de

Moncton's vertebrate collection. Marks were then classified into different categories (see Fig. 3 for the names of the categories). Many species had to be pooled into the same categories because we were unable to distinguish their teeth marks. When an egg had been depredated by more than one type of nest predator (e.g. micro-mammals and black bear) and we were unable to determine which predator was responsible for the initial predation event, the depredated nest was included in the unidentified category. Otherwise, the event was included in the category of the first predator to depredate the egg.

2.4. Vegetation sampling

We quantified vegetation characteristics (structure and composition) around each nest between mid and late July each year. Nest concealment was estimated using a 1 m × 1 m board divided into 16 squares. The board was placed immediately behind the nest and we estimated the percentage of each square that was concealed by the surrounding vegetation, as seen from 2 m in each cardinal direction from

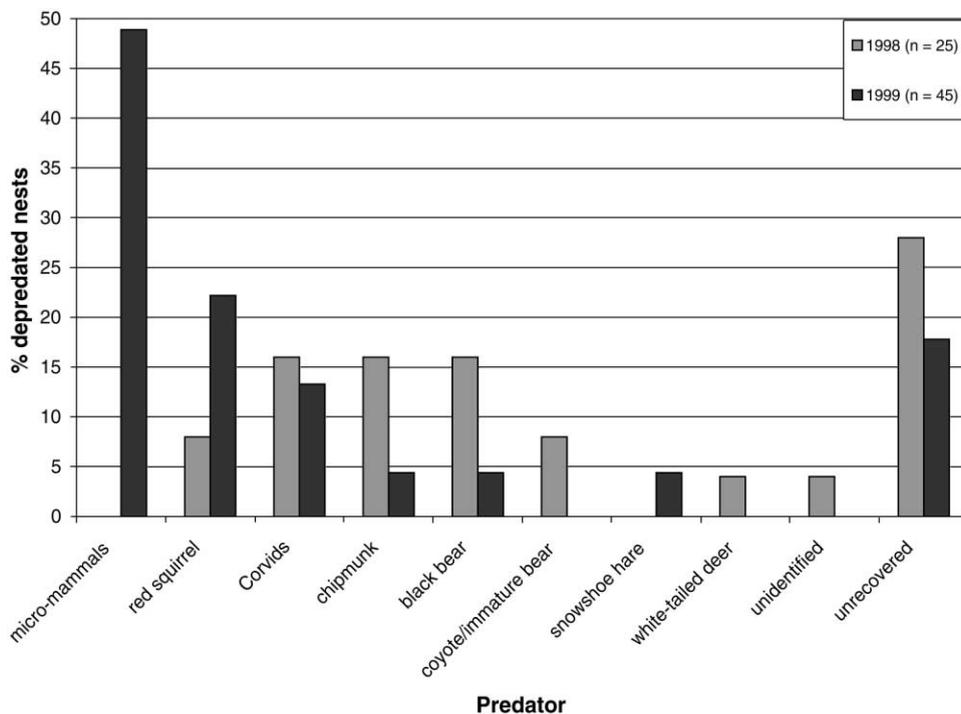


Fig. 3. Relative influence of each nest predator in 1998 and 1999.

Table 1
Independent variables considered in the logistic regression models

Variable	Description
Year	1998 vs. 1999
Habitat type	Conifer plantation vs. deciduous forest
Distance to edge	25 or 50 m increments
Height of nest	Ground vs. 50 cm high
Canopy height	Continuous
Shrub height ^a	Continuous
Percent canopy cover ^b	Percent cover (1% classes)
Percent shrub cover (0.5–8 m) ^b	Percent cover (1% classes)
Percent cover of bare ground ^b	Percent cover (1% classes)
Density of stems 0.5–1 m high ^a	Number of stems
Density of stems 1–2 m high ^a	Number of stems
Density of stems 2–4 m high ^a	Number of stems
Density of stems 4–6 m high ^a	Number of stems
Density of stems 6–8 m high ^a	Number of stems
Above-nest concealment	10% classes
Lateral nest concealment	10% classes (0–6400)

^a Variables measured in 2 m × 10 m quadrats.

^b Variables measured in 10 m × 10 m quadrats.

the nest. Other variables quantified are shown in Table 1.

2.5. Statistical analyses

We used logistic regression models to determine the relative influence of habitat type, distance from the nearest forest/plantation edge, vegetation characteristics, and year on the probability that a nest was depredated. Nest fate after 13 days (predation or not) was the dependent variable since eggs could not be closely examined on all sides on the seventh day. Independent variables included in model building are listed in Table 1. Variables expressed as proportions were arcsine-transformed. We used Pearson correlation coefficients and Mann–Whitney *U*-tests to examine the relationships among independent variables. We entered one variable from each correlated pair and every uncorrelated variable in univariate logistic models. We then incorporated significant variables ($P < 0.10$) in multivariate models, starting with the most significant. The contribution of each independent variable to the model was assessed using the likelihood ratio test (Hosmer and Lemeshow, 1989). Finally, the significance of first- and second-order interactions was examined. We used deciles of

risk to assess the goodness-of-fit of the final multivariate models (Hosmer and Lemeshow, 1989). In cases where goodness-of-fit statistics did not indicate a well-adjusted model, we examined regression diagnostics to identify extreme values. After deleting these cases, we ran additional logistic regressions to determine the effect on the independent variables selected and on the predicted values from the model. Although the predicted values from the original models and models where extreme values were excluded were similar, we used the latter to improve the goodness-of-fit. All statistical analyses were performed using Systat 8.0 (SPSS Inc., 1998).

3. Results

Twenty six percent and 38% of nests were depredated in 1998 and 1999, respectively. The difference between years is statistically significant ($G = 4.47, P = 0.034$). In 1998, there was no significant difference in the proportion of depredated nests between the first and seventh day (42.3%) and the last 6 days (57.7%) of exposure ($G = 1.20, P = 0.27$). In contrast, most nest predation events (73%) occurred during the first 7 days in 1999.

3.1. Selected models

In 1998, the probability of nest predation was (1) higher in plantations (45.8%) than in forests (19.4%), (2) positively related to the density of stems 6–8 m high, and (3) negatively related to the density of stems 0.5–1 m high (Table 2). In 1999, nest predation was (1) positively related to the density of stems 2–4 m high and (2) negatively related to percent cover of bare ground (Table 3). In the model combining the 2 years, the probability of nest predation was (1) positively related to the density of stems 4–6 m high and (2) negatively related to percent cover of bare ground. Although the year effect was significant ($\alpha < 0.10$) in a univariate model ($-2 \log \text{likelihood} = 3.23, P = 0.075$), its addition to the multivariate model did not significantly improve its predictive power. Even after extreme cases were removed, Pearson residuals still indicated an unsatisfactory fit for this model. Owing to the substantial variation in the relative influence of some species of nest predators between

Table 2

Best logistic regression model for predicting the probability of nest predation in 1998^a

Independent variable	Parameter estimate	S.E.	<i>t</i> -ratio	<i>P</i> -value	Odds ratio (95% CI)
Constant	3.87				–
Habitat type	–2.96	0.72	–4.10	<0.001	0.052 (0.21–0.013)
Density of stems 6–8 m high	0.90	0.34	2.68	0.007	2.47 (4.77–1.27)
Density of stems 0.5–1 m high	–0.025	0.012	–2.05	0.041	0.98 (0.10–0.95)

^a –2 log likelihood = 26.70; d.f. = 3; *P* = <0.001.

Table 3

Best logistic regression model for predicting the probability of nest predation in 1999^a

Independent variable	Parameter estimate	S.E.	<i>t</i> -ratio	<i>P</i> -value	Odds ratio (95% CI)
Constant	–0.48				–
Number of stems 2–4 m high	0.095	0.039	2.44	0.015	1.1 (1.19–1.02)
Percent cover of bare ground	–0.013	0.007	–1.99	0.047	0.99 (1.00–0.97)

^a –2 log likelihood = 13.97; d.f. = 2; *P* = 0.001.

the 2 years (see Sections 3.2 and 4), we must caution against the use of this model. Distance to the nearest edge was not a significant predictor of the probability of nest predation in any of our models, although there was a tendency towards higher nest predation far from edges in 1998 (Fig. 4).

3.2. Nest predators

Although we tied all eggs and nests to nearby woody stems, 28 and 17.8% of depredated eggs could not be recovered in 1998 and 1999, respectively. According to the eggs that were recovered, black bear,

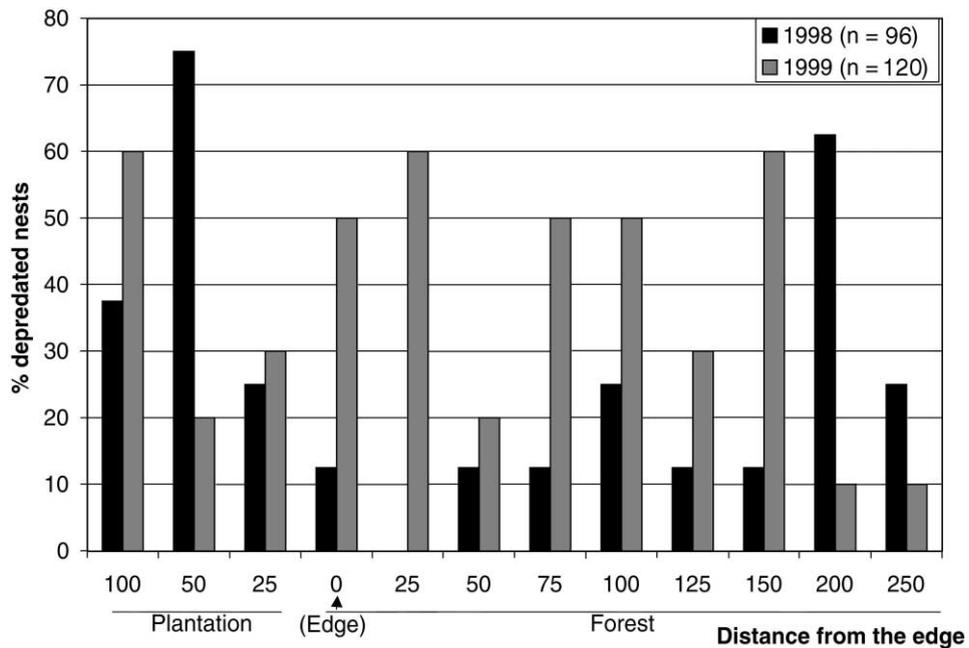


Fig. 4. Proportion of depredated nests for each distance class from the closest edge in 1998 and 1999.

coyote (*Canis latrans*), eastern chipmunk (*Tamias striatus*), and corvids were the most frequent nest predators (Fig. 3). In 1999, micro-mammals (a category that includes rodents such as deer mouse and insectivores such as the short-tailed shrew (*Blarina brevicauda*)), and red squirrel (*Tamiasciurus hudsonicus*) were the most influential nest predators (49.0 and 22.2% of depredated nests, respectively) (Fig. 3). Mammals accounted for 84 and 80% of depredated nests in 1998 and 1999, respectively.

4. Discussion

Between the two successive years of this study, we observed major changes in the significant predictors of nest predation as well as in the relative influence of nest predators themselves. We did not detect a single case of depredation by micro-mammals in 1998, whereas they were the most frequent nest predators in 1999. This probably reflects cyclic variations in the abundance of some of the micro-mammal species inhabiting hardwood stands in our study area (deer mouse and short-tailed shrew). In the same study area, Bowman (2000) detected a two- to seven-fold increase in deer mouse and short-tailed shrew captures in hardwood stands between spring 1998 (3.05 and 1.83 captures per 100 trap nights) and spring 1999 (6.54 and 13.87 captures per 100 trap nights), respectively. This increase may have been important enough for these two species to become relatively common in conifer plantations, where they are normally infrequent (Bowman et al., 2000b).

4.1. Habitat type effects

Nest predation was significantly more frequent in plantations than in forests the first year (1998), as reported by Vander Haegen and DeGraaf (1996). However, this trend was not significant in 1999. Again, temporal variation in the composition of the predator community may be responsible for the observed variation in the results. Generalist mammals with large home ranges, such as the black bear and the coyote, might spend more time foraging in plantations due to the high variety and availability of resources (e.g. fresh leaves, and buds and roots of herbaceous plants certain insects) (Kasbohm et al., 1995; Dumond,

1999) and thus encounter more nests incidentally in that type of habitat than in mature hardwood stands. The foraging behavior of these predators, coupled with the low abundance of micro-mammals in hardwood stands in 1998, may explain the higher nest predation observed in plantations that year. In contrast, the high densities of micro-mammals in hardwood stands may have obscured the influence of predators in plantations in 1999.

4.2. Distance to forest edges

In contrast with Paton's (1994) conclusion, nest predation tended to increase away from edges in 1998, whether nests were located in forests or in plantations. However, this trend was not significant. Other studies have reported higher rates of nest predation far from edges into the forest (Major, 1990; Storch, 1991) or into plantations (Vander Haegen and DeGraaf, 1996). Although many predator species have a heterogeneous distribution within their habitat (Reitsma et al., 1990; Bowman et al., 2000a), the abundance of some of those species (i.e. micro-mammals) in 1999 might have been high enough in forest stands to produce the relatively uniform pattern of predation observed that year.

4.3. Other parameters

The rate of nest predation after 7 days was significantly higher in 1999 (73%) than in 1998 (42.3%). This could have been due to a higher abundance of nest predators in 1999 (i.e. nests were found quicker). Unfortunately, we could not determine whether certain species found nests earlier than others during our trials owing to the incompleteness and inaccuracy of predator identification after 7 days (i.e. eggs could not be examined closely enough after 7 days to allow detection of all predation events by micro-mammals).

In 1998, nest predation was positively related to the density of woody stems 6–8 m high. This could have been due to the fact that some avian nest predators are able to use branches as perch sites to search for prey (Yahner and Wright, 1985; Huhta et al., 1996). Subcanopy perches might be favorable for such nest predators by allowing a better view of the surroundings. The density of stems 0.5–1 m high was also an important factor and was negatively related to nest

predation. It has been suggested that a denser understory could impede predator movements (Bowman and Harris, 1980; Picman, 1988; Seitz and Zegers, 1993) and discourage them to continue to search in a particular direction. In 1999, the density of stems 2–4 m high was positively associated with nest predation. The potential influence of this variable is unclear. Lastly, nest predation rates were higher when there was less ground cover surrounding the nest. There was a significant negative correlation between this variable and the percent cover by vegetation 0–0.5 m high so this last variable was not entered in the logistic models. Kirkland (1990) and Bowman (2000) observed a positive relationship between the abundance of certain species of micro-mammals and the amount of herbaceous vegetation. Hence, nests placed closer to dense herbaceous cover (i.e. this is equivalent to having less bare ground cover in our case) could have been subjected to a higher risk of nest predation, especially when densities of micro-mammals were high in 1999.

As reported in other studies, nest height (Hanski et al., 1996; King et al., 1998) and concealment by surrounding vegetation (Gottfried and Thompson, 1978; Sloan et al., 1998) were not significant predictors of nest success in either year. We would expect the latter to be an important predictor of nest predation, mainly when visual-searching predators are involved. In 1998, Mann–Whitney *U*-tests showed that there was a correlation between this variable and the density of stems 0.5–1 m high ($R^2 = 0.57$), so the importance of nest concealment should be partly reflected by the importance of the density of stems 0.5–1 m high.

Of the 13 habitat variables considered in this study, only one or two were significant each year. The fact that most of the predation events we identified were attributed to mammalian predators may account for this. Many mammals are known to use olfactory cues to detect their prey (Reitsma et al., 1990; Whelan et al., 1994). Although their efficiency would be reduced by denser vegetation, mammals may still move through it after locating a nest using olfactory cues (Holway, 1991).

4.4. Relative influence of nest predators

Black bear, eastern chipmunk and corvids were the three dominant nest predators in 1998. In contrast,

micro-mammals were the dominant nest predators and red squirrel and black bear were the second and third, respectively, in 1999. Although unrecovered eggs represented a large percentage of depredated eggs each year, we are confident that black bear was responsible for the majority of missing eggs, because they often left evidence other than teeth marks near depredated nests (footprints, hair, feces or scratched logs). Black bear has also been shown to be a major nest predator in other artificial nest experiments (see DeGraaf and Angelstam, 1993).

We found no convincing evidence of traplining during our study. There was one case in which four consecutive nests (at least 25 m apart) were depredated by micro-mammals, but this may not have been by the same individual. Owing to the high densities of micro-mammals in 1999, the possibility that the same individual depredated two or more consecutive nests is relatively small and since plasticine eggs provide no nutritional value to a nest predator, there is no incentive to continue searching for such an item (Nour et al., 1993).

Although our study is not the first to implicate micro-mammals as important nest predators (Maxson and Oring, 1978; Hannon and Cotterill, 1998; Keyser et al., 1998; Purcell and Verner, 1999; Buler and Hamilton, 2000; Davison and Bollinger, 2000), it seems to be the first one to quantitatively link the inter-annual variability in their abundance to their relative influence as nest predators. Our results must, however, be interpreted with a certain degree of caution. First, although there is ample evidence in the literature that micro-mammals are able to open many types of eggs (Maxson and Oring, 1978; Bayne and Hobson, 1997b; Maier and DeGraaf, 2000), it is possible that predation rates on plasticine eggs were higher than predation rates on real eggs since plasticine eggs are easier to mark. Indeed, micro-mammals may not have a large enough jaw gape to act as predators on real eggs of the size we used, although DeGraaf and Maier's (1996) experiment suggests that they could still have a potentially significant influence on many forest passerines laying smaller-sized eggs. Further laboratory experiments testing the potential influence of micro-mammals on nest predation should be conducted using a wider variety of egg types (thickness, shapes, sizes) collected from different species to improve our understanding of the actual influence of

such predators. Second, parental defense of the nest might significantly reduce predation by this type of predator (Davison and Bollinger, 2000). Considering all these factors, micro-mammals may indeed have a more restricted role as nest predators than is suggested by our results. Ideally, future researchers using artificial eggs in their experiments should design a type of egg that matches real eggs not only in size and shape, but also in hardness of the outside coating. This would allow detecting predation attempts by micro-mammals without overestimating their importance.

5. Conclusion

The striking differences observed in nest predation patterns between years most likely reflect temporal variations in the nest predator community. These changes may, in turn, determine which variables (landscape, micro- and macro-habitat characteristics, etc.) will be influential in the reproductive success of the avian community. A long-term study would be useful for indicating whether certain nest predators are, on an average, more influential than others in managed forest landscapes and which factors determine their abundance. Because complex interactions have been shown between mast-seeding species and the abundance of granivorous/herbivorous mammals (e.g. Gurnell, 1983 (holarctic tree squirrels); Selas, 1997 (microtine rodents)), it seems likely that there would also be an important effect on nest predation. We suspect that interactions of this nature occur in our study area owing to the abundance of mast-producing species such as the sugar maple, American beech, and naturally-regenerated and planted spruces, and the major changes in micro-mammal abundance recorded in the study area.

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