

# Effects of Red Squirrel (*Tamiasciurus hudsonicus*) Removal on Survival of Artificial Songbird Nests in Boreal Forest Fragments

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**ABSTRACT.**—The importance of red squirrels (*Tamiasciurus hudsonicus*) as predators of songbird nests in the boreal forest was determined by monitoring survival of artificial nests before and after squirrel removal. In eight conifer-dominated forest fragments surrounded by agricultural fields we placed artificial ground and shrub nests along the edge and interior of each fragment. Nests contained one quail and one clay egg, which were monitored for 12 d. We then removed squirrels from four forest fragments and repeated the experiment. Nests located in reference plots, where squirrel numbers were not manipulated, had similar survival rates among trials ( $2 \pm 7\%$  change between trials). In contrast, the percentage of quail eggs surviving 12 d increased  $32 \pm 9\%$  after squirrels were removed. The survival of clay eggs increased  $22 \pm 10\%$  after squirrel removal, although this was not significantly different from changes in clay egg survival between trials in reference plots ( $-2 \pm 6\%$ ). The increase in nest survival when squirrels were removed was consistent for nests on edge and interior transects and ground and shrub nests. Unlike previous studies, we did not observe compensatory predation by other predators, although the relative frequency of mice destroying nests increased after squirrel removal.

## INTRODUCTION

Many populations of North American songbirds, particularly Neotropical migrants, are declining (Askins *et al.*, 1990). Although factors on both the breeding and wintering grounds likely contribute to these declines, increased nest predation caused by fragmentation of temperate breeding areas is thought to be a major factor. Despite the importance of predation as a factor influencing survival of passerine nests, a major limitation in our understanding of nest survival is how predator abundance and type of predator influence nest predation (Yahner, 1996). Determining species responsible for predation has relied on evidence from egg remains, signs of nest disturbance and remote cameras (Major, 1991; Lariviere, 1999). Although these methods provide an index of the relative frequencies of nest predation by a particular predator, they tell us little about the absolute impact of individual predator species, as other predators may compensate when a particular predator is reduced or removed from a system. To evaluate the importance of particular predators, controlled experiments that contrast predation on nests in areas where predator numbers are manipulated and where they remain at natural levels are desirable (Reitsma *et al.*, 1990; Clark *et al.*, 1995).

Red squirrels (*Tamiasciurus hudsonicus*) are ubiquitous in conifer-dominated ecosystems

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across North America and are assumed to be a major predator of songbird nests in such habitats (Vander Haegen and Degraaf, 1996; Darveau *et al.*, 1997; Sloan *et al.*, 1998). In the boreal forest of central Saskatchewan red squirrels are more abundant in forest fragments created by agriculture than in continuous forest (Bayne and Hobson, 1998; Bayne and Hobson, 2000). Similarly, artificial and natural songbird nests have lower survival in forest fragments than in contiguous forest (Bayne and Hobson, 1997a; Hobson and Bayne, 2000). We suspect reduced numbers of squirrel predators such as the barred owl (*Strix varia*) and fisher (*Martes pennanti*) along with abundant anthropogenic food sources in fragmented landscapes have resulted in higher than normal densities of red squirrels in forest fragments. In turn, the higher abundance of red squirrels in forest fragments seems to have increased the likelihood that red squirrels will destroy forest songbird nests in this habitat (Bayne and Hobson, 1997a). Whether increased squirrel density is wholly responsible for higher rates of nest predation in our fragmented landscape relative to continuous forest remains unclear, as other predators such as corvids are also more abundant (Bayne and Hobson, 1997a).

Our objective was to determine the importance of red squirrels as predators of forest songbirds nesting in forest fragments. We compared survival rates of artificial nests before and after squirrels were removed and compared these data to those collected in reference plots where squirrel abundance was not manipulated. We hypothesized that red squirrels were the dominant nest predator in forest fragments and that nest survival would increase when squirrels were removed. We expected this effect to be most pronounced in the interior of forest fragments since previous work indicated a greater richness of predators along forest edges in our study area (Bayne and Hobson, 1997a). Therefore, we predicted that generalist predators, such as corvids, might be more likely to compensate at forest edges than in forest interiors when squirrels were removed.

#### METHODS

Our study was conducted from June through August in 1995 and in 2000, in the southern boreal mixedwood zone of north central Saskatchewan. Forest fragments were located in the rural municipality of Paddockwood, a 135,000 ha area of privately owned land, of which 70% is used for grain, hay or cattle production (Bayne and Hobson, 1997a). Plots were at least 10 km apart, ranged from 7 to 15 ha and were isolated from other forest fragments by at least 100 m. Each forest fragment was dominated by white spruce (*Picea glauca*), with some trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) present. The shrub layer was sparse and dominated by white spruce saplings.

Eight plots were chosen, with four randomly allocated as reference and four as removal plots. In trial 1, beginning in mid-June, we set out a single transect of 12 artificial nests near (<5 m) the edge of each forest fragment and two transects of six nests in the interior. Interior transects were placed 50 m apart and at least 50 m from the edge. Nests were spaced 20 m apart along transects and were alternately placed on the ground or in a shrub (>1 and <3 m high). Artificial nests were constructed from wicker baskets (10 cm diam and 6 cm deep) that were aired outside for 5 d before use and lined with vegetation found on site (Bayne and Hobson, 1997a). In each artificial nest, we placed a Japanese quail (*Coturnix japonica*) egg and a clay egg painted to resemble a quail egg. Rubber boots and latex gloves were worn when handling and checking nests to minimize human scent (Whe lan *et al.*, 1994). Nests were checked every 3 to 4 d for 12 d, a typical incubation period for songbirds at this latitude. Eggs were considered destroyed if they were missing, broken, cracked or if markings were visible on the clay eggs. If only one egg was destroyed at a given visit, we removed the remains of that egg and left the other egg. Based on the con-

dition of the clay egg, we attempted to identify the type of predator that destroyed the egg. Identification of predators followed methods outlined in Bayne and Hobson (1997a). No trapping of squirrels was done during trial 1.

During trial 1 we systematically walked all plots looking for areas where squirrels were present. Based on these observations, we established a series of squirrel trapping lines in the removal plots. Using 12 Havaheart (# 745) squirrel traps, baited with peanut butter and rolled oats, we established two lines of traps 50 m apart. Individual traps were placed on the ground at 20 m intervals. Trapping lines were systematically moved over the entire forest fragment during a 10 d trapping period. Traps were set between 18:00 and 20:00 CST and checked at 08:00 to 10:00 CST the following day. When a red squirrel was captured, it was taken to a new location at least 50 km from where it was captured and released. Trapping took place in late June and early July. In removal plots no squirrels were captured after the seventh night of trapping. However, squirrels were still detected on these plots after trapping, so the remaining squirrels were shot. Trial 2 began in early July, when we re-established the artificial nest transects. In Trial 2 nests were set out on the same transects as Trial 1, but the location of nests (*i.e.*, ground versus shrub) was reversed.

The response variable used in our analyses was the difference between the post- and preremoval periods in the percentage of nests surviving 12 d. The difference in the percentage of nests surviving was calculated separately for ground and shrub nests on the edge and in the interior of each plot. To determine if squirrel removal differentially influenced nest survival relative to nest height (ground vs. shrub) or transect (edge vs. interior), we created a generalized linear model (GLM) that included treatment (removal vs. reference), the two-way interactions treatment  $\times$  transect and treatment  $\times$  nest height and the three-way interaction treatment  $\times$  transect  $\times$  nest height. We used a split-split plot design when calculating the error terms for the GLM models (Steel and Torrie, 1980). A split-split plot design was appropriate for these data because the main factor (squirrel removal) was applied to entire forest fragments, whereas the factors transect and nest height were simply subunits within each forest fragment (not a complete factorial design). Nest height was treated as a subunit of transect in our analyses. In essence, a split-split plot design calculates a separate error term for each factor in the model and in this particular situation avoided problems associated with pseudoreplication. The same GLM model was used to determine if we could detect a difference in the actual rate of nest survival between reference and removal plots using the observed nest survival data from trial 2 only.

Logistic regression was used to determine if the relative importance of small predators, such as mice, changed after red squirrels were removed. In this analysis we were not concerned with the number of nests destroyed, but the proportion of destroyed nests whose destruction could be attributed to a particular type of predator. The response variable in this model was whether or not a mouse-sized predator destroyed a nest. We assumed eggs removed from nests were taken by predators larger than mice. Previous studies in the boreal forest indicate that squirrels, birds and various large mammals tend to remove eggs from artificial nests, whereas mice and voles almost always leave egg remains within the nest bowl (Bayne and Hobson, 1999). The model that was fit to the data included the two-way interaction treatment  $\times$  trial and the three-way interactions treatment  $\times$  trial  $\times$  nest height and treatment  $\times$  trial  $\times$  transect.

Data are reported as means  $\pm$  1 SE. Because of our small sample size, we used a rejection criterion of  $\alpha = 0.10$  to avoid making a Type II error (Steel and Torrie, 1980). Analyses were done in SYSTAT version 9.0.

## RESULTS

Through a combination of trapping and shooting, 18 red squirrels were removed from plot 1, 10 from plot 2, 20 from plot 3 and 15 from plot 4. Although we did not trap squirrels on the reference plots, we visually or acoustically detected at least 10 squirrels on each plot, suggesting the number of squirrels in reference and removal plots was similar. Near the end of trial 2, one red squirrel was observed on plot 4, whereas no squirrels were detected in the other removal plots for the duration of trial 2.

Removing squirrels significantly increased the percentage of quail eggs surviving 12 d in removal plots ( $F_{1,6} = 4.0$ ,  $P = 0.09$ ). In removal plots, quail eggs were  $32 \pm 9\%$  more likely to survive trial 2 than trial 1. In contrast, the percentage of quail eggs surviving was the same between trial 1 and 2 in reference plots ( $2 \pm 7\%$  change). The change in quail egg survival between trials was similar for edge and interior transects in removal ( $31\%$  vs.  $33\%$  change, respectively) and reference plots ( $-4\%$  vs.  $8\%$  change, respectively), as treatment  $\times$  transect was not significant ( $F_{1,6} = 0.$ ,  $P = 0.74$ : Table 1). Nest height  $\times$  treatment was not significant ( $F_{1,12} = 0.1$ ,  $P = 0.75$ : Table 1), indicating squirrel removal did not have a differential effect on survival of ground and shrub nests in removal ( $31\%$  vs.  $33\%$  change, respectively) or reference plots ( $4\%$  vs.  $0\%$  change, respectively). After squirrel removal,  $81\%$  of the transect-nest height combinations in removal plots increased in the percentage of quail eggs surviving (Table 1). The exception was removal plot 2 where quail eggs in ground and shrub nests along the edge had lower survival after removal of squirrels. When we removed the edge transect of plot 2 from our analysis, quail eggs were  $43 \pm 7\%$  more likely to survive trial 2 than trial 1 in removal plots ( $F_{1,6} = 9.2$ ,  $P = 0.02$ ).

The difference in percentage of clay eggs surviving was not significantly different after squirrels were removed in either removal or reference plots ( $F_{1,6} = 2.9$ ,  $P = 0.14$ ). However, the trend was similar to that observed when quail eggs were used to estimate nest survival. The percentage of clay eggs surviving increased  $22 \pm 10\%$  in removal plots between trial 1 and 2, whereas nest survival remained constant in reference plots ( $-2 \pm 6\%$  change). Changes in nest survival using clay eggs were consistent between removal and reference plots for edge-interior transects ( $F_{1,6} = 0.6$ ,  $P = 0.46$ ) and ground-shrub nests ( $F_{1,12} = 0.2$ ,  $P = 0.68$ ). However, only  $56\%$  of the transect-nest height combinations in removal plots showed an increase in nest survival after squirrels were removed when clay eggs were used to establish nest survival (Table 1). When the edge transect of Plot 2 was removed from our analysis, nest survival increased  $30 \pm 9\%$  between trials in the removal plots ( $F_{1,6} = 6.9$ ,  $P = 0.04$ ).

The absolute percentage of quail eggs surviving trial 2 was significantly higher in removal plots ( $77 \pm 6\%$ ) than in reference plots ( $52 \pm 7\%$ ;  $F_{1,6} = 4.2$ ,  $P = 0.09$ ). Similarly, the percentage of clay eggs surviving trial 2 was significantly higher in removal plots ( $58 \pm 8\%$ ) than in reference plots ( $38 \pm 6\%$ ;  $F_{1,6} = 3.8$ ,  $P = 0.10$ ). None of the other terms in the models were significant ( $P > 0.30$ ), indicating patterns of predation on ground vs. shrub and edge vs. interior nests were similar between removal and reference plots.

Of 384 clay eggs,  $55\%$  were destroyed. Of the destroyed clay eggs,  $53\%$  were completely removed from the nest. Based on tooth marks in recovered eggs, squirrels destroyed  $15\%$  of the nests in removal plots during trial 1. After squirrels were removed from removal plots, none of the destroyed clay eggs could be attributed to predation by squirrels. In contrast, squirrels destroyed  $19\%$  of clay eggs in reference plots in trial 1 and  $9\%$  in trial 2. Other large predators that destroyed clay eggs were birds ( $3\%$ ) and coyotes ( $2\%$ ). The proportion of clay eggs destroyed by mice was significantly influenced by the treatment  $\times$  trial interaction ( $\chi^2 = 11.3$ ,  $P < 0.001$ ). In reference plots, mice destroyed  $29\%$  of clay eggs

TABLE 1.—Number of quail and clay eggs surviving 12 d. Data are given for ground and shrub nests along edge and interior transects before (1) and after (2) the removal of red squirrels in each removal and reference plot. In each plot in each trial we placed 12 nests on a transect (edge vs. interior) with 6 nests on the ground and 6 in the shrub layer. Each nest contained one quail egg and one clay egg

Treatment	Edge-Ground						Edge-Shrub						Interior-Ground						Interior-Shrub						
	Quail		Clay		Clay		Quail		Clay		Clay		Quail		Clay		Clay		Quail		Clay		Clay		
	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	
<b>Removal Plots</b>																									
Plot 1	0	2	0	0	0	6	0	6	1	3	0	0	1	2	1	0	3	0	3	0	3	0	3	0	3
Plot 2	5	2	4	1	6	4	5	4	2	5	1	1	2	4	5	2	4	5	2	4	5	2	4	5	2
Plot 3	2	5	2	1	5	6	5	5	4	6	3	3	6	4	6	4	4	6	4	4	6	4	4	4	4
Plot 4	2	5	2	5	1	6	1	5	3	6	2	6	6	4	4	4	4	4	4	4	4	4	4	4	4
Total	9	14	8	7	12	22	11	20	10	20	6	6	15	12	18	10	14	10	14	10	14	10	14	10	14
<b>Reference Plots</b>																									
Plot 5	6	5	3	1	4	6	4	6	3	3	3	3	1	2	3	1	2	3	1	2	3	1	2	3	1
Plot 6	5	1	1	1	6	4	5	4	3	4	2	1	1	4	4	1	4	4	1	4	4	3	3	3	3
Plot 7	1	2	1	2	4	3	4	2	1	2	1	1	1	4	4	1	4	4	1	4	4	3	2	2	2
Plot 8	1	2	1	1	2	4	0	2	2	5	1	1	4	4	2	4	4	2	4	4	2	4	4	2	2
Total	13	10	6	5	16	17	13	14	9	14	7	7	7	14	13	7	14	13	7	14	13	7	14	13	10

in trial 1 and 34% in trial 2. In removal plots, mice destroyed 10% of clay eggs in trial 1 and 61% in trial 2 following squirrel removal. None of the other terms in the model were significant ( $P > 0.30$ ).

#### DISCUSSION

Our primary hypothesis that squirrels were the dominant predators of artificial nests was supported since the removal of red squirrels significantly increased the survival of artificial nests, particularly when quail eggs were used to derive nest survival estimates. Although a wide variety of predators destroy artificial nests in our study area (Bayne and Hobson, 1997a), other species did not compensate numerically when squirrels were removed. This is in contrast to studies on ducks, grouse and ptarmigan where removals of striped skunks (*Mephitis mephitis*) or corvids have rarely increased nest survival (Greenwood, 1986; Clark *et al.*, 1995). Removal experiments involving single predators have typically shown that other predators compensate for the loss of the removed predator species (Reitsma *et al.*, 1990; Clark *et al.*, 1995). Pictures taken by remote cameras at artificial nests suggest that multiple visits to the same nest by different predator species may be the norm rather than the exception (Leimgruber *et al.*, 1994).

Unlike most predator removal studies, we compared nest survival before and after predator removal rather than simply between areas where predators were removed and areas where they were not manipulated (Reitsma *et al.*, 1990; Clark *et al.*, 1995). Variation in nest predation among spatial replicates within an experimental treatment are often high, which, given the small sample size of most predator removal experiments, tends to mask treatment effects (Reitsma *et al.*, 1990; Marini and Weale, 1997). Although we had considerable variation in nest survival among plots within treatments, we also found nest survival in trial 2 was higher in removal plots than the reference plots. This suggests that our findings are robust and that removing squirrels can increase survival of artificial nests even when there is large variation among plots in predation pressure.

The increase in nest survival we observed was consistent among ground and shrub nests and at the edge and interior of forest fragments, suggesting red squirrels were destroying nests in all of the surveyed nesting strata. Thus, predators from the surrounding landscape matrix did not compensate for the loss of red squirrels at edges. Most of the larger predators in our study area likely have home ranges that encompass more than one forest fragment, so that an individual predator may spend relatively little time in any particular fragment. Large generalist predators may not have compensated when squirrels were removed, simply because the amount of time they spend in any particular fragment makes their probability of encountering nests quite low. The exception in our study was plot 2, where nests along the edge were more likely to be destroyed after squirrel removal. Possibly, this forest fragment was encompassed within the home range of a larger predator that only visited this plot in trial 2. After our experiment was completed, we observed a red fox (*Vulpes vulpes*) within this particular forest fragment.

Although predation by other species was insufficient to compensate for the loss of squirrels, the relative frequency with which small predators (*i.e.*, mice) destroyed nests increased with squirrel removal. This suggests that when squirrels were present, they were more likely to find nests than mice and destroyed artificial nests before mice had an opportunity to do so. In areas where squirrels are at naturally low densities (*i.e.*, deciduous forest), mice could be more important predators given their abundance and ubiquity (Bayne *et al.*, 1997). Regardless, higher nest survival following squirrel removal indicates that mice were not able to compensate for the loss of squirrels and suggests mice are not as effective at destroying

nests as red squirrels. Studies examining how intraspecific and interspecific variation in predator abundance influence avian nest predation are needed (Yahner, 1996).

Although artificial nest experiments imply that mice and squirrels are important predators of forest songbirds, it is not clear how accurately artificial nests mimic what happens to natural nests (Roper, 1992; Major and Kendall, 1996). Most artificial nest studies have used quail eggs to simulate passerine eggs (Major and Kendall, 1996). However, mice are unable to break large, thick-shelled quail eggs (Haskell, 1995; Bayne and Hobson, 1999), but are capable of destroying smaller, thin-shelled songbird eggs (DeGraaf and Maier, 1996). If we had not used clay eggs in our nests, we would not have detected the increase in the proportion of nests that were destroyed by mice after squirrels were removed. However, clay eggs may have an odor that allows mice and voles to find artificial nests more easily than natural nests (Rangen *et al.*, 2000). Importantly, clay egg scent does not seem to attract red squirrels to artificial nests (Bayne and Hobson, 1999). Furthermore, predation by mice and voles tends to occur nocturnally (Bayne and Hobson, 1997b), when adult passerines are incubating nests. Whether adult passerines can successfully defend their nests against small mammals requires further study. The effort required to locate sufficient numbers of natural nests in a before/after removal design makes repeating this experiment with natural nests extremely difficult. Future studies examining the role of squirrels as predators of natural nests might be done by comparing nest survival of passerines between years, with squirrel removal occurring in the intervening winter months.

High squirrel density may have been a key factor in our experiment. In contiguous deciduous forest in New Hampshire, Reitsma *et al.* (1990) removed red squirrels and eastern chipmunks (*Tamias striatus*) from six plots and found no difference in artificial nest survival relative to reference plots. They concluded that chipmunks and squirrels were not the most important predators in the forest and/or that other predators were capable of numerically compensating when they were removed. However, the mean squirrel density was lower in New Hampshire ( $0.96 \pm 0.27$  per ha) than in Saskatchewan ( $1.94 \pm 0.23$  per ha). Possibly, high densities of red squirrels in our forest fragments have resulted in a saturated predator community. Replicating our experiment in contiguous boreal forest would help discern whether red squirrels are the dominant predator of forest songbird nests across boreal forest habitats or whether the pattern we observed is a consequence of anthropogenic changes to normal predator-prey relationships.

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