

# Red squirrels and predation risk to bird nests in northern forests

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**Abstract:** Red squirrels (*Tamiasciurus hudsonicus*) are important predators on bird nests in northern conifer forests, and previous work has shown that nest density of understory birds is low in these forests compared with deciduous forest. Here, we examine the relationships between the risk of squirrel predation and nest distribution at a smaller, within-habitat scale using both experimental and comparative studies. Female squirrels depredated experimental nests more quickly than males in interior forests near the Yukon – British Columbia border, but after 2 weeks, there was no difference in the percentage of nests depredated by males and females. The density of squirrels and the risk of experimental nest predation increased but the index of natural nest density did not decrease with the density of cone-bearing Sitka spruce (*Picea sitchensis*) trees in coastal conifer forests of Southeast Alaska. Experimental nests in successional deciduous stands had high risks of predation, in part because squirrels occupied small stands of colonizing spruces in the deciduous matrix and foraged widely in the deciduous stands. In the experimental study site, natural nests occurred at similar densities both next to and away from squirrel-occupied spruce stands, but in other areas, there was a “halo” of low nest density in deciduous vegetation next to spruce stands. Overall, there was little evidence that, within habitats, birds chose nest sites that minimized the risk of squirrel predation.

**Résumé :** Les écureuils roux (*Tamiasciurus hudsonicus*) sont d'importants prédateurs des nids d'oiseaux dans les forêts de conifères boréales et des études antérieures ont signalé que la densité des nids des oiseaux du sous-bois est faible dans ces forêts, par comparaison à la forêt décidue. Nous examinons les relations entre le risque de prédation par les écureuils et la répartition des nids à une échelle plus petite à l'intérieur des habitats à l'aide d'études expérimentales et comparatives. Les écureuils femelles pillent les nids expérimentaux plus rapidement que les écureuils mâles dans des forêts intérieures près de la frontière Yukon – Colombie-Britannique; cependant au bout de 2 semaines il n'y a plus de différence dans le pourcentage de nids pillés par les mâles et les femelles. La densité des écureuils et le risque de pillage des nids expérimentaux augmentent avec la densité des épinettes de Sitka (*Picea sitchensis*) porteuses de cônes dans les forêts côtières de conifères du sud-est de l'Alaska, mais l'indice de densité des nids naturels ne baisse pas. Les nids expérimentaux placés dans des boisés décidus de la succession écologique courent de forts risques de prédation, en partie parce que les écureuils occupent les petites parcelles d'épinettes colonisatrices dans la matrice d'arbres décidus et qu'ils recherchent leur nourriture un peu partout dans les boisés de décidus. Au site expérimental, les nids naturels sont présents à des densités semblables, qu'ils soient à proximité ou à distance des parcelles d'épinettes occupées par les écureuils; ailleurs cependant, il y a une couronne de faible densité de nids dans la végétation décidue adjacente à une parcelle d'épinettes. En résumé, il y a peu d'indications que les oiseaux choisissent leurs sites de nidification à l'intérieur des habitats de manière à minimiser les risques de prédation par les écureuils.

[Traduit par la Rédaction]

## Introduction

Predation is the principal cause of avian nest loss in many regions (Ricklefs 1969; Martin 1993), including coastal rain-

forests of Southeast Alaska and interior forests of northern British Columbia and southern Yukon (Sieving and Willson 1998; Willson and Gende 2000). Red squirrels (*Tamiasciurus hudsonicus*) are major nest predators in northern forests, although corvids and other species can be significant locally (Bayne et al. 1997; Sieving and Willson 1998, 1999; De Santo and Willson 2001; Bayne and Hobson 2002a). Red squirrels are widespread in North America (Wilson and Ruff 1999); in western and boreal regions, they commonly establish territories in conifer forests, although they also hold territories and forage in deciduous stands (Uphoff 1990; M.F. Willson, personal observation). The risk of nest predation, particularly by red squirrels, is higher in the understory of conifer forest than of deciduous forest (Sieving and Willson 1998), creating a landscape of predation pressure by squirrels for understory-nesting birds at a between-habitat scale. Here, we examine the relationship between red squirrels, the

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risk of nest predation, and natural nest density at a smaller, within-habitat scale and discuss nest placement in relation to predation risks.

We tested the following hypotheses in three separate studies. (1) Female squirrels depredate nests more quickly than males and thus create a higher risk to bird eggs. Rationale: pregnant and lactating female sciurids have higher requirements for energy (Smith 1968*a*), protein (Meredith and Redrobe 2002), and perhaps also calcium or other nutrients than do males. Thus, females might be more likely to exploit seasonally available nutrient-rich foods (Uphoff 1990), such as eggs or nestlings, even if overall time budgets of males and females are similar (Ferron et al. 1986). (2A) Red squirrel density and the risk of nest predation in conifer forest increase with increasing density of large, cone-bearing spruce trees. Rationale: conifer seeds are a principal food of red squirrels, although they also eat fungi, buds, berries, and nestlings of both birds and mammals (Smith 1968*a*, 1968*b*; Rusch and Reeder 1978; Ferron et al. 1986; Boonstra et al. 2001). In the forests of Southeast Alaska, spruce cones contain more seeds than hemlock cones, and spruce seeds are also larger than hemlock seeds (Young and Young 1992), so the potential seed supply for squirrels is likely to be greater in spruce-dominated stands than in hemlock-dominated stands. Furthermore, large, mature trees commonly produce large cone crops more regularly than smaller ones (Smith 1968*a*; Gurnell 1984; Benkman 1993; Holimon et al. 1998). Squirrel density is therefore likely to be higher in conifer stands dominated by large, cone-bearing spruces, with concomitantly higher risks of nest predation for birds nesting in these stands. (2B) If nesting birds avoid high-risk areas within conifer forest, then the density of natural nests should decrease in areas with large spruces, *ceteris paribus*. Preliminary observations on Prince of Wales Island, where red squirrels are absent, indicated a higher density of understory nests than in other areas of Southeast Alaska where red squirrels are common. (3) The risk of nest predation is higher, and if nesting birds avoid high-risk areas, then nest density should be lower around squirrel-occupied conifer "islands" in a deciduous forest matrix than in deciduous forest far from conifer islands. This hypothesis is based on previous observations: during the fieldwork for Sieving and Willson (1998), we observed high nest predation rates in very localized portions of deciduous forest, possibly associated with the presence of small clumps of conifers. Also, preliminary observations for this report suggested that nest density was low around small stands of conifers in a matrix of deciduous forest (see below).

## Study area and methods

Three separate studies were conducted in different areas. All three studies used artificial nests to indicate relative risks of nest predation. The use of artificial nests to determine experimentally the rates of natural nest predation has been rightly criticized (e.g., Weidinger 2001 and references therein). However, artificial nests provide a useful and standardized tool to index predation risk for limited comparative analyses, as is done in the present study. Artificial nest experiments are most useful when the results can be seen in re-

lation to natural patterns of predation, which have been previously described for this study system (Sieving and Willson 1998; Willson and Gende 2000).

### 1. Squirrel gender and the risk of nest predation

This study took place in the interior forest of southern Yukon Territory and northern British Columbia, near Atlin, B.C., where white spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*) dominate the uplands.

In June and early July 1995, we determined the gender of 31 red squirrels (18 females and 13 males) in white spruce forest by visual inspection. Red squirrels in conifer forest typically occupy exclusive territories with central caches of stored cones (Smith 1968*a*; Price 1994; Rusch and Reeder 1978), marked by large piles (middens) of discarded cone scales and cores; some middens in this area are 10–20 m in diameter. Middens commonly are areas of high squirrel activity (Price 1994). The territory of each of the 31 squirrels had a large midden, which served as an experimental replicate. Territories were distributed along several transects separated by kilometres. Two observers simultaneously recording squirrel activity on adjacent middens, within each transect, determined that the middens were occupied by different squirrels. Experimental, thrush-size nests ( $n = 62$ ) were constructed of moss and baited with two quail eggs; one nest was placed in a shrub (0.5–1.5 m high) on or within 2 m of each midden and one on the ground on each midden, and egg loss was monitored every 3 days for 15 days. Nonparametric survival analysis was calculated using the Kaplan–Meier method (SPSS version 11.0). A lack of gender difference in levels of depredation would mean that we need not account for squirrel gender in subsequent studies.

### 2. Variation in conifer forest composition, squirrel density, predation risk, and density of natural nests

This study was conducted on the Alexander Archipelago and adjacent mainland in southeast Alaska. Forests in this region are dominated by Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) in varying proportions. We examined the relationship between forest composition, squirrel density, and natural nest density at 38 sites: three sites (separated by 1–2 km) near Suloia Lake on western Baranof Island, five sites (0.4–4 km apart) near Hanus Bay on Catherine Island, seven sites (0.8–3.7 km apart) near Portage Bay on Kupreanof Island, 10 sites (0.3–9 km apart) on north Douglas Island just west of Juneau, and 13 sites (0.3–50 km apart) near Juneau.

From mid-May to mid-July 1999, potential diurnal nest predators (red squirrels and corvids) were recorded in one fixed-radius point-count census (50-m radius) at each site. At each point, observers stood quietly for 2 min before beginning the 15-min count. Censuses were not conducted during periods of heavy rain or high wind. Within each point-count circle, we haphazardly selected six plots of 5-m radius and recorded all live trees greater than 2 m tall, including trees with at least half of their diameter in the plot, tree species, diameter at breast height (DBH), and presence of cones on trees. Near each point-count station, we established a transect of 250 × 50 m. Two experienced observers searched for natural, current-year bird nests in the understory (<4 m

while walking at a pace of 0.5–1.0 km/h; each transect was searched for 1.5–2 person-hours. The nest encounter rate during these searches was used as an index of nest density. Similarly, natural nest density was estimated at 15 sites (0.2–4.8 km apart) near Lancaster Bay on Prince of Wales Island, where red squirrels are absent. These plots were too small to permit adequate sample sizes for assessment of natural nest survival in relation to red squirrel density.

Experimental nests were arrayed at 15 of the census sites. Artificial nests, constructed of moss, mimicked those of Hermit Thrushes (*Catharus guttatus*), with a cup diameter of 6–7 cm and an outside diameter of 10–15 cm. Artificial eggs also mimicked those of Hermit Thrushes in size (approximately 23 × 17 mm) and color. Eggs were constructed of unfired porcelain clay dipped in turquoise plastic polymer (a mixture of blue and yellow Plastidip™, thinned with mineral spirits; D.G. Haskell, personal communication). Each egg was molded around a wire loop, the end of which was pushed through the bottom of the experimental nest and tethered to a twig. Tethering deterred but did not prevent removal of the clay eggs by predators, increasing the number of eggs available for later inspection for bite marks left by would-be predators. Nests and eggs were “aired” in the laboratory for 2 days before placement in the forest. In mid-June, we placed the nests in the field while wearing rubber gloves, boots, and somber-colored clothing and moving as quietly as possible to reduce the likelihood of attracting predators by our scent or activity. Nests were placed in sites typically used by Hermit Thrushes in our region: up to 2.5 m above the ground, on a stump or log, or next to a tree trunk (M.F. Willson, T.L. De Santo, and K.E. Sieving, personal observation). At these 15 sites, experimental nests were placed on either side of a 105-m transect at 15-m intervals (16 nests per site) at least 5 m from the trail. Nests were checked for signs of predation after 10 days. We took all eggs back to the laboratory, dried them in an oven, and removed the plastic coating to uncover the marks made by predators. These marks were compared with a reference collection of clay eggs marked by known predators to determine the agent of predation.

All percent data were angular transformed before analysis. There was a significant negative correlation between the number of cone-bearing spruces and the number of cone-bearing hemlocks ( $r = -0.46$ ,  $p = 0.003$ ,  $n = 38$ ). Therefore, we used only the number of cone-bearing spruces for examination of relationships among forest composition, squirrel numbers, and risk of predation.

### 3. Predation risk and natural nest density around spruce stands in a deciduous forest matrix

The third study was conducted principally in Glacier Bay National Park, Alaska, where postglacial succession creates extensive stands composed chiefly of deciduous trees (cottonwood (*Populus trichocarpa*), alders (*Alnus* spp.), and willows (*Salix* spp.)). Some areas in the southern part of the park, which have been ice free for the longest time, are dominated by Sitka spruce, and small stands of spruce (usually three to six large, cone-bearing trees) have colonized some of the deciduous stands partway up the bay. Red squirrels often occupy these isolated spruce stands, as evidenced by large middens of cone scales, although they also forage well

beyond the spruce stands in the surrounding matrix of deciduous trees.

Observations of natural nest density were made in the coniferous stands of Geikie Inlet and Fingers Bay on the west side of the bay, on the mainland adjacent to Leland Island on the east side of the bay, and near Bartlett Cove in the southern part of the bay. Some ancillary observations were made in Sheep Creek Valley, just south of Juneau, where successional deciduous stands occupy most of the valley floor except for a few groves of spruce. Glacier Bay and Sheep Creek Valley are among the few accessible sites near Juneau that are characterized by extensive deciduous stands. Experienced nest searchers indexed the density of natural understory nests by counting the number of nests encountered per unit time at several sites in Glacier Bay (13.5 person-hours) and Sheep Creek Valley (3 person-hours) in June 1998 and 1999. We also indexed the density of natural understory nests in the experimental and control plots (2 person-hours per plot of about 200-m radius) established in 1999 (below). Searches were conducted at a time of year when the understory is very open, facilitating detection of nests.

In 1999 at Geikie Inlet in Glacier Bay, we examined the risk of predation to artificial nests, each nest baited with one Japanese quail egg and one whitish clay egg. Experimental nests were constructed chiefly of beach-grass roots and leaves and were similar in size to thrush nests. There were eight replicates spaced out along almost 20 km of shoreline. Each replicate consisted of a treatment plot centered on an active squirrel midden in a small spruce stand and a paired (control) plot without a midden in the deciduous matrix. Paired plots in each replicate were at least 400 m apart and most were over 600 m apart; members of two pairs were separated by saltwater channels. Red squirrel territories in deciduous vegetation can be as large as 8 ha (Rusch and Reeder 1978), equivalent to a hypothetically circular area of radius 160 m, so the paired plots of each replicate were thought to be sufficiently far apart to separate control from treatment. In each plot, we placed 10 artificial nests about 10 m apart in shrubs along a transect through the plot and checked them 3 and 6 days after placement (160 nests total).

## Results

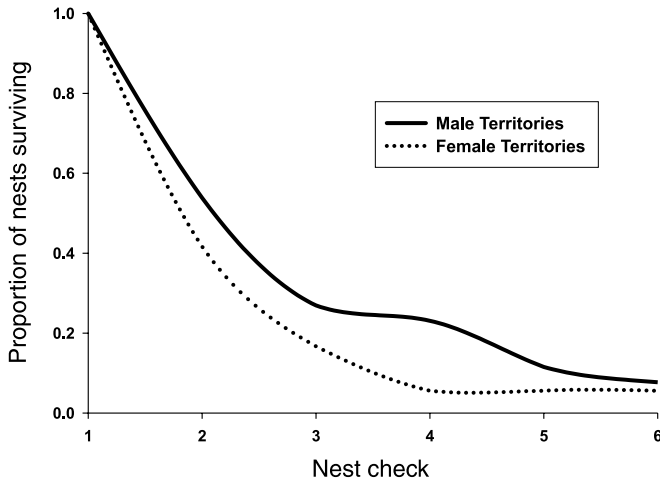
### 1. Squirrel gender and the risk of nest predation

Female and male squirrels depredated experimental ground nests at the same rate (mean number of days the nests survived 5.3 versus 6.0, respectively; log rank statistic = 0.01,  $p = 0.93$ ), but females depredated shrub nests marginally faster than did males (mean number of days the nests survived 4.8 versus 6.3, respectively; log rank statistic = 3.55,  $p = 0.06$ ). However, after 15 days, almost all nests had been found by both males (92%) and females (94%) (Fig. 1). The lack of gender differences in predation risk at the end of the experimental period indicated that squirrel gender was not a major influence in the subsequent studies of nest survival.

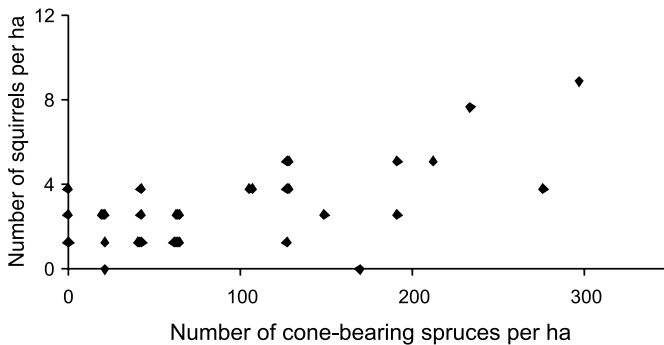
### 2. Variation in conifer forest composition, squirrel density, predation risk, and density of natural nests

Ninety-two predators were detected in the predator surveys; 88% of these were red squirrels and the remainder

**Fig. 1.** Survival of experimental nests on middens of male and female red squirrels (*Tamiasciurus hudsonicus*;  $n = 18$  males, 13 females) in spruce forest near the Yukon – British Columbia border in 1995 was similar at the end of the exposure period. On the  $x$  axis, 1 represents the beginning of the experiment followed by subsequent nest checks at 3-day intervals.



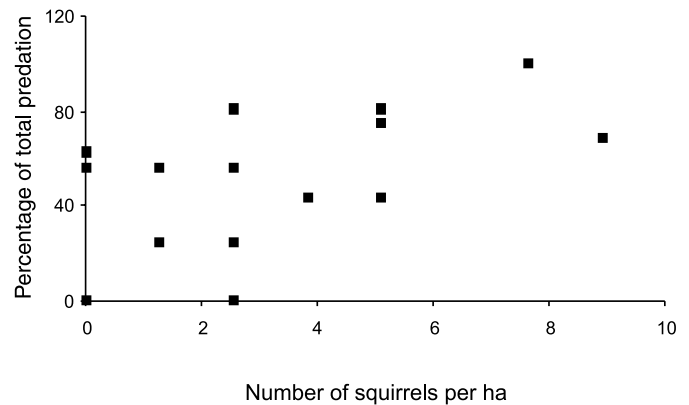
**Fig. 2.** Red squirrel abundance was correlated with number of cone-bearing Sitka spruce (*Picea sitchensis*) in Southeast Alaska in 1999 ( $r = 0.68$ ).



were corvids. Of 240 experimental nests, 123 (51%) were depredated. Predator identification was possible for 35 of these nests: eggs in nine nests were marked by birds, one was marked by a small mammal other than a squirrel, and 25 by the incisors of red squirrels. Eggs or eggs plus tethers were missing from an additional 60 nests, and 28 nests disappeared entirely.

The number of red squirrels detected in the point counts was positively correlated with the number of cone-bearing spruce trees in the plot ( $r = 0.68$ ,  $p < 0.0001$ ,  $n = 38$ ) (Fig. 2) over a range of cone-bearing spruce density of 0–14 trees per plot. All spruces over 80 cm DBH and 86% of those over 45 cm DBH bore cones. The total risk of predation on experimental nests (i.e., the percentage of nests depredated) was correlated with red squirrel abundance ( $r = 0.53$ ,  $p = 0.04$ ,  $n = 15$ ) (Fig. 3). The risk of known squirrel predation to experimental nests, as determined by tooth marks, was not significantly correlated with the number of squirrels per plot ( $r = 0.33$ ,  $p = 0.21$ ,  $n = 15$ ). However, we have observed that squirrels often remove eggs completely

**Fig. 3.** The percentage of experimental nests depredated by all predators was correlated with red squirrel abundance in Southeast Alaska in 1999 ( $r = 0.53$ ).



and sometimes remove or destroy the nest itself (also see Bayne and Hobson 1999); if we include these nest losses with those attributed to squirrels by tooth marks, then the risk of possible squirrel predation is significantly correlated with squirrel abundance ( $r = 0.56$ ,  $p = 0.03$ ,  $n = 15$ ).

The estimated density of natural nests ( $0.6 \pm 0.1$  per plot,  $n = 38$ ) was not related to the abundance of either squirrels or spruces (all  $p > 0.3$ ). However, natural nest density ( $1.9 \pm 0.3$  per plot,  $n = 15$ ) was higher on Prince of Wales Island, where red squirrels are absent, than at the other locations (Wilcoxon two-sample test,  $Z = 3.59$ ,  $p = 0.003$ ).

### 3. Predation risk around spruce stands in a deciduous forest matrix

Overall, 62% of the experimental nests in Glacier Bay in 1999 were depredated. One experimental nest plot was systematically depredated by Northwestern Crows (*Corvus caurinus*), which had a nesting colony nearby, in the latter part of the exposure period. Omitting that replicate and another one lacking data for the 6-day nest check (thus reducing the sample size to six replicates for the second part of the exposure period), there was little overall difference between midden-centered and control plots in the risk of predation: the risk of nest predation was higher in midden-centered plots than in control plots in only two of eight cases after 3 days and in two of six cases after 6 days (sign tests,  $p > 0.10$ ).

Although many of the experimental nests were depredated, only some ( $n = 7$ ) could be attributed specifically and clearly to red squirrels because in most cases, the clay eggs disappeared entirely ( $n = 33$ ). We might assume, as in the second study (above), that all removals could be attributed to squirrels, but that is inappropriate in this case because of the known activity of crows from the nearby nesting colony and our knowledge that crows also remove clay eggs. A number of eggs bore claw marks of unidentified small mammals,

possibly including squirrels. One nest was visited by a bear and one by a weasel.

The apparent density of natural understory nests in or near conifer stands in Glacier Bay and Sheep Creek Valley in 1998 was markedly lower than in nearby deciduous forest. We found an average of 1.1 nests/h (range = 0.0–2.0,  $n = 8$  surveys) in conifer stands and deciduous vegetation <50 m from conifer stands with squirrels, but an average of 5.1 nests/h (range = 2.7–8.2,  $n = 4$  surveys) in deciduous matrix >50 m from conifer stands with squirrels. However, surveys of natural understory nest densities in the experimental midden-centered and control plots in 1999 (means = 4.5 and 4.7 nests per person-hour, respectively) showed no overall difference in the density of nests: nest density in control plots exceeded that in midden-centered plots in only two of eight cases, and the reverse was equally common (sign test,  $p > 0.10$ ). Vegetation in the midden-centered and control plots was very similar: woody stem density, 1.8 versus 2.0/m<sup>2</sup>, respectively; percentage of stems 3–15 cm DBH, 93 versus 90%; percentage of stems 16–30 cm, 2 versus 4%; percentage of stems >30 cm, 5 versus 6%.

## Discussion

### Squirrel gender and nest predation

Consistent with the rationale for hypothesis 1, females tended to depredate shrub nests more rapidly than males, perhaps reflecting their use of different resources. For example, female red squirrels in central Arizona generally occupied areas with more deciduous vegetation than did males, and they were more likely than males to consume certain kinds of foods, including bird eggs or nestlings, bones, and fungi in spring and summer (Uphoff 1990). Uphoff also noted that “several females made systematic searches for bird nests in the upper branches of maple and aspen trees”. In our experiment, most of the shrub nests were placed in deciduous species, which might be explored more often by female squirrels, either in search of nests specifically or in exploring for other particular foods, such as willow buds.

However, there was ultimately little detectable effect of squirrel gender on nest survival at 15 days. Pelech (1999) also reported no difference between risk of predation by male and female red squirrels after a 14-day exposure of experimental nests in southwestern Yukon. Nests of birds with short incubation periods might be more likely to get through this period with eggs intact, but since squirrels also eat small nestlings, it is unlikely that male and female red squirrels have differing effects on overall nest survival in these northern forests.

### Patterns of predation risk

#### *Experimental nest predation*

As expected by the rationale for hypothesis 2A, the density of red squirrels increased with the density of cone-bearing Sitka spruce and the risk of predation to experimental nests increased concomitantly. In contrast, experimental studies in Glacier Bay detected no differences in predation risk in areas around spruce stands and in the surrounding deciduous matrix.

There are at least three reasons why the Glacier Bay experiment did not discriminate between treatment and control. (1) Nest predation by crows was high on one plot and occurred at least sporadically on others, thus masking the effect of squirrel predation. Northwestern Crows nest and forage near shorelines, so these masking effects would be reduced by setting up experiments farther inland. Furthermore, complete removal of clay eggs from many nests prevented examination of predator marks on the eggs. (2) In years when snow stays late on the ground, red squirrel breeding can be delayed as much as a month (Rusch and Reeder 1978; Obbard 1987). Spring was very late in Glacier Bay in 1999 compared with the previous year, and at the time of the experiment, thick snow was still present in some places and few birds had started laying eggs. If the frequency of red squirrel predation on bird nests depends on the density of active nests, then our experiment may have occurred before the peak levels of red squirrel depredation, and the effects of other predators more readily masked the predatory effects of squirrels. (3) Red squirrel territories in this area may be even larger than those in deciduous areas studied by Rusch and Reeder (1978), and the squirrels might range beyond their territorial borders, as suggested by others (Kemp and Keith 1970; Kelly 1978).

#### *Natural nest density*

Natural nest density did not vary with the density of red squirrels in areas where the squirrels are present (hypothesis 2B), nor was nest density lower around squirrel-occupied spruce islands than in deciduous matrix (hypothesis 3), although nest density was higher where red squirrels are absent (on Prince of Wales). One possible explanation for this observation might be that the mere presence of red squirrels in an area is sufficient to depress nest density. However, the structure of understory vegetation and nest site availability might also differ between Prince of Wales and the other areas of southeast Alaska that we studied, but this was not measured.

Do birds select nest sites that minimize predation risk? Birds might choose nest sites to minimize predation risk either by behavioral accommodation (individuals learning to recognize and avoid unsafe places) or by the evolution of risk avoidance via natural selection on habitat and nest site choices (e.g., Martin 1993). The scale at which any avoidance of risky nest sites might occur is still unclear, as are the cues that birds might use. Natural nest density was lower in the understory of conifer forest than in that of deciduous forest in our region (Sieving and Willson 1998) and lower in squirrel-occupied areas than on red-squirrel-free Prince of Wales Island. However, this pattern may be a response not only to the presence of squirrels but also to vegetation structure (e.g., Sieving and Willson 1998). Also, understory birds commonly used high-risk nest sites within these forests (Willson and Gende 2000). The presence of a resident squirrel is readily apparent to human observers and is potentially predictable by breeding birds as well, but we were unable to demonstrate clear evidence of avoidance of squirrel-occupied areas, and Møller (1988) found that predator density did not influence the distribution of passerine nests. Although nest site selectivity may sometimes favor tree species where daily nest survival is high (Schmidt and Whelan

1999), there can be many constraints on safe nest placement: nest sites and suitable nesting habitat may be limiting (Sieving and Willson 1998), areas of lower red squirrel density may have compensatory predation by other species (Reitsma et al. 1990), trade-offs may exist between nest site selection and other requirements, such as foraging or resting, and inexperienced breeders may be more likely to settle in risky areas than birds with previous nesting experience (e.g., Bayne and Hobson 2002b), which could mask actual patterns of risk avoidance behavior. The question of how, when, where, and to what degree forest birds are able to place their nests in safe sites is still open.

### Conclusion

The landscape of nest predation risk resembles a topographic map, with pits in habitats where predation is relatively low (and nest survival is relatively high) and peaks where predation is high (and survival is relatively low). In a northwestern landscape of predation generated by red squirrels, the peaks of predation risk to understory-nesting birds occur in conifer forest and adjacent deciduous stands. Lower levels of squirrel predation usually occur in the interior of extensive deciduous stands. The predation landscape generated by red squirrels may be overlain by one for Northwestern Crows (peaks of risk near their colonies along the coast), for Steller's Jays (*Cyanocitta stelleri*) (peaks near suburban edges, De Santo and Willson 2001; riparian edges, M.F. Willson, personal observation), and so on for other predators. In addition, temporal pits and peaks of predation risk are generated by seasonal variation in predator responses (e.g., high risks of nest predation by Steller's Jays early in the nesting season, Sieving and Willson 1999) and, less predictably, annual variations in predator populations (Sieving and Willson 1998). If there is a "landscape of fear" (Laundré et al. 2001) in the understory of these northern forests, it was seldom evident in nest placement in this study.

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