

THE SQUIRREL CONNECTION: INFLUENCE OF SQUIRRELS AS SONGBIRD NEST PREDATORS IN LASKEEK BAY

Jean-Louis Martin, Mathieu Joron

CEFE/CNRS, 1919 Route de Mende, 34293 Montpellier Cedex 5, France

martin@cefe.cnrs-mop.fr

and

Anthony J. Gaston

National Wildlife Research Centre, 100 Gamelin Blvd., HULL, Quebec K1A 0H3, Canada

ABSTRACT

The introduction of the Black-tailed Deer (*Odocoileus hemionus*) to Haida Gwaii has modified the vegetation of the islands; at the same time, the introduction of the Red Squirrel (*Tamiasciurus hudsonicus*) has added a potential predator of song bird nests to some islands. We compared forested islands with and without these introduced species to understand how predation of song bird nests is affected by the presence of squirrels and the modifications to vegetation caused by deer. We used 506 artificial nests baited with quail eggs placed on nine islands and we monitored predation of natural nests on Reef Island (no squirrels) and Louise Island (with squirrels). Highest predation rates of artificial and natural nests were observed on islands occupied by squirrels, but there was much variation among islands with squirrels. On islands without squirrels, but with native predators (mainly corvids), predation rate was lower for nests placed in shrubs than for nests placed on the ground. On islands with squirrels, rates of nest predation were not affected by nest position. On islands with squirrel, predation of ground nests increased with squirrel abundance and fluctuated from year to year with fluctuations of squirrel abundance. Squirrel abundance was highest in habitats dominated by mature conifers. On islands without squirrels, the predation risk of nests on the ground increased with decreasing vegetation cover, suggesting that removal of the vegetation by deer increases risk of predation by native avian predators (corvids). For nests in shrubs, no link between vegetation cover and predation risk was identified. Direct and indirect interactions among predator community composition, predator abundance, vegetation structure (affected by herbivores) and vegetation dynamics all influence variation and magnitude of nest predation in space and time in these temperate forests. To understand how birds respond to predation risk it is essential to consider spatial and temporal variation in risk of predation.

INTRODUCTION

Nest predation plays a significant role the structure and functioning of bird communities (Martin 1993a, 1993b, 1995). Nest predation is often higher in communities subject to human influences. In altered mainland communities this increase has been usually explained by changes favorable to generalist nest predators. On islands, increase in predation rates has usually been attributed to the introduction of non-native predators

(e.g. Atkinson 1985, Scott *et al.* 1986, Savidge 1987, Drake *et al.* 1989, Sieving 1992, Penloup *et al.* 1997, Martin *et al.* 2000). The usual explanation is that island species tend to lack anti-predation strategies adapted to the introduced predator.

Examining how predation patterns alter after human caused habitat changes can contribute to our understanding of the ecological and evolutionary effects of nest predation. Studies on the impact of edge

effect or of habitat fragmentation on predation patterns, for instance, have demonstrated that different combinations of predators affect nest predation in different ways (Angelstam 1986, Nour *et al.* 1993, Yahner 1996, see also Hannon and Cotterill 1998). Comparing situations with and without introduced predators may provide a more direct way to test the effect of predators on predation risk and how it occurs in space and time. Where nearby islands exist with and without introduced predators they can provide unintentional experiments (e.g. Penloup *et al.* 1997). A similar approach can be used to study the effects of habitat modification on predation pattern by comparing islands affected by the introduction of large herbivores to islands without large herbivores.

The islands of Laskeek Bay, on the East coast of Haida Gwaii, covered by Pacific Northwest temperate rain forests, provide an opportunity to study the relations between predators, nest predation, and habitat quality and structure. Conifers are the dominant trees, but patches of deciduous forests occur locally. The terrestrial mammalian fauna is highly impoverished (Foster 1989). The Red Squirrel (*Tamiasciurus hudsonicus*), a major nest predator (Ehrlich *et al.* 1988, Darveau *et al.* 1997, Bayne *et al.* 1997, Sieving and Willson 1998) and the Black-tailed Deer (*Odocoileus hemionus*), a species that can have a strong impact on vegetation structure (Pojar *et al.* 1980, Daufresne and Martin 1997, Martin and Daufresne 1999), have been introduced to some islands of the archipelago in the course of the 20th century. On the mainland, both species are native to these forests and common; on Haida Gwaii they have become common where they are established. On Haida Gwaii native nest predators with a broad distribution include corvids (Northwestern Crow *Corvus caurinus*, Common Raven *Corvus corax* and Steller's Jay *Cyanositta stelleri*, the latter however only on the larger islands)

and possibly Deer Mice (*Peromyscus maniculatus*). Pine marten (*Martes americana*) and introduced Raccoon (*Procyon lotor*) occur only on the largest island (Louise Island). We have therefore access to islands with and without major mammalian nest predators, and to islands with or without habitat alteration by Black-tailed Deer.

We had 3 focal questions: (1) how does the introduction of red squirrels affect nest predation in these forests (e.g. Nour *et al.* 1993)? (2) Is the pattern of nest predation by native or introduced predators dependent on habitat quality and on habitat modification by Black-tailed Deer? (3) How do predation estimates based on artificial nests relate to predation rates of natural nests in these forests?

Native and introduced fauna

The original mammal fauna of Haida Gwaii had only 8 terrestrial species (Cowan 1989). Eleven terrestrial mammals have been introduced. The Red Squirrel and Black-tailed Deer are currently the most widespread of these exotics. The Forest Commission introduced squirrels on Graham Island in 1950. The Commission thought that the large piles of spruce cones that squirrels accumulate would facilitate the gathering of spruce seeds, which are the staple food for squirrels on the islands (pers. obs. and see Banfield 1974, Rush and Reeder 1978, Gurnell 1984, and for the adjacent mainland Sieving and Willson 1998). The Red Squirrel now occurs on the major islands of Haida Gwaii and on some of the smaller ones (Foster 1989). There is no squirrel native to the archipelago.

The Black-tailed Deer was introduced to Graham Island at the turn of the 20th century (Cowan 1989, Carl and Guiguet 1972). It has colonized the entire archipelago except for a few small isolated offshore islands. The small area of these islands prevents the establishment of stable

populations, and their isolation reduces immigration. Prior to these introductions, the only large native mammalian herbivore known for Haida Gwaii was Dawson's Caribou (*Rangifer tarandus dawsoni*). This subspecies is now extinct. It was formerly restricted to northern parts of Graham Island.

Twenty-six forest bird species breed on the islands studied (Martin *et al.* 1995). Of these, six songbirds are tightly linked to the forest understory, nesting within 1.5m of the ground (Godfrey 1986, Campbell *et al.* 1997). On the islands we studied the most common predators of songbird nests are the Northwestern Crow and Common Raven, and the introduced Red Squirrel on the islands where it occurs. The Deer Mouse is the only other abundant nest predator. It has been recorded on Louise, Ramsay, Reef and East Limestone islands (unpubl. obs.).

Squirrel and vegetation

The frequency of nest predation by a given predator can be partly explained by variation in habitat quality and/or predator density (Andr n and Angelstam 1988, Seitz and Zegers 1993, Major and Kendal 1996). Squirrel populations are controlled by the abundance and fluctuations of their main food, here Sitka Spruce (*Picea sitchensis*) seeds. Seed production in spruce typically varies from year to year (Gurnell 1984). On Haida Gwaii Sitka Spruce, Western Hemlock (*Tsuga heterophylla*) and, locally, redcedar (*Thuja plicata*) form a dense canopy. The importance of spruce varies from place to place (Martin *et al.* 1995) as does the maturity of spruce within and between stands. On small, drier offshore islands, exposed to wind and salt, the forest canopy is not as dense, and Sitka Spruce predominates (Martin *et al.* 1995). On Louise and Lyell Islands extensive parts of the study area were selectively logged early in the 20th century and support

second growth forests. Finally, stands of Red Alder (*Alnus rubra*) develop in moist or recently disturbed areas.

Deer and vegetation

On islands with no deer the shrub layer is an almost continuous cover of Salal (*Gaultheria shallon*), Red huckleberry (*Vaccinium parvifolium*), and Salmonberry (*Rubus spectabilis*), along with a variety of broad-leaved shrubs. The ground layer, when not shaded over by a dense cover of salal, is composed of ferns, herbaceous plants and grass tufts, depending on exposure.

On islands colonized by deer the understory is mostly open (Pojar *et al.* 1980, Martin and Daufresne 1999). It consists of patches of young spruce and hemlock and of a few Red Huckleberry, Salal, False Azalea (*Menziesia ferruginea*) and Salmonberry. These shrubs are found either as relict patches (Salal) or as old isolated individuals. There is little vegetation in the ground layer, which mostly consists of mosses, liverworts, and ferns. In alder-dominated forests, the shrub stratum primarily consists of regenerating conifers with a denser herbaceous stratum.

METHODS

Deployment of artificial nests

We compared predation rates among three types of island: (1) those that had deer and squirrels, (2) those with deer but no squirrels and (3) those without either. All islands with squirrels have deer, making it impossible to assess the effect of squirrels in the absence of deer. To study the impact of squirrel on nest predation we compared islands of types (1) and (2). To assess how the presence of deer affected predation by native predators, we compared islands of types (2) and (3). Island categories are summarized in Table 1.

Table 1. Characteristics of the islands, dates of sampling and sampling protocols in artificial nest predation experiments. Cover = measurements of cover in vegetation layers around the nests, habitat = artificial nests placed in two types of habitats. All islands have native avian nest predators.

Island	Year	Dates	Area (ha)	Ground nests	Shrub nests	Cover	Habitat
No introduced species							
Low	1996	1-15 May	9.6	20	20	x	
Lost	1996	2-16 May	5.3	20	20	x	
South-Low	1996	2-16 May	4.5	20	20	x	
Deer only							
Ramsay	1993	25 May - 17 June	1 622.5	63	63		
Kunga	1996	15-29 May	472.6	30	30	x	
Reef	1996	2-16 May	239.5	30	30	x	
Deer & squirrel							
Louise	1996	4-19 May	27 280.5	30	30	x	
Lyell	1996	15-29 May	17 299.9	30	30	x	
East Limestone	1993	25 May - 17 June	48.0	61*	63		
Year & habitat effect (deer & squirrel)							
East Limestone	1995	4-19 May	48.0	120	0		x
East Limestone	1996	4-19 May	48.0	80	0	x	x

* = 2 nests not found.

We selected three islands in each of the island categories defined in Table 1, all nine situated on the east side of Haida Gwaii in Laskeek Bay and Juan Perez Sound (Figure 1). On each island, we installed 2 to 3 transects separated by at least 100m. Each transect was marked with flagging tape. Transects had 15 to 21 station-points, with 50 m between station-points. On the small offshore islands without deer, we had to reduce the number of station-points to 10, the distance between station-points to 25 m and the distance between transects to 50 m. At each station, we placed artificial nests. We used wicker nests placed in sites

representative of those used by local breeding species (Godfrey 1986, Ehrlich *et al.* 1988), either on the ground, usually against the base of a big tree ("ground nest"), or in shrubs, at 1 to 2 m high, usually hung from a 0.5 - 1 cm-thick branch ("shrub nest").

Nests were lined with moss and dead leaves to reduce their visibility. Shrub nests were more conspicuous to the human eye because the bottom of the wicker basket was not hidden. At each station, one ground nest and one shrub nest was placed on either side of the transect line, at least at

10m from the line. Nests of a given type were placed on alternate sides of the transect at adjacent station-points. On all islands except Louise Island and Lyell Island, transects were placed in mature old growth forest. On Louise and Lyell islands, transects had to be put in 60 year old second growth stands resulting from natural regeneration.

Three field seasons were necessary to run the experiments. In 1993, 63 ground and 63 shrub nests were monitored on each of Ramsay and East Limestone islands. Thirty nests in each category were monitored on the three large islands studied in 1996, and 20 on the four small islands. In addition 80 ground nests were monitored on East Limestone Island in 1995 and 120 in 1996. The latter could thus be used as replicates of experiments in different years (1993, 1995, 1996) on one island (East Limestone Island).

In each experiment empty nests were first placed in the forest. After 1 or 2 days they were baited with two Japanese Quail eggs. Egg exposure time was 15 days, the average incubation time for the local songbirds (Godfrey 1986). Experiments in 1993 were preceded by trial experiments to ensure that predators had time to adjust to the artificial nests. In these trials, nests were exposed for 7 days. No difference was observed between the trials and the actual experiments, hence, trials were not repeated the following years.

Nests were checked four times (on days 4, 8, 12, and 15) on the islands with easiest access, and only twice, on days 8 and 15, on the three most remote islands; Lyell, Kunga and Lost. All experiments took place between 1 May - 17 June (Table 1), during the main breeding season for songbirds.

Measuring nest concealment

In all experiments in 1996, we measured vegetation cover around each artificial

nest. We defined three vegetation layers: 0-1m (ground layer), 1-4m (shrub layer) and >4m (tree layer). The 1m and 4m limits were chosen because they appeared to be the most relevant with respect to the size of shrubs on these islands. We estimated the percentage of vegetation cover in each layer within a 5m radius centered on the nest, using a standard chart of percentage cover (Prodon 1988). The same observer (MJ) did all measurements. For each of these nests we also estimated a visibility value derived from the BBIRD program protocol (Martin 1994): for ground nests, visibility is the percentage of the nest visible from 1 m above the nest. For shrub nests, we estimated the percentage of the nest visible to a human observer placed at 1 m from the nest, averaged over the four cardinal directions. These indices are estimates of vegetation density above or around the nest.

Predator identification

We adopted an approach that was later recommended by Marini and Melo (1998). A nest was considered to have suffered predation when at least one egg was absent, or displaced, or scratched with tooth marks. We did not replace eggs in any nests. We recorded all signs that could help to identify the predator (nest displacement, presence of scratches and shape of broken shells, feathers, hair, feces, etc.). In 1993, on Ramsay Island (no squirrels), and in 1995 on East Limestone Island (with squirrels), we devoted special attention to collect these cues in or around predated nests. The main objective was to be able to distinguish predation caused by (native) birds, by native deer mouse, and by the introduced squirrel.

We considered that birds were responsible for the predation where eggs were 'pierced' and that mammals were responsible where eggshells fragments bore tooth marks. We distinguished between mouse and squirrel predation by differences in the shape of the tooth marks,

using as a reference examples of deer mice scratches obtained by repeatedly placing a quail egg near a “bait station” designed to attract deer mice.

In 1995, we used six automatic cameras connected to artificial nests placed on East Limestone Island to identify predators and quantify their relative importance. The cameras were connected to remote switches that were triggered when the single egg baiting the artificial nest was removed. The system used has been described in Penloup *et al.* (1997). These nests were placed on the ground and were checked at least twice a day. Each system was moved to a different location, at 50 m or more from other active camera nests every two or three days for two weeks.

Analysis of predation risk

We first compared predation rates between transects and islands using two-sample *t*-tests (Statistix software). We transformed predation rates (% of the nests predated) per nest transect using the arcsine of the square root of the proportion of the nests predated (angular transformation - Sokal and Rohlf 1995), in order to obtain normal distribution of the data. We compared average transformed values of predation rates per transect independently for ground and shrub nests between island categories. We used the Wilcoxon’s signed rank test to compare non-transformed predation rates of ground and shrub nests per transects within island categories (with and without squirrels).

Estimating predation risk of natural nests

To assess how the results from artificial nests related to natural nest predation, we searched for natural nests of forest birds on Reef Island (without squirrel) and on Louise Island (with squirrel) in the same areas where artificial nests had been deployed. Natural nests were searched on the ground or in the shrub and sub canopy

layers by following adults, or by systematic searches. Emphasis was put on species with open or roofed (e.g. Winter Wren *Troglodytes troglodytes*) nests rather than on cavity nesters. Each nest, once located, was monitored every fourth day and success of nest was determined. When predation was suspected, evidence that could help identify the predator was searched for in and around the nest (egg shells, fragments, tooth marks etc). Natural nests were searched for opportunistically from early May to early June in 1995, 1996 and 1997 and intensively from early May to mid-July, in 1998 and 1999.

Effect of squirrel on nest predation pattern

To estimate the impact of the squirrels on predation risk for artificial nests, we used data from islands with deer (no variation in vegetation structure) and compared those with and without squirrels. This sample comprised the two islands studied in 1993 (Ramsay, “deer only”; East Limestone “deer and squirrels”) and four of the seven islands studied in 1996 (Reef, Kunga, “with deer only”; Louise, Lyell, “with deer and squirrel”). Because we were unable, for logistic reasons, to study all sites in a single year, a possible year effect is confounded with the squirrel effect. The results obtained for artificial nests were compared with those obtained for natural nests.

Interaction between vegetation cover, nest predation and squirrels

We analyzed how predation risk was affected by vegetation cover around the nest, and by nest visibility when squirrel were present and when they were absent. The islands used were: (1) “with deer and without squirrel”; Reef and Kunga and (2) “with deer and with squirrel”; Louise and Lyell.

Effect of squirrel on spatial distribution of nest predation within a habitat

We used the RANDOM procedure (see Sokal and Rohlf 1995) to test if the presence of squirrels affected the spatial distribution of predation risk within an island. We compared spatial distribution of predation along the transects of artificial nests for all the islands with or without squirrel on which more than 10% and less than 90% of the nests were predated.

Spatial and temporal effect of habitat quality on nest predation by squirrel

We used the transects of ground nests established in 1995 and 1996 on East Limestone Island to study how nest predation by squirrels was affected by variation in habitat quality in space and time. Squirrels are abundant on East Limestone. Nests were distributed between the two main habitat types; hemlock and spruce dominated forests (76 nests in 1995 and 55 in 1996) and alder dominated forests (44 nests in 1995 and 25 nests in 1996). Estimates of the variation in squirrel density within each habitat type were obtained for both year by means of point-counts made along the nest transects within the two habitat categories. Squirrels were counted 10 times, between mid-April and mid-June, by recording every squirrel heard or seen within a 20 m radius during exactly one minute, at each of the 35 stations distributed at 50 m intervals along the trails. Animals heard or seen beyond the 20 m circle were also recorded. Counts were not performed in heavy rain or strong wind.

Effect of deer on nest predation by native predators

We compared predation risk caused only by native predators between islands with and without introduced deer. The islands

used were: (1) with deer and without squirrel; Reef and Kunga, totaling 120 artificial nests equally distributed on the islands; (2) without deer and without squirrel; Low, South Low and Lost, totaling 120 artificial nests equally distributed on the islands.

RESULTS

Direct evidence of squirrel predation

On East Limestone Island, where squirrels were present, we examined 108 depredated nests in 1995. Forty-four of these nests were predated by squirrel, 3 by deer mice and 4 by birds; the remainder, found empty, could have been depredated by large birds or by squirrels (pers. obs. of squirrels removing whole eggs). On squirrel-free Ramsay Island we examined 12 depredated nests in 1993. Six were the result of predation by deer mice, 3 by birds, and 3 by unknown predators. The nests equipped with automatic cameras deployed at East Limestone Island in 1995 were depredated 32 times, in every case by a Red Squirrel.

Squirrel effect on predation risk

On islands with squirrels predation rates were significantly higher for both ground and shrub nests than on islands without squirrels (39% and 36% compared with 17% and 8%; Figure 2, Table 2). On islands with squirrels, predation risks for ground and shrub nests were similar (Wilcoxon's signed rank tests; $P < 0.29$). On islands without squirrels predation risk for ground nests was significantly higher than predation rates for shrub nests ($P < 0.03$).

Table 2. Results of two sample t-tests comparing average predation rates between island categories (proportions transformed to reach normality of distribution within samples ; All “no squirrel” islands include the islands from the “deer only” and “no introduced species” categories. All islands have native avian nest predators.

	Ground nests		Shrub nests	
	Deer & squirrel	Deer only	Deer & squirrel	Deer only
Deer only	P = 0.055(*)	-	P = 0.050*	-
No introduced species	P = 0.024*	P = 0.92	P ¹ = 0.025*	P = 0.40
All “no squirrel” islands	P = 0.017*	-	P ¹ = 0.005**	-

(*) P < 0.06, * P < 0.05; ** P < 0.01.

Variability of predation risk within island categories

There was a large amount of variation in predation rates among individual islands within island categories (Figure 2). On islands with squirrels, predation rates were much higher on East Limestone Island than on other islands for both types of nest sites. This inflated the difference in predation risk between islands with and without squirrels. Predation rates on East Limestone were consistently high during the 3 years that nests were placed on the island (74% in 1993 , 90% in 1995, and 62% in 1996). On islands without squirrels, although predation rates were generally lower than on islands with squirrels, 11 out of 15 ground nests and 5 out of 15 shrub nests in transect 2 on Reef Island were affected. Few nests were affected on the other transects on islands without squirrels.

Predation risk of natural nests in relation to presence of squirrel

Out of 24 natural nests monitored on Reef

Island in 1998 none suffered predation. Of the 16 monitored in 1999, only three suffered predation. Hence, predation rate for the two years combined was 8%. On the islands with squirrels, out of 15 natural nests monitored in 1998 on Louise Island, five (33%) suffered predation, at least 4 of them by squirrels, and out of the 17 nests monitored in 1999 six (35%) suffered predation, at least five of them by squirrels (Figure 3). Over the entire period, 34% of the nests monitored suffered predation on the islands with squirrels, and 81 % (9 out of 11) of these predations were attributed to squirrels. The nests monitored belonged to a variety of forest birds, mostly species breeding above the ground. On Reef Island, none of six thrush nests suffered predation. On Louise Island, 7 of 10 thrush nests found were depredated, six of them by squirrels (Table 3). In several instances, we observed adult thrushes driving squirrels away from their nests containing young birds.

Table 3. Proportion of natural nests suffering predation within island categories for species or species groups with largest sample sizes.

Species	Without squirrels		With squirrels	
	Total	Predation	Total	Predation
<i>Thrushes</i>	8*	0	12**	7 (58%)
Winter Wren (<i>Troglodytes troglodytes</i>)	10	0 (0%)	10	2 (20%)
Song Sparrow (<i>Melospiza melodia</i>)	15	1 (6%)	2	0
Orange-crowned Warbler (<i>Vermivora celata</i>)	6	1	1	0

* 6 Hermit thrushes (*Catharus guttatus*) and 2 Varied thrushes (*Ixoreus naevius*); ** 7 Hermit thrushes, 4 Varied thrushes and 1 American Robin (*Turdus migratorius*).

Effect of vegetation cover on nest predation by squirrel

On islands without squirrels, vegetation cover in all layers was on average lower for depredated ground nests than for untouched nests (Figure 4). On islands with squirrels, vegetation cover of the canopy was, on average, more dense and the ground layer sparser around depredated nests than around untouched nests. For nests in shrubs, neither the vegetation cover nor the conspicuousness of the nests had any effect on predation risk.

Effect of squirrel on spatial distribution of nest predation within a habitat

On islands with squirrels, the distribution of predation events was random. That is, predation risk was not independent from the fate of neighboring nests (tests for randomness of the distribution). On islands with no squirrels, that is, with native predators only (mainly corvids), nests suffering predation were clustered.

Spatial and temporal effect of habitat quality on nest predation by squirrel

The abundance of squirrels on East Limestone Island was in most years higher in forests dominated by hemlock and spruce than in those dominated by alder

(Figure 5). Nest predation rate was higher, in both habitats, in 1995, the year of higher squirrel abundance, than in 1996, a year of lower squirrel abundance (Figure 5). Within each year, predation rate was higher in the Hemlock/Spruce area. These results suggest that variation in squirrel density is habitat- and year- dependent, and that squirrel density can have a strong effect on predation rate: the higher the number of squirrel, the higher the predation rate.

Effect of deer on nest predation by native predators

Considering only islands without squirrels, we compared those with and without deer. Predation rates for both ground and shrub nests were similar (17 and 8% against 13 and 7%, respectively; Figure 2).

DISCUSSION

Changes in predation risk in the presence of Red Squirrel

The predation of artificial nests was significantly higher on islands with squirrels than on islands without squirrels, and there was an unambiguous correlation between squirrel abundance and predation risk (year and habitat effect on both squirrel abundance and predation rate of artificial nests; predation pattern of natural nests). However, the impact of squirrels varied widely among islands with squirrels, to the point that the additional predation risk seemed negligible on some islands. Results from East Limestone Island suggest that levels of nest predation by squirrels were strongly affected by squirrel abundance. Our results suggest that squirrel abundance varied (1) spatially, in relation to habitat type (coniferous versus deciduous, see Bayne *et al.* 1998) and (2) with time, in relation to fluctuations in the production of conifer seeds (Gurnell 1983, Sullivan 1990, Klenner and Krebs 1991, pers. obs.) that are a main staple for Red squirrels (Banfield 1974).

Our observations suggested that fluctuations in squirrel abundance are local. Squirrels peaked on East Limestone in 1995 and in 1999. On nearby Louise Island, we judged squirrel numbers to be medium to low in 1996 in a patch of old growth forest dominated by spruce (Vertical Point), high in 1998 and at a peak in 1999 (pers. obs.). A similar peak in squirrel abundance was also observed by one of us (JLM) in a patch of mature Sitka spruce forest near Yakoun Lake on Graham Island in 1997 (a time when population numbers were low on East Limestone Island). Furthermore, the sites that were available to place artificial nest transects on Louise and Lyell islands were mostly covered by younger mature forests resulting from selective logging carried out at the beginning of the 20th century. It is

possible that cone production of Sitka spruce in these forests, and the overall resources available to squirrels were lower, even in peak years, than in old growth forests such as those of East. This would explain some of the differences observed in predation rates among squirrel-occupied islands. Lower predation rates in younger than in older coniferous forests have been documented by Seitz and Zegers (1993), although they were thought to be the result of more open understory in older forests, rather than being the result of lower resources in younger forests.

Our estimates of predation rates of natural nests were also obtained from a mix of old growth and younger (past logging or natural disturbances) forests. They were of the same order of magnitude as the average figures obtained for artificial nests (overall average for islands without squirrels and deer was 13%, overall average for islands with squirrels and with deer impact was 39% - corresponding figures for natural nests were 8% and 34% respectively). This result is not consistent with the observations of Sieving and Willson (1998) who reported only about 12% of natural nests being subject to predation in comparable coniferous forests as opposed to 60% for their artificial nests.

Mature forests containing abundant Sitka Spruce, high squirrel densities, a declining food source after a good cone crop, coupled with high protein demand in pregnant and lactating squirrel females in spring may be the combination that leads to the kind of peak in predation on artificial nests observed in 1995 on East Limestone (almost 90% of the artificial nests depredated). The results obtained for artificial nests and the monitoring of natural nests both suggested that the presence of squirrels multiplied overall predation risk by four. Observations of natural nests suggested that species such as thrushes were those most affected by additional predation pressure (58% of the

nests depredated on islands with squirrels, none on the islands without squirrels). The risk posed by squirrel aggression, even for clutches and nestlings of large-bodied thrushes, was illustrated by the predation of several Varied thrush (*Ixoreus naevius*) nests, and attacks of Varied Thrush and American Robin (*Turdus migratorius*) broods that resulted in fights between squirrels and adult birds (see also Sieving and Willson 1998). These thrushes nest in shrubs, small trees or against tree trunks at heights varying from 0.5 m to 9m. Observations of natural nests supported the results obtained for artificial nests, which suggested that, in the presence of squirrels, predation pressure increased for shrub nests when compared to islands without squirrels (where they were less subject to predation than ground nests).

In the absence of squirrels, the level of predation on artificial nests was always relatively low during this study, presumably because of the scarcity of native predators on these islands [see Sieving and Willson (1998) for description of predator communities typical of such forests on the adjacent mainland and George (1987) for a comparative study of predation rates between an island and the nearby mainland].

Even in the presence of squirrels, predation rates in our study were low relative to predation rates observed in the adjacent mainland communities. In forests of south east Alaska and northwestern Canada, where the Red Squirrel is also the main predator, followed by jays, Sieving and Willson (1998) found the average predation rates for artificial nests to be 47% (60% in coniferous and 34% in deciduous forests). In these forests, predation by jays accounted for 6 to 32% of the nest losses, a result based on photographic evidence. In forests of central Canada Bayne *et al.* (1997) found similar predation values for artificial nests baited with quail eggs (67% in coniferous

forests, 25% in mixed wood forests and 17% in deciduous forests). Only in the mature forest of East Limestone Island did predation rate exceed 60%, in the presence of squirrels, but in the absence of jays. Steller's Jays breed in Haida Gwaii, but were never observed on the islands studied despite extensive observations carried out over the past 10 years (see Martin *et al.* 1995).

Impact of squirrel on the spatial distribution of nest predation

In the absence of Red squirrel, predation by native predators (corvids, deer mice) was patchy and predation events tended to be concentrated in specific areas. An extreme example was on Reef Island, where predation occurred exclusively on one transect situated in the forest patch occupied by an active colony of Ancient murrelets (*Synthliboramphus antiquus*) which was daily patrolled by corvids during the murrelets' breeding season (Gaston 1992, and pers. obs.). On other islands without squirrels, predation occurred mainly near the forest edge, in areas close to the intertidal zones used by corvids for foraging (Godfrey 1986, Martin *et al.* 1995). In these areas predation risk was, in addition, higher for nests on the ground than for nests in the shrubs, a pattern consistent with the ground foraging behavior of these corvids (Northwestern Crow and Common Raven). Hence in the absence of squirrels, predation risk is related to the distribution of food for corvids and is more affected by nest sites.

On islands with squirrels, predation risk is more uniformly distributed, a reflection of the uniform horizontal and vertical use of the habitat by squirrels. Nests placed in shrubs are as much at risk as nests placed on the ground. Hence the colonization of an island by squirrels alters the relative safety of different nest sites. In the presence of squirrels, predation risk tends,

within an habitat type, to vary more from year to year and less from place to place.

These results differ from those of Yahner and Scott (1988) who found, in mainland forest fragments, that when the community of nest predators was dominated by corvids (as on our islands without squirrels), predation risk was higher for nests placed above the ground. This difference can probably be explained by the higher diversity of corvid species in these communities which, in particular, include jays (Blue jays, *Cyanocitta cristata*), a group of species more prone than crows to rob nests in shrubs (e.g. Sieving and Willson 1998 and pers. obs.). Conversely, Loiselle and Hoppes (1983) and Martin (1987) showed that in mainland communities mammals were mainly responsible for the predation of nests on the ground, with, however, Red Squirrels being an exception, as shown by photographic evidence of predation of nests both on the ground and in shrubs (e.g. Sieving and Willson 1998).

Effect of vegetation cover and nest visibility on predation risk

For nests placed on the ground we have shown that increased vegetation cover around the nests and lower nest visibility or detectability decreased predation risk. This result is in agreement with most studies of nest predation (e.g. Major and Kendal 1996, but see Seitz and Zegers 1993 that find no effect of cover). For these nests we also observed, in the absence of squirrels, an increased predation risk as shrub and tree layer became more open and nest visibility increased. We interpret this as the consequence of a better detection of the nests by avian predators which mainly use visual cues (Ouellet 1970, Ehrlich and McLaughlin 1988, Andr n 1992).

When squirrels are present, predation risk varies only slightly with shrub cover and

increases with increasing tree cover. We interpret the limited effect of shrub cover on these islands by recalling the fact that squirrels mainly use systematic “search and smell” tactics to look for food. We suggest that the significant increase of predation risk observed with increasing tree cover is due to the fact that tree cover is a reflection of the quality of the habitat for squirrels: the more trees the higher the production of cones for the squirrels to eat.

Thus the colonization of an island by deer, by reducing shrub cover (Pojar and Banner 1984, Martin and Daufresne 1999), also increased the risk of nest predation by native predators, but had only a slight effect the risk of nest predation by squirrels. However, the comparison of predation risk between islands with and without deer (all are islands without squirrels) failed to show a direct effect of deer on predation risk. Nevertheless, a significant effect of shrub cover and of nest detectability was found for ground nests for the whole set of islands, confirming that, at least for ground nests, predation rates increased with decreasing vegetation cover.

Small islands without deer are often surrounded by rich intertidal zones which are, as mentioned, one of the favorite foraging areas of the Northwestern Crow. Martin et al. (1995) have shown that the smaller the island the higher the local crow density. Thus, all other things being equal, native predator density may be higher on smaller islands, especially along the shorelines with large intertidal zones used by corvids (a pattern similar to the pattern occurring in forest fragments in an agricultural landscape favorable to avian predators; Wilove 1985, Small and Small 1988, Yahner and Scott 1988, Andr n and Angelstam 1988, Andr n 1992, Nour et al. 1993, Hannon and Cotterill 1998). However, as predation risk decreases with increasing vegetation cover, this edge effect could be compensated for by the

denser vegetation found on these small islands. Alternatively, larger islands provide opportunities for birds to nest further from the shore.

SUMMARY

Average predation rates were higher on islands occupied by squirrels but variability was large among islands used as replicates. Predation rate increased with squirrel abundance which itself varied according to habitat type, possibly habitat age and definitely with year (variation in seed production). Predation was highest in years of peak squirrel abundance.

On islands with squirrels, risk of nest predation was uniform within a habitat type across a given island, did not differ significantly between nests on the ground and in the shrubs and varied only slightly in relation to vegetation cover around the nest. On the islands without squirrels, predation risk was localized in space near predictable food sources for corvids (e.g. active sea bird colonies), and was higher for nests placed on the ground and for nests with less vegetation cover, a feature that we link to the use of visual cues by corvids (Andrén 1992) rather than the olfactory cues used by squirrels (Whelan *et al.* 1994).

The introduction of the Red squirrel has therefore, not only increased overall predation risk (at least on some islands and in some years), but has also modified the spatial and temporal predictability of that risk. The decrease in vegetation cover by deer has increased nest vulnerability to native avian predators, especially for those on the ground.

These results not only show how predation pattern has been altered in these forests by the addition of a new nest predator, and by the changes in vegetation structure caused by the introduction of a large herbivore to the forest community, they also reveal

how several components of a forest ecosystem interact in subtle ways to influence patterns and intensity of nest predation both in time and space. In particular, our results confirm the major and pervasive role of Red Squirrel in the distribution of nest predation at the landscape scale in Pacific northwestern forests as opposed to the more spatially and temporally localized predation pressure caused by avian nest predators (see Sieving and Wilsson 1998). Our data suggest that predation by squirrels not only varies with time in a short term and cyclic fashion related to cycles of spruce cone production, but also, possibly, in a more long term and linear fashion, i.e. it increases with increasing forest maturity. As a consequence, selective pressures on breeding birds that are related to risk of nest predation will greatly (and unpredictably) fluctuate in space and time, and in such a way that years and places with high predation risk may alternate with years and places with lower risk. This may preclude any tight adjustment of breeding strategies, or nest site selections to predation risk. Observed patterns of nest site selection and bird community composition may therefore reflect trade-offs between efficient nest defense and efficient use of the food resources available in the habitat. If nest predation is to influence habitat selection and nest site selection by birds, it is more likely to occur at a landscape scale than at a local or habitat type scale, because of high local spatial and temporal variability in predation risk (see Marini 1997).

Such temporal and spatial fluctuations may also prevent the exclusion from the coniferous forest bird communities of species unable to minimize vulnerability of their nests to predation by squirrels. Indeed several of the thrush species which seem most sensitive to nest predation by squirrels are common in coniferous forests of Haida Gwaii (Martin *et al.* 1995) independently of the presence of squirrels

(JLM unpublished). Nevertheless, some of our unpublished data suggest that Winter Wren nests on islands with squirrels tend to be in sites less accessible to squirrels (e.g. under overhangs) than on islands without squirrels, suggesting possible behavioral adjustments to predation risk.

Beyond confirming the need for coordinated research on both predator ecology and nesting bird ecology, as promoted by Sieving and Willson (1998), our results emphasize that understanding the complexity of habitat interactions and behavioural adaptations may well be one of the challenges in understanding variation in the dynamics of forest bird communities.

ACKNOWLEDGEMENTS

We thank Sylvain Allombert, Janet Brown, Sylvie Blangy, Isabel Buttler, Lorraine Carson, Ginny Collins, Tanguy Daufresne, Joële Fournier, Colin French, Janet Gray, Kathy Heise, Rob Kelly, Sabine Mercier, Marcella Sneider, and Georges Yau for their invaluable assistance in the field. Sally Aitkin, Sylvain Allombert, Doug Burles, Pat Declerc, Bob Elner, Terry and Charlotte Husband, Moira Lemon, Kathy Martin, Greg Martin, Tom Martin, Tarmo Poldmaa, Roger Pradel, Mark Salzl, Gwenaél Vourc'h and Greg Wiggins provided both intellectual and logistic help. This project was possible through the support of the Canadian Wildlife Service, the Laskeek Bay Conservation Society and the Archipelago Management Board. Funding for this research and/or extension project was provided by: Forest Renewal B.C. (a partnership of forest companies, workers, environmental groups, First Nations, communities and government of British Columbia. Research Award: PA97335-BRE.); by the South Moresby Forest Replacement Account ; and by the PICS 489 from

CNRS and Ministry of Foreign Affairs of France. This is a part of a long term research effort by the “Research Group on Introduced Species”. James Aronson very kindly checked the English.

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Legend of figures

Figure 1. Map of study area. Names of study islands in bold. On larger islands shaded areas located by arrows indicate study site.

Figure 2. (a) Variation of squirrel abundance (average number of squirrels encountered per 100 metre transect) with year and habitat on East Limestone Island between 1995 and 1999; and (b) variation of predation rate of artificial nests between spruce-dominated and alder-dominated forests on East Limestone Island in 1995 and 1996.

Figure 3. Vegetation cover around ground nests suffering and not suffering predation on islands with squirrels (FIG. 3a, Louise and Lyell islands) and without squirrels (FIG. 3b, Kunga and Reef islands). When squirrels are absent, nests tend to be more predated when the density of the surrounding vegetation is low. When squirrels are present, there is no consistent relationship between density of vegetation and predation (see also FIG. 4).

Figure 4. Variation of predation risk of artificial nests placed on the ground in relation to vegetation cover in the shrub and canopy layers on islands with and without squirrels. Predation probability curves were established by using the best model (GLM analysis) to estimate predation risk at different values of the vegetation cover variables and then smoothing a curve through these estimates. For the other variables average values were used as fixed values in the model.