

Nest predation in forest birds: influence of predator type and predator's habitat quality

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We used the introduction of a generalist nest predator, the red squirrel *Tamiasciurus hudsonicus*, and of a large herbivore, the Sitka black-tailed deer *Odocoileus hemionus sitkensis*, to the islands of Haida Gwaii (Queen Charlotte Islands, British Columbia, Canada) to study how predator assemblage and habitat quality and structure influenced nest predation in forest birds. We compared losses of natural nests to predators on islands with and without squirrels. We selected nine islands with or without squirrel or deer and used 506 artificial nests put on the ground or in shrubs to further analyse variation of nest predation with predator assemblage and habitat quality for the predators. For both natural and artificial nests predation risk was higher in presence of squirrels. But predation risk varied within island categories. In presence of squirrels it was highest in stands with mature conifers where it fluctuated from year to year, in response to fluctuations in squirrel abundance. Vegetation cover around the nest had little effect on nest predation by squirrels. Where squirrels were absent, nest predation concentrated near predictable food sources for corvids, the main native predators, and increased with decreasing vegetation cover, suggesting that removal of the vegetation by deer increased the risk of predation by native avian nest predators that use visual cues. Predation risk in these forests therefore varies in space and time with predator composition and with quality of the habitat from the predators' perspective. This temporal and spatial variation in predation risk should promote trade-offs in the response of birds to nest predation, rather than fine-tuned adaptations to a given predation pattern.

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Nest predation is thought to affect the structure and function of bird communities (Martin 1993a, b, 1995). Human-induced environmental changes can affect nest predation risk and can be viewed as manipulations that help understand patterns and processes involved in nest predation. Increased nest predation is expected after the introduction of non-native predators, particularly on islands (Atkinson 1985, Scott et al. 1986, Savidge 1987, Drake et al. 1989, Sieving 1992, Penloup et al. 1997, Martin et al. 2000) or after habitat changes favourable to generalist nest predators (Wilcove 1985, Bayne and Hobson 1997, Heske et al. 1999). Although different combinations of predators should affect nest predation in different ways (Angelstam 1986, Nour et al. 1993,

Yahner 1996, Hannon and Cotterill 1998, Söderström et al. 1998), the effects of different predators on the risk of nest predation needs to be further investigated (Buler and Hamilton 2000) as well as the effects of differences in habitat quality for the predator (e.g. the level of other resources for the predator).

The islands of Haida Gwaii (Queen Charlotte Islands, British Columbia, Canada) provide a unique opportunity to study how predator type and habitat quality for the predator affect predation risk of song bird nests. The islands are covered with temperate rain forests dominated by conifers. The native terrestrial mammalian fauna is impoverished (Foster 1989) lacking abundant generalist nest predators and large forest

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herbivores. The only common native nest predators are two species of corvids and one species of mouse. The red squirrel (*Tamiasciurus hudsonicus*), a major nest predator (Ehrlich et al. 1988, Bayne et al. 1997, Darveau et al. 1997, Sieving and Willson 1998), and the Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), a subspecies of the mule deer, both common on the adjacent mainland, were first introduced to the archipelago in 1878 (Dalzell 1968, Carl and Guiguet 1972, Cowan 1989) and in 1947 (Golumbia et al. in press), respectively setting the stage for an unplanned experiment. Both species became common, and only a few islands remain free of deer or squirrel. We took advantage of the existence of islands with and without red squirrel and of islands with and without habitat alteration by Sitka black-tailed deer (Pojar et al. 1980, Daufresne and Martin 1997, Martin and Daufresne 1999), to study how predator type and habitat quality affected predation risk. We expected a decrease in nest survival due to direct predation by squirrels, and an indirect decrease of nest survival through understory simplification by deer. We also expected that habitat suitability to squirrels would affect predation risk.

Material and methods

Biotic community of Haida Gwaii

We worked on a subset of 9 islands situated in Laskeek

Bay and Juan Perez Sound on the eastern side of Haida Gwaii (Fig. 1). On these islands, western hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), and locally western redcedar (*Thuja plicata*), form a dense canopy. The prevalence of spruce varies from place to place (Martin et al. 1995). Stands of red alder (*Alnus rubra*) develop in moist or recently disturbed areas. On larger islands logging has had an increasing impact on the forest. On deer-free islands, the shrub stratum is a nearly 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 colonised 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 scattered red huckleberry, salal, false azalea (*Menziesia ferruginea*) and salmonberry. These shrubs occur either as relict patches (salal) or as old isolated individuals (huckleberry, false azalea). There is little vascular vegetation in the ground layer, which consists mainly of mosses, liverworts, and ferns. In alder-dominated stands, the shrub stratum consists primarily of regenerating conifers, and the herbaceous stratum is denser.

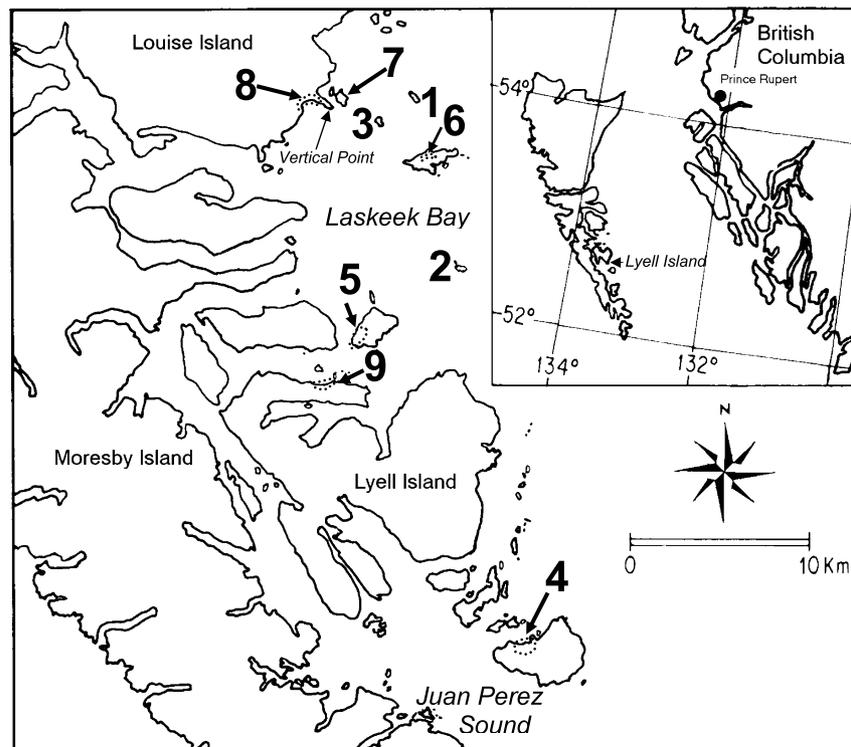


Fig. 1. Study area. Bold numbers identify study islands. On larger islands study sites are outlined in dotted lines indicated by arrows. Type I islands (no deer, no squirrel): 1 = Low Island, 2 = Lost Island, 3 = South Low Island. Type II islands (deer, no squirrel): 4 = Ramsay Island, 5 = Kunga Island, 6 = Reef Island. Type III islands (deer and squirrel): 7 = East Limestone, 8 = Louise Island, 9 = Lyell Island.

The original fauna of Haida Gwaii included only eight terrestrial mammals (Cowan 1989). Of these, Dawson's caribou (*Rangifer tarandus dawsoni*) was the only native large herbivore. It is now extinct, and was formerly restricted to northern parts of Graham Island. Eleven terrestrial mammals were introduced. The red squirrel and the Sitka black-tailed deer are currently the most widespread of these exotics. The red squirrel is the only squirrel found on the archipelago. Spruce seeds are the staple food for squirrels on the adjacent mainland (Banfield 1974, Rusch and Reeder 1978, Gurnell 1983, Sieving and Willson 1998) and they were introduced to Haida Gwaii to facilitate the gathering of Sitka spruce seeds for tree nurseries.

Twenty-six species of forest birds breed in the study area (Martin et al. 1995). Of these, six depend on the forest understory, nesting on average at around 1.5 m in height (Godfrey 1986, Campbell et al. 1997). On the islands used for this study (Fig. 1) the commonest native avian predators of songbird nests are the north-western crow *Corvus caurinus* and the common raven *Corvus corax*. Crows however spend most of their time foraging on the shoreline and in the intertidal zone (Godfrey 1986, pers. obs.). We never observed the native Steller's jay *Cyanositta stelleri* in the study area, despite extensive observations carried out over the past 12 years (Martin et al. 1995). Among the potential native mammalian nest predators, the deer mouse *Peromyscus maniculatus* is present on all islands, except perhaps on the small isolated ones (unpubl.). The American marten (*Martes americana*) occurs on the larger islands only. In our study sites, we only observed it on Louise Island; it may also occur on Lyell and Ramsay Islands but we did not record signs of its presence. The introduced red squirrel is the most abundant nest predator. The introduced common racoon (*Procyon lotor*) is restricted to the shoreline of the islands it has colonised on Haida Gwaii (Louise Island in our study area).

Empirical study of squirrel effect on natural nests

Three people searched intensively for natural nests of songbirds on a set of islands with and without red squirrels from early May to mid-July in 1998 and 1999 (about 40 person-days each year). We also searched nests opportunistically in 1995, 1996, 1997, and 2000 from early May to early June. Two major sites were used for this: Reef Island (249 ha) that had no squirrels but had a long history of deer presence, and an area of similar size to the site on Reef Island, located on Louise Island, which has squirrels as well as a long history of deer presence. In both sites we focused on areas with mature Sitka spruce as an important component of the canopy to ensure the habitat was favourable for squirrel. We found nests on the ground and in the shrub (or

sub-canopy) strata by following the adults and by systematic searches. The nests were found at varying stages (prior to incubation, during incubation, after hatching, and after predation in a few cases). We concentrated on species with open-cup nests and on roofed nests of winter wren (*Troglodytes troglodytes*). The latter typically occur in crevices found in root masses, standing dead trees, or rotting logs.

We checked the nests every fourth day on average to assess their fate (success, predation, desertion). When a nest was preyed upon, we searched it and its vicinity for tooth marks on egg fragments that could identify red squirrel as the predator. Although using egg fragments to identify predators has been questioned (Larivière 1999), tooth marks are a reliable cue in our context: only the red squirrel and the deer mouse are likely to leave scratches on egg shells and these scratches are markedly different in size and shape. This was confirmed using bait stations with eggs accessible to only one of the two rodent species and monitored by automatic cameras (see below).

After dividing the nests found into incubation and nestling period following Mayfield (1975), we estimated daily survival rates, and their standard errors, using the method described by Bart and Robson (1982). This method is based on Mayfield's (1961, 1975) approach but corrects for length of time between observations. We used the method developed by Sauer and Williams (1989; CONTRAST software, Hines and Sauer 1989) to compare the daily survival rates of islands with and without squirrels. Daily survival rates were also used to estimate nest survival over the period of nest exposure. For this, egg exposure time and nestling exposure time were estimated at 15 days, the average length of time for local songbirds (Godfrey 1986). Only nests with known fate were used in the analysis.

Experimental study of spatial and temporal variation in predation risk of artificial nests

Three categories of islands

We identified three categories of islands: (I) those with no introduced species, (II) those with deer but no squirrels, and (III) those with deer and squirrels. We were able to find three islands for each of these categories in the study area (Fig. 1 and Table 1). There were no islands available that had squirrel but no deer, so we could not assess the effect of squirrels in the absence of deer. All the islands available with no deer and no squirrels were small and relatively isolated from the larger islands. Because of the lack of deer impact on the vegetation, these islands, covered by mature forests, had a dense understory (Martin and Daufresne 1999) and a high abundance of the songbirds that depend most on the shrub layer (Martin et al. 1995). The islands available with deer but no squirrels were

Table 1. Comparison by CONTRAST (Hines and Sauer 1989) of natural nest survival in absence or presence of red squirrel. N = number of nests; s = daily nest survival rate; s^{15} = nest survival over a period of 15 days; Diff. s = difference in daily survival rate, χ^2 = chi square value of contrast analysis, df = degree of freedom, P = probability value given by contrast analysis, SL = significance level. n.s. = non significant.

Stage	Without squirrels			With squirrels			Contrast between categories				
	N	s	s^{15}	N	s	s^{15}	Diff. s	χ^2	df	P	SL
Eggs	18	1	1	14	0.922	0.30	0.078	881.7	1	<0.001	***
Nestlings	42	0.990	0.86	22	0.985	0.80	0.005	0.2	1	0.68	n.s.

medium-sized offshore islands, large enough to have deer but remote enough to prevent colonisation by squirrel. Little affected by past logging, they were also mainly covered by mature forest. The islands available with deer and with squirrels were larger on average. On two of them, Louise and Lyell, extensive parts of the study area had been selectively logged early in the 20th century, mainly for mature Sitka spruce (Banner et al. 1989). Compared to the more mature stands, these stands show a reduction of the average height of the canopy ($P < 0.001$, paired t-test on vegetation cover in the canopy layers, after a re-analysis of data from Martin et al. 1995) and a 37% reduction of the cover of mature spruce ($P < 0.001$). Intact and selectively logged stands do not differ significantly in the relative cover of the other main tree species (western hemlock and western redcedar). The third island, East Limestone, was mainly covered by mature forest and by limited areas of stands dominated by red alder. Although habitat structure was relatively homogenous within each site, and even between islands in island categories I and II, it has to be emphasised that our approach was to capture the range of ecological conditions that predators face rather than achieving site replication. The latter would have proved difficult not only because of the limited number of islands available and of the logistics involved, but also for lack of knowledge of the critical environmental variables to be controlled for.

Main protocol

To assess overall variation in predation of artificial nests in relation to predator assemblage, we installed on each island 2 to 3 transects separated by at least 100 m. Each transect was marked with flagging tape. Transects had 15 to 21 stations 50 m apart. On the larger islands transects were laid out over an area of about 25–50 ha, depending on the number of nests per transect. On the three smaller islands without deer we had to reduce the number of stations to 10, the distance between stations to 25 m, and the distance between transects to 50 m and transects covered most of each island (Table 1). At each station, we placed two artificial nests. We used wicker nests placed at 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 large tree (“ground nests” hereafter), or 1 to 2 m

above the ground in a shrub or a young tree and tied to a small branch 0.5 to 1 cm thick (“shrub nests” hereafter). We lined nests with moss and dead leaves to reduce their visibility. Shrub nests were more visible to the human eye because the bottom of the wicker basket was more difficult to camouflage. Their visibility was dependent on the amount of branches around. At each station, one ground nest and one shrub nest were placed on opposite sides of the transect line, at least 10 m from the line. Nest types were placed on alternated sides at the following station. On all islands, except Louise and Lyell, transects run through mature forests. On Louise and Lyell islands, transects run mainly through stands affected by selective logging in the 1930s (see above for characteristics). For logistic reasons, the experiments had to be spread over two field seasons. The data from East Limestone island and Ramsay island were collected in 1993, the data for the other islands in 1996. Table 1 lists the number of nests monitored on each island and the year in which each was studied. In each case, we first placed empty nests in the forest. After 1 or 2 days, we baited each one with two Japanese quail (*Coturnix japonica*) eggs. Egg exposure time was 15 days, the average incubation time for the local songbirds (Godfrey 1986). In 1993, we ran 7-day trials before the experiments, to ensure that predators adjusted to the artificial nests, but we observed no difference between the trials and the actual experiments, so we did not repeat trials the other years. Nests were checked four times (on days 4, 8, 12, and 15) on the islands with easiest access, and twice (days 8 and 15) on the three most remote islands (Lyell, Kunga, and Lost). All experiments took place between 1 May and 17 June (Table 1), during the main breeding season for songbirds on the archipelago. In the warm spring of 1998, for example, Martin et al. (unpubl.) found natural nests ($N = 32$) with eggs between 25 April (first egg laid) and 28 June (last egg hatched). The mean hatching date was 28 May. In the cold spring of 1999, extreme dates of natural nests with eggs ($N = 16$) were 5 May and July 23, with mean hatching date 15 June.

Adopting an approach later published by Marini and Melo (1988), we considered a nest to be preyed upon when at least one egg was absent, 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, shape of broken shells, feathers, hair, faeces, etc.), with the objective of distinguishing predation by birds, deer mice, and introduced squirrels. We considered birds responsible for the predation when eggs were “pierced” and mammals when eggshell fragments bore tooth marks. We distinguished between mouse and squirrel predation by differences in the shapes of the tooth marks, using, as a reference, deer-mouse scratches that we obtained by repeatedly placing quail eggs at a “bait station” attracting deer mice near our camp. These trials showed that deer mice were unable to break through the shells of quail eggs, but left numerous tooth marks on the shells (Roper 1992, Major and Kendal 1996, Yahner and Mahan 1996, Bayne et al. 1997, Hartley and Hunter 1998, Sieving and Willson 1998 for discussion of egg size in experiments with artificial nests). In 1995 we used six automatic cameras connected to artificial nests placed on East Limestone Island, to gain further insights on predator identity and to quantify their relative importance. The cameras were connected to remote switches triggered when the single egg baiting the nest was removed (system described in Penloup et al. 1997). These nests were usually on the ground, and were checked at least twice a day. The systems were moved to a different location, 50 m or more from other active camera nests, every 2 or 3 days for 2 weeks.

Protocol on effect of habitat quality

We established additional transects of ground nests in 1995 and in 1996 on East Limestone Island (Table 1). The purpose was to study how artificial nest predation

by squirrels was affected by prevalence of spruce and varied with time. The nests were assigned to one of the two types of forest cover found on East Limestone Island; hemlock/spruce-dominated forest (76 nests in 1995 and 55 in 1996) and alder-dominated patches (44 nests in 1995 and 25 in 1996). Estimates of the variation in squirrel density within each habitat were obtained for both years by means of point counts made along the nest transects. We censused squirrels 10 times each year, between mid-April and mid-June, by recording every squirrel heard or seen within a 20-m radius during one minute, at each of the 35 stations distributed at a 50-m interval along the transects. Stations were assigned to one of the two forest types. Counts were not performed in heavy rain or strong wind. To confirm the existence of fluctuations in squirrel abundance, we have repeated these censuses every year between 1995 and 2000. Squirrel abundance was calculated per year and per habitat around the census point.

Protocol on effect of nest concealment

On the islands sampled in 1996 for the experiment comparing island categories I to III (Table 2), we measured vegetation cover around each artificial nest. We defined three vegetation layers following Martin and Daufresne (1999): 0–1 m (ground layer), 1–4 m (shrub layer) and > 4 m (tree layer). We estimated the percentage of vascular vegetation cover in each layer within a virtual cylinder of 5-m radius centred on the nest, using a standard chart of percentage cover (Prodon 1988). The same observer (MJ) made all measurements. For each nest we also estimated visibility at 1 m, using an index derived from the BBIRD program

Table 2. Characteristics of the islands, number of artificial nests monitored, and sampling protocols in nest predation experiments. OG = old growth; PSL = past selective logging; Cover = vegetation cover around the nests was measured; Habitat = artificial nests were placed in stands dominated by conifers and in stands dominated by broad leafed trees. All islands have native avian nest predators.

Island	Year	Dates	Island area (ha)	Study site area (ha)	Forest type	Ground nests	Shrub nests	Cover	Habitat
Study of squirrel and deer effect on nest survival									
Category I. No deer, no squirrel									
Low	1996	1–15 May	9.6	9.6	OG	20	20	x	
Lost	1996	2–16 May	5.3	5.3	OG	20	20	x	
South-Low	1996	2–16 May	4.5	4.5	OG	20	20	x	
Category II. Deer only									
Ramsay	1993	25 May–17 June	1 622.5	< 50	OG	63	63		
Kunga	1996	15–29 May	472.6	< 25	OG	30	30	x	
Reef	1996	2–16 May	239.5	< 25	OG	30	30	x	
Category III. Deer and squirrel									
East Limestone	1993	25 May–17 June	48.0	48	OG	61 ¹	63		
Louise	1996	4–19 May	27 280.5	< 25	OG-PSL	30	30	x	
Lyell	1996	15–29 May	17 299.9	< 25	OG-PSL	30	30	x	
Study of year and habitat effect on nest predation by squirrels									
East Limestone	1995	4–19 May	48.0		OG	120	0		x
East Limestone	1996	3–18 May	48.0		OG	80	0		x

¹Two nests not found.

protocol (Martin 1994): for ground nests, visibility at close range is the percentage of the nest visible from 1 m above the nest. For shrub nests, it is the percentage of the nest visible to a human observer placed 1 m from the nest, in each of the four cardinal directions, and averaged to produce a single value. The same observer (MJ) recorded them.

Protocol on effect of nest visitation

Corvids are known to learn quickly to follow experimenters and to find visual trails leading to nests (Picozzi 1975). Mammals may use the human scent trails left by the observers to find artificial nests (Whelan et al. 1994). In addition, some of our nest transects differed in the number of visits, which might create variation of trail intensity between islands. To assess whether the intensity of nest visitation affected nest predation risk in our study (Yahner and Cypher 1987, Major 1990, Reitsma et al. 1990, Mayer-Gross et al. 1997, Skagen et al. 1999, reviewed by Göttmark 1992), we used the 80 artificial ground nests exposed on East Limestone Island in 1996 (Table 1). We implemented a nest check procedure where nests differed in visit frequency, and thus trail intensity. We used four visit frequencies: once (day 1), twice (days 1 and 8), 3 times (days 1, 4, and 8), and 4 times (days 1, 4, 8, and 12) during a 15-day period. We interspersed treatments to control for habitat differences or other spatial sources of variation.

Data analysis

We calculated and compared daily survival rates between samples of artificial nests using the same method as for natural nests. Modified Bonferroni procedures for multiple tests were applied where appropriate (Simes 1986).

We used the Runs test procedure (Sokal and Rohlf 1995, p. 783) to test whether the nests preyed upon occur in a random, regular or clustered sequence along transects, using transects for which more than 10% and less than 90% of the nests had been preyed upon. A rejection of the random sequence hypothesis indicates that nests preyed upon are clustered in specific areas along transects (less runs than random) or regularly distributed (more runs than random).

We used a Generalised Linear Model (GENMOD procedure, SAS software, SAS 1996) to assess the effect of vegetation cover and of nest visibility at close range (1 m, explanatory variables) on predation risk (response variable). Using the individual nest as our basic observation unit, we scored the dependent binary variable, nest predation, as 0 (nest intact) or 1 (nest preyed upon). We assumed a binomial error for the response variable and used the logit link to model the explanatory variables with a logistic regression (Aitkin et al. 1989). In the case of nested models, the difference in deviance between two models follows a χ^2 distribution

with d degrees of freedom, where d is the variation in degrees of freedom between the two nested linear models. The independent variables and factors used in the different analyses were: squirrel (presence/absence); deer (presence/absence); % vegetation cover on ground, shrub, and tree strata within 5 m from the nest (log-transformed); and nest visibility (at 1 m).

Results

Predation of natural nests

We found and monitored a total of 74 natural nests at the nestling and/or incubation stages. Of those 22 were nests of thrushes (hermit thrush *Catharus guttatus*, 13 nests; varied thrush *Ixoreus naevius*, 6 nests; American robin *Turdus migratorius*, 1 nest), 15 song sparrow nests *Melospiza melodia*, 9 orange-crowned warbler *Vermivora coelata* nests and 18 winter wren nests. At the incubation stage, nest survival was significantly lower on islands with squirrels than on islands without squirrels (Table 6). We observed no difference in survival rate at the nestling stage. On the basis of tooth marks left on fragments we could identify squirrels as the predator in 82% of the nests preyed upon on the islands with squirrels.

Predation of artificial nests

The number of visits to the nests had no effect on nest survival (nest survival at 15 days of nests that were visited one, two, three or four times ranged between 36 and 40% and did not differ statistically; P values of pair by pair contrast ranged 0.41 and 0.50).

Squirrels and predation risk

Nest survival was similar on all islands without squirrels for both ground and shrub nests, deer present or not (Tables 3 and 4, contrast between island categories I and II). Nest survival was significantly lower on islands with squirrels (category III) than on islands with no squirrels (categories I and II, Table 4). Overall patterns of nest survival were similar between natural and artificial nests: about 100% of the natural nests with eggs survived on islands without squirrels against 30% on the islands with squirrels; 84% of the artificial nests survived, on average, on islands with deer only (category II) and 50% on islands with squirrels (category III). Of the 108 nests preyed-upon in 1995 that were closely examined during the experiment on East Limestone Island (with squirrels), tooth marks indicated that 44 were preyed upon by squirrels and 3 by deer mice. Pierced shells indicated that 4 had been preyed upon by unidentified birds. Another 57 nests were either found empty, and could have been preyed upon by squirrels (pers. obs. of squirrels removing

Table 3. Survival of artificial nests in the different sets of data. T = number of transects per island; N/T = number of nests per transect; s^{15} = nest survival over a period of 15 days (method of Bart and Robson 1982); s^{15}/T = nest survival per transect. All islands have native avian nest predators.

Island	Year	Transect T(N/T)	Ground nests		Shrub nests	
			s^{15}	s^{15}/T	s^{15}	s^{15}/T
Study of squirrel and deer effect on nest survival						
Category I. No deer, no squirrel						
Low	1996	2 (10)	0.81	0.72; 0.90	0.85	0.71; 1
South-Low	1996	2 (10)	0.95	1; 0.90	0.95	0.90; 1
Lost	1996	2 (10)	0.85	1; 0.70	1	1; 1
Category II. Deer only						
Ramsay	1993	3 (21)	0.86	0.68; 0.90; 1	0.97	1; 0.90; 1
Kunga	1996	2 (15)	0.97	1; 0.93	0.97	1; 0.93
Reef	1996	2 (15)	0.64	1; 0.33	0.83	1; 0.68
Category III. Deer and squirrel						
East Limestone	1993	3 (21)	0.22	0.40; 0.17; 0.10	0.11	0.22; 0.03; 0.11
Louise	1996	2 (15)	0.71	0.71; 0.72	0.86	0.79; 0.93
Lyell	1996	2 (15)	0.83	0.79; 0.86	0.90	1; 0.79
Study of year and habitat effect on nest predation by squirrels						
East Limestone	1995	(120)	0.09			
East Limestone	1996	(80)	0.37			

Table 4. Comparison by CONTRAST (Hines and Sauer 1989) of nest survival between island categories for ground and shrub nests. Diff. s = difference in daily survival rate, χ^2 = chi square value of contrast analysis, df = degree of freedom, P = probability value given by contrast analysis, SL = significance level after modified Bonferroni procedure (Simes 1986) was used to correct statistical significance for multiple tests. n.s. = non significant.

Comparison	Effect	Contrast for ground nests					Contrast for shrub nests				
		Diff. s	χ^2	df	P	SL	Diff. s	χ^2	df	P	SL
I-II	deer	0.005	1.08	1	0.299	n.s.	-0.001	0.05	1	0.811	n.s.
II-III	squirrel	0.013	4.43	1	<0.00001	***	0.046	45.53	1	<0.00001	***
I-III	both	0.034	26.84	1	<0.00001	***	0.465	45.44	1	<0.00001	***

whole eggs) or large birds, or yielded inconclusive clues. The nests equipped with automatic cameras were preyed upon 32 times, in every case by red squirrels.

Within island variation

On all islands nest survival was similar between ground and shrub nests, except on Reef island where shrub nests had a better survival than ground nests (diff. $s = -0.008$, $\chi^2 = 4.63$, $df = 1$, $P = 0.031$, significant at 0.05 level after correction for multiple test by modified Bonferroni procedure, Simes 1986). Nest survival was similar for all transects on the islands with no introduced species (category I) for both ground and shrub nests (no significant differences in CONTRAST analyses). On islands with deer only or with deer and squirrel (categories II and III) nest survival varied between transects on four islands. Daily survival of ground nests was significantly lower in transect 1 on Ramsay Island (Diff. s between transect 1 and transect 2 = -0.049 , $\chi^2 = 20.93$, $df = 1$, $P < 0.00001$, significant at 0.001 level after correction for multiple tests by modified Bonferroni procedure; diff. s between transect 1 and transect 3 = -0.056 , $\chi^2 = 34.25$, $df = 1$, $P < 0.00001$, significant at 0.001 level after correction). Daily survival rates of

ground and shrub nests were higher in transect 1 than in transect 2 on Reef Island (for ground nests diff. $s = 0.072$, $\chi^2 = 11.69$, $df = 1$, $P < 0.001$; for shrub nests diff. $s = 0.026$, $\chi^2 = 5.17$, $df = 1$, $P < 0.05$). On islands with deer and squirrel survival rate of ground nests of transect 1 on East Limestone Island (category III) was significantly higher than survival of ground nests in transect 3 (diff. $s = 0.082$, $\chi^2 = 489.14$, $df = 1$, $P < 0.00001$, significant at 0.001 level after correction for multiple tests) and survival of shrub nests was significantly higher in transect 1 than in transect 2 (diff. $s = 0.108$, $\chi^2 = 4.40$, $df = 1$, $P = 0.036$, significant at 0.05 level after correction for multiple tests). On Louise Island survival of shrub nests was significantly higher in transect 1 than in transect 2 (diff. $s = 0.029$, $\chi^2 = 8.62$, $df = 1$, $P < 0.01$).

Within category variation

Nest survival did not differ from island to island within island category I (Table 5). For island category II (deer only) nest survival was significantly lower on Reef island than on the other two islands. For island category III (deer and squirrel) nest survival rate on East Limestone island is significantly lower (and is so for all 3 years this island has been monitored) than on the two

Table 5. Comparison by contrast (Sauer and Williams 1989) of nest survival rates between islands within island categories for ground and shrub nests. Diff. s = difference in daily survival rate, χ^2 = chi square value of contrast analysis, df = degree of freedom, P = probability value given by contrast analysis, SL = significance level after modified Bonferroni procedure (Simes 1986) was used to correct statistical significance for multiple tests. n.s. = non significant.

	Ground nests					Shrub nests				
	Diff. s	χ^2	df	P	SL	Diff. s	χ^2	df	P	SL
Category I. No deer, no squirrel										
Low – South Low	-0.010	1.92	1	0.166	n.s.	-0.007	1.02	1	0.312	n.s.
Low – Lost	-0.003	0.105	1	0.746	n.s.	-0.011	3.02	1	0.082	n.s.
South Low – Lost	0.008	1.170	1	0.279	n.s.	-0.003	1.00	1	0.317	n.s.
Category II. Deer only										
Ramsay – Kunga	-0.008	3.90	1	0.048	n.s.	0	0	1	1.00	n.s.
Ramsay – Reef	0.083	79.97	1	<0.00001	***	0.010	3.10	1	0.078	n.s.
Kunga – Reef	0.091	104.40	1	<0.00001	***	0.010	2.86	1	0.091	n.s.
Category III. Deer and squirrel										
East Limest. 93 – Louise	-0.074	20.70	1	<0.00001	***	-0.127	44.41	1	<0.00001	***
East Limest. 93 – Lyell	-0.083	29.49	1	<0.00001	***	-0.129	47.19	1	<0.00001	***
Louise – Lyell	-0.009	0.10	1	0.318	n.s.	-0.003	0.133	1	0.684	n.s.

other islands in this category (Table 3). When we restrict the comparison between island categories II and III to the islands with highest and homogenous survival rates in both groups (Ramsay and Kunga for category II and Louise and Lyell for category III) nest survival rate is significantly lower on the islands with squirrels (diff. s = 0.0087, χ^2 = 7.80, df = 1, P = 0.005).

Effect of habitat on squirrels and on nest survival

The abundance of squirrels on East Limestone Island was, in most years, higher in forest stands dominated by hemlock/spruce than in those dominated by alder (Fig. 2). It peaked in 1995 and in 1999. In the hemlock/spruce-dominated stands squirrel abundance dropped from 0.42 squirrel per point count in 1995 to 0.07 in 1996 (P < 0.001, paired t-test) and from 0.26 to 0.02 squirrel per point count in the alder-dominated habitat (P < 0.01). During the year of high squirrel abundance nest survival was significantly lower in the hemlock/spruce stands than in the stands dominated by alder (Table 6). Overall nest survival increased between 1995 and 1996 (Table 6) but the difference was significant only in the hemlock/spruce stands.

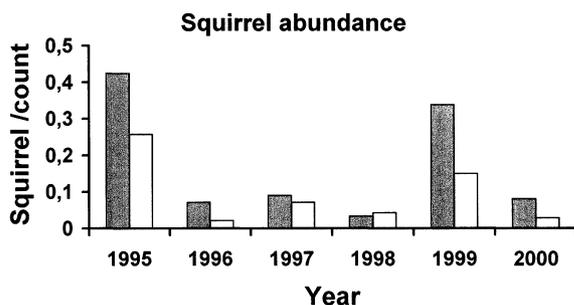


Fig. 2. Variation in squirrel abundance (average number of squirrels observed per point count) with year and habitat quality for squirrels on East Limestone Island between 1995 and 2000.

Effect of nest concealment

Of the nests studied in 1996, for which we had described the surrounding vegetation, only 2 shrub nests were preyed upon on islands of category I, 6 on the islands of category II and another 6 on the islands of category III, precluding the analysis of the effect of nest concealment on shrub nests. Respectively 8, 12 and 13 ground nests were preyed upon in island categories I, II and III, with 52, 48 and 47 nests left intact. Ground vegetation cover and shrub cover around the nests were, on average, three to four times denser, and the canopy more open, on the islands with no introduced species (category I) than on the islands with deer (categories II and III, Fig. 3). The shrub layer was significantly more open around the depredated nests than around intact nests in island categories I and II (χ^2 = 4.55, df = 1, P < 0.05; GENMOD analysis) and nest visibility at 1m was higher (χ^2 = 6.12, df = 1, P < 0.05). On islands with deer only (category II), tree cover was significantly more open (Fig. 3) around depredated nests than on islands with deer and squirrel (category III, tree effect: χ^2 = 5.58, df = 1, P < 0.05; squirrel and tree interaction: χ^2 = 4.40, df = 1, P < 0.05; GENMOD analysis). Shrub cover had no significant effect on nest survival on islands with squirrels. Predation risk increased significantly with higher nest visibility at 1 m (χ^2 = 8.29, df = 1, P < 0.01).

Effect of predator assemblage on spatial distribution of nest predation

On islands with squirrels, depredated nests were randomly distributed along transects in the four samples that could be tested by the Runs test (East Limestone Island 1993, 1996; Louise Island 1996; and Lyell Island 1996 – see Methods, P > 0.05). On two of the islands without squirrels, depredated nests were clustered in certain areas (Reef Island 1996, Low Island 1996) (number of runs significantly lower than random, P < 0.005, Runs test).

Table 6. Nest survival rates at 15 days (s^{15}) and comparison by contrast (Sauer and Williams 1989) of daily nest survival rates s between years and habitat characteristics on East Limestone Island. Diff. s = difference in daily survival rate, χ^2 = chi square value of contrast analysis, df = degree of freedom, P = probability value given by contrast analysis, SL = significance level after modified Bonferroni procedure (Simes 1986) was used to correct statistical significance for multiple tests. n.s. = non significant.

	Hemlock/Spruce	Alder	Diff. s	χ^2	df	P	SL
1995	$s^{15} = 0.02$	$s^{15} = 0.24$	-0.136	23.37	1	<0.001	***
1996	$s^{15} = 0.37$	$s^{15} = 0.32$	0.009	0.09	1	0.758	n.s.
Diff. s	-0.1610	-0.016					
χ^2	28.49	0.315					
df	1	1					
P	<0.001	0.57					
SL	***	n.s.					

Discussion

Predator assemblage and nest survival

Our data from both artificial and natural nests indicate that predation rate can be much higher on islands with squirrels than in absence of squirrels. Results from artificial nests show that predation risk varies between islands with the same predator community. Our data from natural nests suggest that nest predation by squirrels mainly occurs at the incubation stage. We interpret the low level of predation observed in the absence of squirrels (0% for natural nests and between 0 and 36% for artificial nests, Table 3) as the result (1) of the overall scarcity of native predator species on these islands (see Sieving and Willson 1998 for description of predator communities and predation pressures typical of such forests on the adjacent mainland and George 1987 for a comparative study of predation risk between an island and the nearby mainland), (2) of the absence of jays among the corvid predators found in our study sites (jays accounted for 6 to 32% of nest losses in Sieving and Willson 1998) and (3) of the high prevalence of shoreline foraging in Pacific crow (Godfrey 1986).

Habitat effects on predation

Spruce prevalence and nest survival on islands with squirrels

The control of red squirrel abundance by the production of conifer seeds has been repeatedly documented (Banfield 1974, Gurnell 1983, Sullivan 1990, Klenner and Krebs 1991, Christen 1995 for Norway spruce *Picea excelsa*; Osfeld and Keesing 2000, pers. obs.). The production of Sitka spruce seeds, squirrels' main food on Haida Gwaii, typically increases with tree diameter as the number of cones per tree increases with tree size and the number of seeds per cone with the number of cones per tree (Holimon et al. 1998). As a consequence, the number of cones per tree can be about six times higher in mature stands of more than 150 years old than in stands of about 50 years old. Finally,

seed production fluctuates between years (Reinikainen 1937, Gurnell 1983, Christen 1995) being about 50 times higher in good years than in bad years in mature stands of Sitka spruce (Holimon et al. 1998). The peaks in squirrel abundance on East Limestone island were synchronised with non quantified pulses in cone production (pers. obs.). The systematically lower survival of artificial nests on East Limestone island (in 1993, 1995 and 1996) when compared to the other islands with squirrels, was consistent with the higher maturity of Sitka spruce stands on East Limestone than on the other islands with squirrels. It was also consistent with the higher frequency of squirrel observations along transects on East Limestone than on the other islands with squirrels (qualitative pers. obs.). The connection between seed production of the dominant tree, rodent abundance and nest predation has been experimentally demonstrated by McShea (2000). Lower predation risk in younger than in older coniferous forests has also been found by Seitz and Zegers (1993), although they suggested them to result from more open understory in older forests rather than from lower resources in younger forests. The relation between habitat quality, predator density and intensity of nest predation was also underlined in Major and Kendal (1996) and in Andrén and Angelstam (1988).

Vegetation cover, nest visibility and nest predation

The differences we observed in the effect of vegetation cover on nest survival between islands with and without squirrels are consistent with differences in predator biology. On islands where the squirrel is the main predator, the significant positive effect of cover in the tree layer can be another reflection of the dependence of squirrel on the abundance of tree seeds, abundance which is positively correlated with tree cover (Holimon et al. 1998). On islands where corvids are the main predators, the higher predation risk observed when canopy cover is more open, is consistent with the predominant dependence on visual cues of foraging avian predators (Ouellet 1970, Ehrlich and McLaughlin 1988, Andrén 1992) as opposed to squirrels, that mainly use systematic "search and smell" tactics (Whelan et al. 1994). Also consistent with this interpretation is the

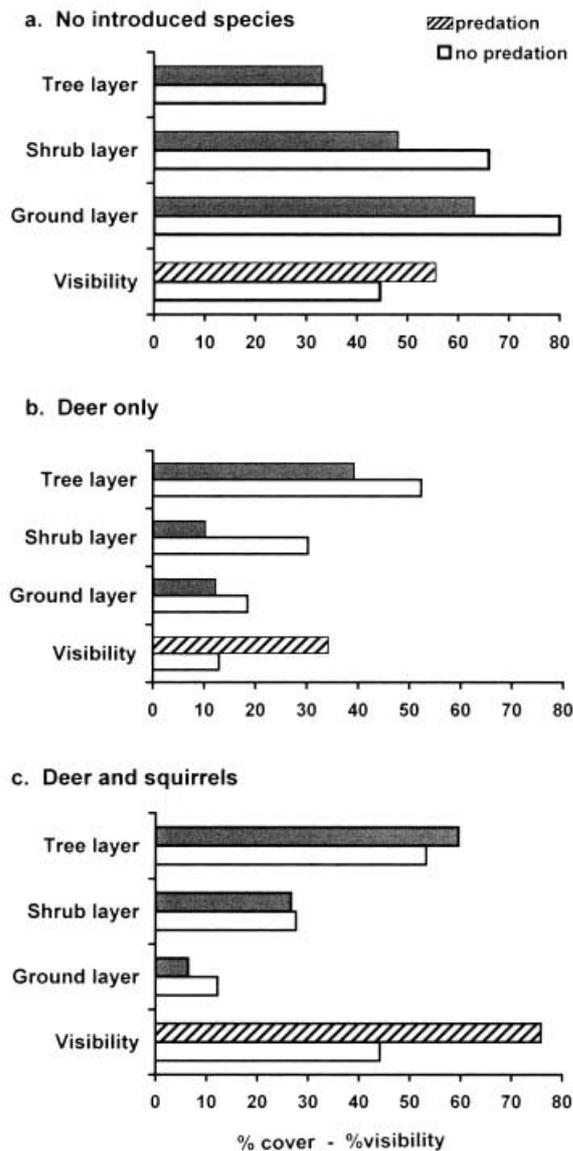


Fig. 3. Vegetation cover around, and visibility at 1 m of, preyed upon (grey and hatched) and intact (white) ground nests. 3a: islands with no introduced species (category I; Low, South Low and Lost islands); 3b: with deer only (category II; Kunga and Reef islands); 3c with deer and squirrels (category III; Louise and Lyell islands);.

lower cover in the shrub layer observed around preyed-upon ground nests on islands without squirrels, as well as the absence of a difference in shrub cover within 5 m of depredated nests on islands with squirrels. However, the significant increase in predation risk, on both types of islands, with higher nest visibility at 1 m in preyed-upon ground nests, suggest that lower vegetation cover in the immediate vicinity of the nest increases its detectability both to corvids and squirrels. This interpretation is in agreement with several studies of nest predation (reviewed by Major and Kendal 1996) but

contradicts others who found no effect of vegetation cover around the nest on predation risk (Seitz and Zegers 1993, Howlett and Stutchbury 1996).

The comparison of predation risk between islands with deer only and islands with no introduced species failed to show a direct effect of deer presence on predation risk of artificial nests. The lower tree cover observed, on average, on the islands without deer is a feature common to all small isolated islands in the area (Martin et al. 1995). The higher vegetation cover in the ground and shrub layers on islands with no introduced species is a direct consequence of the absence of browsing by deer (Daufresne and Martin 1997, Martin and Daufresne 1999). Notwithstanding these differences in vegetation cover, related to the presence or absence of deer, we observed, within each category of islands, a decrease in nest survival with decreasing vegetation cover around and above the nest (shrub layer), a result consistent with our conclusion that predation by native predators increases when the vegetation is more open.

Temporal and spatial variability of predation risk in relation to predator assemblage

The random distribution of predation risk on islands with squirrels suggest that on these islands predation risk can occur anywhere over the area studied. The clusters of preyed-upon nests on islands with only native predators indicate that predation risk tends to be concentrated in specific areas on these islands. These areas actually coincided with the proximity of intertidal zones used by corvids for foraging (Godfrey 1986, Martin et al. 1995) and, on Reef island, with an active breeding site of ancient murrelet (*Synthliboramphus antiquus*) intensively visited by corvids (Gaston 1992, pers. obs.) trying to prey on adult birds or on their eggs. On East Limestone Island (with squirrels) the spatial distribution of predation risk was not affected by the distribution of murrelet colonies. Contrary to Yahner and Scott (1988) and Söderström et al. (1998), we did not find that predation risk was higher for nests placed above the ground when the main predators were corvids. This can reflect the low diversity of corvid species in the communities we studied and particularly the absence of jays (blue jay, *Cyanocitta cristata*), more likely than crows to rob nests in shrubs (Sieving and Willson 1998, 1999, Söderström et al. 1998, pers. obs.) and the habit of the native species to forage mainly on the ground. Conversely, Loiselle and Hoppes (1983) and Martin (1987) showed that in mainland communities mammals were mainly responsible for the predation on nests on the ground. Red squirrels were an exception, however, as shown by photographic evidence of predation on nests both on the ground and in shrubs (Sieving and Willson 1998, 1999).

The introduction of the red squirrel has, therefore, not only increased overall predation risk but has also modified the spatial and temporal predictability of that risk. In the presence of squirrels, predation risk tends, within a habitat type, to vary more from year to year and less from place to place than on islands without squirrels. The relation found between vegetation cover and predation risk suggests that the colonisation of an island by deer, by reducing shrub cover (Pojar and Banner 1984, Martin and Daufresne 1999), should increase nest predation by native avian predators.

Finally the lack of effect of the number of nest visits on predation risk suggests that observer activity had little or no impact on the observed patterns. Bowen et al. (1976), Gottfried and Thompson (1978), Mankin and Warner (1992), O'Grady et al. (1996), Mayer-Gross et al. (1997), and Knutson et al. (2000) obtained similar results for real and artificial nests, but Major (1990) did observe an effect of visit frequency (reviewed by Göttmark 1992).

Conclusions

Our results confirm the major and pervasive role of red squirrels in the distribution of nest predation at the landscape scale in Pacific Northwest forests, as opposed to the more spatially and temporally localised predation pressure caused by avian nest predators (Sieving and Willson 1998, 1999). They also suggest that predation by squirrels varies not only with time in a short-term and cyclic fashion related to cycles of spruce cone production but also, over a longer-term, through increasing cone production with increasing forest maturity. Selective pressures on breeding birds that are related to risk of nest predation appear therefore to fluctuate in space and time and in such a way that years and places with high predation risk alternate with years and places with lower risk. This pattern may preclude any tight adjustment of breeding strategies, or nest site selections, to predation risk. It suggests that, if nest predation is to influence habitat selection and nest site selection by birds, it should occur at the landscape scale rather than at the local or habitat scale (Marini 1997).

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