

NESTING SUCCESS OF FOREST BIRDS IN SOUTHEAST ALASKA AND ADJACENT CANADA¹

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Abstract. Predation caused 78% of nest failures in coastal forests of southeast Alaska and interior forests of adjacent Canada. Nest success tended to be better in coastal than interior forests. Mayfield daily nest survival from predation on open-cup nests was higher in egg than nestling phase for most species. Species building large (thrush-sized) nests had lower Mayfield daily survival from predation than species building smaller (warbler-sized) nests, but there was no difference in daily survival (total and from predation only) among species nesting in different vegetation strata. Nesting success differed little with nest cover or nest site diversity for most species. Total nest success within species was only sometimes higher in commonly used nest sites than in less frequently used sites. Nest survival from predation did not generally decrease with increasing nest density within guilds of species with similar nests or with nest-site similarity. We emphasize the likelihood of varied outcomes of natural selection on nest-site selection in differing circumstances.

Key words: Alaska, British Columbia, nest density, nest predation, nest success, Yukon.

INTRODUCTION

Avian nesting success in North American forests has been studied chiefly in the eastern region, with fewer studies in the west and almost none in the far north. Such studies are important, however, for understanding geographic patterns of life histories, as well as for management of species of conservation concern. We examined patterns of nest success in wooded habitats in southeast Alaska and adjacent parts of Canada, testing several predictions: (1) if nestling calls and parental feeding activity draw attention to nests, then nest survival from predation for a species should be higher during the egg phase than the nestling phase (Skutch 1949), (2) if concealment contributes to better survival of nest contents, nest success (total and specifically with respect to predation) should be greater for species building nests of smaller size and with more cover, (3) if birds usually choose nest sites adaptively, total nest success within species should be greater in commonly used sites than in rarely used sites, and (4) if predators respond to high nest density, nest survival from predation should decrease with increasing density of similar nests and with nest-site overlap among species (Martin 1988b, 1988c, 1998). We also com-

pared nest success of birds in coastal and continental interior forests, cavity vs. open-cup nests, cavity nests with differing nest-hole orientation, and nests in different forest strata.

METHODS

STUDY SITES

Conifer-forest study sites near Juneau, Alaska (about 58°21'N, 134°36'W) were located at Peterson Creek on Douglas Island (separated from the mainland by a shallow channel) and between Herbert River and Eagle River on the mainland. Both lowland forests were composed principally of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) in the overstory, and blueberry (*Vaccinium* spp.), devil's club (*Oplopanax horridum*), western skunk cabbage (*Lysichiton americanum*), and rusty menziesia (*Menziesia ferruginea*) in the understory. Both forests also contained small patches of deciduous overstory, principally Sitka alder (*Alnus sitchensis*) or red alder (*A. rubra*). One deciduous-forest site was located in Sheep Creek valley at about 200 m elevation, where the dominant vegetation was composed principally of alder, willow (*Salix* spp.), black cottonwood (*Populus trichocarpa*), elderberry (*Sambucus racemosa*), salmonberry (*Rubus spectabilis*), and viburnum (*Viburnum edule*), with a few scattered enclaves of spruce. The other principal deciduous-forest

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site (Back Loop) was in the lowland Mendenhall River valley, where the dominant vegetation was alder and willow, with patches of wet meadow and a few isolated spruce trees. A few nests ($n = 14$) were found at miscellaneous other sites near Juneau and are included in the totals. Interior sites were located near Atlin, British Columbia (about 59°35'N, 133°45'W) and included one principal site with deciduous vegetation (mixed alder, willow, cottonwood, with a few scattered white spruce, *Picea glauca*) along Pine Creek south of Atlin. Ancillary sites were located in deciduous stands on Haunka Creek and Snafu Creek north of Atlin in the Yukon Territory. Some nests were also found in an array of other sites and habitats in the region during casual investigations. Further description of the sites can be found in Willson and Comet (1996). Scientific names of the principal bird species mentioned in the text are found in Table 1.

FIELD METHODS AND ANALYTICAL APPROACHES

Standard methods of nest-searching were used (Martin and Geupel 1993), with the most intensive effort from mid May to mid July in 1994 and 1995 (and less intensive efforts in 1996), although the fates of some nests found late in this period were followed into August. In Juneau, regular plots were defined and marked, so that comparisons involving nest density could be made; plots were not the same in both years. Nests were usually checked every 1–3 days during the season. Our measure of nest success is whether or not young were successfully fledged from the nest; brood size is not considered. A nest was considered to be depredated if the clutch or brood disappeared prematurely or, in a few cases, predation was observed directly. Because predation attempts could lead to nest abandonment without immediate loss of clutch or brood, our estimates of predation risk are, to that degree, conservative.

Principal nesting stratum (ground; shrub, defined as ≤ 2 m in height, which encompasses the majority of shrub foliage in these habitats; canopy/subcanopy, defined as > 2 m in height) for each species was determined by the median of the nest-height distribution in our sample, supplemented by standard references such as Ehrlich et al. (1988) and Kaufman (1996). Nest cover, for Juneau nests only, was measured after the nest was empty. Vegetative cover was deter-

mined using a Plexiglas board divided into 25 3-cm squares. The nest was centered within this grid, which was held 1 m from the observer and 1 m from the nest. The amount of vegetation obscuring the nest was determined by counting the number of squares that were $> 50\%$ filled by vegetation in front of the nest in the four cardinal directions. In addition, vegetative cover 1 m above each nest was estimated in relation to the same grid. We recorded nest size at the time that cover was measured. For cavity nests, we recorded the orientation of the opening, in quadrants centered on the four cardinal directions.

Nests for each species were divided into two categories so as to achieve sample sizes as equal as possible: those in more commonly used sites vs. those in less commonly used sites, using three factors: nest-support species (woody plants), support structure (main branch, branchlets, moss wads), and nest height. The number of species that could be examined in this way was limited not only by the number of nests recorded but also by the extent of variation: some species clustered their nests so closely to a single common value, such as Lincoln's Sparrow and Dark-eyed Junco on the ground, Ruby-crowned Kinglet and Varied Thrush in the canopy, that too few other nests were available for comparison. Nest survival was then compared for more- and less-commonly used nest sites, to test the hypothesis that nest success would be higher in commonly used sites, if nest-site selection were adaptive.

For analyses of the relationship between nesting success and nest density, selected species were placed in guilds with similar nest type and placement. Judgements of which species comprised a guild were based on our observations of nests and known occurrences of nest usurpation among guild members. Specifics of guild membership are described in Results.

To assess the relationship between nest success and nest-site diversity, we calculated Simpson's diversity index for nest sites, using samples with at least 15 nests (Smith and Grassle 1977, Levinton 1982). The relationship was examined for three factors (nest height, in meter intervals; nest-support species; nest-support structure) separately and for a composite index obtained by summing the separate indices for each factor. For Simpson's index, low values indicate high diversity.

STATISTICAL ANALYSIS

Preliminary analyses for samples of at least five nests showed that standard percent survival was closely correlated with Mayfield percent survival (Mayfield 1975), as modified by Hensler and Nichols (1981), which accounts for the stage at which the nest was found (Juneau deciduous forest, $R^2 = 0.91$, $P < 0.001$; Juneau coniferous forest, $R^2 = 0.99$, $P < 0.001$; Atlin deciduous, $R^2 = 0.96$, $P < 0.001$; Atlin mixed sites, $R^2 = 0.95$, $P = 0.014$). We have used the more rigorous Mayfield method here, except as noted below. For Mayfield estimates, a sample size of at least 20 is recommended (Hensler and Nichols 1981), but we have used a minimum sample of 15 here. Comparisons of Mayfield daily survival rates were made with the program CONTRAST (Hines and Sauer 1989).

Logistic regression was used to examine nest fate (successful or not) of open-cup nests (for all samples that allowed construction of a model) in relation to (1) the type of plant supporting the nest—deciduous, coniferous, or moss and herbs, (2) vertical vegetation cover (estimated % cover above the nest), and (3) horizontal vegetation cover (number of squares of the sampling grid with >50% cover at four points around the nest). To normalize the data, vertical cover was arcsin transformed and horizontal cover was square-root transformed. Log-likelihood chi-square tests were used to evaluate models with and without each variable, beginning with a full model containing all variables and sequentially eliminating each variable (Trexler and Travis 1993). Multicollinearity between transformed and binomial independent variables was absent. Interaction terms did not contribute to the ability of the model to make predictions and were therefore dropped from analysis. For comparative purposes, logistic regression analysis was done once including all nest failures (depredated and abandoned) and again for depredated nests only.

RESULTS

OVERALL NEST SURVIVORSHIP

For 1,084 nests monitored in this study, 53–85% were successful in the given habitats and locations. The risk of nest predation ranged from 11–42% of nests in a given habitat and location (Juneau deciduous 33%, $n = 701$, conifer 11%, $n = 153$; Atlin deciduous 42%, $n = 160$, miscellaneous mixed habitats 36%, $n = 70$).

Predation was the primary known source of nest mortality (78% of all failures). For individual species with at least 10 nests of known causes of failure, predation caused 65–100% of the failures; the sole exception was Varied Thrushes in Juneau (40%).

NEST SUCCESS IN EGG AND NESTLING PHASES

We tested the prediction that survivorship from predation per day was lower in the nestling than the egg phase (laying + incubation) by comparing Mayfield daily survival estimates for both phases of the nesting cycle. Comparison of survivorship of egg and nestling phases, by species, revealed that most species (11/19, with 5/19 significant) had greater survivorship during the nestling phase (Table 1). For five species, Mayfield daily survivorship in the nestling phase was virtually equal to that in the egg phase. Only 1 of the 19 samples examined exhibited significantly greater survivorship in the egg phase. Thus, the general pattern was for survivorship in the nestling phase to exceed or equal that in the egg phase.

EFFECTS OF NEST COVER, NEST SIZE, AND STRATUM

Juneau species with larger nests averaged lower daily nest survival than species with smaller nests (0.958 vs. 0.977; $\chi^2_1 = 11.3$, $P < 0.001$) overall, as well as survival specifically from predation (0.967 vs. 0.983, $\chi^2_1 = 11.6$, $P < 0.001$). Atlin species building larger nests also had lower daily nest survival than those with smaller nests (0.920 vs. 0.973; $\chi^2_1 = 12.2$, $P < 0.001$). Daily nest survival differed significantly among Juneau species (CONTRAST, $\chi^2_{10} = 53.8$, $P < 0.001$), but such differences were not associated with nesting stratum ($\chi^2_2 = 2.7$, $P = 0.26$). In Atlin, daily nest survival of the only adequately sampled ground nester (Dark-eyed Junco) was higher than that of five species of canopy nesters (0.987 vs. 0.900–0.970).

Within species, logistic regression on nest success revealed no association of success (overall or with respect to predation) with cover, nest size, or stratum for any of the five Juneau species with adequate sample size with one exception: nest success (with respect to predation) of Yellow Warblers was positively associated with nest cover ($P = 0.03$).

TABLE 1. Nesting success (absence of predation) during egg and nestling phases, near Juneau and Atlin, and the combined locations, for samples with $n \geq 15$. Statistically significant ($P \leq 0.05$) or nearly significant ($P \leq 0.10$) differences between egg and nestling phases are marked ** and *, respectively, as determined by the program CONTRAST, P -values adjusted for one-tailed test of the prediction that nestling survival rates would be lower. Samples are from the Juneau area, except those marked (A), which are from the Atlin area. About 32% of the samples exhibited significant differences between nesting phases, a frequency substantially greater than that expected among numerous comparisons from chance alone.

Species		n (nests)	Mayfield daily survival rate		
			Egg phase	Nestling phase	Total
Red-breasted Sapsucker	<i>Sphyrapicus ruber</i>	31	1.000	1.000	1.000
Hammond's Flycatcher	<i>Empidonax hammondi</i> (A)	26	0.958*	0.982*	0.970
Winter Wren	<i>Troglodytes troglodytes</i>	74	0.991	0.995	0.993
Ruby-crowned Kinglet	<i>Regulus calendula</i>	39	0.971**	0.995**	0.983
Swainson's Thrush	<i>Catharus ustulatus</i>	55	0.976	0.984	0.980
Swainson's Thrush	<i>C. ustulatus</i> (A)	21	0.890**	0.983**	0.942
Hermit Thrush	<i>C. guttatus</i>	24	0.939**	0.993**	0.965
Varied Thrush	<i>Ixoreus naevius</i>	15	0.946*	0.991*	0.977
American Robin	<i>Turdus migratorius</i>	139	0.947**	0.982**	0.966
American Robin	<i>T. migratorius</i> (A)	21	0.855*	0.922*	0.897
Orange-crowned Warbler	<i>Vermivora celata</i>	27	0.970*	0.991*	0.982
Yellow-rumped (Myrtle) Warbler	<i>Dendroica coronata</i> (A)	18	0.962	0.965	0.964
Yellow Warbler	<i>D. petechia</i>	60	0.985	0.987	0.986
Wilson's Warbler	<i>Wilsonia pusilla</i>	19	0.938*	0.991*	0.973
American Redstart	<i>Setophaga ruticilla</i> (A)	26	0.979*	0.959*	0.970
Dark-eyed Junco	<i>Junco hyemalis</i>	19	1.000*	0.988*	0.992
Dark-eyed Junco	<i>J. hyemalis</i> (A)	15	0.956*	1.000*	0.987
Fox Sparrow	<i>Passerella iliaca</i>	113	0.937**	0.968**	0.950
Lincoln's Sparrow	<i>Melospiza lincolni</i>	55	0.993**	0.978**	0.984

RELATIONSHIPS BETWEEN NEST-SITE SELECTION AND NEST SUCCESS

Nest success was only sometimes higher in commonly used nest sites than in rarely used sites. Mayfield daily survival was significantly higher in commonly used sites for only 4 of 14 samples (Table 2). Furthermore, two cases had significantly better success in the rarely used sites.

Several species in our study sites nested frequently in more than one stratum, but the consequences of nesting in an alternative stratum for nest success varied (Table 3). When typical understory species nested in the canopy/subcanopy stratum, nest success was improved slightly for Swainson's Thrush and Yellow Warbler and markedly for Winter Wren. In contrast, nest success decreased substantially for Fox Sparrow. When American Robins, a typical canopy nester, nested in the understory, nesting success changed very little.

At the habitat level, although the great majority of Juneau Winter Wrens (83%) nested in conifer forest, simple nest survival was 82% in conifer forest but 93% in deciduous forest. Al-

though we did not have an adequate sample to calculate Mayfield survival for wrens in deciduous stands ($n = 11$), it is clear that nest survival there was at least equivalent to that in the more usual habitat.

Among species in our study, nest success (absence of predation) was higher for samples with low diversity of plant species used for nest support ($r_s = 0.89$, $P < 0.001$, $n = 13$). No significant correlations emerged with other nest-site variables.

NEST SUCCESS IN RELATION TO DENSITY AND NEST-SITE SIMILARITY

Examination of this issue is best conducted using Mayfield survivorship, but our sample sizes were adequate to achieve a minimum of 15 nests per nest-searching plot only for all species combined, for a guild comprising the thrushes, and for American Robins in Juneau. We divided all plots into categories of density above and below the median density and contrasted Mayfield daily survival (from predation) in plots of high and low density. For all open-cup nesters, daily sur-

TABLE 2. Mayfield percent survival (and Mayfield daily survival rates) in nest sites used most commonly or more rarely in Juneau, Alaska, considering all sources of nest failure. Typical ground nesters were excluded because their nests were seldom associated with any woody plant species. Significant differences ($P \leq 0.05$) are marked **. Tests of contrast between Mayfield daily survival rates are one-tailed, because the prediction is that success would be better in the more commonly used sites. Data are for overall survival, but the significance of survival from predation-only is the same in all cases except for Fox Sparrow nests and nest support structure, for which there was no difference in survival from predation in relation to support structure.

Species	Support structure		Support species		Nest height	
	Common	Rare	Common	Rare	Common	Rare
American Robin	33.1 (0.961)	30.3 (0.958)	39.4 (0.967)**	26.8 (0.954)	21.3 (0.946)**	42.8 (0.970)
Fox Sparrow	19.7 (0.932)**	32 (0.952)	29.5 (0.948)	19.8 (0.932)	33.2 (0.953)**	15.3 (0.922)
Swainson's Thrush	55.1 (0.976)	47.7 (0.971)	52.5 (0.975)	52.3 (0.974)	56.5 (0.977)	49.4 (0.972)
Yellow Warbler	68.5 (0.982)	63.5 (0.979)	69.8 (0.983)	58.4 (0.975)	71.1 (0.984)	64.4 (0.979)
Ruby-crowned Kinglet	—	—	—	—	50.6 (0.972)**	79.1 (0.990)
Winter Wren	—	—	—	—	100.0 (1.000)**	58.4 (0.983)

vival rate was statistically indistinguishable at high and low densities (0.974 vs. 0.967, $\chi^2_1 = 2.5$, $P = 0.12$). For all the thrushes taken together, as a guild of medium-to-large nesters, daily survival was marginally higher at high density (0.975 vs. 0.964, $\chi^2_1 = 2.7$, $P = 0.10$); for a modified sample in which robins were randomly sampled such that they outnumbered no other species, the daily survival rate at high density was significantly higher ($\chi^2_1 = 3.8$, $P = 0.05$) than at low density. Survival rates of American Robins (the largest sample for any single species) did not differ with density (0.968 vs. 0.961, $\chi^2_1 = 0.6$, $P = 0.45$), so robins are

unlikely to account for the trend seen in the guild as a whole or in the open-cup nesters. If we were to consider these contrasts as one-sided tests of the specific hypothesis that survival is greater at low densities, in no case was the hypothesis supported: the trend was in the opposite direction. In short, there was no indication that survival rates decreased at higher densities. However, these analyses were limited to densities over 15 nests/plot by the requirements of the Mayfield method, and many low-density plots were therefore omitted.

We then examined patterns of nest success (absence of predation; for all plots with $n \geq 5$

TABLE 3. Mayfield nesting success and daily survival rates of Juneau species that used both understory (≤ 2 m) and subcanopy/canopy (> 2 m) for nesting. Values are for overall survival, but the patterns were exactly the same for survival from predation. Significant differences ($P \leq 0.05$) in daily survival rates are marked **. Habitat structure permitted excellent detection of canopy nests for most of these species, and Winter Wrens were the subject of a separate study (De Santo and Willson, in press), so serious underestimation of canopy nests is unlikely.

	Nesting success		Nest frequency		Daily survival rate	
	Understory	Canopy	Understory	Canopy	Understory	Canopy
Understory Nesters						
Swainson's Thrush	50.5	< 58.4	76	> 24	0.973	0.979
Winter Wren	67.0	< 86.4	49	\leq 51	0.987**	0.995
Fox Sparrow ^a	29.6	> 5.6	87	> 13	0.948**	0.882
Yellow Warbler ^a	64.1	< 73.1	62	> 38	0.979	0.985
Canopy Nester						
American Robin	30.0	\leq 32.8	24	< 76	0.958	0.916

^a Species in which the more common nesting stratum is also that in which the best nesting success is achieved.

ness) in relation to density using simple percent success, which was closely correlated with Mayfield success. The risk of nest predation was density-dependent for open-cup nests in general: percent success of all open-cup nests was inversely related to their density ($R^2 = -0.32$, $P < 0.02$). We then divided the set of open-cup nests into "guilds" of similar nest size and stratum. One guild included Yellow Warbler, American Redstart, Yellow-rumped Warbler, and Hammond's Flycatcher (small nests, outside diameter 6–10 cm; placed in shrubs or low canopy; some nest usurpation known—redstarts using Yellow Warbler nests [Yezerinac 1993] and Hammond's Flycatcher nests, our field observations). Another guild was composed of Lincoln's Sparrow, Dark-eyed Junco, Orange-crowned Warbler, and Wilson's Warbler (small ground nests, outside diameter 7–12 cm). A third guild included Swainson's and Hermit Thrushes and shrub-nesting Fox Sparrows (medium shrub nests, outside diameter 11–14.5 cm), and a fourth contained American Robin and Varied Thrush (large canopy nests, outside diameter 15–19 cm). All four guilds exhibited a nonsignificant positive relationship of nest survival to nest density (with $R^2 < 0.20$). Two reduced guilds (Orange-crowned and Wilson's Warblers; Swainson's and Hermit Thrushes) showed nonsignificant negative relationship between survivorship and density; ($R^2 < 0.30$). Thus, the overall negative correlation of percent success vs. density was not seen within guilds of species with similar nest sizes and sites; most relationships between success and density within a nesting guild were not significant but tended in the positive direction.

Very few species had sufficiently large sample sizes and an adequate spread of densities to allow inspection of the relationship between nest density and survival within species. Three of seven species showed at least marginally significant, positive relationships between percent nesting success and nest density (American Robin, $R^2 = 0.46$, $P = 0.06$; Lincoln's Sparrow, $R^2 = 0.97$, $P = 0.01$; Ruby-crowned Kinglet, $R^2 = 0.75$, $P = 0.08$). Of the four species with nonsignificant correlations, two were positive in direction and two were negative.

The risk of predation did not, in general, increase with increasing similarity of nest sites between species. For example, Yellow-rumped Warblers, American Redstarts, Hammond's Fly-

catchers, and Swainson's Thrushes in Atlin often used similar sites. Simple percent success was somewhat greater in similar sites than in dissimilar sites for the first two species (63% vs. 43%, 54% vs. 44%, respectively) but less for the last two (31% vs. 53%, 20% vs. 57%). Nest success of Hermit Thrush and Swainson's Thrush in Juneau differed little in similar and dissimilar sites (47% vs. 55%, 59% vs. 51%, respectively). Comparable comparisons cannot be made for ground-nesters, because they virtually all occupied the same stratum and were seldom directly associated with woody plant species—the criteria on which nest-site similarity was based.

NESTING IN COASTAL AND INTERIOR FORESTS

Daily nest survival rates (considering all sources of failure) were higher near Juneau than near Atlin (mean Mayfield daily survival = 0.974 vs. 0.950; CONTRAST, $\chi^2_1 = 19.9$, $P < 0.001$; Table 4). The same was true when cavity nesters near Juneau were omitted and the contrast was made only between open-cup nesters ($\chi^2_1 = 12.0$, $P < 0.001$). Five of 6 species in Atlin had <50% nesting success, but in Juneau, only 4 of 12 species had such low success (Table 2). Few species nested in abundance on both sides of the mountain range dividing coastal and interior forests, so only four intraspecific comparisons can be made between locations. Of these, daily survival rate was significantly higher in Juneau for two species (Table 4), but the trend was in the same direction for the remaining two species.

CAVITY VS. OPEN-CUP NESTS

Pooling data from all Juneau sites, daily survival rates averaged 0.966 for open-cup nests; the daily survival rate for one cavity-excavating species (Red-breasted Sapsucker) was 1.00 and for one nonexcavating cavity-nester (Winter Wren) was 0.992.

Neither of the two species of cavity nesters oriented their nest openings randomly (both $\chi^2_3 > 25$, $P < 0.001$). Red-breasted Sapsuckers used more north-facing cavities and fewer east-facing cavities than expected, and Winter Wren nests faced west more often and south less often than expected. However, all sapsucker nests were successful, regardless of orientation; too few wren nests failed, preventing a statistical test of association with nest orientation, but there was

TABLE 4. Nesting success near Juneau and Atlin, for samples with $n \geq 15$; all sources of mortality considered. n = number of nests, MDS = Mayfield daily survival rate, M%S = Mayfield percent survival. ** marks species whose nest success differed significantly ($P < 0.05$) between areas (CONTRAST, $\chi^2_1 > 3.88$).

Species	Juneau			Atlin		
	n	MDS	M%S	n	MDS	M%S
American Restart				28	0.967	48.8
American Robin**	163	0.959	31.2	26	0.888	3.6
Dark-eyed Junco	30	0.979	60.7	26	0.974	54.9
Fox Sparrow	126	0.944	26.5			
Hammond's Flycatcher				30	0.963	32.3
Hermit Thrush	36	0.958	35.9			
Lincoln's Sparrow	55	0.984	69.2			
Orange-crowned Warbler	29	0.98	63.8			
Red-breasted Sapsucker	31	1	100.0			
Ruby-crowned Kinglet	40	0.982	65.1			
Swainson's Thrush**	63	0.975	53.3	24	0.946	24.9
Wilson's Warbler	27	0.958	42.2			
Winter Wren	92	0.992	77.0			
Yellow Warbler	68	0.98	65.2	19	0.961	43

a tendency for north-facing nests to fail more frequently than others (33% vs. $\leq 20\%$).

DISCUSSION

As in many other studies (Ricklefs 1989, Martin 1993a), nest predation was the chief cause of nest failure in this study. Predation risk can directly affect nest distribution, at least of open-field species (Møller 1989, Suhonen et al. 1994), and probably also of forest birds.

NEST SUCCESS IN EGG AND NESTLING PHASES

The risk of predation to eggs was higher than that to nestlings in most cases in our study, suggesting that the supposition of greater risk during the nestling phase is not always true (Cresswell 1997, Roper and Goldstein 1997). However, some species in some places, or at some times, may conform to Skutch's (1949) expectation (Morton et al. 1993, Matsuoka et al. 1997).

EFFECTS OF COVER, NEST SIZE, AND STRATUM ON THE RISK OF PREDATION

We found no difference in nesting success for species nesting in different strata, in contrast to other studies (Martin 1988a, 1992a, 1993c, Seitz and Zegers 1993). Species constructing large nests suffered heavier predation than those with smaller nests, in agreement with findings from artificial-nest experiments in these forests (Sieving and Willson 1998), thus documenting the utility of controlling nest size in artificial-nest

experiments and suggesting that birds building larger nests may be under stronger predation pressure than those with smaller nests. However, we detected no within-species relationships between nest size and risk of predation.

Nest cover near the nest was not closely associated with nest fate for most species. A partial review of the literature shows highly variable relationships between nest cover and success: for example, positive association of nest cover and nest success for some species (Martin and Roper 1988, Cresswell 1997), no effect of cover on success for others (Howlett and Stutchbury 1996), and variable relationships in other cases (Storaas 1988, Martin 1992b). In some cases, cover at greater distances from the nest, at the patch scale, may be effective (Knopf and Sedgwick 1992, Martin 1992b, 1998), and in certain cases the effectiveness of nest cover may vary with nest density (Sugden and Beyersbergen 1986). Just as the effects of nest density on the risk of predation vary with the predator, habitat landscape patterns, and the availability of alternative foods to the predators (see below), so can the effectiveness of nest cover vary with circumstances (Collias and Collias 1984). If future studies of nest predation confirm the identity of principal predators in each locale, it would be feasible to relate the behavior of specific predators to patterns of nest predation. In particular, it would be interesting to know if or when foliage or other cover specifically provides direct concealment or whether cover somehow increas-

es the difficulty of predator searching by diffusing the search effort over multiple potential nest sites (Martin 1992b, 1993b).

NEST-SITE SIMILARITY, NEST DENSITY, NEST SUCCESS, AND THE EVOLUTION OF NEST-SITE SELECTION

If nest predation is higher at higher nest densities, selection may favor nest-site specialization within species and nest-site diversification among species (Martin 1988b, 1993b, 1998). Several of Martin's studies provided evidence for this hypothesis, but our results do not.

One can imagine a logical scenario alternative to that of Martin: if high density increases predation risk, it might, reasonably, do so within as well as among species, because within-species variation in nest appearance and nest site is likely to be even less than among species. So the search-image (if any) of a predator could then drive diversification within species, instead of finer adaptation to one particular kind of nest site. Put another way, if nest-site diversification among species reduces predation by reducing the apparent density of nests, then the same could well be true within species. Here we examine several aspects of Martin's hypothesis for our samples in boreal and north-temperate rain forests; we also propose an alternative approach to understanding the role of predation in the evolution of nest-site selectivity.

Comparison of results. In our study, in contrast to Martin (1998), nest-site selection was not necessarily adaptive (Purcell and Verner 1998, Clark and Shuter 1999). Birds often placed their nests in sites where the risk of nest failure was relatively high. Particularly notable were the cases for two species in Atlin. Many nests of Hammond's Flycatcher were placed on relatively large branches in low-canopy willow (52%), but nesting success there was markedly lower than in other sites (simple percent success: 29% vs. 57%, respectively). Swainson's Thrush nests were often (42%) on large branches in low-canopy willow or alder, but success was much lower than in other sites (simple percent success: 20% vs. 57%, respectively). High usage of apparently poor sites suggests the existence of some kind of constraint (ecological, perceptual, and/or behavioral) on nest-site selection.

Nesting success (absence of predation) decreased significantly with nest density, using simple percent success, or did not change with

density, using Mayfield measures, when all species of open-cup nesters in Juneau were considered together. Schmidt and Whelan (1998) also reported between-guild effects, using experimental shrub and ground nests. However, most of our analyses based on guilds of species with similar nests or single-species samples showed a positive relationship between success and density. In short, there was no apparent cost in nest mortality to increased nest density or coexistence of species with similar nest size and nest-site selection in our sample.

Rationalizing the differences. Although we did not examine all aspects of Martin's hypothesis, much of our study does not seem to support it. Some of the differences may result from differences in data set and methods. Martin had a larger sample size and used different criteria for nesting guilds and nest site (plant species, height, and microhabitat patch, in various combinations).

Some potential problems beset both our study and Martin's. Although the nesting season in our region is typically short, with much overlap of nesting cycles, there was some temporal spread of nesting cycles within sampling plots, which was not explicitly considered in estimates of nest density by either Martin or us. A problem with the analysis of nest density and survival for single species is caused by site fidelity between years and re-nests within years, which may produce some non-independence of data (Martin and Li 1992). We did not know the extent of site fidelity, nor did Martin report on it, and we cannot address it concretely, except to note that our density plots were not the same every year, reducing the problem of site fidelity. Furthermore, this problem afflicts both the overall trend and the trend within species and guilds, and we believe that the differences in trends are probably real for the observed densities.

It is not clear just what traits of nests and nest sites are important in determining predator responses. Other factors may matter, in addition to those used by any single study so far. For instance, nest appearance (Martin 1987, 1988c) within guilds differed in some cases; for example, redstarts in Atlin commonly placed whitish bits of plant down on the nest exterior but Yellow and Yellow-rumped Warblers did not, and Fox Sparrows usually built a nest with an exterior of twigs rather than mosses as the Hermit and Swainson's Thrushes did in Juneau.

Many factors might determine whether or not the risk of nest predation is related to nest density (Schmidt and Whelan 1998). It is possible that birds of a nesting guild settle more densely in locales with certain habitat features because expected reproductive success is higher or equivalent there, despite a risk of density-dependent predation, or because they respond to the previous settlement of other individuals (Muller et al. 1997); in short, habitat or other factors might compensate for the effects of increased density. Many more studies, with large samples, would be needed to detect general patterns and processes.

A more general approach might be to determine geographic differences in predation patterns and avian responses. Because habitat structure, microclimatic constraints, identity of major nest predators, and no doubt many other factors vary enormously among regions, it is reasonable to expect geographic variation in responses to the risk of nest predation. It is possible that density-dependent predation responses are found, for example, only at certain levels of nest density or of predation intensity, or only with certain predators, or only in particular circumstances (Hogstad 1995, Larivière and Messier 1998). For example, red squirrels (*Tamiasciurus hudsonicus*) are one of the chief predators on bird eggs in northern forests (Sieving and Willson 1998; unpubl. data); they are strongly territorial, which may determine the scale at which they respond to nest densities. Clearly, the outcome of nest-site selection may be different when predation is not density-dependent, when other factors compensate for the effects of increased density, or when ecological or behavioral constraints are present. That is, there are multiple outcomes to natural selection on nest placement under different conditions. If so, many of the adjustments of forest birds to the risk of nest predation may be made by behavioral plasticity and may vary in time and space.

OVERALL NESTING SUCCESS

The average levels of nest predation in this study (33–42%, by habitat and location) generally fell within the range (31–46%, averaged by stratum) for forest birds summarized by Martin (1993c, his Table 3). The salient exception was Juneau conifer forest, where the risk of nest predation was only 11%; relatively low levels of predation on natural nests have also been reported for bo-

real forest in Quebec (Darveau et al. 1997). By the model of Schmidt and Whelan (1998), these populations are likely to be self-sustaining.

For many of the adequately sampled species in our study, nest success was high compared to other studies. For these comparisons, we use standard, simple percentages of nest success for all species for which there were at least 5 nests, rather than Mayfield estimates, because most of the other literature reports provide simple percentages. Our data for several species fall at or beyond the high end of reported values for Winter Wren (De Santo et al., in press), Yellow Warbler (58–66% vs. 45–55%; Briskie 1995), Common Yellowthroat (73% vs. 44–52%; Martin 1992b, 1995), Orange-crowned Warbler (72% vs. 38–67%; Martin 1993c, 1995, Sogge et al. 1994), Wilson's Warbler (67% vs. 60%; Martin 1992b), Dark-eyed Junco (73–77% vs. 60–69%, Martin 1993c), Lincoln's Sparrow (80% vs. 49–78%; Ammon 1995), and Hermit Thrush (53% vs. 6–60%; Martin 1993c, 1995, Jones and Donovan 1996). For other species (Yellow-rumped Warbler, Hammond's Flycatcher, American Redstart), our observed values fell near those reported elsewhere (Martin 1992b, 1993c, 1995, Sedgwick 1994). However, success of American Robins in Atlin averaged only 19% and in a Colorado study ranged from 8–24%, compared to 46–49% elsewhere (Martin 1993c, Ortega et al. 1997).

Cavity nesters had higher nesting success than open-cup nesters, as is often reported (Martin and Li 1992), and as we have found for south-temperate rainforest birds in Chile (De Santo and Willson, unpubl. data), but in contrast to Christman and Dhondt (1997) and Mönkkönen and Orell (1997). Similarly, one species of cavity-excavator had higher success than a non-excavating cavity nester, as reported by Martin (1993b). Although we detected differences in frequency of directional orientation of the openings of cavity nests, there was little detectable difference in nesting success in relation to orientation of the opening.

CONCLUSIONS

Attempts to draw general lessons from studies such as ours are frustrated by the enormous variation in many of the described patterns. For instance, responses of nesting success to nest density and nest-site location, as well as temporal patterns of nest failure, vary greatly among stud-

ies. This is not fundamentally surprising, in view of the varied ecological circumstances of the studied populations, but it clearly means that we are a long way from a comprehensive understanding of the determinants of spatial and temporal patterns in nesting biology. Most studies are necessarily case studies at this point, and many more are needed before strong generalizations will emerge. Exceptions to trends are tests of the rule, and the strongest generalizations will account for the exceptions.

It is clear, however, that predation is undoubtedly a critical factor in the evolution of many aspects of nesting biology. Therefore, it is also clear that we need thorough studies of nest predators, not only their identity and searching patterns, but also the distribution of their activities in time and space and variation of their impact across habitats, seasons, and years, with differing levels of availability of alternate prey. Furthermore, the availability of nesting birds as prey varies with their population density and reproductive success, which may be a response to their food availability (Ammon 1994), suggesting that multitrophic-level studies might be appropriate in many cases, as well as records of catastrophic weather events (DeSante and Geupel 1987, Smith et al. 1996). These considerations make it obvious that integrated, long-term comparative studies are probably crucial to achieving comprehension of variation in nesting biology; for this, our limitations are no doubt more financial than intellectual.

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