

PREDATOR RESPONSES TO SIMILARITY AND DISPERSION OF ARTIFICIAL NEST SITES: IMPLICATIONS FOR THE STRUCTURE OF BOREAL FOREST SONGBIRD COMMUNITIES

SHEILA A. RANGEN,^{1,3} ROBERT G. CLARK,^{1,2} AND KEITH A. HOBSON^{1,2}

¹Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, Saskatchewan S7N 5E2, Canada; and

²Canadian Wildlife Service, Prairie and Northern Wildlife Research Centre, 115 Perimeter Road, Saskatoon, Saskatchewan S7N 0X4, Canada

ABSTRACT.—Relatively little is known about the role of predation in shaping patterns of coexistence and nest dispersion of songbird species. It has been hypothesized that predators diversify songbird communities by preying more heavily on individuals and species with greatest similarity in nest-site use. To investigate the importance of predation, we tested how predators responded to assemblages of artificial songbird nests that varied in nest-site placement, vegetation features, and nest dispersion patterns in boreal forest of west-central Alberta, Canada. Variability among nest sites was achieved by deploying wicker nests throughout a gradient of vegetation cover and by deploying nests to simulate two- and three-species assemblages. Two-species assemblages, comprising 20 simulated White-throated Sparrow (*Zonotrichia leucophrys*) and 3 simulated Hermit Thrush (*Catharus guttatus*) nests, and three-species assemblages, comprising 10 simulated White-throated Sparrow, 9 simulated Hermit Thrush, and 4 simulated Chipping Sparrow (*Spizella passerina*) nests, were deployed in eight replicate plots. We hypothesized that predators would be more adept at locating and depredating (1) nests characterized by similar vegetation features in nest patches; (2) nests of similar appearance or nest guild; and (3) clumped versus randomly distributed nests. Contrary to predictions, predation did not increase as variance in vegetation of nest sites decreased across 16 nest-predation plots, nor did variance in vegetation of successful nests increase as predation level increased across 15 nest-predation plots. The addition of one species' nest type to assemblages did not result in lower predation rates. Predators also did not depredate more clumped nests than randomly distributed nests. Overall, predation did not appear to influence patterns of songbird species coexistence or nest dispersion. Abilities of predators to discriminate among less-similar versus more-similar nest sites and nest-dispersion patterns are probably species-specific; that is probably related to the hunting behavior of predators (i.e. use of olfactory and visual cues) and territory size. Received 2 September 1999, accepted 8 August 2000.

A GENERAL GOAL of avian evolutionary ecology is to understand mechanisms driving patterns of community organization (Wiens 1989). Hypotheses advanced to explain the structure of avian communities have focused primarily on interspecific competition and food limitation (Schoener 1974; Martin 1987b, 1991). However, recent research has shown that predation might also be an important factor influencing evolution of forest songbird community structure (Martin 1988a, b, c; Lima and Valone 1991, Forsman et al. 1998), particularly when predation is the primary cause of nesting mortality (Ricklefs 1969). If predators respond to accumulating densities of similar nesting songbird

species as though they were one species, predation may provide a selective pressure for coexisting species to select different nest types and locations, presumably within constraints of stereotypic nest placement that arises from a species' evolutionary history (Martin 1988c, 1993). Such partitioning of nesting sites may yield a more diverse bird community that, in turn, forces predators to search more substrates and height levels, inhibiting the development of predator search images, and decreasing predator searching efficiency (Martin 1988b, 1993, 1996).

An inherent assumption of the predation hypothesis is that predators specialize on nest types. However, the extent to which different predator species hunt for nests of specific songbird species or in locations of specific vegeta-

³ E-mail: sheila.rangen@gov.ab.ca

tion types is unclear. Use of search images that lead to an intensified search for similar nests is generally ascribed to predators that rely on visual cues (Martin 1988b). Thus, if a considerable proportion of the predator community comprises nocturnal mammals, visual cues provided by nest construction, substrate, strata, and vegetation at nest sites may be of limited importance. Rather, olfactory search images may prevail with predators cueing on odors of nest contents, parent birds, and nests (Nams 1997, Pelech 1999). Ultimately, songbird community assemblage patterns may be subject to counteracting selection pressures from different species in the predator community.

Predation pressure may favor coexisting songbirds with different nest types and locations, but also species with nests that are well spaced from neighbors. For that to occur, predators must concentrate their search efforts after cueing on nests, which results in closely spaced nests incurring heavier predation (Tinbergen et al. 1967, Sonerud 1985). Some studies using artificial and natural nests have reported density-dependent predation, whereas others have found no relationship between predation rates and nest density (Zimmerman 1984, Reitsma 1992, Hogstad 1995, Larivière and Messier 1998). Nonetheless, few studies have examined predator responses to nest-dispersion patterns of songbirds (Picman 1988, Major et al. 1994).

We examined predator responses to assemblages of artificial songbird nests that were placed along a gradient of variance in vegetation and that differed in number of coexisting songbird species. We also investigated the influence of clumped and random nest distributions on survival of artificial shrub nests. Because it is difficult to directly test hypotheses that nest predators shape forest songbird community patterns through bird species coexistence and nest dispersion, we evaluated whether predators were more successful at detecting nests when exposed to nest sites of high similarity and to clumped nests. We predicted that (1) as variance in nest-site vegetation increased among nest-predation plots, predation would decrease, and that (2) following predation, variance in nest-site vegetation (of surviving nests only) would be high among nest-predation plots with high predation. Two-species nest assemblages and clumped nests were predicted to suffer higher predation than three-species

assemblages and randomly distributed nests, respectively.

STUDY AREA AND METHODS

Plots were located in the (Boreal) Lower Foothills ecoregion of Alberta, Canada (elevation 1,060 to 1,170 m), approximately 25 km north of Marlboro (53° 31'N, 116° 45'W), and were of postlogging origin (1970 to 1973). Stands were dominated by trembling aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta*). White spruce (*Picea glauca*), balsam fir (*Abies balsamea*), and balsam poplar (*P. balsamifera*) constituted most of the remaining canopy. Understorey was characterized, in decreasing importance, by willow (*Salix* spp.), green alder (*Alnus crispa*), bracted honeysuckle (*Lonicera involucrata*), low-bush cranberry (*Viburnum edule*), *Ribes* spp., and wild rose (*Rosa* spp.).

Potential mammalian predators in the study area included black bears (*Ursus americanus*), red foxes (*Vulpes vulpes*), coyotes (*Canis latrans*), pine martens (*Martes martes*), fishers (*Martes pennati*), least weasels (*Mustela nivalis*), long-tailed weasels (*Mustela frenata*), short-tail weasels (*Mustela erminea*), least chipmunks (*Eutamias minimus*), alpine chipmunks (*Eutamias alpinus*), northern flying squirrels (*Glaucomys sabrinus*), and western jumping mice (*Zapus princeps*), though red squirrels (*Tamiasciurus hudsonicus*), deer mice (*Peromyscus maniculatus*), and red-backed voles (*Clethrionomys gapperi*) were the most common. Potential avian predators included Common Ravens (*Corvus corax*), though Gray Jays (*Perisoreus canadensis*) were more abundant. Key predators, such as red squirrels and Gray Jays, may be at lower abundances than they have been historically, due to the conversion of old growth coniferous forest to young mixed-wood forest by logging.

Response of predators to similarity in nest-site vegetation.—Commercial wicker nests (10 cm outside diameter and 6 cm deep) were dipped in mud, air-dried, and lined with dry grass one week prior to use. Nests were baited with one Japanese Quail (*Coturnix japonica*) and one plasticine egg painted to resemble a quail egg. Quail eggs were washed with tap water prior to use to reduce olfactory cues; that was unnecessary for plasticine eggs because they were made and handled only using rubber gloves.

Six and 10 mixed-wood forest stands were selected in 1995 and 1996, respectively, and in each we established nest plots (100 × 100 m), placed at least 800 m apart. Two stands were used in both 1995 and 1996, but nest plots were separated by a minimum of 150 m between years. In 1995 (17 to 22 June), a total of 150 ground nests was deployed with 25 nests per plot. Twenty ground nests were deployed per plot in 1996 (2 to 4 July), totaling 200 nests. At each plot, nests were randomly assigned to grid coordinates

(10 × 10 m) marked by flagging tape, and subsequently deployed in vegetation that characterized nesting microhabitats of seven ground-nesting songbirds in our study area. Nests were marked 2 m on either side with flagging tape of the same color as grid coordinate markers to help prevent predators from cueing on nest sites. Rims of nest bowls were placed flush with the ground. Rubber gloves and boots were worn during nest deployment and checks (Rudnicki and Hunter 1993). Predation rates on wicker nests were measured by examining loss of eggs from nests every 3 to 5 days during 12 (1995) or 15 days (1996) of exposure to predators. A predation event was recorded if any egg was penetrated or missing, or if a plasticine egg was marked. Incisor widths and bill marks on plasticine eggs were used to identify predators (Bayne and Hobson 1997).

Vegetation characteristics at nest sites were recorded at the end of the experiment. Visual estimates were calibrated among four observers before data collection. Point-quarter sampling was used to obtain tree (>3 m tall) and shrub (>1 m tall) measurements at nest sites (Krebs 1989). The area around each nest was divided into four equal quadrants, and distances to nearest tree and nearest green alder or willow were measured in each of the four quadrants. Tree and shrub density calculations followed Krebs (1989). Plant species and height were identified and measured, respectively, for the nearest tree and shrub in each quadrant (trees ± 0.5 m; shrubs ± 0.1 m). Relative abundance of coniferous versus deciduous trees, individual tree species (e.g. trembling aspen, lodgepole pine), and green alder versus willow were calculated based on frequency of species in the four quadrants. Deciduous and coniferous trees (≤3 m) were counted in a 3 m radius around nests. Percent cover of bare ground and rock, grass or sedge, herbs, lichen, litter, moss, shrubs (≤1 m), water, and woody debris were estimated visually in a 2 m radius surrounding nests. Heights of nest substrates were measured. Horizontal and vertical concealment of nests were estimated visually 1 m from nests in four cardinal directions as well as 1 m above nests. Horizontal estimates were obtained 90 cm above ground. Those estimates were averaged to obtain a single percentage value of each nest obscured by foliage. Tree and shrub closure was measured using a concave spherical densiometer held 110 cm above ground (Lemmon 1956). Subsequent experiments followed the protocols above for nest construction, deployment, monitoring, and concealment unless otherwise stated. Concealment of above ground nests also included an estimate of concealment from 1 m below the nest or from ground level if the distance was <1 m. The densiometer was held at the same height for ground and above-ground nests.

Predator response to two- and three-species assemblages.—Each assemblage of artificial nests contained 23 nests but differed by the ratio of nest types, not nest

number or dispersion. Nest types were chosen to simulate combinations of three common breeding songbird species in our study area, White-throated Sparrows (*Zonotrichia leucophrys*), Hermit Thrushes (*Catharus guttatus*), and Chipping Sparrows (*Spizella passerina*). Nests of those three species were chosen because they permitted ratios of nests within each nest assemblage to fall within the range of ratios of natural densities of those breeding birds recorded on spot-mapping grids in our study area in 1995. Even though ratios of nest types were realistic, densities of artificial nests exceeded those of natural nests. Three-species assemblages consisted of 10 White-throated Sparrow, 9 Hermit Thrush, and 4 Chipping Sparrow nests that were simulated. Two-species assemblages comprised 20 simulated White-throated Sparrow and 3 simulated Hermit Thrush nests.

Wicker and natural nests were used to simulate nest types. Wicker nests (9.5 cm outside diameter by 3.8 cm deep) were lined with dry grass and deer hair (*Odocoileus* spp.) to simulate White-throated Sparrow nests. Wicker nests were lined with dry grass and feather moss (*Pleurozium schreberi*, *Ptilium crista-castrensis*) to simulate Hermit Thrush nests. Nest linings used were representative of White-throated Sparrow and Hermit Thrush nests found on our study area. Natural nests (collected 1995 to 1997) were used to simulate Chipping Sparrow nests, to maximize concealment of above-ground nests. Similar to natural Chipping Sparrow nests, all natural nests of bird species used were open cups constructed of grass with an ungulate hair lining (i.e. 4 Chipping Sparrow, 5 Clay-colored Sparrow [*Spizella pallida*], 12 Dark-eyed Junco [*Junco hyemalis*], 2 Lincoln's Sparrow [*Melospiza lincolni*], 1 Tennessee Warbler [*Vermivora peregrina*], 6 White-throated Sparrow, 2 Yellow Warbler [*Dendroica petechia*] nests).

Nests of each songbird species were deployed in nest substrates identified at natural nests of the respective species on our study area. White-throated Sparrow nests were deployed on the ground under low shrubs including low-bush cranberry, black currant (*Ribes lacustre*), and Labrador tea (*Ledum groenlandicum*) that averaged 0.44 ± 0.20 SE m tall ($n = 16$ nest-predation plots). Hermit Thrush nests were deployed at the base of white spruce and balsam fir seedlings (0.70 ± 0.10 m tall, $n = 16$ plots). Chipping Sparrow nests were deployed above-ground (0.63 ± 0.70 m, $n = 8$ plots) in conifers averaging 2.27 ± 0.20 m tall ($n = 8$ plots). Within paired plots (described below), for both experimental assemblages, the same shrub species were used as nest substrates. Shrub species, however, changed from stand to stand due to local changes in vegetation.

Eight mixed-wood forest stands were selected in which to establish paired plots (2 ha) in turn separated by 100 m. Plots in separate stands were at least 800 m apart. Nest distributions were allocated randomly to one of the paired plots. Twenty-three nests

were deployed per plot, totaling 184 nests per treatment. Nests were deployed (7 to 14 June 1997) at random coordinates in each plot, using numbered cells in a 25×25 m grid. Predation rates on nests were measured by examining loss of eggs from nests every 5 days during 15 days of exposure to predators. Nest concealment, species, and height of nest substrates were recorded. Distance (meters) to nearest-neighbor ground nests or nest trees (for above-ground nests) was recorded.

Predator response to clumped versus random distributions of shrub nests.—Five mixed-wood forest stands were selected in which to establish paired plots (1 ha). One plot of each pair was assigned randomly to a random or clumped nest distribution. Twenty nests were deployed per plot (17 to 20 July 1996). Randomly distributed nests were deployed at random coordinates, using numbered cells in a 10×10 m grid. Four groups of five clumped nests each were deployed in each plot with one group at each corner grid cell. Nests were placed in a shrub closest to the allocated grid location, which was usually within 2 m. Nests for both distributions were randomly, but equally, allocated to a 0.5 m height class (range 0.5 to 2 m). Predation rates on shrub nests were measured by examining loss of eggs from nests every 5 days during 10 days of exposure to predators. Nest concealment and distance (meters) to nearest-neighbor nests were measured (using the base of nest substrates because some nests were above-ground).

Statistical analyses.—To examine response of predators to similarity in nest-site vegetation, we first used reciprocal averaging (RA) ordination to collapse original measurements of vegetation structure and composition at 344 nests into single axes (Pielou 1984). Prior to the analysis, variables with zeros in >50% of the data set were deleted to prevent uncommon variables from disproportionately influencing the analysis (i.e. bare ground or rock, water). Remaining variables (i.e. coniferous trees >3 m tall, tree and shrub closure, deciduous trees >3 m tall, grass or sedge, green alder, herbs, lichen, litter, lodgepole pine, moss, number of conifer trees ≤ 3 m tall, number of deciduous trees ≤ 3 m tall, shrub density, shrub height, tree density, tree height, trembling aspen, willow, and woody debris) were log, arcsine, or square-root transformed to improve normality. The interpretation of RA axes was based on the relative sizes of correlations between axes and originally measured variables. Variances in nest-site vegetation for each nest predation plot were calculated using RAI and RAII scores for the 20 to 25 nests per plot. RAI and RAII were chosen to represent variance in vegetation among plots in regressions (see below) because they accounted for the majority of variation in nest-site vegetation within plots. However, because those axes characterized tree and shrub species composition rather than microhabitat features surrounding nests, which are presumably important in

predator search images, RA analyses were also conducted using only ground vegetation variables.

To evaluate our prediction that predation was directly related to similarity in nest-site vegetation before selective predation occurred, linear regressions of variance in RAI and RAII vegetation scores for all nest sites versus daily nest mortality rate (Johnson 1979) were conducted using 16 nest-predation plots visited 1995 to 1996. To test the prediction that there was a negative relationship between predation and similarity in nest-site vegetation following selection by predators, linear regressions of variance in RAI and RAII vegetation scores of successful nest sites versus daily nest mortality rate were conducted using 15 nest-predation plots. One plot was deleted because all nests failed. Residuals were examined for nonlinear relationships. Nest-predation plots were pooled across years because similar results were found within years and predictions were best tested with a wide range of nest mortality and variance in nest-site vegetation.

Interpretations based on two forest stands in both 1995 and 1996 should have been conservative because plots between years were spatially separated within the same stand and new random nest locations were allocated each year. Moreover, nests between years were likely deployed in territories of different individual red squirrels and mice, due to spatial independence but also high turnover of those species (Banfield 1974, Rusch and Reeder 1978). However, to ensure that pseudoreplication did not influence analyses, linear regressions were conducted with and without 1996 plots located in forest stands also containing 1995 plots. R^2 -values and P -values were similar for both regressions; thus, results only including all 16 nest-predation plots were shown. Due to inconsistencies in patterns obtained for predator responses to two- versus three-species assemblages when nests visited by mice were treated as nonsurviving or were excluded from analyses (see below), the above regressions were also conducted excluding nests depredated by mice. Similarly, results were given for all nest-predation plots.

To examine predator responses to two- versus three-species assemblages, nest fate and number of days nests survived (Johnson 1979) were used as response variables in a two-way analysis of covariance (ANCOVA), with species assemblage (i.e. two, three), and nest type (i.e. White-throated Sparrow, Hermit Thrush, Chipping Sparrow) as main effects, and concealment and nearest-neighbor distance as covariates. Nest-predation plots were used as sampling units; thus, plot means for each nest type within each species assemblage ($n = 40$) were used in ANCOVA. Results for nest fate and number of surviving days were similar except for concealment; therefore, surviving days were reported only, and both response variables were reported for concealment. Home ranges of mice may be only one-fifth to one-tenth the

size of our plots (Williams 1955, McCann 1976), precluding mouse exposure to a sufficient number of artificial nests, and subsequent development or use of search images. Hence, mice may not have had the opportunity to specialize in their choice of nests, an assumption necessary for predation pressure to result in partitioning of nest sites (Tinbergen 1960, Ricklefs 1989). Furthermore, some bird species may be able to defend their nests against mice (Verbeek 1970). Therefore, two additional ANCOVA were conducted, using nest fate and number of days nests survived as response variables, where nests visited by mice were excluded. Trends in rates of predation using number of days surviving were similar to those where all predators were examined; therefore, only predator responses to species assemblages using fate were shown. Fisher's exact test was used to determine the response of different predator groups to both species assemblages.

To examine predator responses to clumped nest distributions, nest fate and number of days nests survived were used as response variables in a one-way ANCOVA, with nest distribution as a main effect and concealment as a covariate. Nest-predation plots were used as sampling units. Because clumped nests were equally spaced, effects of nearest-neighbor distances on plot means of fate and number of days nests survived were examined only for random nests using simple regression. Because results for nest fate and number of surviving days were the same, only those for surviving days were reported. Responses of specific predator groups to nest distributions were examined using Fisher's exact test. Statistical tests followed Zar (1984) and were executed on SAS Institute (1990) with a significance level of 0.05.

RESULTS

Response of predators to similarity in nest-site vegetation.—Axis 1 (RAI) accounted for 44% of total variance in vegetation data and represented a gradient in tree species composition ranging from deciduous (primarily trembling aspen) to coniferous (primarily lodgepole pine) trees. Lodgepole pine and coniferous trees (>3 m tall) were positively correlated and trembling aspen, deciduous trees (>3 m tall), tree and shrub closure, and green alder were negatively correlated with RAI. Axis 2 (RAII) accounted for an additional 20% in total variance, expressing a shift in shrub species composition from willow to green alder. Only shrub species were strongly associated with RAI. Additional axes were not retained as they each accounted for $\leq 7\%$ of total variation, though 36% collectively. Plots with high variance in RAI scores

contained individual nest sites represented by pine, mixed-wood, or trembling aspen. Some plots with low variance contained individual nest sites that were dominated either by pine or mixed-wood, whereas other plots had individual nest sites that were dominated by either trembling aspen or mixed-wood. Plots with high variance in RAI scores had nest sites with green alder, willow, or a mixture of these two species. Low-variance plots had nest sites dominated by willow or green alder, both of which were accompanied by a few patches of both shrub species. Using ground cover only, axis 1 (RAIG) constituted 27% of total variance and expressed a gradient in ground vegetation from lichen to grass. Plots with high variance in RAIG scores contained individual nest sites with lichen, grass, or both. Some plots with low variance contained individual nest sites with lichen or lichen and grass, whereas nests in other plots were dominated by grass or grass and lichen.

Before predation occurred, there was no relationship between nest-site similarity across plots, based on RAI, RAII, and RAIG scores, and nest mortality, respectively (RAI: all predators, $r^2 = 0.05$, $P = 0.41$, $n = 16$; nests depredated by mice were excluded, $r^2 = 0.004$, $P = 0.81$, $n = 16$; RAI: all predators, $r^2 = 0.02$, $P = 0.59$, $n = 16$; nests depredated by mice were excluded, $r^2 = 0.01$, $P = 0.70$, $n = 16$; Fig. 1; RAIG: all predators, $r^2 = 0.07$, $P = 0.32$, $n = 16$; nests depredated by mice were excluded, $r^2 = 0.03$, $P = 0.53$, $n = 16$) nor was there after predation occurred, whether nests depredated by mice were excluded or not (RAI: all predators, $r^2 = 0.04$, $P = 0.47$, $n = 15$; nests depredated by mice were excluded, $r^2 = 0.005$, $P = 0.81$, $n = 15$; RAI: all predators, $r^2 = 0.02$, $P = 0.65$, $n = 15$; nests depredated by mice were excluded, $r^2 = 0.003$, $P = 0.85$, $n = 15$; RAIG: all predators, $r^2 = 0.12$, $P = 0.20$, $n = 15$; nests depredated by mice were excluded, $r^2 = 0.002$, $P = 0.89$, $n = 15$).

Predator response to two- and three-species assemblages.—Of the total nests ($n = 368$), 29% ($n = 107$) were considered depredated on the basis of evidence from quail and plasticine eggs. Within the two-species assemblage, 67% ($n = 123$) of nests survived, whereas mice were responsible for the majority of predation events (mice, 14%; unknown predators, 10%; small mammals, 4%; squirrels, 3%; large mammals,

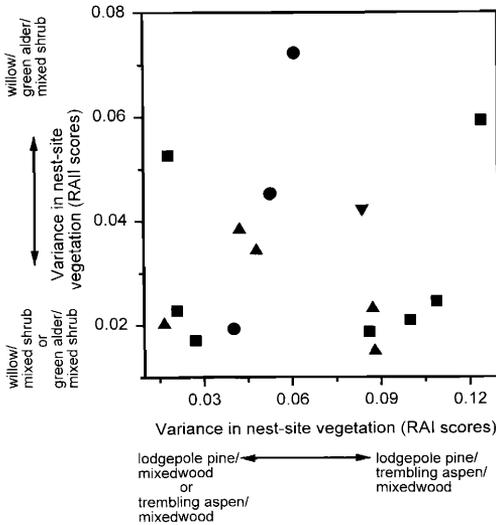


FIG. 1. Distribution of 16 artificial nest-predation plots along gradients of variance in nest-site vegetation; plots categorized by 0–25% (●), 26–50% (■), 51–75% (▲), and 76–100% (▼) nest mortality. Nests were deployed in boreal mixed-wood forest stands in west-central Alberta, Canada (June 1995, July 1996).

2%). Within the three-species assemblage, 75% ($n = 138$) of nests survived and unknown predators attacked most nests (unknown predators, 11%; mice, 10%; squirrels, 3%; large mammals, 0.5%; birds, 0.5%). Small mammals included mice and squirrels that could not be distinguished by incisor widths, and large mammals included predators larger than squirrels. Different types of predators did not destroy one species assemblage any more than another, nor did one predator group destroy more nests of one species assemblage compared to another predator group (Fisher's exact test; $P = 0.06$). Using surviving days, all predators combined did not discriminate between species assemblages ($F = 0.5$, $df = 1$ and 34 , $P = 0.49$; Table 1) and responded similarly to the three nest types ($F = 0.7$, $df = 2$ and 34 , $P = 0.50$). Nearest-neighbor effects were not evident ($F = 0.3$, $df = 1$ and 34 , $P = 0.61$). When surviving days were used, we discovered successful nests were better concealed than failed nests ($F = 4.7$, $df = 1$ and 34 , $P = 0.04$) but that relationship was not detected using nest fate ($F = 2.4$, $df = 1$ and 34 , $P = 0.13$). When nests depredated by mice were excluded from the analysis and fate was used as a dependent variable, the remaining predators appeared to be more adept at de-

TABLE 1. Number of days nests survived (mean \pm SE) or fate (mean \pm SE) in parentheses for species assemblage and nest type, nearest-neighbor distances and concealment for successful and failed nests, combining all predators and treating nests visited by mice as surviving, in boreal mixed-wood forest in west-central Alberta, Canada (June 1997).

Species assemblage ^a	Nest type ^a				Nearest-neighbor distance (m) ^b		Concealment (%) ^b	
	Two	Three	White-throated Sparrow	Chipping Sparrow	Successful	Failed	Successful	Failed
12.1 \pm 0.7 (1.5 \pm 0.1)	12.7 \pm 0.5 (1.6 \pm 0.1)	11.5 \pm 0.7 (1.5 \pm 0.1)	12.9 \pm 0.7 (1.5 \pm 0.1)	12.7 \pm 1.0 (1.5 \pm 0.1)	26.8 \pm 0.8	25.1 \pm 0.7	87.4 \pm 1.3	82.2 \pm 2.1
12.3 \pm 0.7 (1.5 \pm 0.1)	13.1 \pm 0.5 (1.7 \pm 0.1)	12.2 \pm 0.7 (1.7 \pm 0.1)	13.4 \pm 0.7 (1.7 \pm 0.1)	12.6 \pm 0.9 (1.5 \pm 0.1)	26.6 \pm 0.8	25.1 \pm 0.9	87.3 \pm 1.3	79.8 \pm 2.1

^a Least square means are reported.
^b Unadjusted means are reported.

TABLE 2. Number (percentage) of nests in random distributions and clumped distributions that survived and were visited by predators in boreal mixed-wood forest stands ($n = 5$) in west-central Alberta, Canada (July 1997).

Nest distribution	Survivors	Mice	Squirrels	Small mammals	Large mammals	Birds	Unknown predators
Random	47 (47)	2 (2)	8 (8)	7 (7)	0 (0)	9 (9)	26 (26)
Clumped	51 (52)	2 (4)	5 (11)	8 (17)	1 (2)	9 (19)	22 (47)

* Fisher's exact test for predator groups only; $P = 0.93$.

stroying nests of the two-species assemblage ($F = 5.1$, $df = 1$ and 34 , $P = 0.03$; Table 1) but nest losses of the three songbird species did not differ ($F = 1.7$, $df = 2$ and 34 , $P = 0.20$). Nests that were closer together were not more susceptible to predators ($F = 4.9$, $df = 1$ and 34 , $P = 0.06$), though poorly concealed nests were ($F = 11.3$, $df = 1$ and 34 , $P = 0.002$).

Predator response to clumped versus random distributions of shrub nests.—Fifty percent of nests was depredated (99 of 197; three were of unknown fate). About one-half of depredated nests could not be ascribed to specific predators ($n = 48$). Of the remaining nests, birds destroyed most (35%), followed by small mammals (29%), squirrels (26%), mice (8%), and large mammals (2%). Predators did not depredate more clumped versus random nests by the end of the experiment (random nests, surviving days = 7.2 ± 0.7 SE; clumped nests, surviving days = 7.4 ± 0.7 ; $F = 0.03$, $df = 1$ and 7 , $P = 0.86$). Concealment of nests was similar for successful ($54.6 \pm 2.3\%$, $n = 9$) and failed nests ($44.8 \pm 2.5\%$; $F = 3.15$, $df = 1$ and 7 , $P = 0.12$, $n = 10$). Distances to nearest-neighbor nests of the random distribution were 15.5 ± 1.2 m for surviving nests and 12.8 ± 0.8 m for failed nests; those for the clumped distribution were 7.1 ± 0 m for surviving nests and 10.0 ± 2.9 m for failed nests. Loss of random nests to predators was not related to the proximity of nearest-neighbor nests ($r^2 = 0.20$, $P = 0.44$, $n = 5$). Avian and mammalian predators did not prey on a greater number of nests of any one nest distribution, nor were there differences among predator groups in their predation of random and clumped nests (Table 2).

DISCUSSION

Predator response to nest-site similarity.—There was little support for the hypothesis that predators mediate the coexistence of nesting song-

birds, but whether or not similar communities were more susceptible to predation appeared to be closely linked with the composition and abundance of the predator community. Evidence consistent with that hypothesis was strongest when squirrels and birds depredated more two-species assemblages, but the entire predator community did not differentially destroy two- and three-species assemblages when mice were included in the analysis. Our result that predators other than mice might favor partitioning of nesting microhabitat supported the idea that search images based on nest appearance or nest height were probably less important to mice that rely primarily on olfaction for food detection and forage on the ground (Howard et al. 1968, Anderson 1986). Similar to our arguments regarding mice, Schmidt and Whelan (1999) contended that territories of squirrels are too small for individuals to detect and respond to the full range of heterogeneity in nest abundance and placement, but those of corvids are large enough to respond to patterns of nest heterogeneity. However, there were an estimated six artificial nests per squirrel territory with our high nest densities, though we had insufficient data to test squirrels and corvids separately. Pelech (1999) found red squirrels did not use visual search images to locate artificial nests and suggested that squirrels rely on olfactory cues. Mice are more adept at locating ground nests, squirrels tend to destroy similar numbers of ground and above-ground nests, and birds depredate relatively high numbers of above-ground nests (Rangen et al. 1999). Assuming this, and that predator communities were similar between experimental assemblages, additional predation pressure from avian predators on the three-species assemblage may have counteracted any predisposition of more-similar nest sites of the two-species assemblage to be depredated, leading

to similar predation rates of the two-nest assemblages. Support for that explanation was inconsistent, however, with squirrels and Gray Jays destroying more nests of the two-species assemblage when fate was used as the response variable but not when number of surviving days were used. In contrast, studies suggesting that predators can diversify songbird communities either had both ground and above-ground nests destroyed by the same predator species or nest predators were not identified (Martin 1987a, Marini 1997). Alternatively, if predators of forest songbird nests have evolved as generalists to survive in a highly variable and seasonal environment, it may also be difficult to detect patterns of songbird species coexistence induced by predation, particularly if nest losses are opportunistic and nest contents represent only a small proportion of dietary items (Rusch and Reeder 1978, Blancher and Robertson 1985, Strickland and Ouellet 1993, Andr en 1995). That may be especially true of boreal forest communities that can encompass a considerable range in spatial and temporal variability in stand structure and composition.

Differences between our experimental design and that of comparable studies may have led to contrasting results (Martin 1987a, Marini 1997), but again such distinctions in design can be linked to variation in the predator community. Consequently, differences in predator communities among studies could be a contributing factor to inconsistencies in observed patterns, or common predators among studies may have responded differentially under varying experimental conditions. The most abundant mammalian and avian predators in Martin's (1998b) study were red squirrels, least chipmunks, golden mantled ground squirrels (*Citellus lateralis*), deer mice, and Stellar's Jays (*Cyanocitta stelleri*), though larger mammals and snakes were also present. Marini (1997) reported corvids, blackbirds, Tufted Titmouse (*Baeolophus bicolor*), snakes, eastern chipmunks (*Tamias striatus*), gray squirrels (*Sciurus carolinensis*), and larger mammals (e.g. raccoon [*Procyon lotor*], long-tailed weasel) as potential predators. In those studies, trends showing that predators were able to destroy more songbird nests if they had similar nest placements were consistent whether artificial or natural nests were used (Martin 1988b, Marini 1997), a pattern that was only apparent in our study

when nests visited by mice were excluded from analyses. Lower predation on the three-species nest assemblage, under those circumstances, may be related to natural nests used for Chipping Sparrows being less conspicuous to squirrels and jays than wicker nests used in the two-species assemblage (but see Martin 1987a). However, because a similar proportion of Chipping Sparrow versus White-throated Sparrow and Hermit Thrush nests was destroyed, that explanation appears weak. Besides nest type, our study was unique in the use of plasticine and quail eggs, because similar experimental designs used quail eggs only (Martin 1988b, Marini 1997). Because mice can be attracted to plasticine eggs and mice tend to visit more ground nests than above-ground nests (Rangen et al. 1999, 2000), the higher proportion of ground nests in the two-species assemblage may have elevated nest losses, masking an assemblage effect. Moreover, previous experimenters excluded potential effects by mice as members of the predator community by only using quail eggs that are too large to be broken by mice (Haskell 1995, Rangen et al. 2000; but see Blight et al. 1999). Lastly, variation in nest types and nesting guilds may not have been high enough for predators to discriminate between experimental nest assemblages; thus, a greater range in diversity of nest types or nest guilds might have generated predator responses consistent with our hypothesis, as did other investigations that compared different species assemblages (Martin 1988b, Marini 1997).

We have emphasized the importance of understanding the structure of predator communities and behavior of predator species, yet choice of boreal habitats in which to test the predation hypothesis may also be critical. Boreal forest encompasses an array of structural and floristic complexity at both the stand and landscape level (Hobson and Schieck 1999), whereas our experiments were restricted to relatively homogeneous mixed-wood stands, preventing generalizations across cover types and seral stages. In structurally simple habitats, predation may initially act to decrease similarity within nesting guilds, but as predation intensifies and the limited number of nest niches in which species can expand are exhausted, coexisting species may be forced to nest in similar locations, increasing similarity of nesting guilds (Menge and Sutherland 1976, Sih et al.

1985). Thus, if predators had already forced songbird species to deplete finite nesting options in those stands over evolutionary time, predators may have responded to our experiment as though nest assemblages were very similar. Lack of a predation effect also may not be surprising because nests were located in homogeneous forest stands with relatively little variation in nest-site vegetation, only 36–73% of variation in vegetation was actually unaccounted for, and statistical power was probably low (8–16 plots). Both predator community composition and boreal forest heterogeneity are related to spatial scale, which can further lead to contradictory results regarding the influence of predators on species coexistence (Marini 1997).

Predator response to clumped versus random distributions of shrub nests.—Although it has been hypothesized that spacing of nests through territoriality may be an antipredator strategy, we found no evidence that predators depredated more clumped nests versus randomly distributed songbird nests. Predator responses to variation in nest-spacing patterns may be obscured by the composition of the predator community, as various studies have reported marsupials, raccoons, mustelids, canids, felids, squirrels, rats, gulls, corvids, and Eastern Meadowlarks (*Sturnella magna*) as predators or potential predators (Picman 1988, Major et al. 1994, Hogstad 1995). Selection pressures placed on nesting songbirds vary with type of predator, particularly avian predators and ground-dwelling mammals, thereby preventing stereotyped antipredator strategies (i.e. nonclumped nests) from evolving in breeding birds or creating songbird nesting patterns that simply are not detectable at the community level. Alternatively, Gray Jays may have viewed both nest distributions as clumped, because of small plot sizes. High nest densities may have been influential in masking songbird nest dispersion patterns if as many random nests as clumped nests were placed within territories of mice and squirrels; besides, red squirrels tend to find most artificial nests in their territories (Pelech 1999). It is still possible, however, that predators influence songbird nesting patterns by forcing songbirds to select uniform distributions of nests because, in other studies, clumped artificial nests tended to suffer higher rates of predation than regularly dispersed

nests (Picman 1988, Major et al. 1994), though most songbirds tend to nest in semiclumped or semirandom patterns (Rothstein 1971, Mönkönen et al. 1997). Overall, our findings suggest that nesting near neighbors may not be a disadvantage nor beneficial to songbirds breeding in early successional stages of mixed-wood boreal forest. Yet, songbirds that have relatively weak defense mechanisms against predators may benefit from vigilance and alarm calls from con- and heterospecifics (Sealy 1994, Hogstad 1995, Forsman et al. 1998). Some polygynous species can also maximize reproductive success in clumped territories (Herremans 1993).

Summary.—Contrary to predictions, artificial songbird nests deployed to simulate low similarity of breeding birds did not survive better than those mimicking high similarity. In the first experiment, predation of artificial nests did not increase as variance in vegetation at nest sites decreased across nest-predation plots. Likewise, as predation increased across plots, variance among plots in nest-site vegetation of surviving nests did not increase. In the second experiment, predators did not respond differently to two-species versus three-species assemblages, except when nests destroyed by mice were excluded. Those results suggest that predation was not a strong selective force in the partitioning of nest space, leading to coexistence of additional dissimilar species, and subsequently more diverse songbird communities. Although over-dispersion of nests is expected to be the best strategy for songbirds with weak mechanisms of nest defense, predators did not exert more intense selection on clumped nests versus randomly distributed nests. Hence, other biological, physical, and historical factors likely play more important roles in structuring songbird communities relative to predation, synergism among factors may swamp predator effects, or different predator species exert opposing forces of selection on nest-site partitioning, masking patterns at the community level.

More experimentation is required to elucidate and fully understand the role that predation plays in structuring songbird communities. Natural assemblages of songbirds could be evaluated where predator abundance is manipulated across several boreal forest seral stages, thereby controlling for the structure of the predator community as well as forest complex-

ity associated with stand age. Alternatively, point counts could be conducted in a large number of habitat types to capture wide-ranging variation in songbird and predator diversity. Controlling for vegetation, the predicted positive response of songbird diversity to predator diversity could be investigated. Lastly, work that examines the structure of predator communities and predator behavior as it relates to nest predation is needed (Bayne and Hobson 1998, Pelech 1999). In particular, the importance of mice as nest predators and the abilities of parent birds to defend nests against mice are not well known.

ACKNOWLEDGMENTS

We are grateful to field assistants M. F. Ambard, C. Gregoire, S. W. Leach, V. Lester, J. Peters, J. R. Stade, M. Worland, and K. F. Wudkevich. The exceptional dedication of B. D. Login, H. A. Rangen, and K. Stroebel deserves special mention. This study was supported by the Foothills Model Forest, Alberta; a Natural Sciences and Engineering Research Council of Canada research grant and doctoral scholarship to R.G.C. and S.A.R., respectively; a University of Saskatchewan graduate scholarship to S.A.R.; Canadian Circumpolar Institute of the University of Alberta; Canadian Wildlife Service (Prairie and Northern Wildlife Research Center); Alberta Fish and Wildlife (Edson Region); Weldwood of Canada (Hinton Division); and a Cooper Ornithological Society research grant to S.A.R.

LITERATURE CITED

- ANDERSON, P. K. 1986. Foraging range in mice and voles: The role of risk. *Canadian Journal of Zoology* 64:2645-2653.
- ANDRÉN, H. 1995. Effects of landscape composition on predation rates at habitat edges. Pages 225-255 in *Mosaic Landscapes and Ecological Processes* (L. Hansson, L. Fahrig, and G. Merriam, Eds.). Chapman and Hall, London.
- BANFIELD, A. W. F. 1974. *The Mammals of Canada*. University of Toronto Press, Toronto, Ontario.
- BAYNE, E. M., AND HOBSON, K. A. 1997. Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. *Conservation Biology* 11:1418-1429.
- BAYNE, E. M., AND K. A. HOBSON. 1998. The effect of habitat fragmentation by forestry and agriculture on the abundance of small mammals in the southern boreal mixed-wood forest. *Canadian Journal of Zoology* 76:62-69.
- BLANCHER, P. J., AND R. J. ROBERTSON. 1985. Predation in relation to spacing of kingbird nests. *Auk* 102:654-658.
- BLIGHT, L. K., J. L. RYDER, AND D. F. BERTRAM. 1999. Predation on Rhinoceros Auklet eggs by a native population of *Peromyscus*. *Condor* 101:871-876.
- FORSMAN, J. T., M. MÖNKKÖNEN, J. INKERÖINEN, AND P. REUNANEN. 1998. Aggregate dispersion of birds after encountering a predator: Experimental evidence. *Journal of Avian Biology* 29:44-48.
- HASKELL, D. G. 1995. Forest fragmentation and nest predation: Are experiments with Japanese Quail eggs misleading? *Auk* 112:767-770.
- HERREMANS, M. 1993. Clustering of territories in the Wood Warbler *Phylloscopus sibilatrix*. *Bird Study* 40:12-23.
- HOBSON, K. A., AND J. SCHIECK. 1999. Changes in bird communities in boreal mixed-wood forest: Harvest and wildfire effects over 30 years. *Ecological Applications* 9:849-863.
- HOGSTAD, O. 1995. Do avian and mammalian nest predators select for different nest dispersion patterns of Fieldfares *Turdus pilaris*? A 15-year study. *Ibis* 137:484-489.
- HOWARD, W. E., R. E. MARSH, AND R. E. COLE. 1968. Food detection by deer mice using olfactory rather than visual cues. *Animal Behaviour* 16:13-17.
- JOHNSON, D. H. 1979. Estimating nest success: The Mayfield method and an alternative. *Auk* 96:651-661.
- KREBS, C. J. 1989. *Ecological Methodology*. Harper and Row, New York.
- LARIVIÈRE, S., AND F. MESSIER. 1998. Effect of density and nearest neighbours on simulated waterfowl nests: Can predators recognize high-density nesting patches? *Oikos* 83:12-20.
- LEMMON, P. E. 1956. A spherical densiometer for estimation of forest overstorey density. *Forest Science* 2:314-320.
- LIMA, S. L., AND T. J. VALONE. 1991. Predators and avian community organization: An experiment in a semi-desert grassland. *Oecologia* 86:105-112.
- MAJOR, R. E., G. H. PYKE, M. T. CHRISTY, G. GOWING, AND R. S. HILL. 1994. Can nest predation explain the timing of the breeding season and the pattern of nest dispersion of New Holland Honeyeaters? *Oikos* 69:364-372.
- MARINI, M. Â. 1997. Predation-mediated bird nest diversity: An experimental test. *Canadian Journal of Zoology* 75:317-323.
- MARTIN, T. E. 1987a. Artificial nest experiments: Effects of nest appearance and type of predator. *Condor* 89:925-928.
- MARTIN, T. E. 1987b. Food as a limit on breeding birds: A life-history perspective. *Annual Review of Ecology and Systematics* 18:453-487.
- MARTIN, T. E. 1988a. Habitat and area effects on forest bird assemblages: Is nest predation an influence? *Ecology* 69:74-84.
- MARTIN, T. E. 1988b. On the advantage of being different: Nest predation and the coexistence of

- birds species. Proceedings of the National Academy of Sciences USA 85:2196–2199.
- MARTIN, T. E. 1988c. Processes organizing open-nesting bird assemblages: Competition or nest predation? *Evolutionary Ecology* 2:37–50.
- MARTIN, T. E. 1991. Food limitation in breeding birds: Is that all there is? Pages 1595–1602 in *Acta XX Congressus Internationalis Ornithologici* (B. D. Bell, Ed.). New Zealand Ornithological Congress Trust Board, Wellington.
- MARTIN, T. E. 1993. Nest predation, nest sites, and birds: New perspectives on old patterns. *BioScience* 43:523–532.
- MARTIN, T. E. 1996. Fitness costs of resource overlap among coexisting bird species. *Nature* 380:338–340.
- MCCANN, S. A. 1976. Home ranges of the meadow vole and deer mouse (on a reclamation test pit in eastern Montana). Proceedings of the Montana Academy of Sciences 36:11–17.
- MENGE, B. A., AND J. P. SUTHERLAND. 1976. Species diversity gradients: Synthesis of the roles of predation, competition, and temporal heterogeneity. *American Naturalist* 10:351–369.
- MÖNKKÖNEN, M., P. HELLE, G. J. NIEMI, AND K. MONTGOMERY. 1997. Heterospecific attraction affects community structure and migrant abundances in northern breeding bird communities. *Canadian Journal of Zoology* 75:2077–2083.
- NAMS, V. O. 1997. Density-dependent predation by skunks using olfactory search images. *Oecologia* 110:440–448.
- PELECH, S. 1999. Habitat use and nest searching success of red squirrels at a forest edge. M.S. thesis, University of British Columbia, Vancouver.
- PICMAN, J. 1988. Experimental study of ground-nesting birds: Effects of habitat and nest distribution. *Condor* 90:124–131.
- PIELOU, E. C. 1984. *Interpretation of Ecological Data. A Primer on Classification and Ordination*. Wiley-Interscience, New York.
- RANGEN, S. A., R. G. CLARK, AND K. A. HOBSON. 1999. Influence of nest site vegetation and predator community on the success of artificial songbird nests. *Canadian Journal of Zoology* 77:1676–1681.
- RANGEN, S. A., R. G. CLARK, AND K. A. HOBSON. 2000. Visual and olfactory attributes of artificial songbird nests. *Auk* 117:136–146.
- REITSMA, L. 1992. Is nest predation density dependent? A test using artificial nests. *Canadian Journal of Zoology* 70:2498–2500.
- RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* 9:1–48.
- RICKLEFS, R. E. 1989. Nest predation and the species diversity of birds. *Trends in Ecological Evolution* 4:184–186.
- ROTHSTEIN, S. I. 1971. High nest density and non-random nest placement in the Cedar Waxwing. *Condor* 73:483–485.
- RUDNICKY, T. C., AND M. L. HUNTER. 1993. Avian nest predation in clearcuts, forest, and edges in a forest-dominated landscape. *Journal of Wildlife Management* 57:358–364.
- RUSCH, D. A., AND W. G. REEDER. 1978. Population ecology of Alberta red squirrels. *Ecology* 59:400–420.
- SAS INSTITUTE, INC. 1990. *SAS/STAT User's Guide*, version 6, 4th ed. SAS Institute Inc., Cary, North Carolina.
- SEALY, S. G. 1994. Observed acts of eggs destruction, egg removal, and predation on nest of passerine birds at Delta Marsh, Manitoba. *Canadian Field-Naturalist* 108:41–51.
- SCHMIDT, K. A., AND C. J. WHELAN. 1999. Nest predation on woodland songbirds: When is nest predation density dependent? *Oikos* 87:65–74.
- SCHOENER, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27–39.
- SIH, A., P. CROWLEY, M. MCPEEK, J. PETRANKA, AND K. STROHEMEIER. 1985. Predation, competition, and prey communities: A review of field experiments. *Annual Review of Ecology and Systematics* 16:269–311.
- SONERUD, G. A. 1985. Nest hole shift in Tengmalm's Owl as defence against nest predation involving long-term memory in the predator. *Journal of Animal Ecology* 54:179–192.
- STRICKLAND, D., AND H. OUELLET. 1993. Gray Jay (*Perisoreus canadensis*). In *The Birds of North America*, no. 40. (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- TINBERGEN, L. 1960. The natural control of insects in pinewoods. I. Factors influencing the intensity of predation by songbirds. *Archives Néerlandaises de Zoologie* 13:265–343.
- TINBERGEN, N., N. IMPEKOVERN, AND D. FRANCK. 1967. An experiment of spacing out as a defence against predation. *Behavior* 28:307–321.
- VERBEEK, N. A. M. 1970. Breeding ecology of the Water Pipit. *Auk* 87:425–451.
- WIENS, J. A. 1989. *The Ecology of Bird Communities*, vol. 2. Processes and Variations. Cambridge University Press, Cambridge, United Kingdom.
- WILLIAMS, O. 1955. Home range of *Peromyscus maniculatus rufinus* in a Colorado ponderosa pine community. *Journal of Mammalogy* 36:42–45.
- ZAR, J. H. 1984. *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, New Jersey.
- ZIMMERMAN, J. L. 1984. Nest predation and its relationship to habitat and nest density in Dickcissels. *Condor* 86:68–72.