NEST-SITE CHARACTERISTICS AND NEST PREDATION IN HARRIS' SPARROWS AND WHITE-CROWNED SPARROWS IN THE NORTHWEST TERRITORIES, CANADA

CHRISTOPHER J. NORMENT[1]

Museum of Natural History and Department of Systematics and Ecology,
University of Kansas, Lawrence, Kansas 66045, USA

ABSTRACT.—I examined the relationship of nest-site and nest-patch characteristics to nest success in ground-nesting Harris' Sparrows (*Zonotrichia querula*) and Gambel's White-crowned Sparrows (*Z. leucophrys gambelii*) in the forest-tundra ecotone of the Northwest Territories, Canada. I found 34% of all Harris' Sparrow nests depredated, primarily by arctic ground squirrels (*Spermophilus parryii*), while no White-crowned Sparrow nests were disturbed by predators. White-crowned Sparrow nests appeared to be less susceptible to predation than Harris' Sparrow nests because the former were placed in areas with more shrubs and ground cover, and denser vegetation, than were Harris' Sparrow nests. Comparison of successful and depredated Harris' Sparrow nests supported the idea that interspecific differences in rates of nest predation were due to differences in concealment rather than to density-dependent nest predation. Successful Harris' Sparrow nests were placed in areas with more shrub cover and more dense vegetation within 5 m of the nest than were depredated nests. Orientation of the nest entrance did not differ between Harris' and White-crowned sparrow nests, nor between successful and depredated Harris' Sparrow nests. However, nest entrances of both species were nonrandomly oriented, with mean orientation vectors 135° to 170° from prevailing storms. Reasons for the tendency of Harris' Sparrows to select sites where chances of predation are relatively high are unclear, but could be related to a lack of suitable nest sites in the study area. *Received 8 May 1992, accepted 25 November 1992.*

NEST PREDATION is the primary cause of egg and nestling mortality for many bird species (Ricklefs 1969, Best and Stauffer 1980, Nilsson 1984). As such, nest predation may act as a strong selective force, and it has been hypothesized to affect the evolution of clutch size (Lima 1987, Martin 1988a), coexistence of species in avian communities (Martin 1988b, c, d), and nestling developmental rates (Ricklefs 1984, Murphy and Fleischer 1986).

Because nest predation may have important fitness consequences, numerous studies have examined factors affecting nest-predation rates, including nest concealment and nest density, habitat characteristics, and types of predators present. Increased nest concealment is of primary importance in reducing the probability of predation in many species (e.g. Livezey 1981, Skeel 1983, Bédard and LaPointe 1984, Jackson et al. 1988, Martin and Roper 1988), but not in others (e.g. Best 1978, Best and Stauffer 1980,

Holway 1991). However, most nest-predation studies examined only vegetation characteristics in the immediate vicinity of the nest. Few studies of birds have attempted to relate vegetation characteristics at a larger spatial scale—that of the nest patch—to predation and nest success (Martin and Roper 1988, but see Holway 1991).

In this study I examine the relationship between nest-site and nest-patch characteristics and nest success in two ground-nesting passerines, the Harris' Sparrow (*Zonotrichia querula*) and Gambel's White-crowned Sparrow (*Z. leucophrys gambelii*), which breed in the Northwest Territories (NWT), Canada. I use univariate and multivariate techniques to examine differences in nest-site selection between the species, and to evaluate the null hypothesis that nest-site and nest-patch characteristics of successful nests and depredated nests do not differ.

[1] Current address: Department of Biological Sciences, State University of New York College at Brockport, Brockport, New York 14420, USA.

METHODS

The study was conducted at Warden's Grove, Thelon Game Sanctuary, NWT, Canada (63°41'N,

104°26'W). The 2.0-km² study area was located adjacent to the Thelon River on a gentle east-facing slope with an approximate average elevation of 200 m. The Thelon River Valley supports extensive stands of white and black spruce (*Picea glauca* and *P. mariana*) growing beyond the northern forest border. "Tree islands," isolated stands of spruce from less than 0.01 to 12.3 ha, are scattered along drainages and rocky benches throughout the area, and are separated from one another by extensive areas of tundra. Tree islands typically are surrounded by shrubby vegetation 0.3 to 1.5 m high, consisting of dwarf birch (*Betula glandulosa*), willow (*Salix* spp.), green alder (*Alnus crispa*), Labrador tea (*Ledum groenlandicum* and *L. decumbens*), and bilberry (*Vaccinium uliginosum*). This dwarf birch community provides the primary nesting habitat for Harris' and White-crowned sparrows. More detailed descriptions of the study area may be found in Norment (1985, 1992a).

The Harris' Sparrow is a medium-distance, intracontinental migrant that breeds only in the forest-tundra ecotone of northern Canada (Godfrey 1986). The breeding range of the White-crowned Sparrow is much less restricted and extends from New Mexico and California north to Alaska and east to Labrador (AOU 1983). Breeding densities of Harris' Sparrows are about three times those of White-crowned Sparrows at Warden's Grove (Norment 1992a). Breeding biologies of the two species at Warden's Grove are similar (see Norment 1992a). Sex ratios and nesting cycles are almost identical, and males and females of the two species showed very similar patterns of change in body mass and lipid stores during the nesting cycle. Both species exhibit low levels of intra- and interspecific agonistic interactions. Only female White-crowned and Harris' sparrows build nests, incubate, and brood young; both males and females feed nestlings. Length of incubation and nestling periods in the two species do not differ significantly (Norment 1992a); patterns of nestling development also are quite similar, and Harris' and White-crowned sparrow nestlings fledge at the same size relative to adults.

Nest location and visitation.—I studied Harris' and White-crowned sparrows at Warden's Grove from 21 May–23 July 1989, 27 May–21 July 1990, and 24 May–17 July 1991. Nests were located by systematically searching habitat or following females to their nests. Nests were marked for relocation by placing small pieces of plastic flagging about 10 m from the nest. All nests were checked daily to determine if eggs or nestlings had been lost to predation or other causes. Each year I handled nestlings daily in about 80% of the nests while studying the growth rates of juvenile birds (Norment 1992a). I did not disturb nestlings in about 20% of the nests so that I could determine whether nest disturbance affects predation rate (see Westmoreland and Best 1985). In these nests, I checked visually from a distance for presence of the female, eggs, or nestlings, but did not disturb the nest contents or flush the female off the nest. A nest was defined as successful if one or more young fledged from it; unsuccessful nests were those that failed completely for any reason. Unsuccessful nests used in comparisons of successful and unsuccessful nests included only those known to have failed due to predation on eggs, nestlings, or the attendant female. I included nest failures due to loss of the female because nest-patch characteristics probably influence susceptibility of the female to predation.

Vegetation sampling.—Nest-site and nest-patch characteristics were measured at all nests in July after the young had fledged. At each nest I measured 13 variables. Five were nest-site variables: (1) distance from nest rim to top of concealing shrub (SBHT); (2) distance from nest rim to edge of shrub (DESH); (3) distance from nest to edge of nearest stand of trees >0.01 ha (DEST); (4) compass orientation of nest entrance relative to center of shrub or other concealing material (ORIENT); and (5) a measure of vegetation density (ND; Petersen and Best 1985). Vegetation density was measured at 10-cm intervals along 50-cm transects extending outward from the nest in the four cardinal directions. At each sampling point, a thin 1-m rod was passed vertically through the vegetation to the ground, and the number of contacts ("hits") by vegetation counted. The number of hits along the four transects then was summed to derive ND.

The nest patch was considered to be all habitat from 1 to 10 m from the nest. Most nest-patch characteristics were measured along 10-m transects extending outward from the nest in the four cardinal directions. Shrub cover (SHBCOV) was measured by tallying the amount of shrub canopy intercepting the tape; the height of each shrub along the transect was recorded and used to determine the average shrub height for the nest patch (AHTSH). Nest-patch foliage-density profiles were measured at 1-m intervals along each transect. At each sampling point, a thin aluminum pole was passed vertically through the vegetation and the number of contacts by vegetation counted in each of the following intervals: 0–0.5 m; >0.5–1.0 m; >1.0–1.5 m; >1.5–2.0 m; and >2.0–3.0 m. The number of hits within 5 m of the nest gave the 5-m foliage density (FD5), and the number of hits within 10 m of the nest gave the 10-m foliage density (FD10). The percentage of ground cover (GRCOV) was determined by recording the presence or absence of vegetation at each sampling point. I used the foliage-density-profile data to derive indices of horizontal and vertical heterogeneity in the nest patch. Vertical foliage diversity (VDF10) was calculated using the Shannon diversity index:

$$VDF10 = -\sum_{i=1}^{I} P_i \ln P_i, \qquad (1)$$

where I is the number of height intervals, and P_i is the proportion of total vegetation hits along the 10-m

transect in each interval. Horizontal foliage diversity (HDF10) was calculated using a heterogeneity index from Wiens and Rotenberry (1981):

$$HDF10 = \sum_{i=1}^{I} (Max - Min) \Big/ \sum_{i=1}^{I} \bar{x}, \qquad (2)$$

where I is the number of 10-m transects, Max is the maximum number of hits recorded among the 10 sample points in each 10-m transect, Min is the minimum number of hits recorded among the 10 sample points in each 10-m transect, and $\bar{x}$ is the mean number of contacts within a transect, summed over the four transects for each nest. I also counted the number of tree stems greater than 3 cm dbh within a 10-m radius of the nest (NOTR).

Statistical analyses.—I compared successful and depredated Harris' Sparrow nests, as well as Harris' Sparrow and White-crowned Sparrow nests, using univariate and multivariate methods. In either case, variables were log or arcsin transformed to more closely fit a normal distribution if necessary. Most univariate comparisons between nest categories involved t-tests. Because circular variables are nonlinear, Kupier's test was used for between-group comparisons of mean nest-entrance-orientation vectors (r); the Rayleigh test was used to test for nonrandom nest orientation (Batschelet 1981).

I used discriminant-function analysis to further explore relationships between nest-site and nest-patch characteristics and nest predation. This method allows consideration of many variables simultaneously, avoiding redundancy among correlated variables. Also, discriminant-function analysis allows detection of effects due to variables that otherwise may be obscured by noise from correlated variables. Stepwise discriminant-function analysis was performed using the BMDP program 7M (Dixon et al. 1990) and 12 of the 13 nest variables; ORIENT was excluded because it is a nonlinear variable. Equality of the covariance matrices was tested with the program DISCRIM (SAS 1982). In both comparisons (successful vs. depredated Harris Sparrow nests, and Harris' Sparrow vs. White-crowned Sparrow nests), the covariance matrices were not equal ($P < 0.05$). Although equality of the covariance matrices is an assumption of discriminant analysis, statistical inferences are generally considered robust to violations of this assumption (Cooley and Lohnes 1971), and moderate violations probably have little effect on two-group classification success (Williams 1983). Wilks' lambda and F-tests were used to determine the combination of variables providing the best group separation. Because group sample sizes differed, Cohen's kappa statistics (Z-values) were computed for each classification matrix to test whether the model classified the observations significantly better than chance alone (Titus et al. 1984). Means and standard deviations are given throughout the paper; the significance level was set at $P < 0.05$.

RESULTS

Nest success.—Of 64 Harris' Sparrow nests found, 40 (62.5%) were successful; 22 (34.4%) were lost to predators, and 2 (3.1%) were abandoned. Included among those lost to predators were two nests in which the attendant females were killed by Northern Shrikes (*Lanius excubitor*). In contrast to Harris' Sparrow nests, no White-crowned Sparrow nests ($n = 13$) were depredated; 2 nests (15.4%) were abandoned for unknown reasons, and the other 11 (84.6%) were successful. Known predators on Harris' Sparrow eggs and nestlings at Warden's Grove were arctic ground squirrels (*Spermophilus parryii*) and short-tailed weasels (*Mustella ermina*). Suspected nest predators included Gray Jays (*Perisoreus canadensis*) and red squirrels (*Tamiasciurus hudsonicus*). Arctic ground squirrels were most numerous and probably accounted for most losses of eggs or nestlings (Norment 1992a).

Repeated visits to nests did not increase nest predation. No White-crowned Sparrow nests in which nestlings were handled were depredated, and success rates for disturbed (28/40) and undisturbed (10/14) Harris' Sparrow nests did not differ ($X^2 = 0.007$, df $= 1$, $P = 0.935$).

Successful vs. depredated Harris' Sparrow nests.— Means for successful and depredated Harris' Sparrow nests (Table 1) differed significantly for one nest-site variable (ND) and five nest-patch variables (SHBCOV, GRCOV, FD5, FD10, and HDF10). All of the above variables except HDF10 were directly related to vegetation cover and density; successful Harris' Sparrow nests generally were placed in denser vegetation with thicker cover than were depredated nests. Mean horizontal vegetation heterogeneity tended to be lower for successful nests, suggesting that more uniform distribution of the vegetation interfered with the ability of predators to locate nests.

Discriminant-function analysis further emphasized the relationship between concealment and nest success, as well as the importance of nest-patch characteristics. Successful and depredated nests were discriminated significantly (Wilk's lambda $= 0.527$, $P < 0.001$; approximate $F = 17.36$, $P < 0.001$) using 3 of the 12 variables considered (SHBCOV, FD5, AHTSH) in the classification function

$$Y = -1.886 + 3.306X_1 + 0.044X_2 - 0.089X_3,$$

where X_1 is SHBCOV in meters, X_2 is FD5 in

TABLE 1. Untransformed means ± SD for nest-site and nest-patch characteristics of successful (n = 40) and depredated (n = 22) Harris' Sparrow nests, and of White-crowned Sparrow (n = 13) nests. Comparisons involved t-tests; where appropriate, data were transformed before statistical analysis.

	Harris' Sparrow nests				White-crowned Sparrow nests	P^c
Variable[a]	Successful	Depredated	P^b	All		
Nest site						
SBHT (cm)	49.0 ± 24.6	45.09 ± 18.1	ns	47.6 ± 22.4	62.1 ± 27.8	*
DESH (cm)	38.1 ± 26.1	29.7 ± 21.4	ns	35.6 ± 24.5	38.6 ± 21.3	ns
DEST (m)	26.7 ± 31.0	26.8 ± 48.2	ns	27.9 ± 38.8	7.2 ± 6.8	***
ND (no. hits)	165.2 ± 51.9	112.3 ± 39.1	***	145.4 ± 53.3	217.1 ± 56.3	***
ORIENT (°)[d]	143.4 ± 60.1	134.1 ± 54.3	ns	140.5 ± 57.8	106.5 ± 55.0	ns
Nest patch						
SHBCOV (m)	19.6 ± 7.2	10.6 ± 4.9	***	16.1 ± 7.9	27.5 ± 6.9	***
AHTSH (cm)	50.8 ± 21.3	51.4 ± 19.8	ns	50.1 ± 21.3	69.2 ± 21.8	**
GRCOV (%)	94.2 ± 7.6	80.4 ± 14.7	**	88.6 ± 13.2	98.7 ± 2.7	***
NOTR	6.6 ± 12.5	4.7 ± 8.6	ns	5.7 ± 11.0	12.7 ± 11.2	*
FD5 (no. hits)	71.5 ± 32.8	38.9 ± 18.5	***	58.9 ± 32.4	108.7 ± 43.3	***
FD10 (no. hits)	133.8 ± 64.1	80.6 ± 40.3	***	112.9 ± 62.1	210.2 ± 78.6	***
VDF10	0.30 ± 0.30	0.32 ± 0.42	ns	0.31 ± 0.34	0.64 ± 0.28	**
HDF10	2.22 ± 0.54	2.83 ± 1.01	**	2.45 ± 0.80	2.18 ± 0.80	ns

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, $P > 0.05$.

[a] Abbreviations defined in Methods.

[b] Comparison successful vs. depredated nests.

[c] Comparison all Harris' Sparrow nests vs. all White-crowned Sparrow nests.

[d] Mean vector (r) and angular deviation (s); mean vectors compared using Kupier's test (Batschelet 1981).

number of hits, and X_3 is AHTSH in centimeters. This model correctly classified 80.0% of the successful nests (32/40) and 86.4% of the depredated nests (19/22) using a jackknifed procedure, an efficiency 63.2% higher than expected by chance (Cohen's kappa Z = 4.789, P < 0.01). Successful Harris' Sparrow nests tended to be placed in areas with more cover and with denser vegetation within 5 m of the nest than were unsuccessful nests (Fig. 1). Even though the means for AHTSH did not differ significantly (Table 1), this variable did help to separate the groups in combination with the other variables in the discriminant function, with successful nests tending to be located beneath lower shrubs.

Interspecific nest differences.—Harris' Sparrows and White-crowned Sparrows differed significantly in 10 of 13 variables examined (Table 1), including three nest-site (SBHT, DEST, ND) and seven nest-patch (SHBCOV, AHTSH, GRCOV, NOTR, FD5, FD10, and VDF10) variables. White-crowned Sparrow nests generally were placed nearer the edge of spruce stands, and in taller, denser vegetation than were Harris' Sparrow nests. White-crowned Sparrows tended to nest in vegetation with greater vertical complexity, as indicated by the higher mean index for VDF10.

Discriminant-function analysis emphasized nest-patch characteristics in separating nest sites of the species. A model that included four nest-patch variables (SHBCOV, FD10, HDF10, and GRCOV) significantly discriminated Harris' Sparrow and White-crowned Sparrow nests (Wilk's lambda = 0.689, P < 0.001, approximate F = 8.113, P < 0.001) using the classification function

$$Y = -10.204 + 0.097X_1 + 0.016X_2 + 0.955X_3 + 2.470X_4,$$

where X_1 is SHBCOV in meters, X_2 is FD10 in number of hits, X_3 is horizontal diversity, and X_4 is percent ground cover. This model correctly classified 85.9% of the Harris' Sparrow nests (55/64) and 84.6% of the White-crowned Sparrow nests (11/13) using a jackknifed procedure, a classification success 58.1% better than expected from random assignments (Cohen's kappa Z = 3.68, P < 0.001). White-crowned Sparrow nests tended to be placed in areas with a combination of denser vegetation, greater shrub and ground cover, and (less clearly) greater horizontal heterogeneity of cover (Fig. 2).

Nest orientation.—Mean orientation vectors (r) for nest entrances did not differ significantly, either between successful and depredated Harris' Sparrow nests, or between Harris' Sparrow
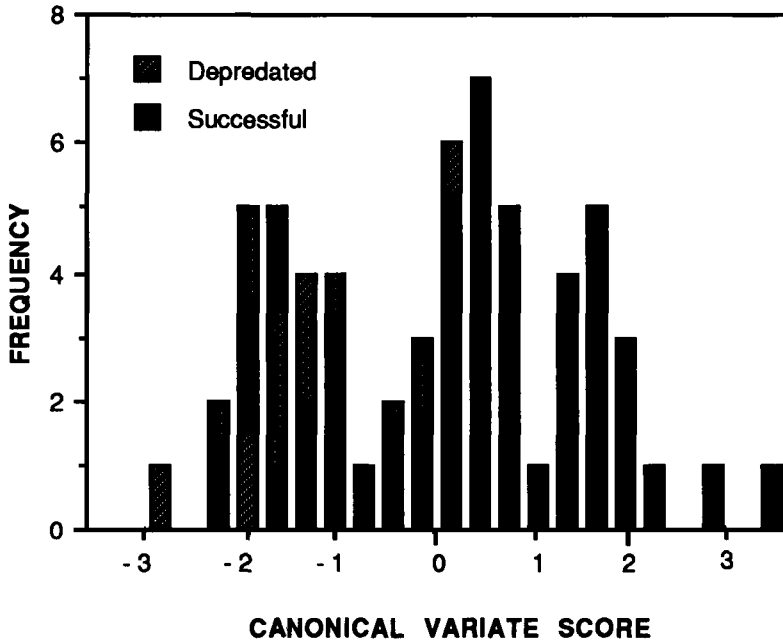
Fig. 1.   Frequency distribution of canonical variate scores for successful ($n = 40$) and depredated ($n = 22$) Harris' Sparrow nests. Nest sites with greater shrub cover, denser vegetation within 5 m of nest, and lower shrubs have higher canonical variate scores.

and White-crowned Sparrow nests (Kupier's tests, $P > 0.05$, Table 1). Both Harris' Sparrow ($r = 140.5°$) and White-crowned Sparrow ($r = 106.5°$) nest entrances were nonrandomly oriented (Rayleigh tests, $P < 0.05$; Fig. 3). Wind direction during the breeding season, as measured on dates when wind speed exceeded 8 km/h, also was nonrandom (Rayleigh test, $P < 0.05$); the mean wind vector was 329° (angular deviation $s = 56.9°$). Wind direction at Warden's Grove during most cyclonic storms was almost always northerly or northwesterly. Winds out of the SW, S, or SE were rare and generally mild. Thus, most *Zonotrichia* nest entrances at WG were placed from 135° to 170° away from the direction of prevailing storms.

DISCUSSION

Results of my study demonstrate a clear relationship between nest concealment and nest success, emphasizing the need to consider nest-patch characteristics, as well as the vegetation immediately surrounding the nest, in studies of nest predation (see Martin and Roper 1988). Successful Harris' Sparrow nests generally were placed in sites with more shrub and ground cover, and with greater density of vegetation, than were depredated nests. Characteristics of the surrounding habitat had a clear effect on the probability of successfully fledging young. The amount of shrub cover within 10 m of the nest (SHBCOV) was the single most useful variable in discriminating between successful and depredated nests, although a measure of vegetation density (FD5) also contributed to the separation of groups. Density of the vegetation immediately surrounding the nest (ND) also differed significantly between the two groups, although the variable did not enter into the DFA.

Comparison of the nest-site and nest-patch characteristics of White-crowned Sparrow and Harris' Sparrow nests emphasized the positive relationship between concealment and nest success, and the effects of habitat patch characteristics on predation rates. Four nest-patch variables (SHBCOV, FD10, HDF10, GRCOV) entered into the model discriminating between species with very different levels of nest predation. Because the breeding biologies of the two species are similar in most respects (Norment 1992a), it is reasonable to ascribe the lack of predation on White-crowned Sparrow nests to their greater concealment, rather than to oth-
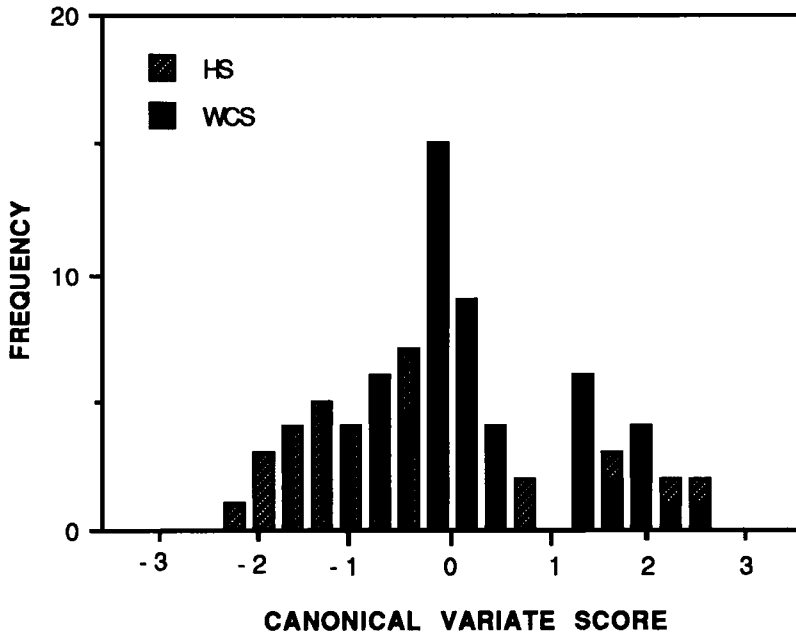
Fig. 2. Frequency distribution of canonical variate scores for Harris' Sparrow ($n = 64$) and White-crowned Sparrow ($n = 13$) nests. Nest sites with greater shrub cover, denser vegetation within 10 m of nest, higher horizontal diversity of vegetation, and greater ground cover have higher canonical variate scores.

er differences in their nesting habits. Additionally, nest-attendance patterns may actually increase the vulnerability of White-crowned Sparrows to predation at Warden's Grove, as they make more trips to and from the nest while incubating eggs and caring for young than Harris' Sparrows (Norment 1992b).

Because different types of predators use different search tactics (Martin 1988d), there may not always be a clear relationship between nest concealment and nest predation. In habitats where the major nest predators are either snakes or nocturnal mammals, which mainly rely on olfactory cues when hunting, nest concealment may not protect nests from depredation (Best 1978, Gottfried and Thompson 1978, Holway 1991). For example, concealment did not affect the ability of snakes to locate Field Sparrow (*Spizella pusilla*) nests, but nests placed in large expanses of tall grass were not detected by mammalian predators (Best 1978). Arctic ground squirrels are the major nest predator at Warden's Grove and appear to locate nests while wandering randomly through suitable habitat (pers. obs.). Ground squirrels apparently rely on their good eye sight to detect predators at a distance and generally avoid thick vegetation

(Kenneth B. Armitage pers. comm.). Thus, increased nest concealment may decrease the ability of ground squirrels to locate *Zonotrichia* nests. Nest concealment also may reduce nest losses to other predators in the area, including short-tailed weasels and red squirrels, because they are, by necessity, diurnal during the arctic summer.

Because the search intensity of a nest predator may increase with prey density (Martin 1988d), and White-crowned Sparrows are much less abundant than Harris' Sparrows at Warden's Grove, differences in rates of nest predation between Harris' and White-crowned sparrows also could be explained by density-dependent effects. Density-dependent nest predation occurs in some situations (Fretwell 1972, Caccamise 1977, Martin 1988d, Reitsma et al. 1990), but not in others (Best 1978, Gottfried and Thompson 1978, Zimmerman 1984). Reasons for the presence or absence of density-dependent effects on nest predation are unclear, but may be related to the density and type of predators, and the degree of similarity of nest types (Best 1978, Zimmerman 1984, Martin 1988d). Density-dependent predation is an unlikely explanation for the observed trend at Warden's Grove be-
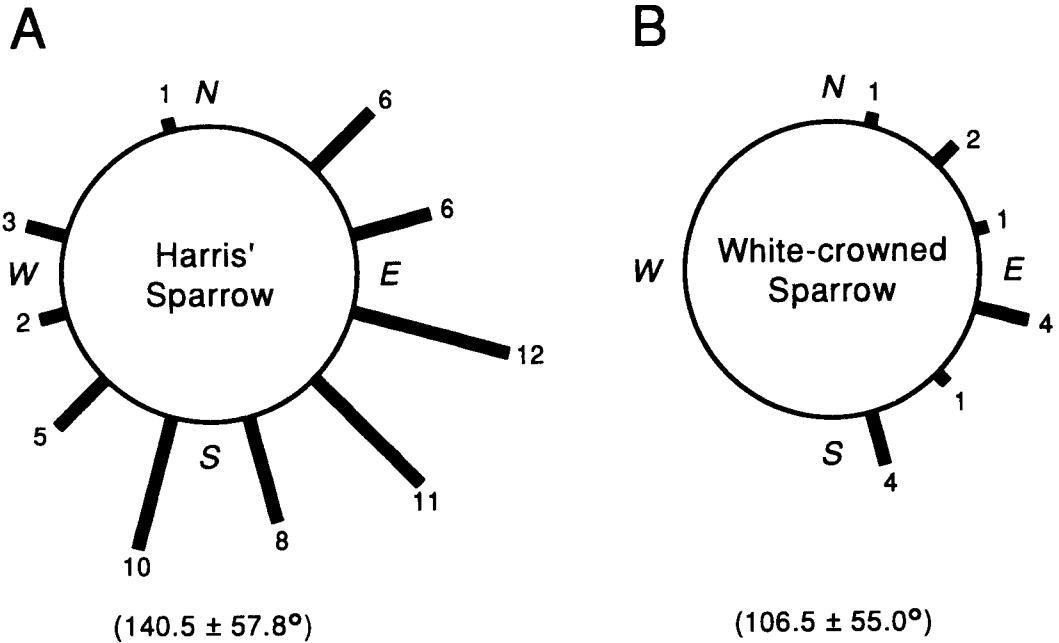
A

B

Fig. 3.   Nest entrance orientation of (A) Harris' Sparrow and (B) White-crowned Sparrow nests at Warden's Grove, 1989–1991. Number of nests in 30° subdivisions of compass shown. Mean vector (*r*) ± angular deviation (*s*) given in parentheses.

cause the nest sites of Harris' Sparrows and White-crowned Sparrows probably do not differ enough to elicit specialization on one nest type (see Martin 1988d). Although White-crowned Sparrow nests are generally placed in thicker vegetation, both species build their nests on the ground beneath the same species of shrubs and have almost identical nest cups (Norment 1992a). Additionally, nest-site characteristics of the two species overlap (Fig. 2). Density-dependent effects on predator search intensity also would not explain the effects of concealment on the success rate of Harris' Sparrow nests alone.

Predators destroyed 34% of all Harris' Sparrow nests found at Warden's Grove, including 50% in 1990, and more than 30% of all eggs and nestlings. Because nest predation was the primary mortality factor for Harris' Sparrow eggs and nestlings, and accounted for 62.5% of all known losses at Warden's Grove (Norment 1992a), it seems that selection should favor those Harris' Sparrows that use concealed nest sites, and that few Harris' Sparrows should nest in open habitats.

Several factors could be important criteria for nest-site selection and operate in opposition to

any preferences for increased nest concealment. First, habitat selection and nest placement could be influenced primarily by proximity to areas with abundant supplies of preferred resources (see Rosenzweig 1981, 1985). Given the need for rapid maturation of altricial young during the short breeding season at high latitudes (Morton 1976, Custer and Pitelka 1977), and the high energetic demands placed upon parents feeding young (Custer et al. 1986), Harris' Sparrows could select nest sites that offer the best resource availability, so as to maximize food delivery rates to young. Behavioral observations are consistent with this explanation. Harris' Sparrows and White-crowned Sparrows at Warden's Grove differ in their preferred foraging habitats; Harris' Sparrows forage in more open habitats and farther from cover than do White-crowned Sparrows (Norment 1992b). However, I cannot determine if nest-site selection is a consequence of foraging habitat selection, or if foraging habitat is a consequence of nest-site selection.

Second, nest placement may be influenced primarily by microclimatic factors. Harris' Sparrows may generally orient their nest entrances in a SE direction and place them in more open

vegetation to increase diurnal heat gain and protect the nests from prevailing winds. Both factors could decrease the energy required by nestlings for thermoregulation, and increase growth rates. However, this explanation is unlikely because *Zonotrichia* nesting at high latitude or altitude may suffer heavy losses of eggs and/or nestlings due to inclement weather (Jehl and Hussell 1966, Ehrlich et al. 1972, Jehl 1971, King and Mewaldt 1987). Accordingly, mortality caused by inclement weather should select for increased nest cover to reduce cold stress (Walsberg 1985). Although harsh weather was rare during my study, severe inclement weather at Warden's Grove may cause significant mortality among nesting passerines in some years (Norment 1985).

A third possibility is that White-crowned Sparrows are behaviorally dominant over Harris' Sparrows and exclude them from preferred nest sites. This explanation also seems unlikely because Harris' Sparrows and White-crowned Sparrows at Warden's Grove show little evidence of interspecific agonistic interactions. Substantial territorial overlap occurs between the species, nests of which may be within 10 m of one another (Norment 1992b; see also Rees 1973). If anything, Harris' Sparrows would be expected to be behaviorally dominant over White-crowned Sparrows, as they are about 30% larger and tend to displace the latter species at trap locations baited with seed (pers. obs.).

Finally, although high-quality nest sites are generally considered to be abundant, they may be less common than usually assumed (Martin and Roper 1988). At Warden's Grove, thick dwarf birch/willow habitat is usually limited to the perimeter of forest stands, whereas more open dwarf birch vegetation extends farther out into tundra habitats. Thus, Harris' Sparrows may place their nests in more open vegetation than White-crowned Sparrows because of the relative lack of high-quality, concealed nest sites. I do not have the data to examine this relationship, but future studies of nest-site characteristics and nest success should include an analysis of nest-site availability.

LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1983. Checklist of North American birds. 6th ed. Am. Ornithol. Union, Washington, D.C.

BATSCHELET, E. 1981. Circular statistics in biology. Academic Press, Orlando, Florida.

BÉDARD, J., AND G. LAPOINTE. 1984. The Savannah Sparrow territorial system: Can habitat features be related to breeding success? Can. J. Zool. 62: 1819–1828.

BEST, L. B. 1978. Field Sparrow reproductive success and nesting ecology. Auk 95:9–22.

BEST, L. B., AND D. F. STAUFFER. 1980. Factors affecting nesting success in riparian bird communities. Condor 82:149–158.

CACCAMISE, D. F. 1977. Breeding success and nest-site characteristics of the Red-winged Blackbird. Wilson Bull. 89:396–403.

COOLEY, W. W., AND P. R. LOHNES. 1971. Multivariate data analysis. Wiley, New York.

CUSTER, T. W., AND F. A. PITELKA. 1977. Demographic features of a Lapland Longspur population. Auk 94:505–525.

CUSTER, T. W., R. G. OSBORN, F. A. PITELKA, AND J. A. GESSMAN. 1986. Energy budget and prey requirements of breeding Lapland Longspurs near Barrow, Alaska, USA. Arct. Alp. Res. 18:415–427.

DIXON, W. J., M. B. BROWN, L. ENGLEMAN, AND D. I. JENNRICH. 1990. BMDP statistical software manual. Univ. California Press, Berkeley, California.

EHRLICH, P. R., D. E. BREEDLOVE, P. F. BRUSSARD, AND M. A. SHARP. 1972. Weather and the "regulation" of subalpine populations. Ecology 53:243–247.

FRETWELL, S. D. 1972. Populations in a seasonal environment. Monogr. Pop. Biol. 5. Princeton Univ. Press, Princeton, New Jersey.

GODFREY, W. E. 1986. The birds of Canada, 2nd ed. National Museums of Natural Sciences, Ottawa.

GOTTFRIED, B., AND C. F. THOMPSON. 1978. Experimental analysis of nest predation in oldfield habitat. Auk 95:304–312.

HOLWAY, D. A. 1991. Nest-site selection and the im-

portance of nest concealment in the Black-throat-
ed Blue Warbler. Condor 93:575–581.

JACKSON, S. L., D. S. HIK, AND R. F. ROCKWELL. 1988.
The influence of nesting habitat on reproductive
success of the Lesser Snow Goose. Can. J. Zool.
66:1699–1703.

JEHL, J. R. 1971. Patterns of hatching success in sub-
arctic birds. Ecology 52:169–173.

JEHL, J. R., AND D. J. T. HUSSELL. 1966. Effects of
weather on reproductive success of birds at Chur-
chill, Manitoba. Arctic 19:185–191.

KING, J. R., AND L. R. MEWALDT. 1987. The summer
biology of an unstable insular population of
White-crowned Sparrows. Condor 89:549–565.

LIMA, S. L. 1987. Clutch size in birds: A predation
perspective. Ecology 68:1062–1070.

LIVEZEY, B. C. 1981. Locations and success of duck
nests evaluated through discriminant analysis.
Wildfowl 32:23–27.

MARTIN, T. E. 1988a. Nest placement: Implications
for selected life-history traits, with special ref-
erence to clutch size. Am. Nat. 132:900–910.

MARTIN, T. E. 1988b. Processes organizing open-
nesting bird assemblages: Competition or nest
predation? Evol. Ecol. 2:37–50.

MARTIN, T. E. 1988c. Habitat and area effects on for-
est bird assemblages: Is nest predation an influ-
ence? Ecology 69:74–84.

MARTIN, T. E. 1988d. On the advantage of being
different: Nest predation and the coexistence of
bird species. Proc. Natl. Acad. Sci. USA 85:2196–
2199.

MARTIN, T. E., AND J. J. ROPER. 1988. Nest predation
and nest-site selection of a western population
of the Hermit Thrush. Condor 90:51–57.

MORTON, M. L. 1976. Adaptive strategies of Zono-
trichia breeding at high latitude or high altitude.
Pages 322–326 in Proceedings 16th International
Ornithological Congress (H. J. Firth and J. H.
Calaby, Eds.). Canberra, 1974. Australian Acad-
emy of Sciences, Canberra.

MURPHY, M. T., AND R. C. FLEISCHER. 1986. Body size,
nest predation, and reproductive patterns in
Brown Thrashers and other mimids. Condor 88:
446–455.

NILSSON, S. G. 1984. The evolution of nest-site se-
lection among hole-nesting birds: The impor-
tance of nest predation and competition. Ornis
Scand. 15:167–175.

NORMENT, C. J. 1985. Observations on the annual
chronology for birds in the Warden's Grove area,
Thelon River, Northwest Territories, 1977–1978.
Can. Field-Nat. 99:471–483.

NORMENT, C. J. 1992a. Comparative breeding biol-
ogy of Harris' Sparrows and White-crowned

Sparrows in the Northwest Territories, Canada.
Condor 94:955–975.

NORMENT, C. J. 1992b. Comparative breeding ecol-
ogy of the Harris' Sparrow (Zonotrichia querula)
and White-crowned Sparrow (Zonotrichia leuco-
phrys) in the Northwest Territories, Canada. Ph.D.
dissertation, Univ. Kansas, Lawrence.

PETERSEN, K. L., AND L. B. BEST. 1985. Nest-site se-
lection by Sage Sparrows. Condor 87:217–221.

REES, W. R. 1973. Comparative ecology of three sym-
patric species of Zonotrichia. Ph.D. dissertation,
Univ. Toronto, Toronto.

REITSMA, L. R., R. T. HOLMES, AND T. W. SHERRY. 1990.
Effects of removal of red squirrels (Tamiasciurus
hudsonicus) and eastern chipmunks (Tamias stria-
tus) on nest predation in northern hardwood for-
est: An artificial nest experiment. Oikos 57:375–
380.

RICKLEFS, R. E. 1969. An analysis of nesting mortality
in birds. Smithson. Contrib. Zool. 9:1–48.

RICKLEFS, R. E. 1984. The optimization of growth
rate in altricial birds. Ecology 65:1602–1616.

ROSENZWEIG, M. L. 1981. A theory of habitat selec-
tion. Ecology 62:327–335,

ROSENZWEIG, M. L. 1985. Some theoretical aspects of
habitat selection. Pages 517–540 in Habitat selec-
tion in birds (M. L. Cody, Ed.). Academic Press,
Orlando, Florida.

SAS INSTITUTE. 1982. SAS user's guide: Statistics. SAS
Institute, Inc., Cary, North Carolina.

SKEEL, M. A. 1983. Nesting success, density, philo-
patry, and nest-site selection of the Whimbrel
(Numenius phaeopus) in different habitats. Can. J.
Zool. 61:218–225.

TITUS, K., J. A. MOSHER, AND B. K. WILLIAMS. 1984.
Chance-corrected classification for use in dis-
criminant analysis: Ecological applications. Am.
Midl. Nat. 111:1–7.

WALSBERG, G. E. 1985. Physiological consequences
of microhabitat. Pages 389–413 in Habitat selec-
tion in birds (M. L. Cody, Ed.). Academic Press,
Orlando, Florida.

WESTMORELAND, D., AND L. B. BEST. 1985. The effect
of disturbance on Mourning Dove nesting suc-
cess. Auk 102:774–780.

WIENS, J. A., AND J. T. ROTENBERRY. 1981. Habitat
associations and community structure of birds in
shrubsteppe environments. Ecol. Monogr. 51:21–
41.

WILLIAMS, B. K. 1983. Some observations on the use
of discriminant analysis in ecology. Ecology 64:
1283–1291.

ZIMMERMAN, J. L. 1984. Nest predation and its re-
lationship to habitat and nest density in Dick-
cissels. Condor 86:68–72.