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NEST-SITE SELECTION AND THE IMPORTANCE OF NEST CONCEALMENT IN THE BLACK-THROATED BLUE WARBLER[1]

DAVID A. HOLWAY[2]
Department of Biology, University of California, Los Angeles, CA 90024

Abstract. Nest-site selection of Black-throated Blue Warblers (*Dendroica caerulescens*) was studied for two summers in a northern hardwood forest in the White Mountains of New Hampshire. Nest placement in the shrub layer was examined to evaluate several alternative hypotheses concerning the selection of nest-site microhabitat. Nest-sites tended to be in dense patches of hobblebush (*Viburnum alnifolium*) with denser vegetation below 1.5 m and more open vegetation between 1.5–3 m than at random points. Shrub densities at nests and at random points within hobblebush patches were, in nearly all cases, statistically indistinguishable. Nests were placed in large patches of shrubs much more often than at random points and in larger patches of hobblebush more often than at random points within hobblebush patches. Black-throated Blue Warblers placed their nest in more concealed locations compared to empty nests placed at random locations. Concealment indices of successful and depredated nests, however, were not significantly different from one another. Several reasons why this species chose particular microhabitats within the shrub layer are discussed.

Key words: Nest-site; nest microhabitat; nest concealment; Black-throated Blue Warbler; Dendroica caerulescens; *hobblebush; nest predation.*

INTRODUCTION

Nest-site selection is of central importance to the reproductive success of most birds (Pleszczynska 1978, Clark et al. 1983) and at least some other vertebrate taxa as well (Sargent et al. 1980). Adults must take into account a suite of biotic and abiotic variables when selecting a nest-site, any one of which can jeopardize the reproductive investment, and even the survival, of the parents. For example, the selection of favorable microclimatic conditions at nest-sites is important to meet the metabolic demands of the rapidly developing chicks as well as the parents (Calder 1973, Austin 1974). Accessible and seasonally stable resources must be available near the nest-site to meet the high energetic demands of the young, because food is often important in determining reproductive success (Rodenhouse 1986, Simons and Martin 1990). Lastly, nests must be placed in locations to minimize predation of eggs and young. Nest failure due to predation in open-cup nesting birds, in particular, can be high: 54.9% for six species of passerines (reviewed by Ricklefs [1969]), 52% for the Black-throated Blue Warbler (*Dendroica caerulescens*) (Rodenhouse 1986), 80–93% for the Hermit Thrush (*Catharus guttatus*) (Martin and Roper 1988). Such heavy nest predation may be an important mechanism of population regulation for some species of birds (Ricklefs 1969, George 1987).

This study examines nest-site selection and the importance of nest concealment as a determinant of nesting success in the Black-throated Blue Warbler. Throughout its range this species nests in the shrubby understory of deciduous or mixed deciduous–coniferous forests (Nice 1930, Harding 1931, Walkinshaw and Dyer 1953). Steele (1988) found that this species nests in areas of low, dense shrubs, especially hobblebush (*Viburnum alnifolium*). The propensity of this species to nest in the shrub layer is intriguing since this substrate seems to offer less protection from nest predators than either the forest floor, where nests could be relatively cryptic, or the forest canopy, where nests could be spatially diffuse. The Black-throated Blue Warbler is the only species on the study site which nests exclusively in the shrub layer (R. T. Holmes, pers. comm.).

First, I attempted to identify the microhabitat parameters that distinguished nest-sites of Black-throated Blue Warblers. I compared microhabitat at nest-sites to that at two different null data sets (random points and random points within hobblebush patches) to determine if Black-

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[2] Present address: Department of Biology, University of Utah, Salt Lake City, UT 84112.

throated Blue Warblers nested in areas of dense shrubs, if they nested in hobblebush patches of specific densities, and if they nested in shrub patches of a specific size. Then, I measured nest concealment and evaluated its possible importance for safeguarding Black-throated Blue Warbler nests from nest predators.

STUDY AREA

This study was conducted at the Hubbard Brook Experimental Forest in the White Mountain National Forest, West Thornton, Grafton County, New Hampshire on several plots between 500–600 m in elevation. All plots were gridded with flagging at 50 m intervals. The forest at Hubbard Brook is composed of northern hardwoods, dominated by American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*). White ash (*Fraxinus americanus*), paper birch (*Betula papyrifera*), red spruce (*Picea rubens*), and eastern hemlock (*Tsuga canadensis*) also occur throughout the forest. The shrub layer is composed mainly of hobblebush and saplings of American beech, sugar maple, striped maple (*Acer pensylvancium*), and mountain maple (*Acer spicatum*) (pers. observ.; Siccama et al. 1970). Ferns (mainly *Dryopteris spinulosa*) are widespread. The shrub layer varies in density and structural complexity from being relatively open (especially under closed canopy) to being quite dense (especially within tree fall gaps). Areas dominated by beech saplings and by hobblebush are common. For a more detailed description of the study site, see Holmes et al. (1986).

METHODS

Monitoring of Black-throated Blue Warbler nests was part of an ongoing study of the breeding ecology and habitat selection of this species (Holmes et al., in prep.). We examined nests every other day to determine the onset of incubation, date of hatching, and fate of the nest. Black-throated Blue Warblers typically fledge chicks on the eighth day after hatching; nests that held chicks at least seven days after hatching were considered successful.

In 1989, microhabitat measurements were made at 40 warbler nests (NM = nest microhabitat) and 40 random points (RM = random point microhabitat). In 1990, microhabitat measurements were made at 40 random points within hobblebush patches (RHM = random hobblebush microhabitat). Measurements at nests were taken soon after predation or fledging of young; NM points were centered directly on nests. Nest height and substrate were recorded at all nests. Each RM point was located 25 paces, along a randomly selected compass bearing, from a randomly selected 50 m grid intersection. RHM points were selected as the nearest hobblebush patch (4-m^2 area which had a hobblebush stem density >2 stems/m^2) from randomly selected grid intersections.

Microhabitat measurements. Microhabitat measurements (expanded and modified from Steele [1988]) included the following: percent cover (at NM and RM), shrub density (at NM, RM, and RHM), and foliage profiles (at NM and RM). Percent cover directly over nests was estimated for three circular areas (radii: 0.15 m, 0.30 m, and 1 m) centered on each nest. Percent-cover estimates were made by looking straight down through a tube onto the three circular areas (the radii of which were marked off on the floor of the forest). Shrub density measurements were taken in four belt segments (1 × 10 m) radiating at right angles from a central point in the configuration of the crossed blades of a windmill (Steele 1988). Each belt segment was subdivided into four partitions at increasing distances from a central point: 0–1 m, 1–2 m, 2–5 m, 5–10 m. Plant species for shrub density analyses included hobblebush and saplings of beech and maple. Shrubs were defined as woody vegetation >0.50 m in height and with a stem diameter <2 cm. Shrub density was measured in terms of stems/m^2. Foliage profiles were measured at points along concentric circles around a central point. The foliage profile points were distributed at equal intervals around the circumference of circles of the following radii: 0.15 m (4 points + 1 point at center), 0.30 m (4 points), 1 m (8 points), 2 m (16 points), 5 m (16 points), and 10 m (16 points). The 0.15 m and 0.30 m circles were combined for analysis into a <0.50 m category. At each point I placed a 3 m pole divided into 6 height increments of 0.50 m each, and recorded the number of leaves of each understory plant species that touched the pole (foliage density for data analysis). Plant species used in foliage profile analyses included hobblebush, ferns, and saplings of beech and maple.

Shrub patch size. I used the shrub density data (at NM, RM, and RHM) to determine whether Black-throated Blue Warblers selected particular sized shrub patches for their nests. I defined a shrub patch as an area with a mean shrub stem density >2 stems/m^2 within 1 m of a central point (the mean shrub density within 1 m of random points was 1.7 stems/m^2). Shrub patches were of the following size radii: 1 m, 2 m, 5 m, 10 m. These measurements provided an index of the extent of shrubby vegetation surrounding a central point.

Nest concealment. I measured nest concealment at three levels parallel to the horizontal plane of the nest: ground-level, nest-level, and 1.5 m. At each level, the visibility of the nest was measured from 1 m away at eight points (45-degree compass intervals). Overhead visibility was also measured by looking directly down at the nest from 1.5 m. Concealment at each point was scored on a scale from 0–5 corresponding to increasing visibility of the nest (0 = 0% visibility, 1 = 20% visibility, 2 = 40% visibility, etc.). Scores of each of the eight points at each level were then added such that a score of 40 = 100% visibility. Concealment scores were an estimate of the amount of the nest (to the nearest 20%) that was visible from a point. I measured the concealment of nests placed at random points by conducting concealment measurements on empty Black-throated Blue Warbler nests that I placed at RM points. These randomly placed nests were placed at RM points about 0.50 m from the ground (the average height of real nests) and were not adjusted to the nearest shrub patch or likely nest site. Concealment was measured at 31 warbler nests (22 successful and 9 depredated) in 1989 and 42 warbler nests (21 successful and 21 depredated) in 1990. I measured concealment at 33 randomly placed nests in 1989. Nests believed to have been lost due to inclement weather or desertion were excluded from analyses of nest concealment. Concealment measurements were also used to determine if warbler nests were oriented in a particular direction.

Statistical analysis. I made pairwise comparisons of the means (NM vs. RM, NM vs. RHM) of all microhabitat measurements. I used the F-test for equality of variance to determine if the variances of the means in each pairwise comparison were different. If the variances were not different ($P > 0.05$, F-test), then I analyzed the microhabitat data using two-sample t-tests. If the variances of the means were different ($P < 0.05$, F-test), then I used the Cochran-Cox two sample t-test. The Cochran-Cox two-sample t-test is suited for comparing two means when the population variances are not equal and is more conservative than the two-sample t-test (Woolson 1987).

RESULTS

Nest-site characteristics. Black-throated Blue Warblers placed their nests in the shrub layer about 0.50 m above the ground: 49 ± 28 cm (mean ± 1 SD; n = 82, 1989 and 1990 combined). Nests were placed most commonly in hobblebush (73%), but saplings of beech (12%), maple (5%), spruce (5%), balsam fir (*Abies balsamea*) (3%), and elderberry (*Sambucus* spp.) (1%) were used, in addition to ferns (1%). All nests were situated in crotches of intersecting branches. More than half of these nests (56%) had a dead branch or twig forming part of this crotch which lent additional support to the nest.

Nest microhabitat. Black-throated Blue Warbler nests had a nearly complete canopy of vegetation over the immediate vicinity of the nest (Table 1). Percent cover measurements over nests (NM) were significantly greater than over nests placed at random points (RM) in circular areas immediately encompassing (radii of 0.15 m and 0.30 m) the nest (two-sample t-tests, $P < 0.005$; Table 1).

Shrub density measurements in NM were significantly greater than in RM for all total shrub density and hobblebush density comparisons (two-sample t-tests, $P < 0.005$; Table 1). Hobblebush density accounted for most of the total shrub density in NM, but not in RM; this suggests that Black-throated Blue Warblers selected areas with disproportionately dense hobblebush from that available at random locations. Shrub densities in NM and RHM were quite similar, with only two significant differences (two-sample t-tests, $P < 0.05$; Table 1). The congruence between NM and RHM shrub density measurements suggests that Black-throated Blue Warblers were not discriminating between specific kinds of hobblebush patches.

Foliage profile measurements demonstrated that Black-throated Blue Warblers selected areas with denser hobblebush below 1.5 m and more open areas between 1.5–3 m than at random points. Densities of total shrub foliage in NM were significantly greater (two-sample t-tests, $P < 0.05$; Table 2) than in RM in the three lower strata (0.–0.5 m, 0.5–1 m, 1–1.5 m) in 80% (12/15) of the comparisons; densities of hobblebush

TABLE 1. Percent cover and shrub density (stems/m[2]) comparisons of Black-throated Blue Warbler nest microhabitat (NM, n = 40) with microhabitat at random points (RM, n = 40) and at random points within hobblebush patches (RHM, n = 40). Values represent mean ± 1 SD.

Measurement	NM	RM	RHM
% Cover			
0.15 m	94 ± 14	26 ± 33[b]	—
0.30 m	87 ± 14	28 ± 29[b]	—
1.0 m	65 ± 21	82 ± 31	—
Shrub density 0–1 m			
Hobblebush	3.0 ± 1.7	0.7 ± 1.1[a]	3.3 ± 1.2
Beech	0.4 ± 0.6	0.6 ± 0.8	0.2 ± 0.3[a]
Maple	0.4 ± 0.6	0.4 ± 0.6	0.5 ± 0.5
All spp.	3.8 ± 1.3	1.7 ± 1.3[b]	4.0 ± 1.3
Shrub density 1–2 m			
Hobblebush	2.1 ± 1.4	0.6 ± 0.7[b]	2.1 ± 1.4
Beech	0.4 ± 0.4	0.7 ± 0.6	0.4 ± 0.4
Maple	0.5 ± 0.6	0.4 ± 0.5	0.9 ± 0.8
All spp.	3.0 ± 1.0	1.7 ± 0.9[b]	3.4 ± 1.3
Shrub density 2–5 m			
Hobblebush	1.1 ± 0.8	0.4 ± 0.4[b]	0.8 ± 0.7
Beech	0.4 ± 0.3	0.5 ± 0.4	0.4 ± 0.3
Maple	0.5 ± 0.4	0.4 ± 0.4	0.6 ± 0.5
All spp.	2.0 ± 0.6	1.3 ± 0.6[b]	1.8 ± 0.6
Shrub density 5–10 m			
Hobblebush	0.8 ± 0.4	0.4 ± 0.4[b]	0.6 ± 0.4[a]
Beech	0.4 ± 0.3	0.5 ± 0.3	0.5 ± 0.3
Maple	0.4 ± 0.3	0.3 ± 0.2	0.5 ± 0.4
All spp.	1.6 ± 0.4	1.2 ± 0.3[b]	1.6 ± 0.4

[a] $P < 0.05$ (distribution different from NM; two-sample t-test).
[b] $P < 0.005$ (distribution different from NM; two-sample t-test).

foliage in NM were significantly greater (two-sample t-tests, $P < 0.05$; Table 2) in 93% (14/15) of the comparisons in these same strata. Below 1 m, total shrub and hobblebush foliage was significantly denser in NM (two-sample t-tests, $P < 0.05$; Table 2) than in RM in all comparisons. In the three upper strata (1.5–2 m, 2–2.5 m, 2.5–3 m), vegetation was significantly denser in RM (two-sample t-tests, $P < 0.05$; Table 2) than in NM in 67% (10/15) of the comparisons; densities of beech foliage were significantly greater in RM in 60% (9/15) of these comparisons.

Shrub patch size. Because Black-throated Blue Warblers nested in areas of dense shrubs, they may have selected shrub patches of a particular size for their nest-sites. Frequencies of both total shrub and hobblebush patch sizes in NM, RM, and RHM are listed in Table 3. Nest-sites (NM) were much more likely to be centered in both patch categories than RM (both frequency distribution comparisons were significantly different, χ^2-test, $P < 0.005$; Table 3). More than half of all nest-sites (NM) were in 10 m total shrub patches suggesting that expansive areas of dense shrubs were selected as nest-sites. NM and RHM hobblebush patch size frequency distributions were significantly different (χ^2-test, $P < 0.005$; Table 3) with a greater tendency for nest-sites (NM) to have been in large hobblebush patches than RHM. This result suggests that Black-throated Blue Warblers selected areas of more expansive hobblebush for their nest-sites.

Nest concealment. Black-throated Blue Warbler nests (in NM) had significantly lower visibility indices than those placed at random points (in RM) for all four measures of visibility (Mann-Whitney U-Test, $P < 0.01$; Table 4). In situ nests were more concealed primarily because dense hobblebush acted as an effective visibility screen. Overhead visibility of nests (in NM) differed strikingly from nests placed at random locations (in RM); these results are in accord with the percent cover comparisons (Table 1), which showed significantly greater cover above and immediately around nests (in NM) than those placed at random points (in RM). Successful and depre-

TABLE 2. Foliage height profile comparisons between Black-throated Blue Warbler nest microhabitat (NM, $n = 40$) and random points (RM, $n = 40$) at five distances from the nest-site (real or randomly placed). Listed vegetation types in each height increment are significantly greater ($P < 0.05$, two-sample t-test) for either category (NM or RM). Vegetation types are: T = total shrubs (sum of all categories), H = hobblebush, B = beech, and M = maple.

Foliage profile strata	Horizontal distance from center of nest or point: <0.5 m NM	<0.5 m RM	1 m NM	1 m RM	2 m NM	2 m RM	5 m NM	5 m RM	10 m NM	10 m RM
0–0.5 m	T, H	–	T, H	–	T, H	–	T, H	–	T, H	–
0.5–1 m	T, H	–	T, H, M	–	T, H	–	T, H	–	T, H	–
1–1.5 m	–	B	H	B	H, M	B	T, H	–	T, H	–
1.5–2 m	–	–	–	B	–	B	–	–	–	–
2–2.5 m	–	T, B	–	T, B	–	T	–	B	–	–
2.5–3 m	–	T, B	–	T, B	–	–	–	T, B	–	B

dated warbler nests had levels of concealment which were not significantly different (Mann-Whitney U-test, $P > 0.5$; data from 1989 and 1990 pooled; Table 4).

Nest orientation. Visibility measurements were also used to determine if Black-throated Blue Warbler nests were consistently oriented in any specific direction for thermal benefits (e.g., southern exposures). I made pairwise comparisons between each of the eight 1.5 m visibility measurements. No statistically significant differences were found (two-sample t-test, $P > 0.5$) between these measurements indicating that nests are not oriented in or exposed towards a particular direction.

DISCUSSION

NEST-SITE CHARACTERISTICS

It seems likely that Black-throated Blue Warblers at Hubbard Brook are responding to some general feature of hobblebush rather than to hobblebush per se. For instance, Black-throated Blue Warblers nest in the shrub layer throughout their range, but commonly place their nests in plant species other than hobblebush. In other areas of central New Hampshire, for instance, they have been reported to nest only in Mountain Laurel (*Kalmia latifolia*) (Harding, 1931). Bent (1953) cites various authors who describe nests in rhododendrons, laurels, and both coniferous and deciduous saplings. Given this, it seems likely that Black-throated Blue Warblers nest in whatever understory shrub affords the most protection from either the elements or from nest predators. Hobblebush is a stout-petioled, large-leaved plant that grows in dense patches and could conceivably provide more cover than the other common understory plant species at Hubbard Brook.

NEST MICROHABITAT SELECTION

There are three primary reasons why Black-throated Blue Warblers might select dense shrubs for nesting. First, dense shrubs could provide concealment from predators. Second, dense shrub patches may be favored foraging sites. Third, areas of low, dense shrubbery could be selected because they contain favorable microclimates. These hypotheses are not mutually exclusive and may interact in the selection of nest-sites. The

TABLE 3. Shrub patch size frequency distributions for nest microhabitat (NM, $n = 40$), random point microhabitat (RM, $n = 40$), and microhabitat at random points in hobblebush patches (RHM, $n = 40$). Patch sizes are expressed as radial distances from a central point and are defined as areas with a shrub stem density >2 stems/m^2. The total shrub patch size category is all shrub species combined.

Sample	Total shrub patch size: No patch	1 m	2 m	5 m	10 m	Hobblebush patch size: No patch	1 m	2 m	5 m	10 m
NM	2	1	6	10	21	8	2	13	13	4
RM	21	4	4	1	10[a]	36	2	2	0	0[a]
RHM	0	1	8	9	22	0	9	20	10	1[a]

[a] $P < 0.005$ (frequency distribution different from NM; χ^2-test).

TABLE 4. Visibility scores for all Black-throated Blue Warbler nests (1989 and 1990) and real warbler nests placed at random locations. Visibility scored on a scale of 0–5 with eight measurements for each level such that a score of 40 = 100% visibility. Overhead visibility includes only one measurement of visibility. Statistical tests compared all nests to randomly placed nests and successful nests to depredated nests. Values represent means ± 1 SD.

	Black-throated Blue Warbler nests			Randomly placed nests (n = 33)
Visibility category	Successful (n = 43)	Depredated (n = 30)	All nests (n = 73)	
Ground-level	22.8 ± 7.4	25.2 ± 7.5	23.7 ± 7.5	31.6 ± 8.9[a]
Nest-level	29.1 ± 6.9	31.0 ± 6.5	29.7 ± 6.5	36.9 ± 4.7[a]
1.5 m	17.2 ± 6.4	17.2 ± 8.1	17.2 ± 7.4	33.6 ± 9.5[a]
Overhead	1.4 ± 1.4	1.2 ± 1.7	1.2 ± 1.5	4.5 ± 1.2[b]

[a] $P < 0.01$, Mann-Whitney U-test. All nests vs. randomly placed nests.
[b] $P < 0.001$, Mann-Whitney U-test. All nests vs. randomly placed nests.

remainder of the discussion will consider each of these three explanations separately.

Concealment from predators. Black-throated Blue Warblers select large, dense shrub patches for their nest sites. The extent of shrubby vegetation around nest sites may influence the chance of nest predation in several ways. First, large shrub patches will contain more potential nest-sites for a visually searching predator to investigate (Martin and Roper 1988). Second, dense shrub patches may physically impede some species of foraging mammals (Bowman and Harris 1980). Finally, large patches of vegetation may more effectively screen nests and the actions of the parents than those in small patches simply by the greater extent and volume of surrounding vegetation.

Black-throated Blue Warblers do place their nests in concealing locations, but fine-scale variation in nest concealment was not an important determinant of the fate of nests. It seems improbable, however, that behaviors that confer nest concealment would not be under strong natural selection. Why should subtle concealment factors not be important in a system which is at least occasionally affected by high (> 50%; Rodenhouse 1986) levels of nest predation?

There are several factors that may obscure the importance of fine-scale variation in nest concealment. First, nest predation is, to some extent, a stochastic event; nest predators almost certainly find some nests by chance alone. Second, the chance that a given nest is depredated might depend more on its proximity to the home range of a potential nest predator than to subtle concealment factors. Third, several species of nocturnal mammals have been documented at artificial nests baited with *Coturnix* eggs (Reitsma et al. 1990). If nocturnal mammals are important predators of Black-throated Blue Warbler nests and if these nest predators detect nests primarily by olfactory cues, then visual concealment might not protect nests from depredation. Lastly, repetitive behavioral patterns of the parents (e.g., fixed routes used to and from the nest) may be important cues for visually oriented predators.

Nest concealment is of demonstrated importance in some systems (Martin and Roper 1988). Tests with artificial nests, however, have demonstrated no statistically significant relationship between nest predation and either nest concealment or shrub density around artificial nests (Kelso 1989, Reitsma et al. 1990). The results of this study concur with these studies of artificial nests. The degree of nest concealment may be an important contributing factor to the success or detriment of some Black-throated Blue Warbler nests at Hubbard Brook, but its importance is probably masked largely by random events and the variation in levels of nest predation in space and time.

Foraging substrate. For some species of birds, proximity to resources is the principal criterion of nest-site selection (Lenington 1980). It seems unlikely, however, that Black-throated Blue Warblers nest in low, dense shrubs simply to be close to preferred foraging sites. Black-throated Blue Warblers forage low in the understory (Holmes 1986), but neither sex forages preferentially in areas of low, dense shrubs (Steele 1988). Hobblebush, ferns, and herbs are used as foraging substrates by females more than twice as much as by males (21% vs. 9% of total foraging time), but both sexes forage more than 50% of the time in the beech and maple midstory (Holmes 1986). In addition, Black-throated Blue Warblers forage over a much larger area than the vicinity of the nest (B. B. Steele, pers. comm.).

Microclimate selection. Nest placement could be influenced by microclimatic variation. The shrub layer could serve as a wind screen to reduce convective heat loss or as insulation to reduce nocturnal heat loss or diurnal heat gain (Walsberg 1985). The data to adequately address this class of hypotheses are not available, but two lines of evidence are pertinent here. First, Black-throated Blue Warbler nests were not oriented to southern exposures. Some species of shrub-nesting forest passerines, however, do orient their nests non-randomly, apparently to increase incident insolation (Martin and Roper 1988). Second, both overhead visibility and percent-cover measurements showed that Black-throated Blue Warbler nests are typically covered by vegetation. Overhead cover at nests is typically attributed to provide shading or concealment from predators, but Walsberg (1985) emphasizes that overhead cover may be selected to prevent precipitation-induced cold stress that is potentially lethal to both young and adults. Shelter could be an important component of Black-throated Blue Warbler nest-site selection at Hubbard Brook, since the early portion of the breeding season (late May and early June) typically includes periods of cold, rainy weather (Holmes et al. 1986).

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LITERATURE CITED

AUSTIN, G. T. 1974. Nesting success of the cactus wren in relation to nest orientation. Condor 76: 216–217.

BENT, A. C. 1953. Life histories of North American wood warblers, Part 1. Dover Publications, New York.

BOWMAN, G. B., AND L. B. HARRIS. 1980. Effect of spatial heterogeneity on ground-nest predation. J. Wildl. Manage. 44:806–813.

CALDER, W. A. 1973. Microhabitat selection during nesting of hummingbirds in the Rocky Mountains. Ecology 54:127–134.

CLARK L., R. E. RICKLEFS, AND R. W. SCHREIBER. 1983. Nest-site selection by the red-tailed tropicbird. Auk 100:953–959.

GEORGE, T. L. 1987. Greater land bird densities on island vs. mainland: relation to nest predation level. Ecology 68:1393–1400.

HARDING, K. C. 1931. Nest habits of black-throated blue warblers. Auk 48:512–522.

HOLMES, R. T. 1986. Foraging patterns of forest birds: male–female differences. Wilson Bull. 98:196–213.

HOLMES, R. T., T. W. SHERRY, AND F. W. STURGES. 1986. Bird community dynamics in a temperate deciduous forest: long term trends at Hubbard Brook. Ecol. Monogr. 56:201–210.

KELSO, J. 1989. An analysis of density dependent nest predation in northern hardwoods forest. Senior Honor's Thesis. Dartmouth College, Hanover, NH.

LENINGTON, S. 1980. Female choice and polygyny in red-winged blackbirds. Anim. Behav. 28:347–361.

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

NICE, M. M. 1930. A study of nesting black-throated blue warblers. Auk 47:338–345.

PLESZCZYNSKA, W. K. 1978. Microgeographic prediction of polygyny in the lark bunting. Science 201:935–937.

REITSMA, L. R., R. T. HOLMES, AND T. W. SHERRY. 1990. Effects of removal of red squirrels (*Tamiasciurus hudsonicus*), and eastern chipmunks (*Tamias striatus*) on nest predation in northern hardwood forest: 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.

RODENHOUSE, N. L. 1986. Food limitation for forest passerines: effects of natural and experimental food reductions. Ph.D.diss. Dartmouth College, Hanover, NH.

SARGENT, R. C., AND J. B. GEBLER. 1980. Effects of nest site concealment on hatching success, reproductive success, and parental behavior of the threespine stickleback (*Gasterosteus aculeatus*). Behav. Ecol. Sociobiol. 7:137–142.

SICCAMA, T. G., F. H. BORMANN, AND G. E. LIKENS. 1970. The Hubbard Brook ecosystem study: productivity, nutrients, and phytosociology of the herbaceous layer. Ecol. Monogr. 40:389–402.

SIMONS, L. S., AND T. E. MARTIN. 1990. Food limitation of avian reproduction: an experiment with the cactus wren. Ecology 71:869–876.

STEELE, B. B. 1988. Habitat selection of breeding black-throated blue warblers. Ph.D.diss. Dartmouth College, Hanover, NH.

WALKINSHAW, L. H., AND W. DYER. 1953. Nesting of black-throated blue warblers in Michigan. Jack Pine Warbler 31:47–54.

WALSBERG, G. E. 1985. Physiological consequences of microhabitat, p. 389–413. *In* M. L. Cody [ed.], Habitat selection in birds. Academic Press, Orlando, FL.

WOOLSON, R. F. 1987. Statistical methods for the analysis of biomedical data. John Wiley & Sons, Inc., New York.