

# SELECTION OF FORAGING AND NESTING SITES BY BLACK-THROATED BLUE WARBLERS: THEIR RELATIVE INFLUENCE ON HABITAT CHOICE<sup>1</sup>

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*Abstract.* To understand why breeding Black-throated Blue Warblers (*Dendroica caerulescens*) select forests with dense shrubs, I assessed the value of this habitat in supplying opportunities for foraging and nesting. I predicted that these warblers would select shrub foliage for foraging if foraging substrate was important in their selection of habitat and that they would place their nests in areas of dense shrubs if nest-site availability affected habitat choice. To measure foraging and nest-site selection, I compared the proportion of foraging or nests in a particular habitat element to the availability of that element expressed as a proportion of all habitat elements. Foraging males under-utilized shrub foliage (below 3 m) in relation to its relative availability and over-utilized the sparse foliage between 3-9 m high. On a horizontal plane, males over-utilized areas of their territories with dense shrub foliage, but this could be due to the greater number of shrubs in these areas. Small samples of females and males feeding fledglings indicated that the lower foliage strata, but not necessarily dense shrub patches, might be important to these groups. These results demonstrate differences in foraging patterns between the sexes and between stages of the breeding cycle. More importantly, foraging Black-throated Blue Warblers showed no consistent selection of dense shrubs. As this species is more abundant in forests with dense shrubs, these analyses suggest that foraging may have a minor influence on habitat selection.

Black-throated Blue Warblers consistently selected areas of dense shrubs for nesting. Number of shrub stems and amount of foliage (0-1 m high) were significantly higher at nests than at random points. Furthermore, on an experimental plot with chemically defoliated shrubs, males continued to forage, but nesting was markedly reduced. These results suggest that, while shrubs are used for both foraging and nesting, nest-site requirements may be more important in determining what habitat is selected by Black-throated Blue Warblers. If nest-site requirements determine habitat choices in other forest birds, then the availability of suitable nest-sites should have an important effect on community structure.

*Key words:* Foraging; nest-site selection; habitat selection; Black-throated Blue Warblers; *Dendroica caerulescens*; community structure.

## INTRODUCTION

Breeding bird species are associated with specific habitats, presumably because of an evolved behavior to select habitats that provide resources necessary for reproduction and survival. These resources include food, foraging sites, nesting sites, favorable microclimates, and places to avoid predators, parasites, or competitors. Although numerous studies have identified habitats selected by a species (see studies in Cody 1985 and Verner et al. 1986), we rarely know which resources are important in restricting a species to

a particular habitat. For insectivorous forest birds, availability of nesting sites and places to find food or foraging sites vary widely from habitat to habitat and thus should have a strong effect on habitat selection (Martin 1988b).

Many studies associate a selected habitat with the use of foraging sites (Pearson 1975; Partridge 1976; Franzreb 1978, 1983a, 1983b; Stanton 1986; Yahner 1986; Carrascal et al. 1987). For Black-throated Blue Warblers (*Dendroica caerulescens*), reproductive output is affected by food abundance (Holmes et al. 1992, Rodenhouse and Holmes 1992), suggesting that this species might select habitat because of food resources and foraging sites provided.

Recently, several investigators suggested that some species select habitats primarily because they supply nesting sites (Bilke 1984, Martin 1988b). Nest-site availability has been shown to affect distribution and abundance of some cavity

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nesting species (Connor et al. 1976, Evans and Connor 1979, Brawn and Balda 1988). High nest predation in open-nesting birds (Ricklefs 1969, Best and Stauffer 1980, Martin and Roper 1988, Rotenberry and Wiens 1989, Rodenhouse and Holmes 1992) suggests that availability of protected nest-sites might be important in determining what habitats are selected in these species as well.

In this study, I investigated foraging and nest-site selection of Black-throated Blue Warblers. This species breeds in northern hardwood forests throughout eastern North America, selecting forests with dense shrubs (Black 1975, Sherry and Holmes 1985, Steele 1992). I predicted first, that if foraging site availability is important in the choice of habitat, the birds would selectively forage in the shrub stratum compared to foliage at other heights and that they would also selectively forage in areas of their territories where shrubs were dense. I tested the null hypothesis that the birds forage in direct proportion to the availability of these resources. Secondly, I predicted that if nest-site availability influenced habitat choice, then birds would nest where shrubs are dense and would select a particular species of shrub as a nest substrate. I tested the null hypothesis that nests are placed randomly with respect to shrub density and species. I supported these tests experimentally by removing shrub foliage on a 14-ha plot and monitoring subsequent nesting and foraging.

## STUDY AREA

This study was conducted at the Hubbard Brook Experimental Forest in the southern White Mountains of New Hampshire. This northern hardwood forest is dominated by beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula allegheniensis*) with lesser amounts of red spruce (*Picea rubens*) and eastern hemlock (*Tsuga canadensis*). Trees provided nearly complete canopy cover except in occasional tree-fall gaps. Sub-canopy trees and saplings included small beech and maple trees along with striped maple (*A. spicatum*). The shrub layer was dominated by hobblebush (*Viburnum alnifolium*), and sugar maple and beech seedlings and saplings. Lower branches of beech and sugar maple trees also contributed foliage to the lower strata. Ground cover consisted of Lycopodium, wood fern (*Dryopteris spinulosa*), and various herbaceous species.

Foraging and nests of Black-throated Blue Warblers were studied on a 53-ha plot located within continuous forest encompassing the long-term census plot described by Holmes et al. (1986). The foliage removal experiment was conducted on a 14-ha plot of similar slope, elevation and vegetation composition, approximately 3 km distant. Both plots were gridded with flagging at 50 m intervals.

## METHODS

*Vegetation measurements.* Black-throated Blue Warblers feed primarily on insects captured from leaves, so the availability of foraging substrates was measured with foliage profiles (vertical distribution of foliage) and sketch maps of different categories of shrub density (horizontal distribution of foraging resources). To detect foraging selection, I compared foraging heights and locations to the availability of foraging resources. Nest-site selection was identified by comparing shrub densities and foliage profiles at nest-sites with those at random points.

Shrub density was measured in 1986 at 23 nests and 41 randomly selected sites (a subset of the measurements on a larger plot). At nests and random sites I recorded all shrub stems within four 1 m wide quadrats extending 10 m in each of the four cardinal directions. I counted and identified all stems >0.5 m tall and <2 cm diameter at breast height.

Foliage profiles were measured at 15 randomly selected sites and at 12 nests, distinct from those nests at which shrub density was measured. Profiles at each random point were measured by placing a 3 m pole vertically at 30 spots located along a 20 m tape extending in a randomly selected direction from the point. At 2 m intervals along the tape, the pole was placed 1, 2, and 3 m from the tape and the heights of all leaves striking the pole were recorded. Profiles above 3 m were constructed using a camera fitted with a 135 mm lens and a gridded focusing screen. The camera was placed at six random points along the 20 m tape and aimed at the canopy. At each of the 15 grid points on the focusing screen, height to the nearest leaf was read from the focusing ring. I calculated a foliage profile from these data by the method of MacArthur and Horn (1969). At nests, the 3 m pole was placed at 44 locations evenly spaced on concentric circles around each nest. At 0.15 m from the nest, the pole was placed at four locations, at 0.3 m it was

placed at eight locations, and at both 1.0 and 2.0 m, it was placed at 16 locations. Again heights of all leaves striking the pole were recorded. Only foliage below 3 m was considered at nests because all nests were below 1 m high.

Sketch maps of foliage density types were made by visually categorizing patches of shrub foliage as either low, medium, or high density. Medium and high density foliage was further subdivided into areas where most of the foliage was below 2 m (shrub areas) and areas with most of the foliage between 2 and 5 m, so that the ground was easily visible (shrub/sapling areas). I mapped areas of 5 × 5 m and larger. Sketch maps were made in the field by orienting myself from labeled grid points and sketching borders on a map of the grid. A total of 143 50 × 50 m squares or 35.75 ha were mapped.

*Foraging observations.* Foraging heights (to identify selection in the vertical dimension) were recorded for males from 1984 to 1987, and for females in 1986 and 1987. Locations where foraging occurred (for horizontal selection) were mapped in 1986 and 1987 for both sexes. Birds were color-banded to distinguish individuals.

For each foraging bird encountered, I estimated its height at 10 sec intervals (Wiens et al. 1970). For analysis, I used the mean height of each foraging sequence, with a sequence defined as a string of consecutive observations separated from other strings by either a flight out of sight or a one-minute interval during which no observations were recorded. In general, each sequence included observations in only one height stratum because when a bird flew higher or lower, they usually flew out of sight. Using means from sequences of observations limits the serial dependence that is inherent in sequential observations of the same bird (Wiens et al. 1987). Although this method does not ensure complete independence of observations (mean height of a sequence), I attempted to maximize independence by spreading observation periods throughout the day and breeding season (mid May to late July, see Morrison et al. 1992). This technique includes rare or less conspicuous observations that are omitted if only one observation of each individual is recorded (Wagner 1981, Morrison 1984, Bradley 1985, Morrison et al. 1992).

Foraging location was mapped each time I encountered a foraging bird. Subsequent locations were recorded after either a flight out-of-sight or

two minutes of elapsed time. Maps of foraging locations were overlaid on the maps of foliage density to record the proportion of foraging in each category of foliage density. This eliminated a possible bias that could have occurred if I had classified shrub density as I was observing foraging birds.

*Experimental removal of foliage.* Shrubs and lower branches (up to 3 m) were defoliated on the experimental plot by applying DuPont Krenite®, a relatively non-toxic herbicide used in brush control. In late summer 1984, the herbicide was applied using a Stihl® back-pack mist blower at the rate of 5 L of concentrate per ha. Krenite® allows normal leaf fall in autumn but prevents bud expansion the following spring. Thus, only the foliage was removed, no dead leaves were left, and stems remained in place for the duration of the experiment.

*Analysis.* Holmes et al. (1978), Werner and Sherry (1987), and others identified significant variation among individual birds in how they forage. Thus, foraging data with more observations from some individuals than others is potentially biased towards individuals seen more often. To eliminate this bias, I weighted each bird equally to obtain a pooled estimate of the amount of foraging done in different height strata (vertical analysis) or shrub density category (horizontal analysis). In the vertical analysis, I characterized foraging with proportions of mean heights that occurred in each height interval. Thirty-one males and nine females were used in the foraging height analysis. Four males recorded in two different years were treated as separate birds, with the assumption that different prey distribution and territory placement would create independent foraging distributions. Horizontal foraging patterns were characterized by calculating the proportion of foraging locations occurring in each shrub density category. Sixteen male and eight female birds were weighted equally and pooled in the horizontal analysis.

I detected selection of foraging sites by comparing use of sites to their availability using the method of Neu et al. (1974, also see Allredge and Ratti 1986). In this method, the number of observations in each class (height interval or shrub density category) is compared to expected values with a  $\chi^2$  test. Expected values are based on foraging in direct proportion to the amount of foraging sites (foliage, area, or number of shrubs) available in each class. Repeated observations of

TABLE 1. Availability and use of foliage strata by 31 male Black-throated Blue Warblers, 1984–1987. All height intervals that are labeled over- or under-used are significant at  $P < 0.01$ , except 1–3 m which is significant at  $P < 0.05$ .

Height interval	Number of foraging sequences	Observed proportion (p)	99% C.I. of p	Foliage available <sup>a</sup>	Expected proportion foraging <sup>b</sup>	Selection
>9 m	150	0.287	0.226–0.348	1.467	0.383	under-used
6–9 m	115	0.220	0.164–0.276	0.303	0.079	over-used
3–6 m	125	0.239	0.181–0.297	0.314	0.082	over-used
1–3 m	85	0.163	0.121–0.204 <sup>c</sup>	0.801	0.209	under-used
0–1 m	48	0.092	0.053–0.131	0.943	0.246	under-used
Total	523	1.001		3.828	1.000	

<sup>a</sup> The mean number of leaves striking a vertical line through that height interval.

<sup>b</sup> Expected if foraging is directly proportional to foliage available.

<sup>c</sup> 95% C.I. (no significant preference at 99%).

individuals may violate the assumption of independence of data points (Morrison et al. 1992). Although weighting individual birds equally may partially alleviate this problem, I interpreted the results conservatively, only considering very strong differences (those with  $P < 0.01$ ) to represent real patterns. For data sets with significant  $\chi^2$  values, I constructed confidence limits around the proportion of observations in each class using a Bonferonni  $z$  statistic, a normal approximation for a variable that follows a binomial distribution (Neu et al. 1974). Statistically significant over- or under-utilization was indicated where confidence limits did not overlap expected proportions. To correct for the several simultaneous confidence limits being calculated, the alpha level was divided by the number of classes (five in this study, see Byers et al. 1984, Neu et al. 1974).

In the horizontal analysis, foraging resource availability was defined as the proportional area of each foliage density category in all mapped territories. Territories were defined as the polygon encompassing all observations of a particular bird (Odum and Kuenzler 1955, Reed 1985). I mapped the areas used by females separately because not all of a male's territory may be available to its mate. For a few females with very small foraging territories (<0.1 ha) foraging areas were expanded by adding 5 m to all sides to obtain a better estimate of the shrub density types available to that bird while I was observing it.

## RESULTS

*Vertical analysis—foraging height selection.* Analysis of foraging heights confirmed that individual birds foraged differently. For this analysis, I constructed a contingency table with four

height strata (0–3 m, 3–6 m, 6–9 m, >9 m) and foraging height measurements of seven males for which I had at least 29 foraging sequences. These individuals differed significantly in their foraging heights distributions ( $\chi^2 = 57.92$ ,  $df = 18$ ,  $P < 0.001$ ). In all subsequent analyses each bird was weighted equally.

Male Black-throated Blue Warblers did not select the shrub stratum foliage for foraging (Table 1, Fig. 1). The  $\chi^2$  test showed a highly significant difference between observed male foraging heights and expected foraging heights based on foliage availability ( $\chi^2 = 358.58$ ,  $df = 4$ ,  $P < 0.001$ ). Subsequent calculation of confidence limits showed significant over-utilization of the sparse foliage in the sapling and sub-canopy strata (3–9 m) and significant under-utilization of shrub (0–3 m) and canopy (>9 m) foliage (Table 1, Fig. 1). Shrub foliage was used >25% of the time by foraging male Black-throated Blue Warblers (Table 1), but >45% of the total foliage in the profile is in this layer, resulting in under-utilization of the lower strata (Fig. 1).

I observed some males that were feeding fledglings and also some females. Small sample sizes preclude firm conclusions, but suggest that these birds forage differently from males feeding alone. Foraging heights of males feeding fledglings (99 sequences, seven birds) differed significantly from expected foraging heights ( $\chi^2 = 148.43$ ,  $df = 4$ ,  $P < 0.001$ ). In contrast to all observations of males, however, males feeding fledglings over-utilized tall shrub foliage (1–3 m, Fig. 1). Otherwise, the pattern of selection was similar. Females (96 sequences, nine birds) observed throughout the breeding season also foraged differently than expected based on foliage avail-

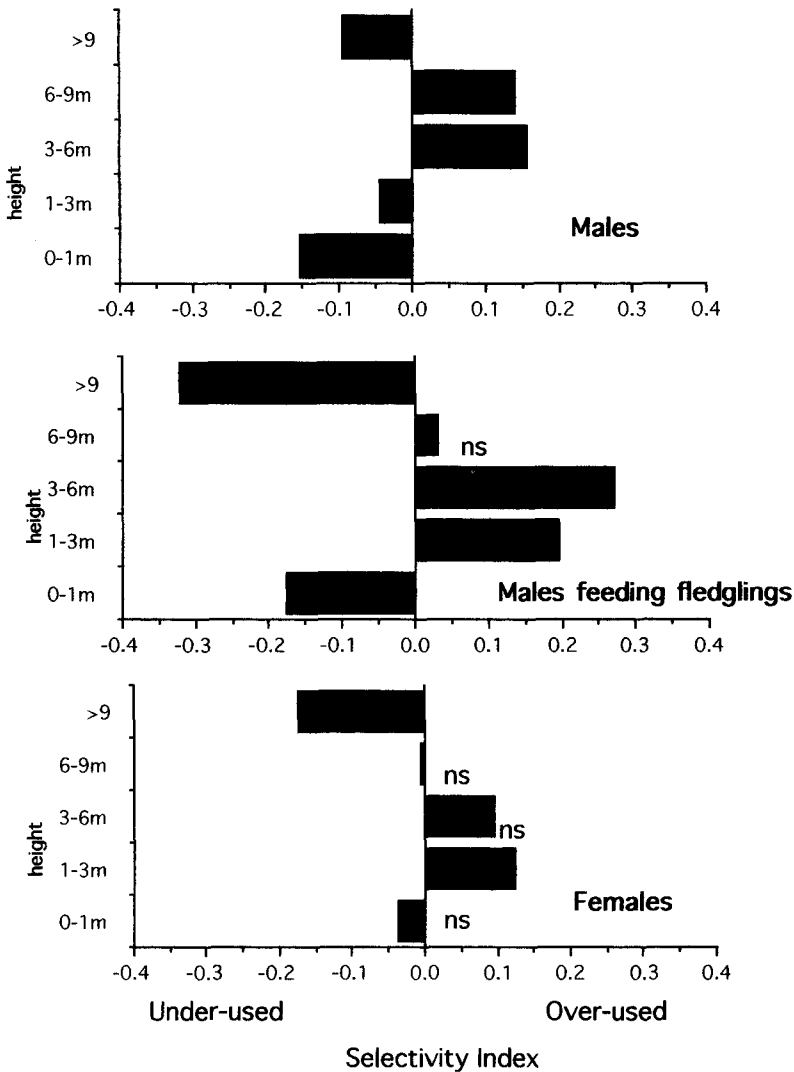


FIGURE 1. Selection of foliage at different heights by foraging Black-throated Blue Warblers. The values graphed are Strauss's (1979) selectivity index,  $L = (\text{proportion used}) - (\text{proportion available})$  for each height stratum. Positive values represent over-utilization, negative values show under-utilization. All values represent significant selectivity except those denoted by ns.

ability ( $\chi^2 = 25.93$ ,  $df = 4$ ,  $P < 0.001$ ). Females significantly over-utilized tall shrub foliage and under-utilized canopy foliage (Fig. 1).

*Horizontal analysis—foraging locations.* Quantitative shrub sampling confirmed that the categories of shrub density sketched in the field represented real differences in shrub density (Table 2, one-way analysis of variance (ANOVA),  $F_{4,192} = 12.84$ ,  $P < 0.0001$ ). These density estimates are based on counts of shrub stems, however, and probably underestimate the differences

in amount of foliage among the categories. The sketch maps take into account foliage on lower branches of trees and they compensate for the fact that some shrubs have much more foliage than others.

In the horizontal foraging analysis, male Black-throated Blue Warblers selected areas with high density shrub or sapling foliage (Table 3). Their use of shrub categories differed significantly from that predicted by the availability of each category ( $\chi^2 = 25.33$ ,  $df = 4$ ,  $P < 0.001$ ). Confidence limits

TABLE 2. Shrub density in five foliage density categories mapped visually (see text).

Category (height)	Mean stems/10m <sup>2</sup>	SE	n <sup>a</sup>
Low density	10.14	1.18	14
Medium density			
Shrub (<2 m)	17.28	0.93	53
Shrub/sapling (2–5 m)	15.13	0.86	80
High density			
Shrub (<2 m)	28.18	2.27	22
Shrub/sapling (2–5 m)	20.16	2.53	28

<sup>a</sup> Number of 1 × 10 m quadrats.

showed that these birds over-utilized high density shrub and shrub/sapling areas. Other density classes were used in proportion to their availability. The area of each density category reflects the amount of each category available, but not the amount of foraging substrate available within each category, since high density areas contained more shrub stems and thus more foliage. When expected proportion of foraging locations was recalculated from the number of shrubs in each density category (calculated from the average shrub density in each category, Table 2), rather than the area, no significant selection was found ( $\chi^2 = 9.24$ ,  $df = 4$ ,  $P > 0.05$ , Table 3, Fig. 2), indicating that male Black-throated Blue Warblers forage in these areas in relation to the number of shrubs they contain.

Foraging females (80 locations, eight birds) under-utilized areas with high density shrub/sapling foliage, based on both area of the categories

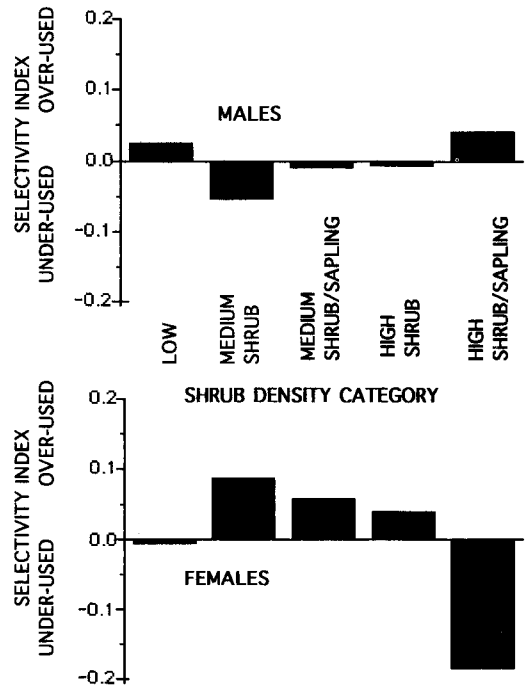


FIGURE 2. Selection of shrub density categories within territories. Selectivity index is as in Figure 1. Availability of each type is calculated from the total number of shrubs available in each type. Females show significant under-utilization ( $P < 0.05$ ) of the high density shrub/sapling type. All others are not significant.

( $\chi^2 = 17.11$ ,  $df = 4$ ,  $P < 0.01$ ) and on number of shrubs ( $\chi^2 = 13.49$ ,  $df = 4$ ,  $P < 0.01$ , Fig. 2). Females used all other categories in approximate relation to their availability.

TABLE 3. Availability and use of shrub density categories for 16 male Black-throated Blue Warblers.

	Foliage density category					Total
	Low	Medium shrub <sup>a</sup>	Medium shrub/sapling <sup>b</sup>	High shrub <sup>a</sup>	High shrub/sapling <sup>b</sup>	
Number of foraging locations	33	108	68	48	95	352
Observed proportion (p <sub>i</sub> )	0.094	0.307	0.193	0.136	0.270	1.000
95% C.I. of p <sub>i</sub>	0.054–0.134	0.243–0.370	0.139–0.248	0.089–0.184	0.209–0.331	
Expected proportion (area) <sup>c</sup>	0.116	0.365	0.234	0.088	0.198	1.000
Selection	ns <sup>d</sup>	ns	ns	over-used	over-used	
Expected proportion (shrubs) <sup>e</sup>	0.067	0.360	0.202	0.142	0.228	1.000
Selection	ns	ns	ns	ns	ns	

<sup>a</sup> Most foliage <2 m high.

<sup>b</sup> Most foliage 2–5 m high.

<sup>c</sup> Expected proportion if foraging in each patch category is directly proportional to its area.

<sup>d</sup> No selection.

<sup>e</sup> Expected proportion if foraging is based on the number of shrubs in each type.

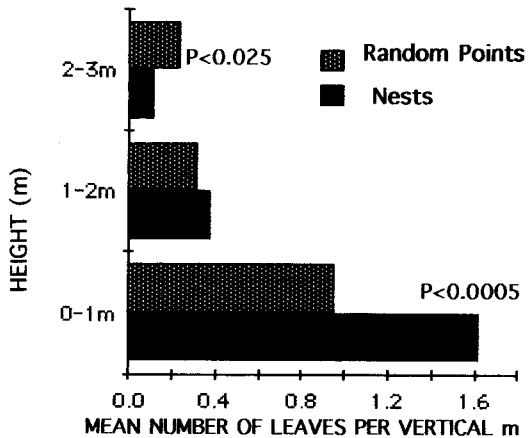


FIGURE 3. Mean foliage profiles at nests ( $n = 12$ ) and random points ( $n = 30$ ).  $P$  values are calculated from unpaired  $t$  tests.

*Selection of nest-sites.* Black-throated Blue Warblers placed their nests in areas with dense shrubs. Shrubs were significantly denser at nests than at randomly selected points (Table 4). One species, hobblebush, makes up 35% of the shrubs and was denser at nests than at random points. Two variables used to identify edges of patches of shrubs—standard deviation and range of density among the four quadrats—did not differ between nests and random points, suggesting that nests are not commonly placed on edges of dense shrub patches.

Foliage profiles confirmed the shrub density result. Foliage density below 1 m was higher at nests than at random points (Fig. 3). Foliage between 1 and 2 m was similar between nests and random points, but that between 2 and 3 m was denser at random points. All 53 nests (from both analyses) were below 1 m in height.

Hobblebush shrubs were strongly selected as a nest substrate. The proportion of each shrub species that was used as a nest substrate differed significantly from the proportion of each shrub species available on the plot ( $\chi^2 = 88.01$ ,  $df = 4$ ,  $P < 0.001$ ). Nests were placed in hobblebush more than twice as frequently as expected from shrub stem abundances (Table 5). All other species were strongly under-utilized. Most nests were placed where two or three separate shrub stems intersected (30 of 53 nests) and many were also supported by a fallen dead branch (30 of 53 nests again).

*Experimental removal of foliage.* On the experimental plot, 80% of shrub foliage was removed (Steele 1992). Before the herbicide treatment in 1984, four pairs successfully reared young on the experimental plot. In the three years following shrub defoliation, only one nest was found, despite the fact that territories of four males were in the defoliated area. In 1985, two males defended territories in the defoliated area. One never attracted a mate; the other's nest was at the extreme edge of its territory, 50 m into undisturbed vegetation. In 1986, one resident male disappeared in early June without attracting a mate. In the same year, a peripheral pair expanded its territory onto the plot in late June and fledged young from a nest on the defoliated area. This nest (0.5 m high) was in a small isolated beech on which most of the foliage had survived. In 1987 no Black-throated Blue Warblers had territories in the defoliated area. In all years, birds with neighboring territories foraged into the edges of the defoliated area. During the same four years, the number of territories remained relatively constant on both a 10-ha control plot (declining from 7.5 to 5.5) and a 10-ha plot censused since

TABLE 4. Density and other shrub characteristics at 23 Black-throated Blue Warbler nest sites compared to 41 randomly located points.

	Mean (SD)		Unpaired $t$	$P$
	Nest sites	Random points		
Total shrub density	85.0 (21.6)	67.5 (30.5)	2.43	<0.02
SD of density <sup>a</sup>	7.84 (3.67)	7.29 (3.50)	0.60	ns
Range of density <sup>a</sup>	17.2 (7.7)	16.3 (8.0)	0.43	ns
Number of species	4.78 (.60)	4.80 (1.03)	0.09	ns
Density of sugar maple	19.6 (20.5)	13.3 (17.4)	1.31	ns
Density of beech	18.6 (9.4)	20.9 (12.6)	0.77	ns
Density of striped maple	15.7 (9.9)	14.4 (10.8)	0.44	ns
Density of hobblebush	29.6 (15.0)	17.1 (17.8)	2.81	<0.01

<sup>a</sup> Calculated from four  $1 \times 10$  m quadrats at each point.

TABLE 5. Shrub species supporting Black-throated Blue Warblers nests and availability of each species. Data are from 53 nests in 1985–1987. Total shrubs used is greater than 53 because most nests were supported by more than one shrub.

Species used	Number of nests	$p_i^a$	99% C.I. of $p_i$	No. of shrubs <sup>b</sup>	Expected nest use <sup>c</sup>	Selection
Hobblebush	58	0.69	0.53–0.85	704	0.25	over-used
Striped maple	9	0.11	0.002–0.212	592	0.214	under-used
Beech	10	0.12	0.01–0.23	856	0.31	under-used
Sugar maple	5	0.06	–0.02–0.14	547	0.20	under-used
Red spruce	2	0.02	–0.03–0.08	69	0.02	—

<sup>a</sup> Observed proportion (proportion used).

<sup>b</sup> Stems per 1,640 m<sup>2</sup>.

<sup>c</sup> Expected proportion based on shrubs available.

1969 (Holmes et al. 1986, increasing from 9.5 to 12.5).

## DISCUSSION

Black-throated Blue Warblers showed no consistent selection of shrub foliage while foraging. Males over-utilized areas with dense shrub foliage on the horizontal plane, but no horizontal selection was apparent when availability was calculated from the number of shrubs in each density category, rather than from the area of each category. This suggests that the birds were simply foraging in direct proportion to amount of foliage available. In a vertical dimension, males under-utilized shrub foliage below 3 m and over-utilized foliage between 3 and 9 m. Thus, they spend much of their foraging time above dense patches of shrubs. Males often sing while foraging and their songs may be more effective when delivered from above the dense shrub foliage. A small sample of observations, however, suggests that shrubs may be important for foraging by females and for feeding of fledglings. Males feeding fledglings over-utilized lower foliage (1–3 m). Females also over-utilized the lower strata, but showed no horizontal selection of dense shrubs. Thus, dense shrub foliage does not appear to be important as a foraging substrate for males when one considers the entire breeding season, but may be important to females and to males when feeding fledglings.

Foraging males selected sparse foliage between 3 and 9 m in height, suggesting that lack of foliage in this stratum might be an element of habitat important to this species. However, in an analysis of habitat associations by Black-throated Blue Warblers, I found neither positive or negative relationships between bird density and sapling or small tree density (Steele 1992). In the same analysis, I found a strong association between

shrub density and bird density ( $R^2 = 0.79$ ,  $P < 0.0005$ ).

Evidence for the selection of dense shrub habitat for nesting sites is unambiguous. Two independent analyses, using different nests, showed higher shrub and foliage density around nests than at randomly selected points. A similar result was reported by Holway (1991). Following the experimental removal of shrub foliage, nesting was nearly eliminated while several males foraged and defended territories. It is reasonable, then, that nest-site selection would affect choice of habitat by this species.

## USE OF HABITAT FOR FORAGING: MALE-FEMALE AND BREEDING CYCLE DIFFERENCES

My foraging analyses demonstrate that male Black-throated Blue Warblers forage differently from females, (as noted by Black 1975 and Holmes 1986; see also Morse 1968, Power 1980, Grubb 1982, Franzreb 1983a, and Peters and Grubb 1983 for other species). Male Black-throated Blue Warblers generally foraged higher than females, often over areas of dense shrub foliage. Females foraged low, but showed no clear selection of dense shrub patches for foraging. Also, stage of the breeding season can affect use of foraging sites (Sakai and Noon 1990). Male Black-throated Blue Warblers feeding fledglings foraged similarly to females: consistently low. These differences emphasize that the habitat that is selected must not only meet the needs of the male, but also provide resources needed by their mates and offspring. The period when adults are feeding fledged young and energy needs are high may be critical in determining what habitat is chosen by birds. Thus, in studies of habitat use, observations should be made at all stages of the breeding season and should include both sexes.



## USE OF HABITAT FOR NESTING

The dense shrub foliage at nest-sites may function as visual screening from predators (Murphy 1983, Yahner and Cypher 1987, Martin and Roper 1988, Holway 1991, Knopf and Sedgwick 1992). Holway (1991) found no difference in visual screening between successful and unsuccessful Black-throated Blue Warblers nests, but the value of dense foliage may not be in direct screening of the nest but in forcing a predator to search all dense shrub patches and decreasing the chance that a nest will be found. Shrubs on these plots typically occur in dense patches, as evidenced by the high standard deviation of density at random points (Table 4, mean = 67.5, SD = 30.5). By locating their territories on plots with high shrub density (Steele 1992), Black-throated Blue Warblers increase the number of dense patches of shrubs that are potential nesting sites thus making search by predators less efficient. Martin and Roper (1988) suggest that Hermit Thrushes (*Catharus guttatus*) select habitat with many potential nest-sites to reduce nest predation.

In this study, most nests were placed in hobblebush shrubs, especially where stems overlap, a situation which occurs commonly in dense patches. Thus, selection of hobblebush as a nest substrate could restrict this species to forests with dense shrub patches. However, Black-throated Blue Warblers also breed where hobblebush is rare or nonexistent in New Hampshire (Harding 1931 and pers. observ.) and in New York (B. Noon and S. Droege, pers. comm.). Consequently, selection of a single shrub species for a nest substrate is unlikely to affect habitat choice.

## IMPLICATIONS FOR COMMUNITY STRUCTURE

My results suggest that nesting sites may be more important than foraging sites in determining the habitat that Black-throated Blue Warblers select. Similar suggestions have been made for other species. The importance of nest-site availability in the distribution of cavity nesting species is well known (Connor et al. 1975, 1976; Evans and Connor 1979; Brawn and Balda 1988). MacKenzie et al. (1982) and Martin (1988a, 1988b, 1988c) argued that nest-site selection has a strong effect on distribution of open-nesting species as well. Several empirical studies concur. First, Hermit Thrushes are limited to sites with small

white fir trees (*Abies concolor*) which are used for nesting but not foraging (Martin and Roper 1988). Second, nest-site selection by Willow Flycatchers is more restrictive than perch-site selection (Sedgwick and Knopf, 1992). Third, the disappearance of several bird species during habitat change has been attributed to a loss of nesting habitat (Kilgore 1971, Raphael et al. 1987). Finally, nesting requirements may be responsible for the narrower habitat breadths of passerines in summer (Bilke 1984).

Assemblages of birds therefore probably contain species that are restricted to certain habitats because of nesting sites requirements plus others whose foraging requirements are more restrictive. This means that the diversity of nesting opportunities on a site should affect which species occur and their abundances. If nesting sites are a limiting resource, then competitive interactions and resource partitioning should occur over nesting sites rather than over food resources. Several studies have shown differences among related species in how they obtain prey (MacArthur 1958, Holmes et al. 1979, Sabo and Holmes 1983). These foraging differences are often attributed to resource partitioning caused by competition (Schoener 1974). These same studies, however, also show broad overlap among species in their foraging behavior. In contrast, nesting sites of many species show very little overlap (Martin 1988b). In the forest at Hubbard Brook, Black-throated Blue Warblers' nests are within 2 m of the ground but not on the ground, Ovenbirds (*Seiurus aurocapillus*) nest on the ground, Veerys (*Catharus fuscescens*) nest on the ground or in low shrubs, American Redstarts (*Setophaga ruticilla*) nest in a crotch along the main trunk of a sapling or tree, Red-eyed Vireos (*Vireo olivaceus*) nest on a branch away from the trunk, Hermit Thrushes nest on or near the ground or above 8 m, and Black-capped Chickadees (*Parus atricapillus*), White-breasted Nuthatches (*Sitta carolinensis*) and woodpeckers (*Picoides* spp.) nest in cavities (Holmes 1990). These distinct nesting requirements might be caused by resource partitioning resulting from interspecific competition, but are more likely due to lower nest predation because a diversity of types of nest sites might inhibit the development of a search image by predators (Martin 1988c). Thus, an alternative explanation for how vegetation structure affects bird communities is that

the diverse physical structures of plants (such as trunks, crotches, cavities, crossed branches), plus the foliage that conceals nests, provide opportunities for a variety of nest-sites and thus may allow species with diverse nest-site requirements to co-occur.

Certainly, foraging sites are a necessary element of habitat for bird species, but a more complete picture of how birds use resource space may be possible if nesting sites as well as foraging behaviors are considered. For example, multivariate descriptions of the relationships among species may be clearer or more complete if they include measurements of nesting site and substrate (see MacKenzie et al. 1982); differences among species may be greater and species may be more evenly spread out over resource space. Also, quantitative descriptions of habitat might be more precise if they included habitat variables associated with nest-sites as well as those describing foraging sites. I suggest that habitat descriptions should include variables such as density of certain types of crotches, branching patterns, branch angles, cavities in dead and alive trees, intersecting shrub branches, and fallen dead branches among shrubs. These variables might improve the predictive capabilities of habitat models.

My results also have implications for habitat management. Habitat enhancement might prove more effective if nesting requirements were understood and duplicate nest-sites were created. Conversely, control for some undesirable species might better be accomplished by removing nesting substrates rather than food.

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