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GEOGRAPHIC VARIATION IN HABITAT STRUCTURE OF THE BLACK-THROATED GREEN WARBLER (*DENDROICA VIRENS*)

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Abstract.—Habitat structure of the Black-throated Green Warbler (*Dendroica virens*) was examined at five study sites: (1) Mount Desert Island, Maine; (2) Mount Blue State Park, Maine; (3) White Mountain National Forest, New Hampshire; (4) southern Adirondacks, New York; and (5) Itasca State Park, Minnesota. Principal component analysis of 13 habitat-structure variables measured at each site produced habitat gradients from tall to shorter canopies, large to smaller trees, and coniferous to deciduous forests. A second ordination indicated that the habitat sampled included five plant-community types: pine forests, spruce-arbor vitae, balsam fir, mixed spruce-fir-deciduous, and beech-maple-birch. Consistent structural features within the total range of habitats sampled were difficult to identify. I suggest that widely occurring species such as the Black-throated Green Warbler have a wide range of habitats with a suitable structure and that regional analyses, even within a single plant-community type, may be of limited value with regard to habitat management when considering the entire range of many species. *Received 10 September 1981, resubmitted 24 May 1982, accepted 20 October 1982.*

Geographic variation has been analyzed for several aspects of avian biology—song dialects (Nottebohm 1975), morphology (James 1970), foraging behavior (Roth 1979), and plumage (Pratt 1980)—yet most analyses of avian habitat have been confined to single-site comparisions (Whitmore 1975, Smith 1977, Collins et al. 1982). Community-level comparisons between sites are common (e.g. Karr 1971, Rabenold 1978, Rotenberry and Wiens 1980), but these studies were based upon a defined habitat structure so that bird-species diversity, niche parameters, and behavior could be compared within a similar habitat type.

Some detailed analyses of geographic habitat differences for a single species do exist (Noon and Able 1978, Cody 1978, Noon et al. 1980, Noon 1981). In particular, Noon et al. (1980) determined that habitat structure was consistent within the range of most eastern United States breeding birds. Their analysis was cast in a community-oriented context, however, so some important differences in habitat structure between sites may not have been detectable with their techniques. In this study I have used the 0.04-ha circle technique, a more direct approach, to elucidate local habitat structure at five sites within the range of the Black-throated Green Warbler (*Dendroica virens*). In this paper, "habitat" refers to the specific life form or structure of the vegetation in which a species occurs (Grinnell 1917, James 1971). The Black-throated Green Warbler was selected because of its wide geographic range and because this species is reported from a number of plant-community types (Brooks 1940, Bent 1953), including pine forests (Collins et al. 1982), deciduous vegetation (Maurer and Whitmore 1981), and spruce-fir (*Picea-Abies*) forests in the northeast (MacArthur 1958). Although differences in vegetation structure between plant-community types would appear obvious intuitively some characteristics of this species' habitat may not vary between sites. Therefore, data were gathered in Maine, New Hampshire, New York, and Minnesota to determine: (1) is the habitat structure of the Black-throated Green Warbler different at several points in its range, and (2) if differences exist, which structural variables change and which are similar between sites? Knowledge of the range of habitat structure may facilitate development of regional models for predicting the future extent of a species' habitat (Shugart 1981).

Materials and Methods

To analyze patterns of habitat structure of the Black-throated Green Warbler, five study sites were selected: (1) Mount Desert Island (MDI), a large island about 300 m off the coast of Maine, the vegetation of which consists of large areas of spruce and arbor vitae (*Thuja occidentalis*) forests (Davis 1966) and of

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TABLE 1.   Mean and standard error for the habitat-structure variables per 0.04-ha sample. Differences were tested by Kruskal-Wallis one-way analysis of variance (H-statistic). Site abbreviations are given in the text; variable abbreviations are presented in Table 2.

Site		GC	SC	CC	CH	CO	SPT	T1	T2	T3	T4	T5	T6	T7
MDI	$\bar{x}$	52.5	21.0	84.0	46.2	79.0	5.5	44.2	43.2	15.7	7.0	2.9	0.0	0.0
($n = 10$)	SE	6.8	4.5	2.9	1.9	3.5	0.7	6.7	3.4	1.4	0.8	1.0	0.0	0.0
MBP	$\bar{x}$	36.8	32.7	92.7	46.7	34.5	8.5	34.4	21.4	9.9	3.8	1.5	0.6	0.2
($n = 11$)	SE	3.9	5.8	1.9	2.3	5.4	0.6	4.0	3.1	1.4	0.6	0.5	0.4	0.1
WMF	$\bar{x}$	45.5	43.5	94.5	49.9	23.5	6.9	29.5	19.0	10.6	4.9	3.9	1.4	0.3
($n = 10$)	SE	5.9	7.7	1.8	1.6	5.2	0.5	2.6	2.2	1.1	0.7	0.6	0.2	0.2
NYA	$\bar{x}$	28.8	78.8	92.5	66.8	36.2	7.0	25.5	6.5	2.2	4.2	4.8	3.0	2.2
($n = 4$)	SE	6.2	2.7	2.2	4.1	5.7	0.9	2.8	1.3	0.4	1.0	0.9	0.6	0.7
ISP	$\bar{x}$	52.7	39.0	84.3	66.1	50.3	5.7	15.1	10.5	5.7	4.4	3.3	1.9	0.9
($n = 15$)	SE	4.3	5.7	3.4	3.8	7.7	0.3	2.2	1.5	0.7	0.9	0.7	0.7	3.9
H-statistic[a]		4.3	6.2	5.6	20.5*	22.1*	0.7	25.0*	27.3*	20.9*	2.9		24.9*[b]	

[a] * = Significant at $P < 0.01$.
[b] T5, T6, T7 were combined for the analysis of variance.

deciduous forests of beech (*Fagus grandifolia*) and maples (*Acer* spp.); (2) Mount Blue State Park and vicinity (MBP) in west central Maine, a region of deciduous-coniferous vegetation, with spruce and fir occurring in the upper elevations; (3) White Mountain National Forest (WMF) in central New Hampshire, a large multi-use national forest containing old growth stands of yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), beech, and red spruce (*Picea rubens*) at lower elevations and increasing dominance of spruce and fir at higher altitudes (Bormann et al. 1970); (4) Southern Adirondacks (NYA) in east central New York, containing a deciduous component similar to that of WMF, with increasing red spruce at higher elevations (Braun 1950); and (5) Itasca State Park (ISP) in north central Minnesota, a site having deciduous, mixed, and coniferous forests of white spruce (*Picea glauca*)-fir along with groves of large red and white pine (*Pinus resinosa* and *P. strobis*). These five sites do not cover the entire range of the Black-throated Green Warbler, but they do provide a sample of the habitat structure at different points in this species' range.

At each study site, 13 vegetational characteristics (Table 1) were measured in 0.04-ha circles centered on the song perch of a singing male Black-throated Green Warbler. Only one sample per individual was recorded, and samples were located without regard to vegetation type, elevation, or topography. The number of circles recorded per site was: MDI = 10 (16–17 June 1980), MBP = 11 (30 May–11 July 1980), WMF = 10 (26–28 June 1980), NYA = 4 (17 July 1980), and ISP = 15 (1 June–7 July 1978, 1979). Because differences in habitat occupancy may be a function of year-to-year variation (Wiens 1981), an effort was made to sample as many sites as possible within one breeding season. Thus, the time available at several

locations was limited. Potential habitats at ISP and MPB are well represented, however, because of extensive field reconnaissance during an entire breeding season. Samples from MDI and WMF represent the most abundant local vegetation types, as well as some other forest types. NYA was not adequately sampled, but the data are included in an effort to identify, to some extent, habitat features that may be constant at all sample areas.

Statistical differences for each variable at the four sites with 10 or more samples were determined using a non-parametric Kruskal-Wallis one-way analysis of variance by ranks. Multivariate methods, however, elicit comparisons of habitat structure between sites by incorporating all variables into one analysis. Therefore, habitat structure for the 50 samples at the five sites was analyzed by principal component analysis (PCA) from a correlation matrix (standardized data) of the habitat variables. To facilitate presentation and to visualize general habitat variability of within-site samples, 95% concentration ellipses (Sokal and Rohlf 1969) were drawn around the means for each site in the space defined by the first two principal components. These ellipses depict relationships of the Black-throated Green Warbler's habitat at each site along structural gradients defined by a subset of the 13 habitat variables, and they provide a visual representation of between-site habitat differences. Distortion is induced by dimensionality problems, sample size differences, and the amount of variance accounted for by the PCA axes (Collins et al. 1982). Therefore, the ellipses do not imply a statistical test of differences in habitat structure between sites, nor do the sizes of the ellipses represent within-site variance in habitat, because ellipse size is affected by sample size (Sokal and Rohlf 1969).

To determine the plant-community types in which

TABLE 2.   Summary of the first four and last two principal components. Values are correlations with original variables. Boldface highlights important correlations. All variables were expressed as per 0.04 ha.

Variable	Mnemonic	Principal component					
		I	II	III	IV	XII	XIII
Eigenvalue		3.72	1.79	1.56	1.29	0.19	0.10
Percentage of variance		28.6	13.7	12.0	9.9	1.5	0.8
Percentage ground cover	GC	0.111	**0.577**	0.261	−0.051	−0.023	0.023
Percentage shrub cover	SC	**−0.532**	−0.314	0.160	−0.294	−0.027	−0.007
Percentage canopy cover	CC	−0.072	**−0.496**	−0.329	**0.551**	−0.139	0.010
Percentage conifer	CO	0.238	**0.709**	**−0.423**	0.258	−0.176	0.126
Canopy height	CH	**−0.739**	0.466	−0.281	0.111	0.128	−0.155
Number of tree species	SPT	0.056	**−0.510**	−0.016	**0.508**	0.015	0.028
Trees 7.5–15 cm dbh[a]	T1	**0.677**	0.019	0.264	0.299	0.092	0.038
Trees 15.1–23 cm dbh	T2	**0.876**	0.205	−0.154	0.160	0.066	**−0.233**
Trees 23.1–30 cm dbh	T3	**0.818**	0.059	−0.368	−0.032	**0.300**	0.066
Trees 30.1–38 cm dbh	T4	0.267	−0.196	**−0.549**	**−0.601**	−0.088	−0.023
Trees 38.1–53 cm dbh	T5	−0.397	−0.076	**−0.711**	0.002	0.069	0.036
Trees 53.1–68 cm dbh	T6	**−0.657**	0.208	−0.167	0.270	0.066	0.009
Trees > 68 cm dbh	T7	**−0.511**	0.169	0.166	0.175	0.077	0.014

[a] Diameter at breast height.

the Black-throated Green Warbler was found, importance percentages [IP = (relative density + relative dominance)/2; Curtis and McIntosh 1951] were calculated for tree species in each of the 50 circular plots. Tree species with less than four occurrences were deleted from the analysis, and red spruce and white spruce data were pooled for analysis. Both species occur at the four eastern sites; only the latter occurs at ISP. The IP's of the species were $\log_{10}$ transformed and subjected to reciprocal averaging-polar ordination (PO-RA; Hill 1973, Gauch 1982). Untransformed variables were analyzed by an unweighted pair group cluster analysis using arithmetic averaging (UPGMA, Sneath and Sokal 1973), and DFA of the groups was determined by cluster analysis (del Moral 1975). The restructured groups were then located on the vegetation ordination and identified by leading dominants. [See Collins et al. (1981) for a detailed description of the vegetation analysis procedures.]

Although the vegetation variables chosen for measurement are thought to be important aspects involved in habitat selection, it is important to note that this study does not analyze habitat selection by the Black-throated Green Warbler. Instead, my data characterize the types of places that are acceptable to the species based upon habitat correlations (Wiens 1976). One could address habitat selection to some extent by comparing occupied and unoccupied sites (Smith 1977), but this was not done here. Measurements of unoccupied sites may be difficult to interpret due to the uncertain meaning of absence (Johnson 1981). Vegetation types lacking territories cannot be interpreted as unsuitable habitat, because occupation may simply be a function of population density.

RESULTS

Based on the Kruskal-Wallis one-way analysis of variance by ranks, six habitat variables [canopy height, percentage conifer, and trees of 7.5–15 cm, 15.1–23 cm, 23.1–30 cm, and greater than 38.1 cm diameter at breast height (dbh)] were significantly different between the four sites with 10 or more samples (Table 1). Forest canopy was tallest in Minnesota due to the occurrence of large red and white pines. In addition, pine stands contributed to the high average percentage of coniferous vegetation at ISP. Conifers were frequent at MDI also, but these trees were mainly spruce and arbor vitae. Differences in tree-size class reflect dissimilar forest-tree population structure primarily between MDI and ISP. In general, the more northerly MDI forests contained many individuals in the smaller size classes, while ISP forests contained more large trees.

Four components with eigenvalues greater than 1.0 (total variance = 64.3%) were extracted from the correlation matrix of habitat variables (Table 2). Principal component I (28.6% of the variance) is a forest-height component separating habitats with large trees, tall canopies, and a low percentage of shrub cover (CH, T6 SC, T7) from areas characterized by smaller trees (T2, T3, T1). Component II (13.7% of the variance) is a deciduous to coniferous component in which deciduous samples have greater tree-species richness and canopy cover, while

coniferous stands have fewer tree species and greater ground cover. Component III (12.0% of the variance) has large negative loadings for medium-sized trees and the percentage of coniferous vegetation (T5, T4, CO). The fourth component (9.9% of the variance) has high positive loadings for CC and SPT and a negative loading for T4, suggesting that more tree species occur as the forest canopy closes.

Distribution of sites in the space defined by the first two principal components (Fig. 1) shows that Black-throated Green Warbler habitat at NYA and ISP contained larger trees and taller canopies, whereas the MBP and MDI habitats had smaller trees of lower stature. WMF and MBP overlap considerably in PCA space, with the habitat of the former containing, on the average, more large trees than that of the latter. Along the second component, ISP and MDI habitats had more coniferous vegetation than did NYA, WMF, or MBP. Indeed, some circular plots at the latter sites contained only deciduous forest components. In summary, differences in habitat structure, based primarily upon tree size and the percentage of coniferous vegetation, occur at points within the range of the Black-throated Green Warbler. In other words, habitats ranged from taller to shorter, more dense forests and from coniferous to mixed and deciduous forests.

It is difficult to determine which structural variables, if any, represent consistent features of habitat throughout a species' range. Pearson's plane of closest fit (Morrison 1967) may provide some insight into this problem. This technique focuses on variables with the largest correlations on components with the lowest eigenvalues. These variables are considered to be relatively constant within a data set; therefore, when considering habitat structure, such high, variable correlations may represent consistent aspects of a species' habitat. The largest correlations on the 13th and 12th components were with trees 15–23 cm dbh and 23–30 cm dbh, respectively; both correlations were low (Table 2), however. These two variables were important along the first component as well. This may reflect a high degree of variability in the actual number of small trees in the habitat, yet the presence of some small trees may be an essential feature of the Black-throated Green Warbler's habitat. Alternatively, the presence of small trees may simply be a consequence of the population structure of forest vegeta-
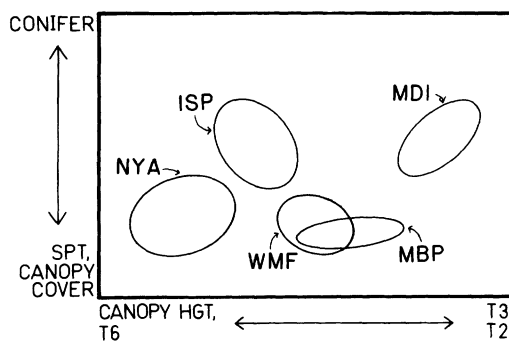

Fig. 1. A two-dimensional principal component analysis showing the position of the five study sites within habitat structure space. The 95% concentration ellipses were drawn to indicate the variability of within-site habitat structure. Axis I is a gradient from tall, large trees and low shrub cover to more smaller trees. Axis II is a deciduous to coniferous forest gradient. See text for site abbreviations and Table 2 for variable abbreviations.

tion (e.g. Goff and West 1975). Interpretations of Pearson's plane of closest fit must be extremely cautious, because the analysis is applicable only to measured variables that are hypothesized to be important structural features of a species' habitat. In addition, if habitat features have threshold values above which a territory becomes suitable, then, because only occupied territories were sampled, the variance noted for these variables would not be meaningful. As previously mentioned, though, the analysis of absence is difficult to interpret. Essentially, any statement relating variable correlations to habitat selection would be invalid until experimental manipulations of habitat structure had been conducted.

Based upon the tree-species analysis, the vegetation sampled at the five sites can be classified into five general plant-community types (Fig. 2). MDI and ISP, the most distant sites sampled within the range of the Black-throated Green Warbler, support vegetation that is unique with respect to that of the other three sites. MDI had arbor vitae-spruce forests, whereas ISP supported large red and white pines. Stands dominated by balsam fir (*Abies balsamea*) were common in MBP and ISP, although these stands differed in the less important tree components. Deciduous stands of yellow birch, sugar maple, and beech were common at the NYA, MBP, and WMF sites.
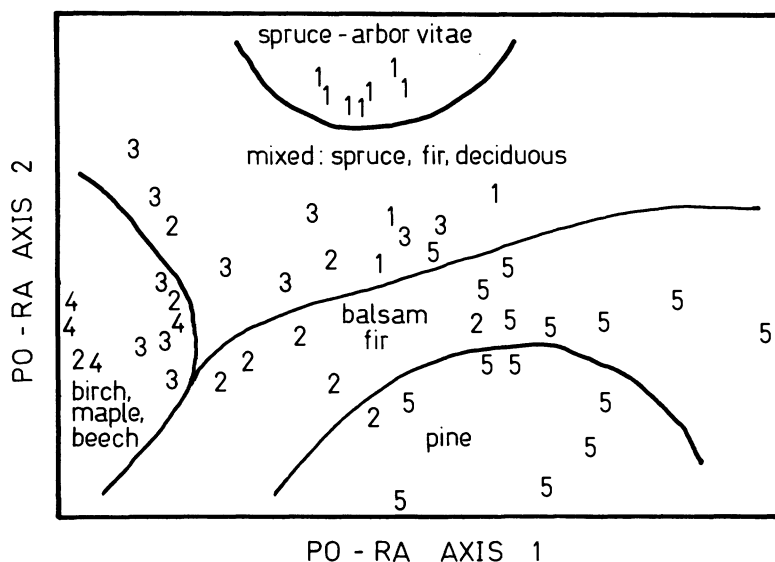
Fig. 2. A two-dimensional reciprocal averaging-polar ordination of the vegetation in the sample plots showing the general plant-community types of the study areas. 1 = Mount Desert Island, Maine; 2 = Mount Blue State Park, Maine; 3 = White Mountain National Forest, New Hampshire; 4 = southern Adirondacks, New York; 5 = Itasca State Park, Minnesota. Location of the lines is based upon the UPGMA cluster analysis.

The most abundant vegetation type sampled, however, was mixed forest of spruce-fir and deciduous species, including red maple (*A. rubrum*), sugar maple, yellow birch, paper birch (*B. papyrifera*), and beech. Hemlock (*Tsuga canadensis*) was found in several stands, yet it was rarely a major component in the habitat of the Black-throated Green Warbler. Thus, it appears that some vegetation types occur at more than one study site and that ISP and MDI additionally contain unique plant-community types.

Discussion

Previous analyses of the Black-throated Green Warbler indicated that this species breeds in a variety of plant-community types (Brooks 1940, Bent 1953, Greenberg 1979). These plant communities, however, were rarely analyzed to determine what structural features of the habitat were stable or variable at different sites within the range. My findings indicate that the habitat of the Black-throated Green Warbler differs in three-dimensional structure as well as in plant-species composition (Figs. 1 and 2). Structural differences primarily reflect gradients in tall to

shorter canopies, large to smaller trees, and coniferous to deciduous forests. Five plant-community types were identified, two of which were localized: pine forests at ISP and spruce-arbor vitae vegetation at MDI. The three other community types, balsam fir, birch-maple-beech, and spruce-fir-deciduous, were found in two or more sites, with the latter being the most abundant type.

Sites with similar plant-community types did not necessarily have the same habitat structure. For instance, MBP and ISP were the only sites sampled containing the balsam-fir community type (Fig. 2), yet these sites were very different in habitat structure (Fig. 1). Habitat descriptions based only upon dominant plant species are not always useful, because habitat structure may be dissimilar at different sites within any widely distributed vegetation type.

Much quantitative habitat research has focused on identifying habitat variables consistently associated with and characteristic of a given species' habitat or niche-gestalt (James 1971, Smith 1977, Collins et al. 1982). Rarely have common features of the habitat been determined for species at different points in their range (Cody 1978, Noon and Able 1978). Noon

et al. (1980) detected "habitat shifts" in only 2 of 25 comparisons of eastern United States breeding passerines. Interestingly, both were warblers. In general, warblers are considered to be opportunistic foragers (Morse 1971, 1973), although the Black-throated Green Warbler may be more stereotyped than some others (Morse 1980); thus, habitat shifts are not surprising, because these species may be responding to variable food resources. Futuyma and Gould (1979) demonstrated that tree species support different populations of phytophagous insects. In addition, Holmes and Robinson (1981) showed that some tree species contained more insects than others and that foliage gleaners responded to increased insect density by spending a greater proportion of time foraging in these trees. Also, foliage gleaners such as the Black-throated Green Warbler showed a preference for trees with multilayered leaf arrangements (Horn 1974, Holmes and Robinson 1981). These factors, which to a large extent are a function of tree-species composition, will vary across a species' range and conceivably may influence territory selection, resulting in structural differences in habitat at different points within the range.

There is some agreement between the univariate and multivariate comparisons of habitat variables for the Black-throated Green Warbler with regard to differences in the number of small trees and canopy height between sites (Tables 1 and 2). These analyses do not provide a clear indication of structural similarity between sites, however, several explanations apply as to why no common thread in habitat structure between sample areas could be identified. Smith (pers. comm.) found that 0.04-ha circles were too large to characterize the vegetation used by Dark-eyed Juncos (*Junco hyemulis*) in northern Utah. The low amount of variance accounted for by the PCA suggests an overall uniformity of habitat among all samples. Perhaps the variables are not sensitive enough to detect subtle patterns of structural similarity (Anderson 1981). Alternatively, habitat selection may be based upon an evaluation by the bird of the gross physiognomy of the vegetation. Thus, large fluctuations noted in habitat structure may indicate that a considerable range exists for each variable. A combination of these variables within the suitable range may then elicit a territorial settling re-

sponse (Hildén 1965). Therefore, in a comparison of widely scattered sites, similarities in habitat structure beyond the presence of trees need not exist and would not be detected by variance-reduction procedures such as principal components analysis.

The large breeding range of the Black-throated Green Warbler incorporates a broad spectrum of plant communities and vegetation structure. These plant communities are subject to different disturbance frequencies and intensities, which affect vegetation on a scale from a highly localized level (i.e. one tree) to large-scale disturbances such as fire (White 1979, Runkle 1981). The increasing fragmentation and destruction of available habitat by man's activities may have enhanced an opportunistic adaptation to local variations in habitat structure by local bird populations. Future habitat analyses, for management purposes in particular, must be based upon site-specific vegetation variables, especially for wide-ranging habitat generalists such as the Black-throated Green Warbler, because wide-scale application of local habitat data may often be of limited predictive value at a regional level.

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