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HABITAT RELATIONSHIPS AND HABITAT VARIABILITY OF THE WOOD WARBLERS (PARULIDAE)

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# HABITAT RELATIONSHIPS AND HABITAT VARIABILITY OF THE WOOD WARBLERS (PARULIDAE)

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HABITAT RELATIONSHIPS AND HABITAT VARIABILITY OF THE WOOD WARBLERS (PARULIDAE)

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# PREFACE

This study examines the habitat structure, relationships, and variation of the wood warblers (Parulidae) in the north-central and northeastern United States. The dissertation has been written in manuscript form for publication. Chapter I, "A comparison of nest-site versus perch site vegetation structure for seven species of warblers," has been accepted for publication in the Wilson Bulletin. Chapter II, "Habitat relationships of the wood warblers (Parulidae) in north-central Minnesota," will be submitted to Oikos. Chapter III, "Geographic variation in the habitat of the Black-throated Green Warbler (*Dendroica virens*)," will be submitted to the Auk.

Special thanks go to my major professor, Dr. Paul Risser, for his support and guidance throughout this project, along with his willingness to let me venture beyond the scope of plant ecology. Also, special thanks to Dr. Frances James for her guidance, encourangement, and valuable theoretical opinions.

I would like to express my appreciation to the other members of my committee, Dr. James Estes, Dr. Douglas Mock, and Dr. Gary Schnell, for their interest and helpful editorial comments.

Many friends, especially Dwight Adams, Tom Antonio, Susan Barber, Karen Dooley, and Gordon Uno, have provided moral support, encouragement, and theoretical comments for which I am sincerely grateful.

I thank Dr. Bernd Heinrich for letting me study the warblers on his property and for useful maps and habitat locations.

My deepest thanks go to my parents for their support and understanding of my many years of graduate school. Finally, I thank my wife, Pat, for her help with the field work, her love, and her patience throughout my graduate career.

This research was supported by two grants from the Chapman Memorial Fund of the American Museum of Natural History, and by a Malvin and Josephine Herz Foundation Summer Fellowship at the University of Minnesota Biological Station.

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ABSTRACT

Habitat relationships of wood warblers (Parulidae) were examined for within-territory, within region, and between-region patterns. By examining nest-site versus song perch site vegetation structure, within territory variation was identified. Circular samples of vegetation structure should be centered not only on song perch sites, but also on nest-sites or female foraging areas, because song perch sites alone may over-estimate the tree component in the habitat of some species.

Based on 13 structural variables, the habitat structure of 16 species of wood warblers breeding in north-central Minnesota can be divided into three general habitat types: open country, shrub-forest edge, and mature forest. Reciprocal averaging ordination produced a gradient of habitat relationships from forest to open country species, the latter being somewhat distinct. Based on principal components analysis, most species had habitats with variable vegetation structure. These habitat characteristics are discussed in relation to competition theory.

The habitat of Black-throated Green Warbler (*Dendroica virens*) was examined at five sites in the north-central and northeastern United States. Principal components analysis of 13 habitat variables showed between site differences in canopy height, tree size, canopy cover, and percent of

coniferous vegetation. Although some sites supported unique plant community types, tree species composition was not related to difference in habitat structure. Instead, habitat differences were mostly attributable to differences in the structure of the vegetation.

CHAPTER I

# A COMPARISON OF NEST-SITE AND PERCH SITE VEGETATION STRUCTURE FOR SEVEN SPECIES OF WARBLERS

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One aspect of the study of avian niches has been the analysis of habitat relationships among breeding birds. In general, each species appears to select a characteristic conformation of vegetation structure, its niche-gestalt (James 1971), in which to establish a territory (Hilden 1965). The territory includes for many breeding passerines suitable sites for singing, feeding, and nesting. Some previous descriptions of avian habitat relationships (James 1971, Whitmore 1975, Smith 1977) have been based on data collected from within 0.04-ha (0.1-a) circular plots centered on song perches within the territory of a singing male. Various structural attributes of the vegetation are recorded in these plots (James and Shugart 1970), and data from several circles can be pooled to determine the general habitat for each species. In the past, these data have been presented as averages and thus, do not permit analysis of within-habitat differences. The purpose of my research was to determine if predictable differences in vegetation structure occur within territories of each of several species of parulid warblers (Table 1). This is part of a larger project analyzing the habitat relationships and geographic habitat variation for warblers in Maine and Minnesota.

Study area and methods. The study was conducted in Itasca State Park located in Clearwater, Hubbard, and Becker counties, north-central Minnesota. The park contains 12,500 ha of which 941 ha (7%) are lakes and ponds (Hansen, Kurmis, Ness 1974). The area is in the hemlock-white pine-northern hardwoods forest region (Braun 1950). Both logging and fire have contributed to the diversity of vegetation types in the region, such as aspen coppice, mature upland spruce-fir forest, hardwood stands, and pine stands. Parmelee (1977) reported 27 species of warblers in the park, of which 13 are considered common nesting species.

Data were also obtained for the Nashville and Palm warblers from the Redlake Peatlands Natural Area, northern Beltrami Co., Minnesota. The vegetation in this region consists of forested islands of small black spruce and tamarack; dense, low ericacious shrubs; and a continuous ground cover of sedges and Sphagnum spp.

The criterion used to determine if consistent within-habitat variability occurs was a comparison between 0.04-ha circular plots at the nest site and at a song perch site, sampled within the territory of a breeding male bird. Thirteen structural characteristics of the vegetation were measured in each circle (Table 2). Supplimental song perch site data were obtained from another data set in which nest-sites were not located. A total of 23 nest-sites and 75 perch sites was sampled (Table 1).

Differences between the vegetation structure of the nest-sites and song perch sites were compared by the Wilcoxon matched-pairs signed-ranks test (Seigel 1956) between the structural characteristics of nest and song perch sites.

Comparisons for each species were made at two levels: nest-sites with corresponding perch sites, and average nest-site structure versus average perch site structure.

Typically, 0.04-ha plot data are analyzed by multivariate ordination techniques. These methods elicit habitat patterns and indicate the most important vegetation variables that produce these patterns. In this case, discriminant function analysis (DFA) was applied to each species' habitat data to determine whether nest and song perch sites differ within species. DFA combines the habitat variables in a stepwise fashion into the linear discriminant function that can best segregate nest-sites from perch sites. The advantage of the multivariate DFA over the univariate Wilcoxon test is that only the former incorporates the variability inherent in any habitat structure data set. For a description of DFA see Morrison (1979). Discriminant function analysis was performed with BMDP (Dixon 1977).

Results and discussion. The habitat of the seven species of warblers ranged from open country to forest and forest-edge (Table 1). In spite of the small sample size, some patterns and differences in nest-site and song perch site structure can be extracted.

Five of 17 samples of nest-sites had vegetation structure that was significantly different from the corresponding perch site structure within a territory (Table

3). Four of the five differences were for open country nesting species. The differences in the structurally simple open habitats of the Yellow and Chestnut-sided warblers were due to the greater number of trees at song perch sites which increased canopy cover, tree height, and percent conifer in the canopy. The song perch site of the Northern Parula had higher ground and shrub cover, and percent conifer in the canopy than at the nest location.

If the nest-site and song perch site data for each species are averaged and again compared by the Wilcoxon test, the within-territory habitat differences between nest and song perch sites of the Northern Parula were no longer statistically different (N=12, T=21). However, both the Yellow and Chestnut-sided warblers still showed significant differences (N=12, T=1 and T=9, respectively). Average perch site variables for these species contained greater tree component structure than average nest-sites, supporting the conclusion based on the within-territory comparisons.

F-values for six discriminant functions were significant for only two species, Common Yellowthroat and Northern Parula (Table 4). Percent conifer and canopy height significantly separate Common Yellowthroat nest and perch sites. However, the DFA reclassified one perch site into the nest-site group, and _vice versa_. Thus, within this data set, some structural overlap occurs between the two types of sites. Eight variables entered into the Northern Parula discriminant function, most of which were tree size-class variables. The nests of this species were located in forest to forest-edge habitat with variable numbers of large, deciduous and coniferous trees, and a relatively open canopy. Perch site locations were also variable yet they were most often found in the forest rather than at the forest edge. No nest or perch sites were reclassified, so complete discrimination between these sites was possible.

In summary, it appears that for the ground nesting Palm Warbler, Nashville Warbler, and Ovenbird, minimal differences exist between nest-site and perch site structure. The Yellow and Chestnut-sided warblers showed significant differences in individual and average nest-site-perch site comparisons, yet these differences did not appear in the DFA. The Common Yellowthroat showed a difference only in the multivariate analysis. Lastly, both uni- and multivariate comparisons of the Northern Parula nest and perch site variables imply locally different within habitat vegetation structure.

Several factors may cause the differences observed in these tests, one of which is the inherent variability of the vegetation. Curtis (1959) stressed the compositional variation of vegetation and concluded that the same plant communities in a region resemble each other only to the extent of 50 to 70 percent. Many territories of forest nesting species are greater than 0.5 ha (Bent 1953), thus incorporating the natural variability of the vegetation.

Generally, the male selects and defends the territory, whereas, the female chooses the nest-site. Different criteria are probably important at each site: conspicuousness for the displaying male, versus a sheltered nest location. Thirdly, previous ecological studies of warblers have shown that males and females use different parts of the territory (Morse 1968, 1973, Busby and Sealy 1979). In particular, males forage farther from the nest and higher in the canopy than do females. Finally, the selection of a perch site as the center of a circular plot assumes some degree of vegetation structure. Therefore, the wide ranging foraging behavior of males, large territories, and differential territory use combine to introduce within-habitat variability.

Many stimuli such as specific aspects of vegetation structure, presence of other birds, food, and previous breeding success are proximate factors that can combine to elicit a territorial settling response in breeding birds (Hilden 1965). The measurement of vegetation structure is a reliable means of summarizing these stimuli since the physical habitat provides the background for the variables in the life cycle of a breeding bird. The suitability of the 0.04-ha circle technique for summarizing and describing the three-dimensional habitat structure for bird species remains valid. Certain caveats, however, should be considered. James (1971) stated that centering a circular plot on a song perch "... may give a biased view of habitat for species which occur in open areas and choose singing perches in places different from their foraging areas, but this objection is minimized in the forest." She later suggested that the 0.04-ha circle method was only suitable for areas with trees (James 1978). However, my evidence for the Northern Parula suggests that within-habitat variability exists in forest and edge nesting species. Even in forest, numerous samples may be necessary to incorporate habitat variability. Locating circular samples on nest-sites or on female foraging areas is recommended whenever possible as a means of incorporating within-habitat variation. Otherwise, caution should be used when interpreting habitat structure because song perch sites of forest and open country nesting species may over-estimate the tree component of the habitat.

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## LITERATURE CITED


Bent, A. C. 1953. Life histories of North American wood warblers. U. S. Natl. Mus. Bull. 203.

Braun, E. L. 1950. Deciduous forests of eastern North America. Blakeston Press, Philadelphia, Pa.

Busby, D. G. and S. G. Sealy. 1979. Feeding ecology of a population of nesting Yellow Warblers. Can. J. Zool. 57: 1670-1681.

Curtis, J. T. 1959. The vegetation of Wisconsin. Univ. Wisconsin Press, Madison, Wi.

Dixon, W. J. 1977. Biomedical computer programs, P-series. Univ. California Press, Los Angeles, Ca.

Hansen, H. L., V. Kurmis, and D. D. Ness. 1974. The ecology of upland forest communities and implications for management in Itasca State Park, Minnesota. Univ. Minnesota Agric. Exp. Sta. Bull. 298, For. Ser. 16.

Hilden, O. 1965. Habitat selection in birds. Ann. Zool. Fenn. 2: 53-75.

James, F. C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bull. 83: 215-236.

James, F. C. 1978. On understanding quantitative surveys of vegetation. Am. Birds 32: 18-21.

James, F. C. and H. H. Shugart. 1970. A quantitative method of habitat description. Audubon Field Notes 24: 727-736.

Morrison, D. F. 1979. Multivariate statistical methods. 2nd

Ed. McGraw-Hill Book Co., New York, NY.

Morse, D. H. 1968. Quantitative study of male and female spruce-woods warblers. Ecology 49: 779-784.

Morse, D. H. 1973. The foraging of small populations of Yellow Warblers and American Redstarts. Ecology 54: 346-355.

Parmelee, D. F. 1977. Annotated checklist of the birds of Itasca State Park and surrounding areas. Loon 49: 81-95.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., New York, NY.

Smith, K. G. 1977. Distribution of summer birds along a forest moisture gradient in an Ozark watershed. Ecology 58: 810-819.

Whitmore, R. C. 1975. Habitat ordination of breeding passerine birds of the Virgin River Valley, southwestern Utah. Wilson Bull. 87: 65-74.

Table 1. Bird species and number of 0.04-ha circular samples.

| Species | General habitat[a] | Number of nests | Number of perches | Additional song perches |
|---|---|---|---|---|
| Nashville Warbler (*Vermivora ruficapilla*) | forest edge, bog | 3 | 3[b] | 7 |
| Northern Parula (*Parula americana*) | forest, forest edge | 4 | 3 | 9 |
| Yellow Warbler (*Dendroica petechia*) | shrub & grass | 4 | 4 | 6 |
| Chestnut-sided Warbler (*D. pensylvanica*) | deciduous, second growth | 2 | 2 | 12 |
| Palm Warbler (*D. palmarum*) | wet, open bog | 2 | 2 | 0 |
| Ovenbird (*Seiurus auricapillus*) | forest | 4 | 3 | 11 |
| Common Yellowthroat (*Geothlypis trichas*) | shrub & grass | 4 | 0 | 13 |
| Total | | 23 | 17 | 58 |

[a]Collins, unpubl., based upon analysis of 207 plots for 16 species of warblers.

[b]Number of song perch samples with corresponding nest-site samples.

Table 2. Variables of the structure of the vegetation considered in the analysis of 0.04-ha nest and perch site samples (James and Shugart 1970). All values expressed as per 0.04-ha.

| | |
|---|---|
| GC | Percent ground cover - No. of sightings of ground cover vegetation at 20 evenly spaced points across a transect dividing the circle multiplied by 5. |
| SC | Percent shrub cover - No. of contacts of shrub vegetation by the outstretched arms at 20 evenly spaced points across a transect dividing the circle multiplied by 5. |
| CC | Percent canopy cover - No. of sightings of canopy vegetation at 20 evenly spaced points across a transect dividing the circle multiplied by 5. |
| CO | Percent coniferous vegetation - No. of sightings of coniferous vegetation in the canopy at 20 evenly spaced points across a transect dividing the circle multiplied by 5. |
| CH | Canopy height (m). |
| SPT | No. of species of trees. |
| T1 | No. of trees 7.5-15 cm dbh. |
| T2 | No. of trees 15.1-23 cm dbh. |
| T3 | No. of trees 23.1-30 cm dbh. |
| T4 | No. of trees 30.1-38 cm dbh. |
| T5 | No. of trees 38.1-53 cm dbh. |
| T6 | No. of trees 53.1-68.5 cm dbh. |
| T7 | No. of trees greater than 68.5 cm dbh. |

Table 3. Comparison of nest-site versus song perch site vegetation structure by Wilcoxon matched-pairs signed-ranks test.

| Species | Number of pairs | Number different[a] |
|---|---|---|
| Northern Parula | 3 | 1 |
| Nashville Warbler | 3 | 0 |
| Yellow Warbler | 4 | 2 |
| Chestnut-sided Warbler | 2 | 2 |
| Palm Warbler | 2 | 0 |
| Ovenbird | 3 | 0 |

[a]Significant at $P < 0.05$.

Table 4. Discriminant function analysis of nest-site versus perch site vegetation structure. Variables are listed in order of entry into the discriminant function. See Table 2 for explanation of variables.

| Species | Variables entered | F-value (df) | P | Number reclassified |
|---|---|---|---|---|
| Nashville Warbler | T2,CO | 3.49 (2, 10) | NS | 1 |
| Northern Parula | T3,T2,T6,CH, T5,SPT,GC,T1 | 5.69 (8, 7) | 0.02 | 0 |
| Yellow Warbler | CH,SPT,SC,T1 | 1.79 (4, 9) | NS | 2 |
| Chestnut-sided Warbler | CC | 3.83 (1, 14) | NS | 2 |
| Ovenbird | T3,T5 | 2.36 (2, 15) | NS | 5 |
| Common Yellowthroat | CO,CH | 4.50 (2, 14) | 0.05 | 2 |

CHAPTER II

# HABITAT RELATIONSHIPS OF THE WOOD WARBLERS (PARULIDAE) IN NORTH-CENTRAL MINNESOTA

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ABSTRACT

Habitat relationships are analyzed for 16 species of wood warblers (Parulidae) breeding in north-central Minnesota. Thirteen variables of the structure of the habitat were measured in 207 0.04-ha circular plots located in the territories of breeding males. Cluster analysis of the average habitats of the 16 species produced three major groups of species that occupy (1) open fields with shrubs (*Dendroica pensylvanica*, *D. petechia*, *Geothlypis trichas*, *Oporornis philadelphia*, *Vermivora chrysoptera*), (2) shrub-forest edge (*D. magnolia*, *Mniotilta varia*, *Setophaga ruticilla*, *V. ruficapilla*, *Wilsonia canadensis*), and (3) mature forest (*D. coronata*, *D. fusca*, *D. pinus*, *D. virens*, *Seiurus aurocapillus*, *Parula americana*). A reciprocal averaging ordination of the average habitat for each species produced an ordination extending from species occurring in areas with few trees and dense ground cover to those in deciduous, mixed, and coniferous forest habitats. A second axis separated species of mature coniferous forest from younger deciduous and mixed forest habitats.

A principal components analysis of 199 circular samples showed that the habitat of each species was variable. These habitat relationships suggest that interspecific competition for habitat is rarely an important factor governing the local distribution of these species. Also, habitat relationships

are important correlaries to analyses of foraging behavior. Differences between species foraging behaviors should not be attributed to interspecific interactions without attention to differences imposed by the structure of the habitat.

# INTRODUCTION

There are many species of wood warblers (Parulidae) that may breed in north-central Minnesota (Parmelee 1977). Each has a unique distribution based at least partly on affinities to specific elements in the structure of the habitat. The extent to which these distributions are partly the result of interspecific interactions is difficult to determine. Nevertheless, many previous workers have assumed that these interactions are the main factor affecting species distributions. That is, birds inhabiting predetermined habitat types were considered to be interacting members of an avian community (MacArthur 1958, Morse 1967, 1976, Rabenold 1978, Holmes, Bonney, and Pacala 1979, Sabo 1980). Different foraging behaviors and locations in the canopy that permitted co-existence were defined for the species in these communities. One problem with this community approach is that it does not treat the potentially important influence of specific characteristics of vegetation structure in considering the habitat relationships of breeding birds. Here we take the alternative approach and ask - to what extent can the distribution of birds be explained merely on the basis of habitat affinities?

Because the family Parulidae has many species breeding in North America, it is an ideal group for the study of interspecific relationships. Clearly, descriptive analyses of habitat relationships are necessary to provide baseline data prior to implementing community-type comparisons of other behavioral characteristics. The purpose of this report is to provide an explicit comparative study of the habitat structure and relationships of the sympatric breeding warblers in north-central Minnesota. Specific questions addressed are (1) What is the habitat structure and variability of each of the breeding species? (2) Are these species found in well-defined communities or are they distributed at specific sites along habitat gradients? (3) Can the habitat relationships of the warblers be interpreted with regard to community phenomena such as interspecific competition?

## MATERIALS AND METHODS

Study area. All field work was conducted within or near Itasca State Park in Becker, Clearwater, and Hubbard counties, north-central Minnesota. Fire has been an important natural factor affecting the vegetation of this region. Until fire control began in the early 1920's fires burned all sections of the park on the average of once every 22 years (Frissell 1973). Recent fire control has limited the occurrence of fire-induced clearings but logging has created new regrowth areas. Thus, intermittent natural and man-caused destruction of vegetation, followed by plant succession, have created a diversity of vegetation types in the region. These types are pine forests (*Pinus banksiana*, *P. resinosa*, *P. strobus*; plant nomenclature follows Gleason and Cronquist 1963), spruce-fir stands (*Picea glauca*-*Abies balsamea*), hardwood forests (*Acer saccharum*, *Betula papyrifera*, *Fraxinus pennsylvanica*, *Populus* spp., *Quercus* spp., and *Tilia americana*), bogs, second growth, and old fields. Within the park, 27 species of warblers have been reported, 13 of which are considered by Parmelee (1977) to be commonly nesting species.

*Field methods*. Thirteen structural characteristics of the habitat (Table 1) were measured from 1 June to 7 July (1978 and 1979) in 0.04-ha (0.1-acre) circles (James and Shugart 1970, James 1971). A total of 207 circles was recorded for the 16 species of warblers (Table 2). All habitat types were sampled, and the number of circular plots per species generally represents the relative abundance of that species during the breeding season. Most of the circles were located by centering on a song perch of a male bird but some additional circles were centered on nest sites (Collins 1981). The 0.04-ha circle technique is designed to determine "...relationships among birds based upon the basic life form of vegetation that each species requires" (James 1971). As such, it is an extension of the individualistic concept of the distribution of organisms (Gleason 1926) in which species populations are treated independently. This technique permits analysis of the habitats of individual species before interspecific comparisons are considered.

*Data analyses*. To classify the general patterns of habitats by species, 13 habitat variables for each species were averaged, standardized ($\bar{X} = 0, \sigma^2 = 1$) and subjected to an unweighted pair group cluster analysis (UPGMA, Sneath and Sokal 1973, Rohlf, Kishpaugh, and Kirk 1974) based upon an Euclidean distance resemblance matrix. UPGMA is an agglomerative, polythetic, hierarchical clustering procedure. Because patterns of continuous variation may not be obvious in a cluster analysis, untransformed average species habitat variables were subjected to reciprocal averaging ordination (RA, Hill 1973). RA is related to principal components analysis and weighted averaging ordination (Curtis and McIntosh 1951). Through an iterative procedure, RA simultaneously obtains species scores based upon the variables, and variable scores based upon the species. After each iteration, the scores are rescaled from 0 to 100. The eigenvalue is the contraction in range of species scores in one iteration after convergence is reached (Hill 1973, Gauch 1977). RA has been shown to be a reliable ordination method for vegetation analysis (Gauch, Whittaker, and Wentworth 1977), and it has recently been applied to the analysis of avian niche relationships by Sabo and Whittaker (1979).

A multivariate analysis of average habitat values can only provide the most general picture of habitat relationships. An additional ordination was deemed necessary to assess variation in the habitat of a single species as well as patterns of interspecific habitat relations. For 199 circular plots of 14 species of warblers (Yellow-rumpted and Canada warblers were deleted because of small sample size), a principal components analysis (PCA) was produced from a correlation matrix of the 13 habitat variables. To facilitate presentation and to assess the variability of a species' habitat, bivariate 95% concentration ellipses (Sokal and Rohlf 1969: 528) were drawn in the space determined by the first two principal components. PCA was selected over RA because the latter method provided poor separation of the samples.

Since the concept of niche and its corresponding terminology is confusing, we need to clarify our definitions of habitat and niche. Although James (1971) referred to the characteristic vegetational requirements of a species as the niche-gestalt, we follow the terminology of Whittaker, Levin, and Root (1973) separating the concepts of niche and habitat. Therefore, habitat is not equal to niche, however, niche-gestalt reflects habitat structure. In general, we are extracting resource axes from the vegetation structure data to determine the structure and amount of variation in the habitat of each species along these habitat gradients.

PCA and RA were performed using ORDIFLEX (Gauch 1977); clustering was done with the TAXON subroutine of NT-SYS (Rohlf et al. 1974).

## RESULTS

Based on cluster analysis, the habitats of the 16 species of warblers can be divided into three general habitat types (Figure 1). The cophenetic correlation coefficient (r = 0.83) indicates that the dendrogram adequately summarized the Euclidean distance habitat matrix. The 40.0 distance line on the dendrogram was selected as the level at which relatively homogeneous groups could be identified because distortion between the distance matrix and the dendrogram matrix greatly increased above this level.

Group I contains five species and represents second growth and forest edge habitats each with a high percent shrub cover. Of these species, the American Redstart, Black-and-white, and Nashville warblers were common, Magnolia Warblers were less common, and the Canada Warbler was rare during the breeding season. The habitat structure for the American Redstart is old growth aspen-birch stands and edges of other deciduous forest vegetation. Very little coniferous vegetation occurs within its habitat ( Table 3 ). The Black-and-white Warbler was found in forests similar to that of the American Redstart but with more coniferous vegetation. Nashville Warblers occupied shrubby edges of deciduous forests similar to that of the American Redstart but with more coniferous vegetation. Nashville Warblers occupied shrubby edges of deciduous forests as well as densely vegetated bogs and swamps. A dense cover of bryophytes and graminoids was usually present yielding the high percent ground cover (Table 3). The Canada Warbler was found in small forest openings with dense shrub and ground cover. Finally, coniferous shrub vegetation was the most predictable component in the habitat of the Magnolia Warbler.

The six species in Group II occur primarily in mature undisturbed forests containing coniferous vegetation. All species in this group are considered common in the Itasca region; however, the Yellow-rumped Warbler was observed infrequently during the study period. Distinctive features of the habitat of the group are moderate ground and shrub cover values and greater than 75% canopy cover for nearly every member of this group (Table 3). Additionally, the territories of these species consistently contained greater than 50% coniferous vegetation, mostly in the large tree categories (T5-T7). For the Northern Parula, Blackburnian, and Yellow-rumped warblers, the coniferous component was usually spruce or fir. Red, white and jack pines appeared regularly in Pine and Black-throated Green warbler habitats. The coniferous component of the Ovenbird was variable but more often spruce-fir than pine.

The five species that prefer open habitats with dense ground cover and usually moderate shrub cover make up Group III. All are common and may co-occur in one large open area. Within the group there is a gradient of shrub and canopy cover, the latter to about 40% (Table 3). The habitat of this group, therefore, grades from open marshland with few or no trees (Common Yellowthroat, Yellow Warbler) to areas of dense aspen coppice (Mourning Warbler) and parkland vegetation where Chestnut-sided and Golden-winged warblers were frequently observed singing and foraging.

The correlation matrix of the 13 habitat variables (Table 4) indicates that ground cover is negatively correlated with increasing vegetation structure. That is, as the forest develops, ground cover decreases, shrub and canopy cover increase, and trees become larger. Also, shrub cover decreases as the forest gains stature and percent coniferous vegetation increases. The high correlations between similar tree size classes (T1-T2, T6-T7) and low correlations between divergent tree size classes (T1-T7) are attributable to regeneration after fire which causes the even-aged structure of many of these forests.

A two-dimensional ordination of the bird species by reciprocal averaging (Figure 2, Table 5) shows that a gradient of habitat structure exists among the warblers in the Itasca region, but Group I species are separated from other species in the ordination. Axis 1, accounting for 73.8% of the variance, is a gradient from large coniferous trees and little ground cover to increasing ground cover and low percent coniferous vegetation (Table 5). Axis 2 (12.3% of the variance) grades from medium and small trees (T4, T3) to large trees (T7, T6). Thus, a species-habitat continuum from coniferous forest inhabitants such as Pine and Yellow-rumped warblers grades to mixed and deciduous forest species, i.e. Blackburnian Warbler. Next are species of second growth and edge habitats with increasing shrub coverage such as the Magnolia Warbler and American Redstart. At the extreme of the gradient are those species like the Common Yellowthroat and Yellow Warbler whose habitats contain few trees, more shrubs, and high percent ground cover.

The variability of each species habitat can be visualized by ordinating all circular plots by PCA and summarizing the results for each species with 95% concentration ellipses (Figure 3). Some distortion of the ellipses is introduced by the scaling of the PCA axes. However, we feel that ellipses are useful descriptive tools for displaying the variability of the habitat-types of species and no statistical tests are implied by use of these ellipses. The first PCA axis (38.5% of the variance, Table 5) is a gradient from most tree components to ground cover, that is from forest to open field vegetation. Axis 2 (14.5% of the variance, Table 5) grades from large, coniferous trees to medium and small (T4, T3, T2) deciduous trees. These variables correspond, in general, with the RA ordination of average habitat variables (Figure 2, Table 5).

The orientation and shape of the concentration ellipses in Figure 3 provide a qualitative indication of the variability of a species habitat structure. However, the size and orientation of each species' ellipse can not be used to quantify whether or not a species is a habitat specialist or generalist, nor do the ellipses measure interspecific overlap of habitat preference. First, due to dimensionality problems, interspecific habitat overlap would be over-estimated by concentration ellipses in PCA space. Secondly, as Major (1979) has indicated, overlapping curves along derived gradients imply that species co-occur at a given point when in fact they may be negatively associated. Third, the species are not necessarily normally distributed around their means as confidence ellipses would imply (Smith 1977). This distribution must be considered when evaluating measures of habitat breadth or overlap. Finally, bird species are probably cueing on a portion of the total habitat structure but not all structural characteristics change at the same rate along the habitat gradient. For, example, the Magnolia Warbler, which had the largest ellipse, always had some dense growth of spruce and fir saplings within its habitat. This dense growth was found in open bogs, deciduous and coniferous forest. Other members of Group I, American Redstart, Black-and-white, and Nashville warblers, had equal sized ellipses which were generally oriented along the first axis indicating variability in canopy coverage. Forest species (Group III) had small, oval ellipses or were somewhat extended along the second axis suggesting variability in the number of large trees in their habitats. The Black-throated Green and Pine warblers had habitats with variable amounts of pine vegetation, whereas, the Blackburnian

Warbler, Ovenbird, and Norther Parula maintained habitats with some spruce and fir vegetation. Mourning, Golden-winged, and Chestnut-sided warblers, three open field species, showed large ellipses incorporating some edge habitat. The Yellow Warbler and Common Yellowthroat were found in structurally simple habitat containing patches of shrubs or scattered trees.

A schematic diagram summarizing the habitat utilization patterns of each species along the structural gradient is presented in Figure 4. Each species occupies lengthy portions of the gradient and the habitats of many species overlap at any given point. These distributions emphasize the high degree of interspecific overlap of habitat and reflect the relatively independent nature of these species in this region. Therefore, based upon habitat relationships, these birds do not appear to form distict avian communities. Instead, birds are probably tracking specific subsets of habitat structure and are most likely limited to regions of the gradient by the structure of the vegetation.

## DISCUSSION

Ostensibly, the selection of breeding territory is initiated at least partly by species-specific responses to elements of vegetation structure (Svardson 1949, Hilden 1965, James 1971). This selection results in species-specific habitat distributions due to individualistic responses to various characteristics of the habitat. Rapid selection of optimal habitat based upon vegetation structure seems advantageous because intraspecific competition for territories may occasionally be keen during some breeding seasons.

It is possible to arrange the habitats of the 16 species of warblers based upon vegetation structure into three broad habitat groups: open country, shrub-forest edge, and mature forest, each of which contains about the same number of species (Figure 1). However, a habitat gradient, again based upon vegetation structure, was also ident. ied for the 16 warblers (Figure 2) and has been schematically diagrammed in Figure 4. This gradient includes all vegetation types present in the region from old fields and bogs, shrub thickets, forest edges, second growth forest, to mature deciduous and coniferous vegetation. Many of the open habitats are the result of logging or fire. In either case, large trees, particularly pines, remain as a seed source for forest regeneration (Hansen, Kurmis, and Ness 1974). The large trees occur in the habitat of open county species and account for the location of the Yellow Warbler and Common Yellowthroat at the large tree end of the gradient (Figure 2, axis 2). In summary, habitat groups can be identified, particulary for open country species, but the gradient suggests that the 16 warblers do not form a subset of a specific bird community based either upon vegetation structure or plant species criteria. The utility of the clustering procedure is to identify those species with closely related habitat structure for future comparitive analyses of other ecotope parameters such as foraging behavior or food preference.

An important facet of community ecology is the effect of interspecific competition on community structure. Previous studies (Anderson and Shugart 1974, Cody 1978, Dueser and Shugart 1979) have interpreted the distribution of species along habitat gradients as a form of resource partitioning resulting from interspecific competition. The warblers in this study were distributed along a habitat gradient and this distribution can be interpreted as conforming to the resource partitioning hypothesis. However, these habitat structure data are probably neutral to this hypothesis. The habitat structure and variability of the warblers may be interpreted in regard to other aspects of competition theory. For example, the great variability of habitat structure noted for many of the warblers naturally leads to interspecific overlap of habitat, a factor observed in the field. Unfortunately, interpretations of resource overlap are inconsistent because some suggest overlap implies competition (Cody 1974, Schoener 1974) while others interpret overlap to mean reduced interspecific interactions due to resource abundance (Colwell and Futuyma 1971, Wiens 1977). Klopfer and Hailman (1965) predicted that individuals living with many competitors should exhibit rigid habitat selection. Our results are counter to this prediction (Figure 3, 4) and the broad overlap of the warbler's habitats may be interpreted as indicating resource abundance and reduced interspecific interaction.

Cody (1974) stated that if species overlapped broadly along one resource dimension such as habitat, they would show greater segregation and less niche overlap along another resource dimension, e.g. foraging behavior. The foraging behavior of several warblers in Maine has been intensively studied by Morse (1971, 1973). He concluded that these species were opportunistic foragers and that food was not a limiting resource to these birds. In fact, Black-throated Green Warblers prefered to forage in red spruce (*Picea rubens*) even though more food could be found in white spruce (*Picea glauca*; Morse 1976). Clearly, species prefer certain food types and the abundance of some prey items may at times be significantly reduced. Holems, Schultz, and Nothnagel (1979) demonstrated that birds depress the levels of defoliating insects, especially Lepidoptera, yet significantly lower levels of Arachnida, Coleoptera, Homoptera, and Hemiptera were rarely observed. The average weekly removal rate of insects was approximately 37% indicating that insect prey usually remains available as a food source during the breeding season.

Competition theory implies that if resources are abundant, species can specialize on certain components of their environment. Yet, the high habitat variability and opportunistic feeding behavior is evidence that specialization by the warblers has not occurred at the community level. As Ricklefs and Travis (1980) pointed out, populations occurring in a variety of habitats interact with a wide spectrum of other species. These interactions prohibit fine tuning of behavior to that of other taxa because interactions are not consistent throughout each population.

We think that the distribution of the warblers along habitat gradients is the result of individualistic responses by the species to characteristics of vegetation structure and we disagree with the statement of Richardson (1980) that animals are more likely than plants to be found in tightly co-evolved, organismal communities. Although species habitats are variable and overlapping, the average habitat structure of each species is separated along the vegetation gradient. This pattern of habitat relationships suggests a situation conforming to the model of Wiens (1977) in which during most breeding seasons resources are abundant and support broadly overlapping habitat and foraging utilization patterns. Years of reduced resource productivity may be encountered during which species narrow and segregate their utilization patterns possibly as a result of interspecific interactions.

In conclusion, the high habitat breadth, opportunistic foraging behavior, and resource abundance imply that there is no need to invoke interspecific competition as a major force governing distribution of these warblers. The individualistic response of the warblers along the habitat gradient determined by vegetation structure suggests that the most reasonable paradigm for examining the niche variables of these birds is the structure of the habitat and interspecific habitat relationships. These conclusions do not result from a test of competition theory, but are based upon habitat correlation analyses (Wiens 1976). Experimental manipulation of (adding or removing) species or habitat is required to truely test the validity of these conclusions. Until such studies are feasable, distributional observations in conjunction with theoretical interpretation must suffice to explain interspecific relationships.

## ACKNOWLEDGEMENTS

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## LITERATURE CITED


Able, K.P. and B.R. Noon. 1976. Avian community structure along elevational gradients in the northeastern United States. Oecologia 26: 275-294.

Anderson, S.H. and H.H. Shugart. 1974. Habitat selection of breeding birds in an east Tennessee deciduous forest. Ecology 55: 828-837.

Beals, E. 1960. Forest bird communities of the Apostle Islands of Wisconsin. Wilson Bull. 72: 156-181.

Bent. A.C. 1953. Life histories of North American wood warblers. U.S. Natl. Mus. Bull. 203.

Busby, D.G. and S.G. Sealy. 1979. Feeding ecology of a population of nesting Yellow Warblers. Can. J. Zool. 57: 1670-1681.

Cody, M.L. 1974. Competition and the structure of bird communities. Princeton Univ. Press, Princeton, NJ.

Cody, M.L. 1978. Habitat selection and interspecific territoriality among the sylviid warblers of England and Sweden. Ecol. Monogr. 48: 351-396.

Collins, S.L. 1981. A comparison of nest-site and perch site vegetation structure for seven species of warblers. Wilson Bull. 93: in press.

Colwell, R.K. and D.J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52: 567-576.

Confer, J.L. and K. Knapp, 1981. Golden-winged Warblers and

Blue-winged Warblers: the relative success of a habitat specialist and a generalist. Auk 98: 108-114.

Cox, G.W. 1960. A life history of the Mourning Warbler. Wilson Bull. 72: 5-28.

Curtis, J.T. and R.P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32: 476-496.

Dueser, R.D. and H.H. Shugart. 1979. Niche pattern in a forest floor small mammal fauna. Ecology 60: 108-118.

Ficken, R., M. Ficken, and D.H. Morse. 1968. Competition and character displacement in sympatric pine-dwelling warblers. Evolution 22: 307-314.

Frissell, S.S. 1973. The importance of fire as a natural ecological factor in Itasca State Park, Minnesota. Quat. Res. 3: 397-407.

Gauch, H.G. 1977. ORDIFLEX: a flexible computer program for four ordination techniques. Release B. Ecology and Systematics, Cornell Univ., Ithaca, NY.

Gauch, H.G., R.H. Whittaker, and T.R. Wentworth. 1977. A comparitive study of reciprocal averaging and other ordination techniques. J. Ecol. 65: 157-174.

Gleason, H.A. 1926. The individualistic concept of the plant association. Bull. Torrey Bot. Club 53: 7-26.

Gleason, H.A. and A. Cronquist. 1963. Manual of vascular plants of northeastern United States and adjacent Canada. D. van Nostrand Co., New York, NY.

Green, R.H. 1974. Multivariate niche analysis with temporally varying environmental factors. Ecology 55: 73-83.

Greenberg, R. 1979. Body size, breeding habitat, and winter exploitation systems in Dendroica. Auk 96: 756-766.

Griscom, L. and A. Sprunt, eds. 1979. The warblers of North America. Doubleday and Co., Garden City, NJ.

Hansen, H.L., V. Kurmis, and D.D. Ness. 1974. The ecology of upland forest communities and implications for management in Itasca State Park, Minnesota. Univ. Minnesota Agric. Exp. Sta. Bull. 298, For. Series 16.

Hilden, O. 1965. Habitat selection in birds. Ann. Zool. Fenn. 2: 53-75.

Hill, M.O. 1973. Reciprocal averaging: an eigenvector method of ordination. J. Ecol. 61: 237-249.

Holmes, R.T., R.E. Bonney, and S.W. Pacala. 1979. Guild structure of the Hubbard Brook bird community: a multivariate approach. Ecology 60: 512-520.

Holmes, R.T., J.C. Schultz, and P. Nothnagel. 1979. Bird predation on forest insects: an exclosure experiment. Science 206: 462-463.

Howe, R.W. 1979. Distribution and behavior of birds on small islands in northern Minnesota. J. Biogeog. 6: 379-390.

James, F.C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bull. 83: 215-236.

James, F.C. and H.H. Shugart. 1970. A quantitative method of habitat description. Audubon Field Notes 24: 727-736.

Klopfer, P.H. and J.P. Hailman. 1965. Habitat selection in birds. Advances in the Study of Behavior 1: 279-303.

MacArthur, R.H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39: 599-619.

Major, J. 1979. Overlapping tolerance curves of plant species. Phytocoenologia 6: 26-34.

Morse, D.H. 1967. Competitive relationships between Parula Warblers and other species during the breeding season. Auk 84: 490-502.

Morse, D.H. 1971. The foraging of warblers isolated on small islands. Ecology 52: 216-228.

Morse, D.H. 1973. The foraging of small populations of Yellow Warblers and American Redstarts. Ecology 54: 346-355.

Morse, D.H. 1976. Variables determining the density and territorial size of breeding spruce-woods warblers. Ecology 57: 290-301.

Osterhaus, M.B. 1962. Adaptive modifications in the leg structure of some North American warblers. Am. Midl. Nat. 68: 474-486.

Parmelee, D.F. 1977. Annotated checklist of the birds of Itasca State Park and surrounding areas. Loon 49: 81-95.

Rabenold, K.N. 1978. Foraging strategies, diversity, and seasonality in bird communities. Ecol. Mongr. 48: 397-424.

Richardson, J.L. 1980. The organismic community: resilience of an embattled ecological concept. BioScience 30: 465-471.

Ricklefs, R.E. and J. Travis. 1980. A morphological approach to the study of avian community organization. Auk 97: 321-338.

Rohlf, F.J., J. Kishpaugh, and D. Kirk. 1974. NT-SYS: numerical taxonomy system of multivariate statistical programs. Tech. Rep. State Univ. New York, Stoney Brook, NY.

Sabo, S.R. 1980. Niche and habitat relations in subalpine bird communities in the White Mountains of New Hampshire. Ecol. Monogr. 50: 241-259.

Sabo, S.R. and R.H. Whittaker. 1979. Bird niches in a subalpine forest: an indirect ordination. Proc. Natl. Acad. Sci. 76: 1338-1342.

Schoener, T.W. 1974. Resource partitioning in ecological communities. Science 185: 27-39.

Sherry T.W. 1979. Competitive interactions and adaptive strategies of American Redstarts and Least Flycatchers in a northern hardwoods forest. Auk 96: 265-283.

Smith, K.G. 1977. Distribution of summer birds along a forest moisture gradient in an Ozark watershed. Ecology 58: 810-819.

Sneath, P.H.A. and R.R. Sokal. 1973. Numerical taxonomy. W.H. Freeman and Co., San Francisco, CA.

Sokal, R.R. and F.J. Rohlf. 1959. Biometry. W.H. Freeman and Co., San Francisco, CA.

Stenger, J. and J.B. Falls. 1959. The utilized territory of the Ovenbird. Wilson Bull. 71: 125-140.

Svardson, G. 1949. Competition and habitat selection in birds. Oikos 1: 157-174.

Whittaker, R.H., S. Levin, and R.B. Root. 1973. Niche, habitat, and ecotope. Am. Nat. 107: 321-338.

Wiens, J.A. 1976. Population responses to patchy environments. Ann. Rev. Ecol. Syst. 7: 81-120.

Wiens, J.A. 1977. On competition and variable environments. Am. Sci. 65: 590-597.

Table 1. Variables of the structure of the vegetation considered in the analysis of 0.04-ha circular samples (James and Shugart 1970).

1. Percent ground cover (GC) - No. of sightings of ground vegetation at 20 evenly-spaced points across a transect dividing the circle multiplied by 5.
2. Percent shrub cover (SC) - No. of contacts of shrub vegetation by the outstretched arms at 20 evenly-spaced points across a transect dividing the circle multiplied by 5.
3. Percent canopy cover (CC) - No. of sightings of canopy vegetation at 20 evenly-spaced points across a transect dividing the circle multiplied by 5.
4. Percent conifer (CO) - No. of sightings of coniferous vegetation in the canopy at 20 evenly-spaced points across a transect dividing the circle multiplied by 5.
5. Canopy height in meters (CH).
6. No. of species of trees per 0.04-ha circle (SPT).
7. No. of trees 7.5-15 cm dbh (T1) per 0.04-ha.
8. No. of trees 15.1-23 cm dbh (T2) per 0.04-ha.
9. No. of trees 23.1-30 cm dbh (T3) per 0.04-ha.
10. No. of trees 30.1-38 cm dbh (T4) per 0.04-ha.
11. No. of trees 38.1-53 cm dbh (T5) per 0.04-ha.
12. No. of trees 53.1-68 cm dbh (T6) per 0.04-ha.
13. No. of trees greater than 68.1 cm dbh (T7) per 0.04-ha.

Table 2. General breeding habitat for the 16 species of warblers.

| Species | No. of samples | General Habitat | Reference |
|---|---|---|---|
| Black-and-white Warbler (BW) *Mniotilta varia* | 10 | Dry deciduous forest | Bent 1953, Osterhaus 1962, Able and Noon 1976 |
| Golden-winged Warbler (GW) (*Vermivora chrysoptera*) | 11 | Shrubby areas, forest edge | Confer and Knapp 1981, Pers. Observ. |
| Nashville Warbler (NA) (*V. ruficapilla*) | 13 | Pine, spruce-fir, bog, shrubby areas | Beals 1960, Able and Noon 1976, Pers. Observ. |
| Northern Parula (NP) (*Parula americana*) | 16 | Coniferous, mixed forest, swamps | Bent 1953, Beals 1960, Morse 1967, Rabenold 1978 |
| Yellow Warbler (YE) (*Dendroica petechia*) | 14 | Open, deciduous shrubby areas | Morse 1973, Busby and Sealy 1979, Greenberg 1979 |
| Magnolia Warbler (MA) (*D. magnolia*) | 9 | Coniferous, mixed forest, bogs | Morse 1976, Greenberg 1979, Pers. Observ. |
| Yellow-rumped Warbler (YR) (*D. coronata*) | 5 | Coniferous forest, bogs | MacArthur 1958, Morse 1976, Greenberg 1979, Howe 1979 |
| Black-throated Green Warbler (BG) | 15 | Pine, coniferous | MacArthur 1958, Osterhaus 1962 |

Table 2, con't.

| | | | |
|---|---|---|---|
| (*D. virens*) | | mixed forest | Morse 1976, Greenberg 1979 |
| Blackburnian Warbler (BB) | 15 | Coniferous, mixed | MacArthur 1958, Morse 1976 |
| (*D. fusca*) | | forest | Greenberg 1979 |
| Chestnut-sided Warbler (CS) | 16 | Deciduous forest, | Greenberg 1979 |
| (*D. pensylvanica*) | | shrubby areas | |
| Pine Warbler (PI) | 15 | Pine forest | Picken et al. 1968, Greenberg |
| (*D. pinus*) | | | 1979, Howe 1979 |
| Ovenbird (OV) | 18 | Spruce-fir, mixed | Stenger and Falls 1959 |
| (*Seiurus aurocapillus*) | | pine, deciduous | |
| Mourning Warbler (MO) | 15 | Clearings, edges, | Cox 1960 |
| (*Oporornis philadelphia*) | | dense second growth | |
| Common Yellowthroat (CY) | 17 | Open, marsh, bog, | Bent 1953, Osterhaus 1962, |
| (*Geothlypis trichas*) | | tall grasses | Pers. Observ. |
| Canada Warbler (CA) | 3 | Mixed forest, | Bent 1953, Able and Noon 1976, |
| (*Wilsonia canadensis*) | | forest openings | Pers. Observ. |
| American Redstart (AR) | 15 | Deciduous forest | Morse 1973, Sherry, 1979, |
| (*Setophaga ruticilla*) | | forest edge | Pers. Observ. |

Table 3. The average habitat characteristics of the 16 species of warblers.

| Variable[a] | AR[b] | BW | NA | CA | MA | BB | NP | OV | BG | PI | YR | CS | GW | MO | CY | YE |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1[c] | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 3 | 3 | 3 | 3 | 3 |
| GC | 67.7 | 65.5 | 81.1 | 88.3 | 51.1 | 56.7 | 60.3 | 65.3 | 52.7 | 64.0 | 84.0 | 92.8 | 92.3 | 92.3 | 98.2 | 96.1 |
| SC | 70.7 | 51.5 | 53.9 | 73.3 | 76.1 | 41.0 | 50.0 | 42.3 | 39.0 | 44.3 | 44.0 | 66.9 | 45.0 | 52.7 | 39.0 | 38.9 |
| CC | 66.3 | 72.5 | 59.4 | 56.7 | 61.1 | 77.3 | 76.4 | 78.3 | 84.3 | 75.7 | 66.0 | 40.3 | 31.4 | 23.0 | 12.4 | 10.6 |
| CH | 47.6 | 48.4 | 48.7 | 61.7 | 55.3 | 52.7 | 55.2 | 50.8 | 66.1 | 72.1 | 53.0 | 43.1 | 34.5 | 35.6 | 17.0 | 19.6 |
| CO | 4.7 | 30.5 | 36.7 | 33.3 | 40.0 | 55.0 | 49.3 | 46.5 | 50.3 | 66.7 | 58.0 | 9.1 | 10.4 | 6.7 | 6.8 | 2.9 |
| SPT | 4.0 | 5.8 | 4.2 | 6.0 | 4.6 | 6.1 | 6.0 | 5.4 | 5.7 | 4.9 | 4.8 | 3.4 | 3.2 | 3.1 | 0.9 | 1.1 |
| T1 | 10.7 | 17.5 | 16.5 | 5.3 | 18.0 | 16.1 | 10.0 | 10.2 | 15.1 | 8.4 | 31.4 | 7.2 | 5.7 | 4.9 | 3.4 | 0.9 |
| T2 | 10.7 | 8.8 | 10.5 | 9.7 | 12.4 | 11.7 | 11.0 | 12.4 | 10.5 | 8.3 | 11.8 | 6.7 | 4.6 | 2.7 | 2.1 | 1.8 |
| T3 | 8.2 | 8.6 | 4.5 | 8.0 | 8.9 | 9.5 | 7.3 | 9.8 | 5.7 | 4.1 | 6.4 | 3.2 | 2.4 | 1.9 | 0.4 | 0.5 |
| T4 | 4.6 | 5.7 | 2.1 | 3.7 | 3.8 | 4.9 | 3.6 | 5.1 | 4.4 | 4.1 | 3.2 | 1.1 | 1.0 | 0.9 | 0.2 | 0.1 |
| T5 | 1.1 | 2.6 | 1.1 | 4.3 | 2.1 | 2.7 | 2.8 | 3.4 | 3.3 | 5.7 | 1.6 | 0.3 | 0.5 | 0.5 | 0.1 | 0.1 |
| T6 | 0.3 | 0.3 | 0.1 | 0.0 | 0.6 | 0.4 | 0.4 | 0.4 | 1.9 | 2.0 | 0.2 | 0.4 | 0.3 | 0.3 | 0.1 | 0.2 |
| T7 | 0.1 | 0.0 | 0.2 | 0.3 | 0.2 | 0.2 | 0.2 | 0.3 | 0.9 | 1.1 | 0.0 | 0.2 | 0.1 | 0.1 | 0.1 | 0.1 |

[a]Variables from Table 1.

[b]Bird species abbreviations are give in Table 2.

[c]Group number are given in Figure 1.

Table 4. Correlation matrix of habitat characteristics. Data are from species averages. Correlations of ± .48 are significant ($P < 0.05$). Abbreviations are explained in Table 1.

| | GC | SC | T1 | T2 | T3 | T4 | T5 | T6 | T7 | CC | CH | CO |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SC | -.06 | | | | | | | | | | | |
| T1 | -.46 | .01 | | | | | | | | | | |
| T2 | -.77 | .28 | .70 | | | | | | | | | |
| T3 | -.76 | .34 | .54 | .90 | | | | | | | | |
| T4 | -.84 | .14 | .52 | .83 | .91 | | | | | | | |
| T5 | -.61 | -.01 | .22 | .58 | .57 | .73 | | | | | | |
| T6 | -.54 | -.26 | .13 | .21 | .03 | .34 | .60 | | | | | |
| T7 | -.43 | -.20 | -.08 | .18 | .01 | .29 | .70 | .92 | | | | |
| CC | -.86 | .07 | .60 | .91 | .83 | .92 | .76 | .47 | .43 | | | |
| CH | -.70 | .22 | .51 | .79 | .66 | .76 | .85 | .61 | .62 | .88 | | |
| CO | -.68 | -.22 | .61 | .73 | .56 | .66 | .81 | .55 | .54 | .81 | .82 | |
| SPT | -.75 | .20 | .44 | .81 | .84 | .87 | .77 | .30 | .33 | .90 | .85 | .72 |

Table 5. Ordination statistics for reciprocal averaging (RA) and principal components analysis (PCA). RA scores are listed as scaled by the ordination program (Gauch 1977). PCA values are correlations with original variables. See Table 1 for abbreviations.

| Variable | RA | | PCA | |
|---|---|---|---|---|
| | I | II | I | II |
| GC | 100.0 | 59.1 | 0.752 | -0.020 |
| SC | 75.3 | 15.4 | 0.134 | 0.308 |
| CC | 23.8 | 30.4 | -0.916 | 0.036 |
| CH | 41.4 | 39.4 | -0.715 | -0.433 |
| CO | 1.1 | 80.7 | -0.720 | -0.343 |
| SPT | 34.2 | 28.7 | -0.801 | 0.081 |
| T1 | 22.1 | 42.2 | -0.450 | 0.266 |
| T2 | 27.4 | 22.0 | -0.660 | 0.326 |
| T3 | 19.6 | 0.0 | -0.662 | 0.476 |
| T4 | 10.4 | 10.5 | -0.636 | 0.340 |
| T5 | 0.0 | 59.7 | -0.519 | -0.155 |
| T6 | 5.5 | 92.6 | -0.281 | -0.691 |
| T7 | 11.6 | 100.0 | -0.218 | -0.669 |
| Eigenvalue | 0.97 | 0.16 | 5.01 | 1.88 |
| % Var[a] | 73.8 | 12.3 | 38.5 | 14.5 |

[a]Percent of variance accounted for by each axis.

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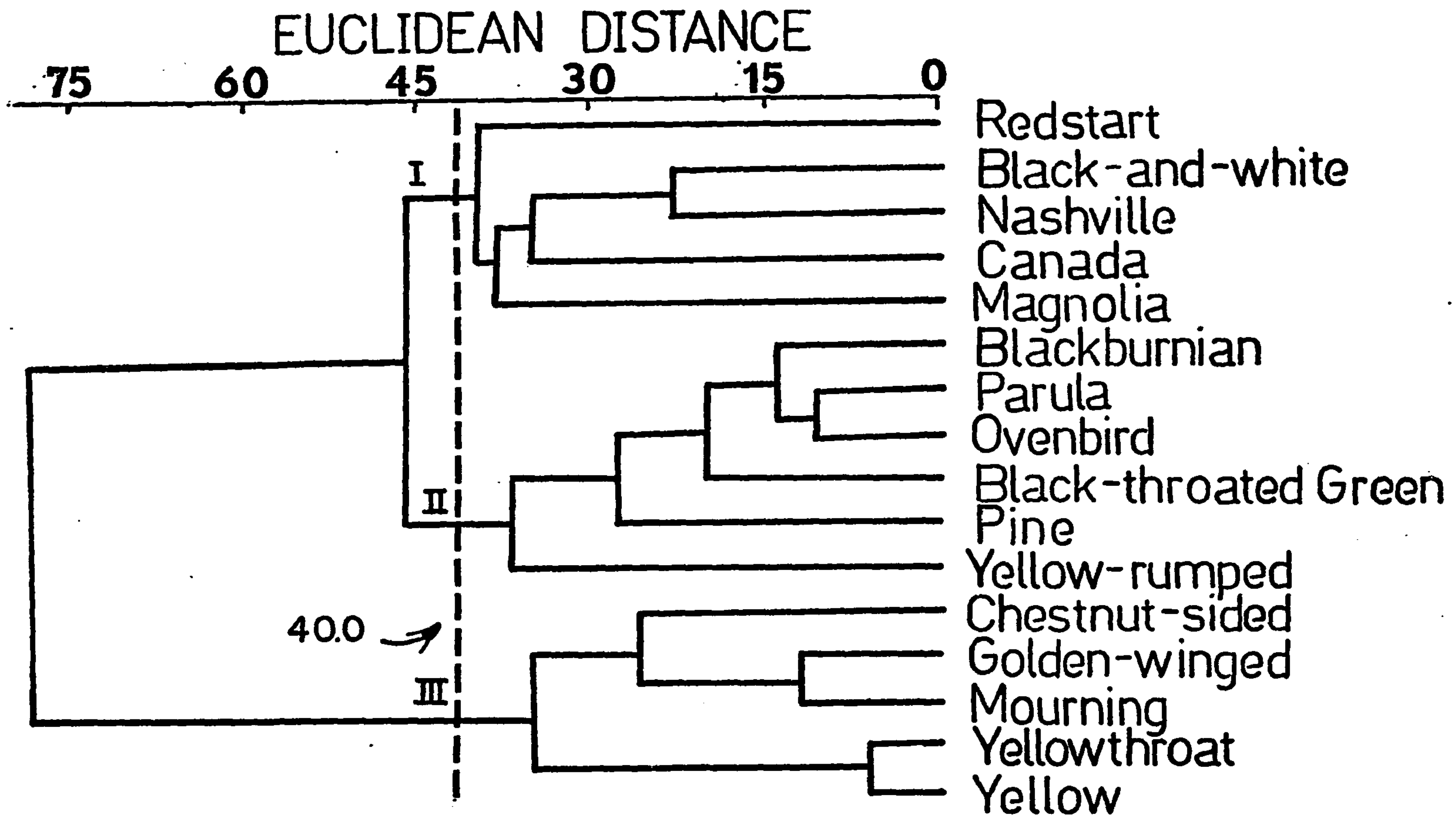
along the gradient. Letters specify the species mode. Vertical arrangement is arbitrary. Species abbreviations are given in Table 2.


EUCLIDEAN DISTANCE
75
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I
II
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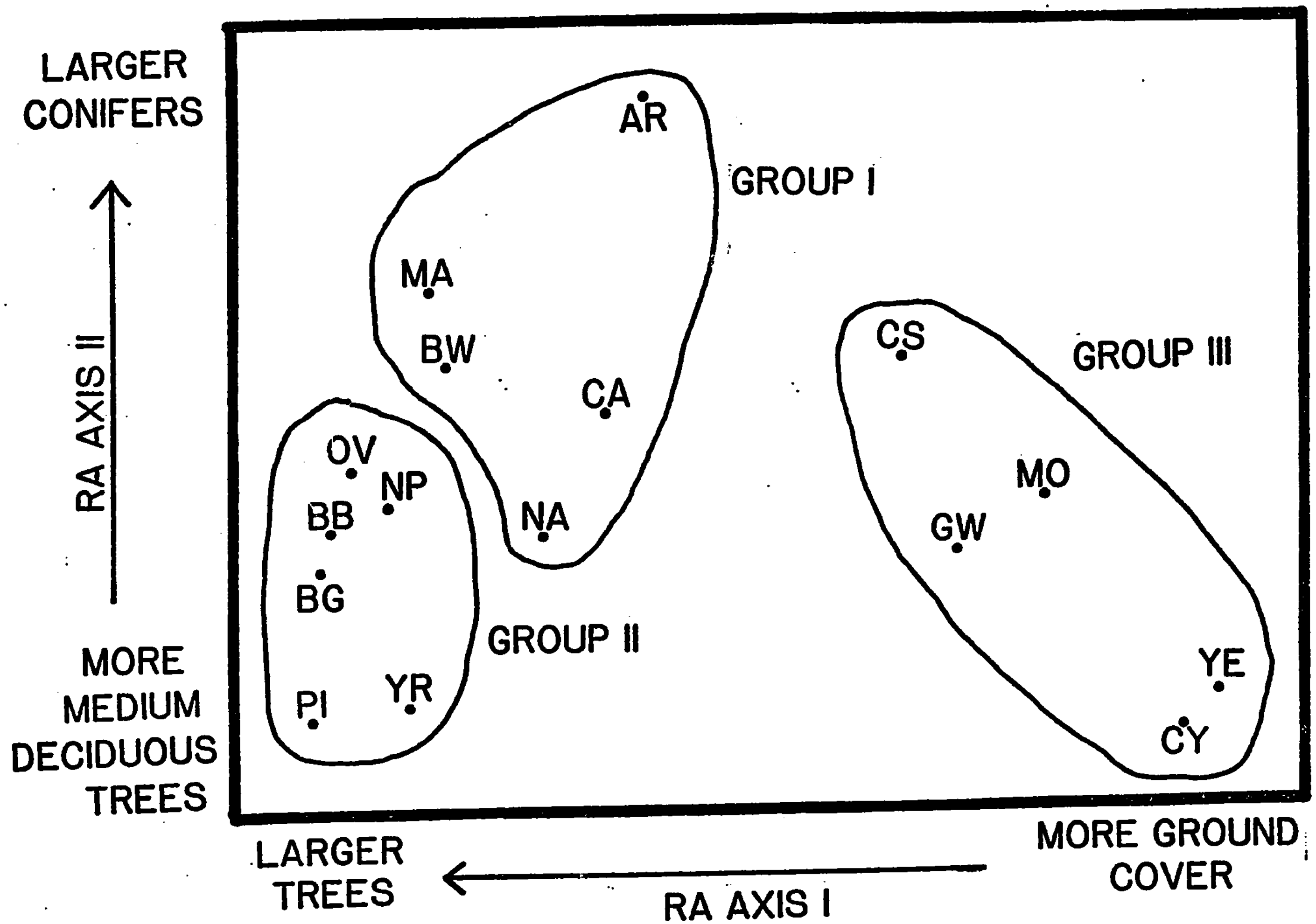
Redstart
Black-and-white
Nashville
Canada
Magnolia
Blackburnian
Parula
Ovenbird
Black-throated Green
Pine
Yellow-rumped
Chestnut-sided
Golden-winged
Mourning
Yellowthroat
Yellow


LARGER CONIFERS
RA AXIS II
MORE MEDIUM DECIDUOUS TREES
AR
GROUP I
MA
BW
CA
NA
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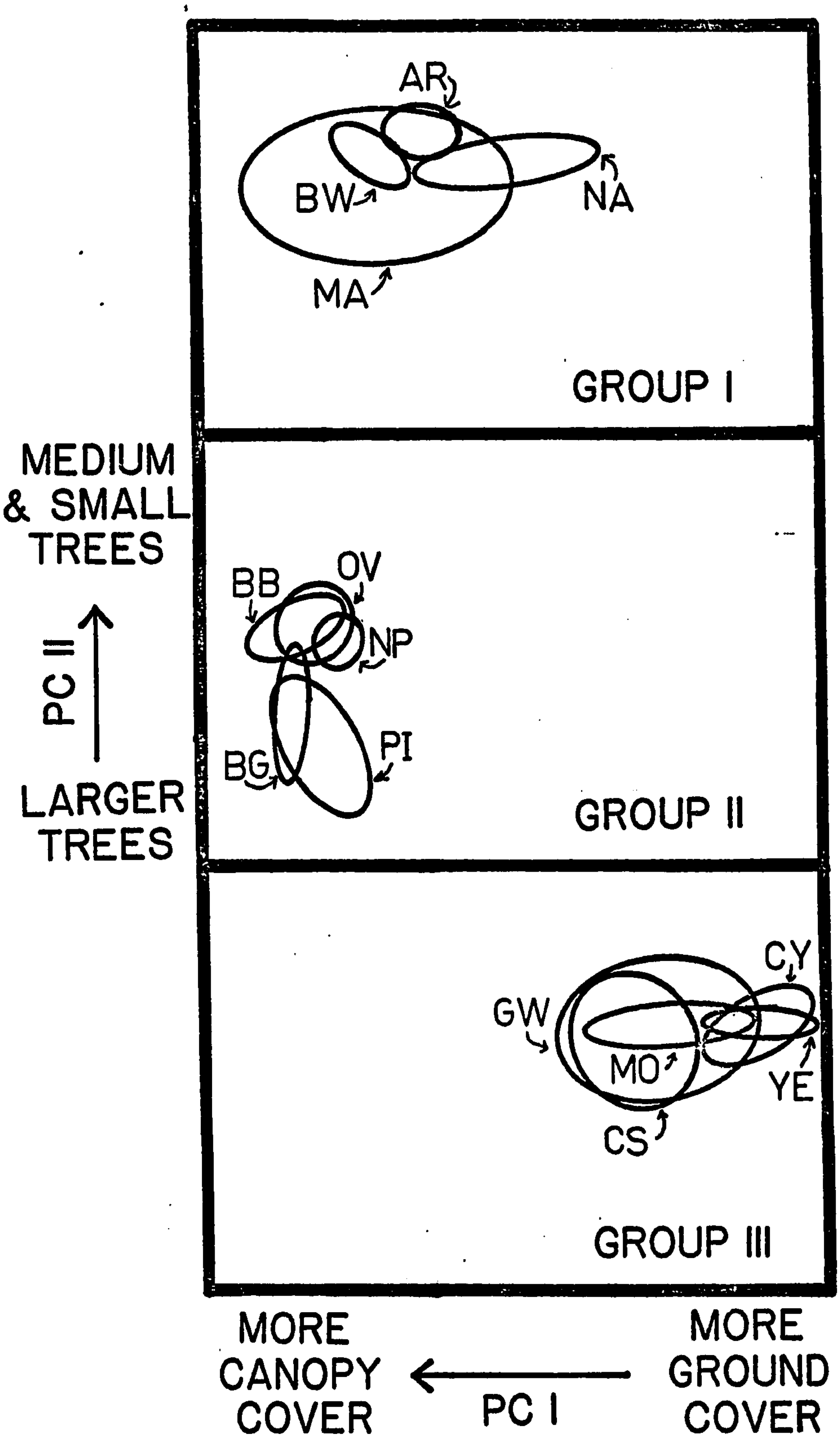
YR
GROUP II
CS
GROUP III
MO
GW
YE
CY
LARGER TREES
RA AXIS I
MORE GROUND COVER



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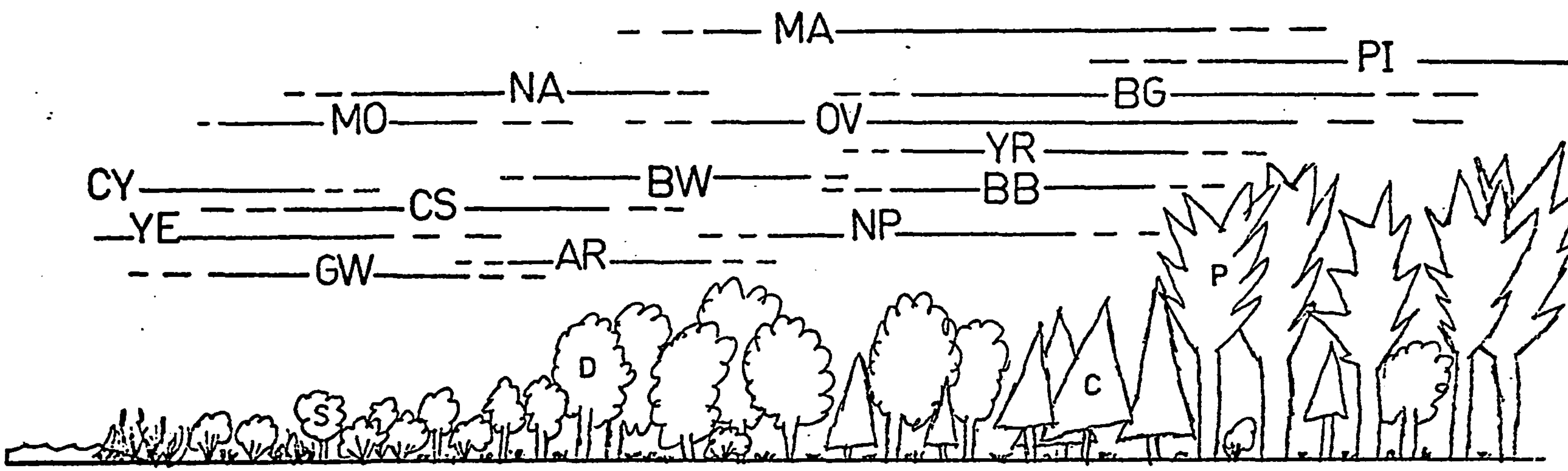

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CHAPTER III

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

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## ABSTRACT

The habitat of the Black-throated Green Warbler was examined at five study sites: (1) Mount Desert Island (MDI), 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 components analysis of 13 habitat structure variables showed between site differences in canopy height, tree size, canopy cover, and percent coniferous vegetation. New York and Minnesota sites had larger trees, whereas, the more northern Mount Blue and MDI habitats contained more small trees. The New Hampshire site was intermediate. Minnesota and MDI had greater percent coniferous vegetation than the other three sites, but Minnesota had more pines (*Pinus*), MDI had more spruce (*Picea*) and arbor vitae (*Thuja occidentalis*).

Comparison of tree species composition and habitat structure between the five sites showed no relationship even though Minnesota and MDI had unique plant community-types. Habitat differences among the five sites may be due to plant species composition, but the major differences seemed to be in the structure of the vegetation. Of importance is the evidence that composition and structure of the habitat are not uniform throughout the range of some species. Potential reasons for these differences are discussed.

Recent studies of avian habitat structure have shown that birds, like plants, are found in continua along habitat gradients and do not form well-defined communities (James 1971, Whitmore 1975, Smith 1977, Johnston 1979, Collins 1981). To date analyses of avian habitat structure have been confined to within-region comparisons, even though geographic variation has been analyzed for other aspects of bird behavior -- e.g. song dialects (Nottebohm 1975), morphology (James 1970), foraging behavior (Roth 1979), and plumage (Pratt 1980). Comparisons of avian communities between regions are common (e.g. Karr 1971, Rabenold 1978, Diamond 1979, Rotenberry and Wiens 1980). However, these studies were based upon *a priori* defined habitat structure so that bird species diversity and behavior could be determined and compared within a similar habitat physiognomy. Detailed analyses of habitat structure and geographic habitat differences for a species are few (Cody 1978). Perhaps differences in habitat may provide a basis for interpreting morphological or behavioral variation.

The purpose of this study was to analyze the habitat of the Black-throated Green Warbler (*Dendroica virens*) to determine if habitat, like other behavioral characteristics, shows geographic variation. This species was selected because of its wide geographic range (Figure 1) and its known within-region habitat variability (Bent 1953, Griscom and Sprunt 1979, Collins 1981). General accounts of the Black-throated Green Warbler have indicated that this species prefers pine (*Pinus*) forests in southern New England and spruce-fir (_Picea_-_Abies_) vegetation farther north (Bent 1953). However, Brooks (1940) stated that, in the central Allegheny Mountains, the Black-throated Green Warbler occurred at high elevations, in spruce, hemlock (_Tsuga_), northern hardwoods, oak-pine (_Quercus_-_Pinus_) scrub, and oak-hickory (_Quercus_-_Carya_) forests. Specific questions addressed in this study were: (1) Is the habitat structure of the Black-throated Green Warbler different at several points in its range? (2) Is the habitat variability greater within or between regions? (3) What are the habitat structure variables that differ between regions?

## MATERIALS AND METHODS

_Study sites_. To analyze the potential pattern of habitat variation five study sites were selected (Figure 1): (1) Mount Desert Island (MDI), Maine; (2) Mount Blue State Park and vicinity (MAINE), west-central Maine; (3) White Mountain National Forest (WMF), central New Hampshire; (4) southern Adirondacks (NYA), east-central New York; and (5) Itasca State Park (MINN), north-central Minnesota. These sites are located throughout the hemlock-white pine-northern hardwoods forest region that extends from northern Minnesota through the Great Lakes region into New England. This forest type is characterized by "...the pronounced alteration of deciduous, coniferous, and mixed forest communities" (Braun 1950: 337). Specifically, this heterogeneous regional vegetation type includes upland spruce-fir stands, pine forest, deciduous forests of maple (_Acer_), basswood

(*Tilia*), birch (*Betula*), aspen (*Populus*), and ash (*Fraxinus*) along with bogs and old fields (Braun 1950).

At each study site, 13 structural characteristics of the vegetation (Table 1) were recorded in 0.04-ha (0.1-a) circles centered on the song perch of a singing male Black-throated Green Warbler. Samples were located without regard to vegetation types, elevation, or topography. The number of circles recorded per site was: MDI=10 (16-17 June 1980), MAINE=11 (30 May-7 July 1980), WMF=10 (26-28 June 1980), NYA=4 (17 July 1980), and MINN=15 (1 June-7 July 1978,1979).

Habitat structure for the 50 samples at the five sites was analyzed by a principal components 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 for each site in the space defined by the first two principal components. These ellipses depict relationships of the Black-throated Green Warbler habitat at each site along structural gradients defined by the 13 habitat variables, and they provide a visual representation of within and between site habitat differences. They do not imply a statistical test of differences in habitat structure between sites.

To quantify the differences in habitat structure between sites, data from the five sample areas were also analyzed by discriminant function analysis (DFA). This technique employs all variables necessary to discriminate between *a priori* defined groups. By using the habitat variables for each study site, treating each site as a separate group, DFA determines if the habitat structure at one site can be discriminated from the structure of another site. If groups can be distinguished, DFA will provide a stepwise analysis that yields a linear function including those habitat variables that can be combined to identify group membership. In addition, DFA will reclassify samples from an original group to a group in which the sample has a higher probability of membership. If no samples are reclassified, complete discrimination between groups is possible. Certain caveats are in order. DFA cannot be used in a predictive manner because the habitat data are not normally distributed, nor do all the variables show homogeneity of variances. However, DFA can provide a means of identifying discriminating variables, reducing the dimensionality of the variable matrix and graphically representing the differences between groups (Neff and Marcus 1980).

Structural differences between sites in the habitat ordination may be due to differences in tree species composition at the study areas. Tree species similarity between the five sites was quantified by the coefficient of community:

$$CC_t = 2S_{ab}/(S_a + S_b)$$

where $CC_t$ is the tree species similarity, $S_a$ is the number of species in sample *A*, $S_b$ is the number in sample *B*, and $S_{ab}$

the number common to both samples (Whittaker 1975: 118).

To compare similarity of the vegetation at the five sites, importance percentages (IP = [relative density + relative dominance]/2; Curtis and McIntosh 1951) were calculated for tree species in each of the circular plots. Tree species with less than four occurrences were deleted from the analysis, and red spruce (*Picea rubens*) and white spruce (*P. glauca*) data were pooled for analysis. The IP's of the species were $\log_{10}$ transformed and subjected to reciprocal averaging-polar ordination (PO-RA, Hill 1973, del Moral and Watson 1978). Untransformed variables were analyzed by an unweighted pair group cluster analysis using arithmetic averaging (UPGMA, Sneath and Sokal 1973), and DFA of the groups determined by the cluster analysis (del Moral 1975). The re-structured groups were then located on the vegetation ordination and identified by leading dominants. See Collins, Risser, and Rice (1981) for a detailed description of the vegetation analysis procedures.

## RESULTS

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 low percent shrub cover (CH, T6, SC, T7) from those areas characterized by smaller trees (T2, T3, T1). Component II (13.7% of the variance) is a deciduous-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) had large negative loadings for medium sized trees and percent coniferous vegetation (T5, T4, CO). The fourth component (9.9% of the variance) had high positive loadings for CC and SPT, and a negative loading for T4, suggesting that as the forest canopy closes, more tree species occur.

The distribution of the sites in the space defined by the first two principal components (Figure 2) shows that Black-throated Green Warbler habitat in NYA and MINN contains large trees and tall canopies, whereas, the MAINE and MDI habitats had more small trees of lower stature. WMF and MAINE overlap considerably in PCA space with the habitat of the former containing, on the average, more large trees than the latter. Along the second component, MINN and MAINE habitats had more coniferous vegetation than did the NYA, WMF, and MAINE sites. Indeed, some circular plots at the latter sites included only deciduous forest components. In summary, differences in habitat structure occur within the range of the Black-throated Green Warbler based primarily upon tree size and percent coniferous vegetation. That is, habitats ranged from tall canopied to shorter, more dense forests, and from coniferous to mixed and deciduous forests.

Ten variables entered into the stepwise discriminant function analysis (Table 3). The F-statistic (not given) from the analysis can not be treated as a measure of significance because the habitat data do not meet the rigid criteria of this multivariate technique. Instead, the order of entry by the variables into the analysis is an indication of the relative importance of each variable for separating the regions. Also, the sign of each variable's coefficient contributes to the effect of each variable when discriminating between sites. Thus, based on the ten variables (Table 3), habitat group membership can be estimated (Table 4). Number of species of trees, canopy cover, and canopy height had high positive coefficients in each site classification function. High negative coefficients were found for T5 and T7 except the latter variable had a positive value at the NYA site.

Based upon the classification functions in Table 3, most of the circular plots at each site were more similar to each other than to the members of the other groups (Table 4). All MDI samples could be discriminated from the other four groups. There is enough similarity in habitat structure between WMF and MINN, and WMF and MAINE that some stands were reclassified between these pairs of groups. However, no samples from MAINE were re-grouped within MINN samples or vice versa.

One means of estimating the effect of plant species composition on differences in habitat structure is the correlation of similarity of tree species ($CC_t$) and the similarity of between-site habitat structure. Structural similarity of the five sites was determined by the Euclidean distance between the group means in the first two canonical axes of the DFA. These distances were correlated with the coefficient of community values and no relationship was found ($r^2 = 0.006$) suggesting that differences in habitat structure at the five sites are not strictly a function of tree species composition.

My results indicated that the composition of the vegetation sampled at the five sites can be classified into five general plant community types (Figure 3). MDI and MINN, the most distant sites sampled in the range of the Black-throated Green Warbler, support vegetation which is relatively unique to their respective locations compared to the other five sites. MDI had arbor vitae (*Thuja occidentalis*)-spruce forests, whereas, MINN supported groves of large red and white pine (*Pinus resinosa* and *P. strobus*, respectively). Stands dominated by balsam fir (*Abies balsamea*) were common in MAINE and MINN although these stands differed in the less important tree components. Deciduous stands of yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), and beech (*Fagus grandifolia*) were common in NYA, MAINE, and WMF sites. The most abundant vegetation type sampled, however, was the mixed forest of spruce-fir, and deciduous species including red maple (*Acer rubrum*), sugar maple, yellow birch, paper birch (*Betula papyrifera*), and beech. Hemlock (*Tsuga canadensis*) was found in several stands yet it was rarely a major component of the habitat of the Black-throated Green Warbler. Thus, it appears that vegetation composition, to some extent, is the same within the sample areas at the five sites even though some sites supported unique plant community types. Therefore, the dissimilarities in habitat structure at the five sites are partly the result of tree species compostion but, more importantly, they are due to different vegetation structure at each site.

## DISCUSSION

Previous descriptions of the habitat of the Black-throated Green Warbler have indicated that this species breeds in a variety of habitat types (Brooks 1940, Bent 1953, Griscom and Sprunt 1979, Greenberg 1979). These habitats were often described as plant community types and were not analyzed to determine if the structure of the habitat varied within or between regions. My findings indicate that the habitat of the Black-throated Green Warbler differs in three-dimensional structure as well as in plant species composition both within and between sites. However, the differences between-sites are greater than within-sites (Table 4).

The differences in habitat structure between sites were not strictly the result of plant community composition. For instance, MAINE and MINN sites had both similar and different plant community types (Figure 3), yet structurally the habitat of the Black-throated Green Warbler at each site was very different (Table 4, Figure 2). Several factors contribute to this dissimilarity between sites including elevational changes in MINN being slight, whereas, the topography at MAINE is mountainous producing upper elevational forests of short, dense fir and spruce trees. Secondly, the vegetation of the MAINE study area was younger than that of Itasca, Minnesota, because of more recent forestry activity at the former site. Thus the MAINE second growth mixed and deciduous forest contained many trees in the smaller size classes. Finally, groves of large red and white pine, a prefered habitat type (Bent 1953), occurred at several locations in MINN yet this vegetation type was not found at the MAINE study site. Therefore, the differences in the Black-throated Green Warbler habitat at these two sites are the result of both vegetation composition and habitat structure.

MDI, a large island about 300 m off the coast of Maine, contains large areas of spruce and arbor vitae forests (Davis 1966) that increase the total coniferous component of the habitat. Deciduous forests of beech and maple also occur on the island. WMF, a large multi-use national forest, contains old growth deciduous forests of yellow birch, sugar maple, beech, and red spruce in lower elevations with an increasing importance of spruce and fir at higher elevations (Bormann et al. 1970). The Black-throated Green Warbler was observed in all these plant communities. The NYA study site was not adequately sampled but the four plots contained large deciduous trees, especially yellow birch, and scattered large individuals of red spruce. Overall, canopy cover was the most predictable component in the habitat of the Black-throated Green Warbler among the five regions, and the other habitat characteristics were more variable.

Reasons for the regional differences may be available habitat (as previously described), food resources, predators, other species, foraging behavior, or a plastic response to different habitat configurations. Evidence indicates that certain tree species support different communities of insects (Futuyma and Gould 1979). The birds may adjust their foraging behavior and territories in response to this factor. Conceivably, competitive interactions may govern habitat and foraging patterns (MacArthur 1958, Cody 1974); however, others feel that interspecific competition may not be an important factor affecting the warblers during the breeding season (Morse 1976, Lister 1980, Collins 1981). Unfortunately, information on foraging behavior, response to predators, or resource levels does not exist for this species at any but the MDI site. Clearly, more detailed analyses of the Black-throated Green Warbler as well as other species are necessary to determine the causes of geographical shifts in behavior.

In conclusion, the habitat of the Black-throated Green Warbler does show differences in structure at the five sites. The variability of the habitat was greater between sites than within sites although structural overlap did occur between some regions. Finally, the dissimilarity of the habitat at the five locations was partly due to changes in vegetation composition, but, it is mostly attributable to differences in the structure of the vegetation at the sites.

## ACKNOWLEDGEMENTS

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## LITERATURE CITED

Bent, A.C. 1953. Life histories of North American wood warblers. U.S. Natl. Mus. Bull. 203.

Bormann, F.H., T.G. Siccama, G.E. Likens, and R.H. Whittaker. 1970. The Hubbard Brook ecosystem study: composition and dynamics of the tree stratum. Ecol. Monogr. 40: 373-388.

Braun, E.L. 1950. Deciduous forest of eastern North America. Blakeston Press, Philadelphia, Pa.

Brooks, M. 1940. The breeding warblers of the central Allegheny region. Wilson Bull. 52: 249-266.

Cody, M.L. 1974. Competition and the structure of bird communities. Princeton Univ. Press, Princeton, NJ.

Collins, S.L. 1981. Habitat relationships and habitat variability of the wood warblers (Parulidae). Ph. D. dissertation, University of Oklahoma, Norman, Ok.

Collins, S.L., P.G. Risser, and E.L. Rice. 1981. Ordination and classification of mature bottomland forests in north-central Oklahoma. Bull. Torrey Bot. Club 108: in press.

Curtis, J.T. and R.P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32: 476-496.

Davis, R.B. 1966. Spruce-fir forests of the coast of Maine. Ecol. Monogr. 36: 79-94.

Diamond, J.M. 1979. Population dynamics and interspecific competition in bird communities. Fortschr. Zool. 25: 389-402.

Futuyma, D.J. and F. Gould. 1979. Associations of plants and insects in a deciduous forest. Ecol. Monogr. 49: 33-50.

Greenberg, R. 1979. Body size, breeding habitat, and winter exploitation systems in Dendroica. Auk 96: 756-766.

Griscom, L. and A. Sprunt (eds). 1979. The warblers of North America. Doubleday and Co., Garden City, NJ.

Hill, M.O. 1973. Reciprocal averaging: an eigenvector method of ordination. J. Ecol. 61: 237-249.

James, F.C. 1970. Geographic size variation in birds and its relationship to climate. Ecology 51: 365-390.

James, F.C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bull. 83: 215-236.

James, F.C. and H.H. Shugart. 1970. A quantitative method of habitat description. Audubon Field Notes 24: 727-736.

Johnston, R.F. 1979. Woodland breeding bird communities in eastern Kansas. Trans. Kansas Acad. Sci. 82: 246-251.

Karr, J.A. 1971. Structure of avian communities in selected Panama and Illinois habitats. Ecol. Monogr. 41: 207-233.

Lister, B.C. 1980. Resource variation and the structure of British bird communities. Proc. Natl. Acad. Sci. 77: 4185-4187.

MacArthur, R.H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39: 599-619.

Moral, R. del. 1975. Vegetation clustering by means of ISODATA: revision by multiple discriminant analysis. Vegetatio 29: 179-190.

Moral, R. Del and A.F. Watson. 1978. Gradient structure of forest vegetation in the central Washington Cascades. Vegetatio 38: 29-48.

Morse, D.H. 1976. Variables determining the density and territorial size of breeding spruce-woods warblers. Ecology 57: 290-301.

Neff, N.A. and L.F. Marcus. 1980. A survey of multivariate methods for systematics. New York: privately published.

Nottebohm, F. 1975. Continental patterns in Zonotrichia capensis: some possible ecological correlates. Am. Nat. 109: 605-624.

Pratt, H.D. 1980. Intra-island variation in the 'Elepaio on the island of Hawai'i. Condor 82: 449-458.

Rabenold, K.N. 1978. Foraging strategies, diversity, and seasonality in bird communities. Ecol. Monogr. 48: 397-424.

Rotenberry, J.T. and J.A. Wiens. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology 61: 1228-1250.

Roth, R.R. 1979. Foraging behavior of Mockingbirds: the effect of too much grass. Auk 96: 421-422.

Smith, K.G. 1977. Distribution of summer birds along a forest moisture gradient in an Ozark watershed Ecology 58: 810-819.

Sneath, P.H.A. and R.R. Sokal. 1973. Numerical taxonomy. W.H. Freeman and Co., San Francisco, Ca.

Sokal, R.R. and F.J. Rohlf. 1969. Biometry. W.H. Freeman and Co., San Francisco, Ca.

Whitmore, R.C. 1975. Habitat ordination of breeding passerine birds of the Virgin River Valley, southwestern Utah. Wilson Bull. 87: 65-74.

Whittaker, R.H. 1975. Communities and ecosystems. MacMillan Co., New York, NY.

Table 1. Variables of the structure of the vegetation considered in the analysis of 0.04-ha circular samples (James and Shugart 1970).

1. Percent ground cover (GC) - No. of sightings of ground vegetation at 20 evenly-spaced points across a transect dividing the circle multiplied by 5.
2. Percent shrub cover (SC) - No. of contacts of shrub vegetation by the outstretched arms at 20 evenly-spaced points across a transect dividing the circle multiplied by 5.
3. Percent canopy cover (CC) - No. of sightings of canopy vegetation at 20 evenly-spaced points across a transect dividing the circle multiplied by 5.
4. Percent conifer (CO) - No. of sightings of coniferous vegetation in the canopy at 20 evenly-spaced points across a transect dividing the circle multiplied by 5.
5. Canopy height in meters (CH).
6. No. of species of trees per 0.04-ha circle (SPT).
7. No. of trees 7.5-15 cm dbh (T1).
8. No. of trees 15.1-23 cm dbh (T2).
9. No. of trees 23.1-30 cm dbh (T3).
10. No. of trees 30.1-38 cm dbh (T4).
11. No. of trees 38.1-53 cm dbh (T5).
12. No. of trees 53.1-68 cm dbh (T6).
13. No. of trees greater than 68.1 cm dbh (T7).

Table 2. Summary of the first four principal components. Values are correlations with original variables.

| Variable | Principal component I | II | III | IV |
|---|---|---|---|---|
| Ground cover | .111 | .577 | .261 | -.051 |
| Shrub cover | -.532 | -.314 | .160 | -.294 |
| Canopy cover | -.072 | -.496 | -.329 | .551 |
| Canopy height (m) | -.739 | .466 | -.281 | .111 |
| Percent conifer | .238 | .709 | -.423 | .258 |
| No. tree species | .056 | -.510 | -.016 | .508 |
| Trees 7.5-15 cm dbh | .677 | .019 | .264 | .299 |
| Trees 15.1-23 cm | .876 | .205 | -.154 | .160 |
| Trees 23.1-30 cm | .818 | .059 | -.368 | -.032 |
| Trees 30.1-38 cm | .267 | -.196 | -.549 | -.601 |
| Trees 38.1-53 cm | -.397 | -.076 | -.711 | .002 |
| Trees 53.1-68 cm | -.657 | .208 | -.167 | .270 |
| Trees > 68.1 cm | -.511 | .169 | .166 | .175 |
| Eigenvalue | 3.72 | 1.79 | 1.56 | 1.29 |
| Percent of variance | 28.6 | 13.7 | 12.0 | 9.9 |
| Sum of variance | 28.6 | 42.4 | 54.4 | 64.3 |

Table 3. Classification functions for the habitat of the Black-throated Green Warbler at the five sites. Variables are listed in order of entry into the discriminant function.

MDI = - 88.21 + 2.77SPT - 0.15CO + 0.88CH + 0.21SC - 1.63T7 + 0.24GC - 0.85T5 + 1.01CC + 0.72T3 + 0.42T1

WMF = -119.11 + 4.80SPT - 0.43CO + 1.32CH + 0.27SC - 1.85T7 + 0.22GC - 1.58T5 + 1.24CC + 0.26T3 + 0.39T1

MINN = -108.64 + 4.22SPT - 0.36CO + 1.37CH + 0.27SC - 1.79T7 + 0.24GC - 1.94T5 + 1.16CC - 0.04T3 + 0.27T1

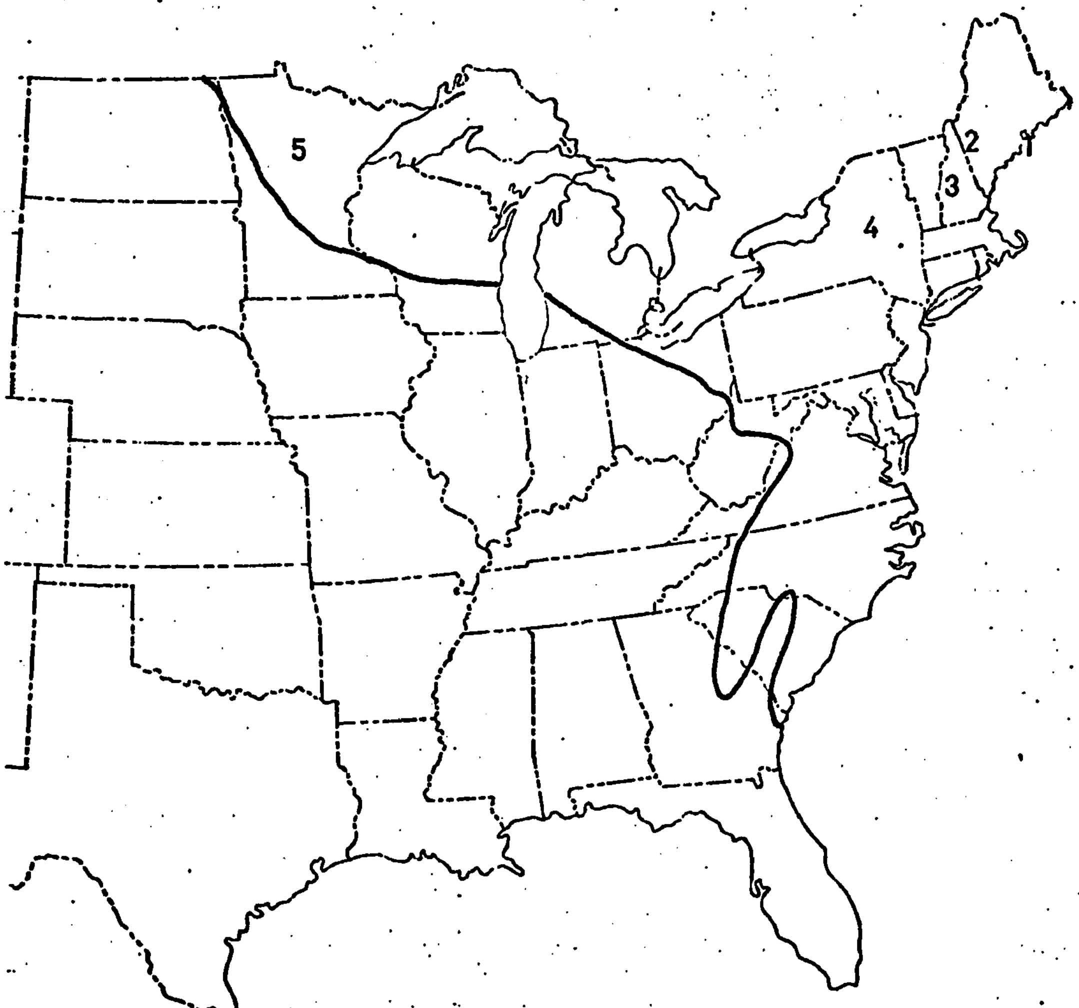
MAINE = -118.49 + 5.49SPT -0.40CO + 1.27CH + 0.25SC - 2.34T7 + 0.18GC -2.15T5 + 1.26CC + 0.08T3 + 0.37T1

NYA = -139.18 + 5.28SPT - 0.45CO + 1.49CH + 0.39SC + 0.80T7 + 0.16GC -1.79T5 + 1.26CC - 0.18T3 + 0.40T1

Table 4. Summary of the classification results from the discriminant function analysis.

| | MDI | WMF | MINN | MAINE | NYA | % CORRECT |
|---|---|---|---|---|---|---|
| MDI | 10 | 0 | 0 | 0 | 0 | 100 |
| WMF | 0 | 8 | 0 | 2 | 0 | 80 |
| MINN | 0 | 3 | 12 | 0 | 0 | 80 |
| MAINE | 0 | 2 | 0 | 9 | 0 | 82 |
| NYA | 0 | 0 | 0 | 0 | 4 | 100 |

## LIST OF FIGURES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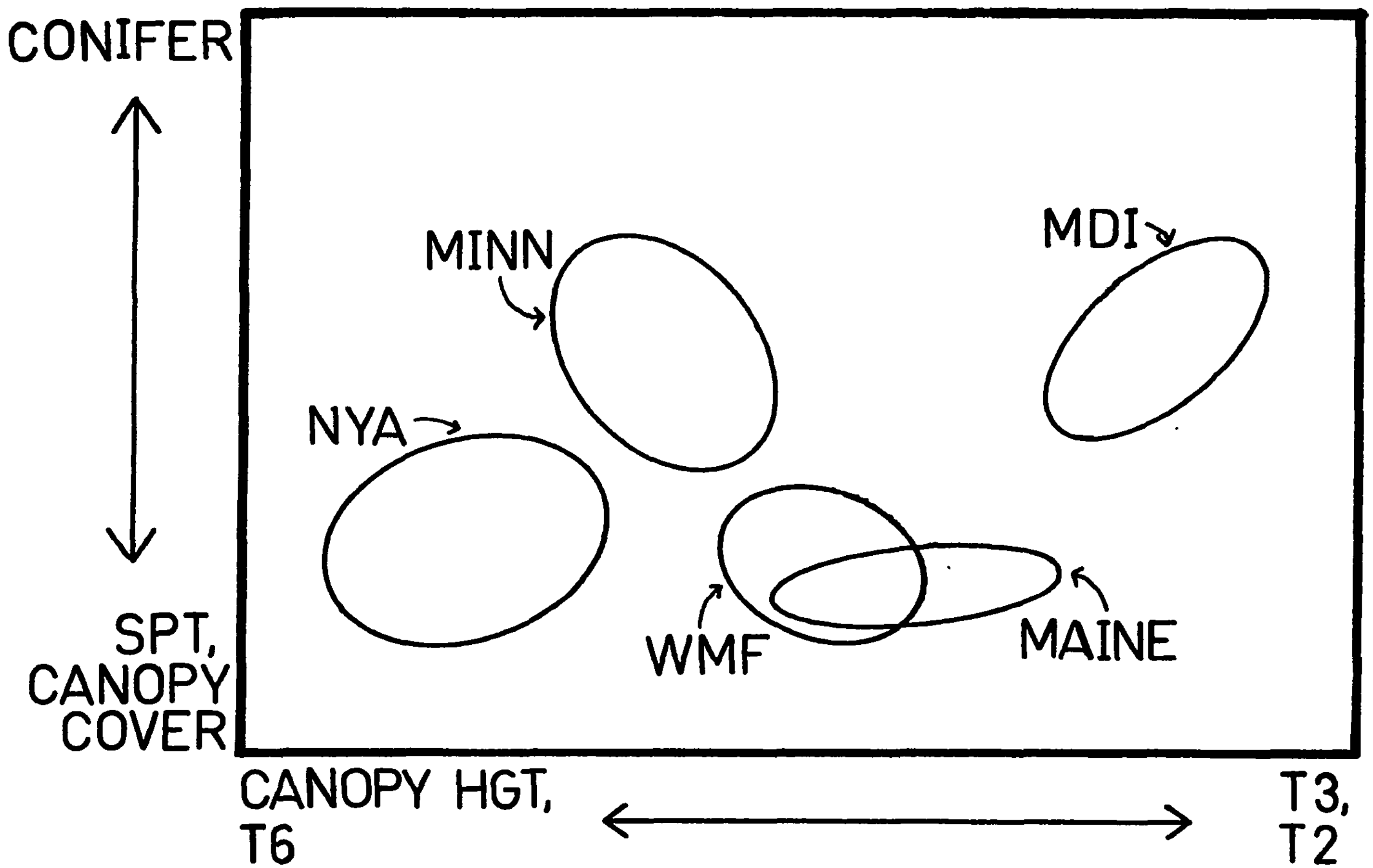
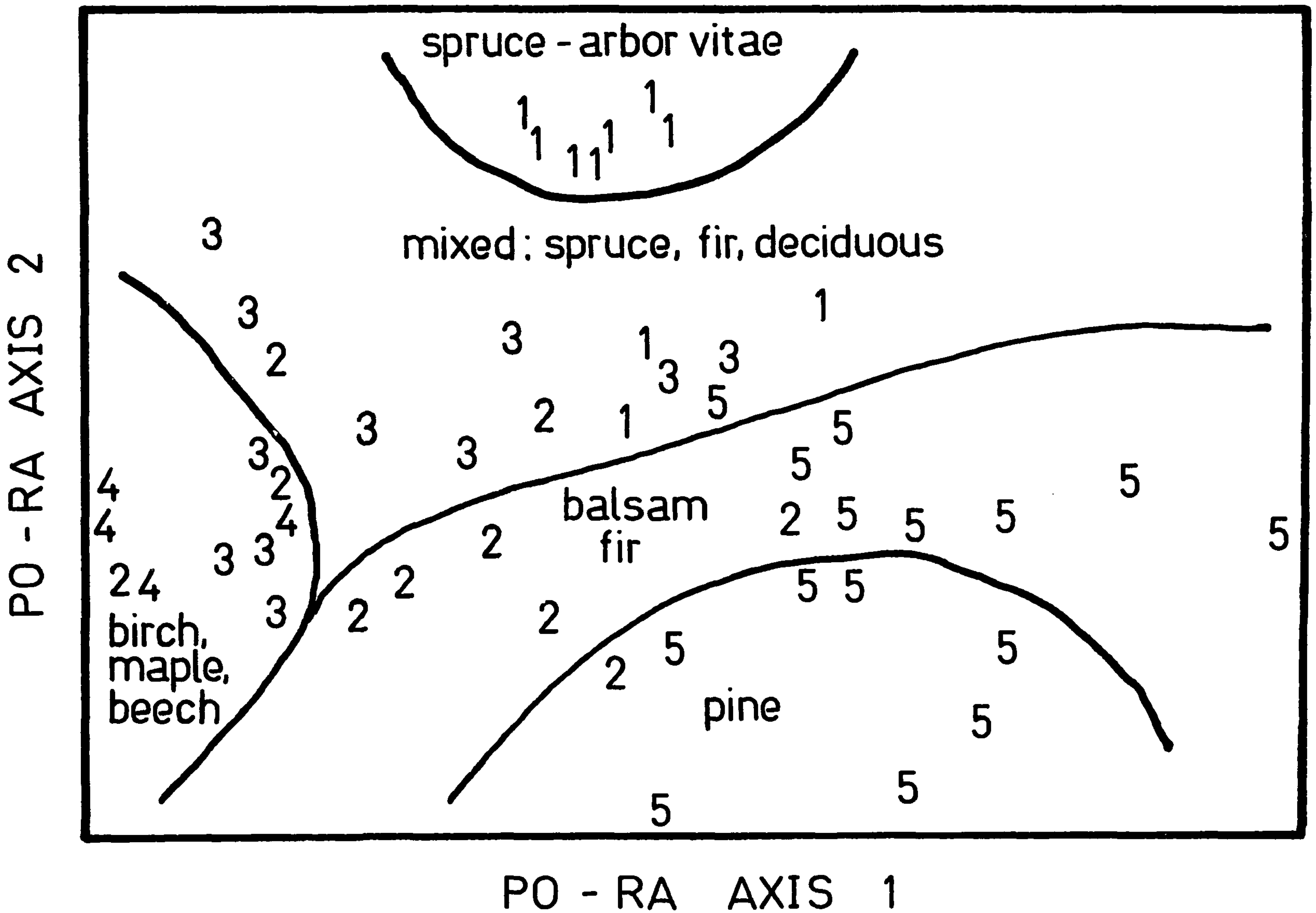

CONIFER
SPT, CANOPY COVER
CANOPY HGT, T6
T3, T2
MINN
MDI
NYA
WMF
MAINE



spruce - arbor vitae
mixed: spruce, fir, deciduous
balsam fir
birch, maple, beech
pine
PO - RA AXIS 2
PO - RA AXIS 1

Appendix I. Variables of the structure of the vegetation considered in the analysis of 0.04-ha (0.1-acre) circular plots for 17 species of warblers in Minnesota.

| SPECIES | | GC[a] | SC | CC | CH | CO | SPT | T1 | T2 | T3 | T4 | T5 | T6 | T7 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Black and White Warbler | | 65 | 80 | 90 | 54 | 35 | 6 | 14 | 8 | 12 | 3 | 2 | 0 | 0 |
| | | 75 | 40 | 75 | 49 | 30 | 6 | 28 | 7 | 11 | 5 | 0 | 0 | 0 |
| | | 50 | 90 | 55 | 65 | 30 | 5 | 8 | 4 | 1 | 7 | 2 | 0 | 0 |
| | | 50 | 45 | 90 | 33 | 80 | 5 | 7 | 15 | 6 | 3 | 1 | 0 | 0 |
| | | 55 | 50 | 55 | 59 | 55 | 6 | 17 | 10 | 11 | 6 | 6 | 0 | 0 |
| | | 70 | 50 | 60 | 35 | 0 | 7 | 27 | 14 | 11 | 3 | 0 | 0 | 0 |
| | | 85 | 45 | 75 | 59 | 45 | 6 | 21 | 6 | 13 | 8 | 6 | 0 | 0 |
| | | 90 | 45 | 80 | 30 | 15 | 8 | 36 | 4 | 8 | 5 | 2 | 2 | 0 |
| | | 55 | 30 | 50 | 53 | 15 | 4 | 1 | 4 | 3 | 2 | 3 | 1 | 0 |
| | | 60 | 40 | 95 | 47 | 0 | 5 | 16 | 16 | 10 | 15 | 4 | 0 | 0 |
| | $\bar{X}$ | 65.5 | 51.5 | 72.5 | 48.4 | 30.5 | 5.8 | 17.5 | 8.8 | 8.6 | 5.7 | 2.6 | 0.3 | 0.0 |
| Golden-winged Warbler | | 100 | 100 | 35 | 39 | 0 | 2 | 2 | 5 | 2 | 0 | 0 | 0 | 0 |
| | | 100 | 95 | 15 | 20 | 0 | 4 | 11 | 0 | 2 | 0 | 0 | 0 | 0 |
| | | 100 | 60 | 30 | 40 | 0 | 2 | 0 | 6 | 1 | 1 | 0 | 0 | 0 |
| | | 100 | 55 | 15 | 20 | 0 | 3 | 7 | 0 | 0 | 0 | 0 | 0 | 0 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 55 | 50 | 65 | 63 | 55 | 5 | 11 | 10 | 5 | 5 | 0 | 0 | 0 |
| | 95 | 90 | 50 | 29 | 0 | 4 | 15 | 15 | 9 | 0 | 0 | 0 | 0 |
| | 85 | 45 | 35 | 75 | 35 | 5 | 4 | 4 | 0 | 1 | 0 | 3 | 1 |
| | 100 | 80 | 10 | 30 | 0 | 2 | 1 | 2 | 0 | 0 | 0 | 0 | 0 |
| | 100 | 45 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 100 | 35 | 20 | 26 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| | 80 | 35 | 70 | 38 | 25 | 7 | 12 | 7 | 9 | 4 | 2 | 0 | 0 |
| $\bar{X}$ | 92.3 | 45.0 | 31.4 | 34.5 | 10.4 | 3.2 | 5.7 | 4.6 | 2.4 | 1.0 | 0.5 | 0.3 | 0.1 |
| Nashville Warbler | 95 | 60 | 65 | 40 | 65 | 4 | 41 | 27 | 3 | 2 | 0 | 0 | 0 |
| | 70 | 50 | 75 | 73 | 40 | 3 | 11 | 14 | 5 | 3 | 6 | 1 | 0 |
| | 95[b] | 90 | 30 | 19 | 30 | 2 | 17 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 100 | 80 | 15 | 22 | 15 | 2 | 7 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 100 | 65 | 40 | 25 | 40 | 2 | 39 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 90[b] | 50 | 35 | 27 | 35 | 3 | 35 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 85 | 80 | 50 | 37 | 10 | 4 | 24 | 12 | 2 | 0 | 0 | 0 | 0 |
| | 70 | 50 | 60 | 80 | 40 | 5 | 5 | 8 | 6 | 1 | 2 | 0 | 2 |
| | 75 | 80 | 40 | 35 | 20 | 3 | 3 | 2 | 2 | 2 | 0 | 0 | 0 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 70 | 60 | 35 | 40 | 0 | 6 | 9 | 3 | 2 | 1 | 1 | 0 | 0 |
| | 70 | 55 | 80 | 43 | 30 | 4 | 5 | 5 | 10 | 3 | 0 | 0 | 0 |
| | 95[b] | 25 | 55 | 55 | 55 | 6 | 10 | 2 | 8 | 7 | 1 | 0 | 0 |
| | 100 | 25 | 75 | 35 | 75 | 3 | 41 | 22 | 3 | 0 | 0 | 0 | 0 |
| $\bar{X}$ | 81.1 | 53.9 | 59.4 | 48.7 | 36.7 | 4.2 | 16.5 | 10.5 | 4.5 | 2.1 | 1.1 | 0.1 | 0.2 |
| Northern Parula | 75 | 45 | 80 | 73 | 30 | 9 | 16 | 10 | 4 | 2 | 3 | 3 | 0 |
| | 85[b] | 40 | 75 | 70 | 45 | 8 | 23 | 5 | 2 | 0 | 4 | 1 | 0 |
| | 75 | 40 | 95 | 57 | 60 | 6 | 8 | 20 | 13 | 8 | 3 | 0 | 0 |
| | 60[b] | 10 | 95 | 49 | 45 | 6 | 11 | 17 | 9 | 7 | 0 | 0 | 0 |
| | 75 | 40 | 75 | 49 | 30 | 6 | 28 | 7 | 11 | 5 | 0 | 0 | 0 |
| | 95[b] | 75 | 50 | 49 | 50 | 8 | 14 | 10 | 5 | 3 | 0 | 0 | 0 |
| | 60[b] | 85 | 85 | 61 | 85 | 4 | 1 | 5 | 3 | 5 | 5 | 0 | 0 |
| | 50 | 65 | 70 | 55 | 50 | 6 | 4 | 9 | 9 | 4 | 0 | 1 | 1 |
| | 30 | 70 | 75 | 69 | 25 | 3 | 10 | 11 | 13 | 1 | 0 | 0 | 0 |
| | 60 | 5 | 75 | 55 | 40 | 8 | 6 | 10 | 8 | 2 | 3 | 1 | 2 |
| | 30 | 35 | 90 | 41 | 30 | 5 | 18 | 14 | 7 | 6 | 8 | 0 | 0 |
| | 80 | 60 | 80 | 45 | 50 | 6 | 17 | 7 | 6 | 2 | 0 | 0 | 0 |
| | 45 | 55 | 80 | 45 | 80 | 3 | 1 | 14 | 9 | 4 | 2 | 0 | 0 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 45 | 60 | 55 | 38 | 50 | 6 | 8 | 0 | 3 | 6 | 7 | 0 | 0 |
| | 55 | 55 | 65 | 50 | 50 | 6 | 3 | 12 | 11 | 1 | 4 | 0 | 0 |
| | 85 | 45 | 60 | 69 | 50 | 5 | 19 | 6 | 6 | 6 | 2 | 1 | 0 |
| $\bar{X}$ | 60.3 | 50.0 | 76.4 | 55.2 | 49.3 | 6.0 | 10.0 | 11.0 | 7.3 | 3.6 | 2.8 | 0.4 | 0.2 |
| Yellow Warbler | 80[b] | 35 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 80 | 40 | 30 | 80 | 30 | 3 | 1 | 0 | 0 | 0 | 0 | 2 | 1 |
| | 100[b] | 40 | 20 | 20 | 0 | 2 | 1 | 3 | 0 | 0 | 0 | 0 | 0 |
| | 100 | 10 | 15 | 25 | 0 | 1 | 10 | 1 | 3 | 0 | 0 | 0 | 0 |
| | 85 | 65 | 10 | 40 | 10 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| | 100 | 11 | 28 | 40 | 0 | 2 | 4 | 7 | 5 | 1 | 0 | 0 | 0 |
| | 100 | 60 | 45 | 70 | 10 | 3 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 100 | 75 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 100[b] | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 100[b] | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 100 | 60 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 100 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 100 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 100 | 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | X̄ | 96.1 | 38.9 | 10.6 | 19.6 | 2.9 | 1.1 | 0.9 | 1.8 | 0.5 | 0.1 | 0.1 | 0.2 | 0.1 |
| Magnolia Warbler | | 50 | 90 | 70 | 63 | 70 | 4 | 7 | 21 | 19 | 4 | 6 | 0 | 0 |
| | | 20 | 60 | 85 | 69 | 65 | 7 | 20 | 9 | 9 | 8 | 5 | 0 | 0 |
| | | 35 | 75 | 80 | 51 | 5 | 4 | 34 | 11 | 9 | 4 | 0 | 0 | 0 |
| | | 55 | 85 | 60 | 45 | 20 | 6 | 23 | 11 | 8 | 9 | 1 | 0 | 0 |
| | | 60 | 80 | 30 | 40 | 25 | 3 | 9 | 7 | 5 | 3 | 2 | 0 | 0 |
| | | 100 | 100 | 10 | 30 | 10 | 2 | 5 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | 50 | 60 | 65 | 67 | 65 | 5 | 26 | 16 | 5 | 2 | 2 | 2 | 2 |
| | | 45 | 60 | 80 | 63 | 60 | 5 | 9 | 22 | 14 | 2 | 5 | 2 | 0 |
| | | 45 | 75 | 70 | 70 | 40 | 7 | 29 | 15 | 11 | 2 | 2 | 1 | 0 |
| | X̄ | 51.1 | 76.1 | 61.1 | 55.3 | 40.0 | 4.6 | 18.0 | 12.4 | 8.9 | 3.8 | 2.1 | 0.6 | 0.2 |
| Yellow-rumped Warbler | | 55 | 30 | 65 | 53 | 60 | 6 | 23 | 12 | 9 | 6 | 4 | 0 | 0 |
| | | 80 | 70 | 60 | 39 | 60 | 5 | 12 | 1 | 0 | 0 | 0 | 0 | 0 |
| | | 85 | 45 | 60 | 69 | 50 | 5 | 19 | 6 | 6 | 6 | 2 | 1 | 0 |
| | | 100 | 10 | 85 | 67 | 60 | 5 | 13 | 22 | 11 | 4 | 1 | 0 | 0 |
| | | 100 | 65 | 60 | 37 | 60 | 3 | 90 | 18 | 6 | 0 | 0 | 0 | 0 |
| | X̄ | 84.0 | 44.0 | 66.0 | 53.0 | 58.0 | 4.8 | 31.4 | 11.8 | 6.4 | 3.2 | 1.6 | 0.2 | 0.0 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Black-throated Green Warbler | 40 | 50 | 75 | 63 | 60 | 5 | 31 | 11 | 2 | 3 | 0 | 3 | 0 |
| | 40 | 30 | 80 | 53 | 55 | 5 | 10 | 21 | 7 | 4 | 3 | 1 | 0 |
| | 95 | 15 | 85 | 73 | 65 | 7 | 19 | 20 | 9 | 5 | 1 | 2 | 2 |
| | 80 | 15 | 85 | 77 | 85 | 5 | 34 | 11 | 6 | 0 | 4 | 4 | 2 |
| | 40 | 80 | 90 | 51 | 10 | 7 | 11 | 4 | 3 | 6 | 4 | 0 | 0 |
| | 60 | 45 | 95 | 73 | 60 | 7 | 9 | 14 | 5 | 5 | 2 | 2 | 3 |
| | 65 | 55 | 90 | 71 | 60 | 8 | 8 | 13 | 5 | 2 | 11 | 2 | 0 |
| | 40 | 50 | 95 | 89 | 95 | 5 | 10 | 4 | 2 | 1 | 7 | 11 | 0 |
| | 45 | 15 | 100 | 55 | 20 | 4 | 11 | 13 | 6 | 0 | 2 | 3 | 3 |
| | 35 | 90 | 90 | 51 | 40 | 5 | 9 | 12 | 11 | 5 | 1 | 0 | 0 |
| | 55 | 35 | 80 | 51 | 0 | 6 | 29 | 7 | 8 | 5 | 3 | 0 | 0 |
| | 60 | 40 | 95 | 47 | 0 | 5 | 16 | 16 | 10 | 15 | 4 | 0 | 0 |
| | 55 | 45 | 45 | 57 | 45 | 8 | 13 | 3 | 4 | 9 | 1 | 1 | 0 |
| | 40 | 35 | 70 | 90 | 70 | 5 | 8 | 3 | 1 | 2 | 3 | 0 | 3 |
| | 40 | 15 | 90 | 90 | 90 | 5 | 9 | 6 | 6 | 4 | 3 | 0 | 0 |
| $\bar{X}$ | 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 |
| Blackburnian Warbler | 70 | 45 | 85 | 61 | 55 | 5 | 7 | 10 | 10 | 5 | 3 | 2 | 0 |
| | 25 | 85 | 85 | 70 | 60 | 6 | 28 | 2 | 2 | 0 | 4 | 1 | 1 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 30 | 20 | 95 | 63 | 85 | 6 | 24 | 22 | 11 | 6 | 4 | 0 | 0 |
| | 50 | 20 | 75 | 55 | 55 | 6 | 27 | 20 | 22 | 7 | 1 | 0 | 0 |
| | 65 | 15 | 85 | 57 | 70 | 6 | 22 | 21 | 5 | 3 | 1 | 1 | 1 |
| | 70 | 35 | 70 | 75 | 35 | 5 | 11 | 3 | 5 | 5 | 4 | 1 | 0 |
| | 50 | 50 | 90 | 41 | 35 | 6 | 22 | 13 | 5 | 9 | 0 | 0 | 1 |
| | 60 | 20 | 90 | 51 | 5 | 5 | 27 | 10 | 8 | 4 | 5 | 0 | 0 |
| | 80 | 60 | 80 | 45 | 50 | 6 | 17 | 7 | 6 | 2 | 0 | 0 | 0 |
| | 55 | 60 | 45 | 57 | 45 | 8 | 13 | 3 | 4 | 9 | 1 | 1 | 0 |
| | 25 | 10 | 85 | 53 | 55 | 7 | 4 | 13 | 18 | 5 | 3 | 0 | 0 |
| | 35 | 60 | 90 | 35 | 90 | 10 | 18 | 12 | 9 | 8 | 6 | 0 | 0 |
| | 20 | 50 | 65 | 59 | 65 | 7 | 13 | 13 | 10 | 6 | 2 | 0 | 0 |
| | 80 | 0 | 65 | 29 | 55 | 5 | 3 | 19 | 14 | 2 | 0 | 0 | 0 |
| | 50 | 85 | 55 | 40 | 55 | 4 | 5 | 8 | 12 | 3 | 7 | 0 | 0 |
| $\bar{X}$ | 56.7 | 41.0 | 77.3 | 52.7 | 55.0 | 6.1 | 16.1 | 11.7 | 9.5 | 4.9 | 2.7 | 0.4 | 0.2 |
| Chestnut-sided Warbler | 100[b] | 80 | 25 | 30 | 0 | 3 | 2 | 6 | 0 | 0 | 0 | 0 | 0 |
| | 100 | 85 | 40 | 30 | 20 | 4 | 3 | 5 | 0 | 0 | 0 | 0 | 1 |
| | 100[b] | 25 | 5 | 50 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| | 100 | 75 | 35 | 52 | 0 | 2 | 2 | 3 | 4 | 2 | 0 | 0 | 0 |
| | 100 | 80 | 55 | 35 | 0 | 6 | 7 | 10 | 6 | 0 | 0 | 1 | 0 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 85 | 80 | 50 | 37 | 10 | 4 | 24 | 12 | 2 | 0 | 0 | 0 | 0 |
| | 95 | 90 | 50 | 29 | 0 | 4 | 15 | 15 | 9 | 0 | 0 | 0 | 0 |
| | 100 | 25 | 30 | 75 | 0 | 5 | 1 | 6 | 2 | 0 | 0 | 1 | 1 |
| | 100 | 75 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 55 | 90 | 75 | 52 | 0 | 4 | 15 | 8 | 6 | 6 | 0 | 0 | 0 |
| | 60 | 95 | 55 | 33 | 0 | 6 | 13 | 12 | 9 | 1 | 0 | 0 | 0 |
| | 100 | 20 | 55 | 100 | 55 | 3 | 2 | 1 | 0 | 0 | 0 | 4 | 1 |
| | 100 | 30 | 45 | 100 | 45 | 2 | 0 | 2 | 0 | 0 | 0 | 1 | 2 |
| | 90 | 75 | 60 | 38 | 0 | 3 | 8 | 13 | 3 | 0 | 0 | 0 | 0 |
| | 100 | 70 | 10 | 25 | 0 | 3 | 6 | 9 | 3 | 0 | 0 | 0 | 0 |
| | 100 | 70 | 55 | 38 | 15 | 6 | 18 | 4 | 6 | 8 | 5 | 0 | 0 |
| $\bar{X}$ | 92.8 | 66.9 | 40.3 | 43.1 | 9.1 | 3.4 | 7.2 | 6.7 | 3.2 | 1.1 | 0.3 | 0.4 | 0.2 |
| Pine Warbler | 55 | 65 | 100 | 67 | 85 | 5 | 3 | 15 | 7 | 2 | 0 | 0 | 6 |
| | 95 | 0 | 85 | 79 | 60 | 4 | 7 | 4 | 0 | 0 | 7 | 1 | 1 |
| | 80 | 35 | 55 | 90 | 55 | 4 | 20 | 19 | 1 | 0 | 4 | 6 | 2 |
| | 40 | 90 | 75 | 83 | 75 | 4 | 1 | 2 | 6 | 12 | 15 | 1 | 0 |
| | 55 | 60 | 90 | 83 | 65 | 8 | 25 | 3 | 1 | 4 | 12 | 2 | 0 |
| | 60 | 10 | 55 | 57 | 50 | 6 | 13 | 27 | 13 | 14 | 3 | 0 | 0 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 70 | 70 | 95 | 69 | 70 | 4 | 4 | 13 | 5 | 5 | 5 | 2 | 0 |
| | 100 | 50 | 75 | 63 | 70 | 6 | 6 | 10 | 10 | 5 | 4 | 0 | 0 |
| | 65 | 60 | 75 | 67 | 70 | 3 | 5 | 2 | 0 | 1 | 3 | 7 | 2 |
| | 30 | 5 | 60 | 65 | 55 | 9 | 7 | 3 | 2 | 2 | 4 | 7 | 1 |
| | 100 | 15 | 55 | 100 | 55 | 2 | 0 | 3 | 0 | 0 | 0 | 0 | 3 |
| | 45 | 40 | 90 | 90 | 90 | 5 | 5 | 8 | 5 | 1 | 2 | 3 | 2 |
| | 55 | 55 | 90 | 44 | 70 | 5 | 4 | 7 | 10 | 3 | 1 | 0 | 0 |
| | 65 | 80 | 70 | 61 | 70 | 3 | 3 | 2 | 2 | 9 | 17 | 0 | 0 |
| | 45 | 30 | 65 | 63 | 60 | 5 | 20 | 9 | 3 | 2 | 8 | 1 | 0 |
| $\bar{X}$ | 64.0 | 44.3 | 75.7 | 72.1 | 66.7 | 4.9 | 8.4 | 8.3 | 4.1 | 4.1 | 5.7 | 2.0 | 1.1 |
| Palm Warbler | 100[b] | 85 | 5 | 21 | 5 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 90 | 85 | 30 | 20 | 30 | 2 | 14 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 100[b] | 95 | 20 | 23 | 20 | 2 | 11 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 95 | 50 | 5 | 15 | 5 | 2 | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| $\bar{X}$ | 96.2 | 78.8 | 15.0 | 19.8 | 15.0 | 1.8 | 7.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Ovenbird | 75 | 85 | 60 | 59 | 25 | 6 | 16 | 3 | 2 | 3 | 7 | 0 | 0 |
| | 30[b] | 60 | 85 | 57 | 85 | 6 | 4 | 1 | 13 | 4 | 1 | 0 | 2 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 70 | 30 | 85 | 70 | 40 | 7 | 28 | 23 | 10 | 3 | 7 | 3 | 0 |
| | 85[b] | 35 | 65 | 65 | 50 | 6 | 13 | 19 | 4 | 6 | 4 | 1 | 0 |
| | 60 | 20 | 90 | 73 | 55 | 7 | 5 | 8 | 4 | 7 | 3 | 1 | 3 |
| | 60[b] | 45 | 90 | 49 | 45 | 6 | 9 | 15 | 9 | 8 | 0 | 0 | 0 |
| | 100[b] | 55 | 75 | 43 | 20 | 7 | 14 | 19 | 5 | 3 | 0 | 1 | 0 |
| | 75 | 30 | 80 | 60 | 55 | 3 | 5 | 28 | 14 | 4 | 1 | 0 | 0 |
| | 60 | 25 | 90 | 53 | 0 | 5 | 7 | 17 | 20 | 5 | 1 | 0 | 0 |
| | 75 | 15 | 95 | 51 | 0 | 5 | 9 | 11 | 12 | 14 | 2 | 1 | 0 |
| | 55 | 55 | 85 | 42 | 45 | 5 | 11 | 6 | 8 | 5 | 0 | 0 | 0 |
| | 55 | 30 | 75 | 38 | 55 | 8 | 16 | 23 | 17 | 6 | 4 | 0 | 0 |
| | 65 | 70 | 90 | 39 | 50 | 5 | 12 | 8 | 16 | 6 | 2 | 0 | 0 |
| | 45 | 90 | 75 | 40 | 75 | 7 | 17 | 9 | 8 | 7 | 2 | 0 | 0 |
| | 45 | 10 | 70 | 53 | 65 | 2 | 3 | 2 | 1 | 0 | 10 | 0 | 0 |
| | 65 | 80 | 70 | 61 | 70 | 3 | 3 | 2 | 2 | 9 | 17 | 0 | 0 |
| | 75 | 35 | 65 | 30 | 20 | 5 | 8 | 11 | 17 | 0 | 0 | 0 | 0 |
| | 80 | 0 | 65 | 32 | 55 | 5 | 0 | 3 | 19 | 14 | 2 | 0 | 0 |
| $\overline{X}$ | 65.3 | 42.3 | 78.3 | 50.8 | 46.5 | 5.4 | 10.2 | 12.4 | 9.8 | 5.1 | 3.4 | 0.4 | 0.3 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Common Yellowthroat | 100[b] | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 95[b] | 25 | 30 | 35 | 30 | 3 | 12 | 4 | 0 | 0 | 0 | 0 | 0 |
| | 75[b] | 85 | 60 | 40 | 60 | 1 | 17 | 15 | 0 | 0 | 0 | 0 | 0 |
| | 100 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 100 | 30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 100[b] | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 100 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 100 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 100 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 100 | 50 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 100 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 100 | 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 100 | 45 | 15 | 24 | 0 | 2 | 8 | 3 | 0 | 0 | 0 | 0 | 0 |
| | 100 | 100 | 50 | 30 | 0 | 5 | 18 | 8 | 1 | 0 | 0 | 0 | 0 |
| | 100 | 50 | 5 | 75 | 5 | 2 | 2 | 0 | 0 | 0 | 0 | 1 | 0 |
| | 100 | 5 | 40 | 35 | 10 | 2 | 1 | 6 | 5 | 3 | 2 | 0 | 0 |
| | 100 | 30 | 10 | 50 | 10 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| $\bar{X}$ | 98.2 | 39.0 | 12.4 | 17.0 | 6.8 | 0.9 | 3.4 | 2.1 | 0.4 | 0.2 | 0.1 | 0.1 | 0.1 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mourning Warbler | 95 | 50 | 0 | 0 | 0 | 4 | 16 | 0 | 2 | 0 | 0 | 0 | 0 |
| | 55 | 80 | 20 | 53 | 20 | 4 | 5 | 8 | 2 | 2 | 0 | 0 | 0 |
| | 100 | 80 | 5 | 45 | 0 | 4 | 3 | 1 | 1 | 0 | 0 | 0 | 0 |
| | 100 | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 95 | 55 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 100 | 75 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 100 | 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 95 | 15 | 50 | 45 | 0 | 4 | 7 | 2 | 6 | 0 | 0 | 0 | 0 |
| | 80 | 65 | 70 | 47 | 5 | 8 | 13 | 10 | 6 | 2 | 3 | 0 | 0 |
| | 100 | 45 | 5 | 80 | 5 | 2 | 2 | 0 | 0 | 0 | 0 | 1 | 0 |
| | 65 | 90 | 90 | 49 | 25 | 7 | 19 | 11 | 4 | 9 | 2 | 1 | 0 |
| | 100 | 45 | 55 | 35 | 5 | 8 | 8 | 7 | 5 | 0 | 1 | 0 | 0 |
| | 100 | 70 | 25 | 80 | 25 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| | 100 | 40 | 15 | 55 | 15 | 2 | 1 | 0 | 0 | 0 | 1 | 3 | 0 |
| | 100 | 15 | 5 | 20 | 0 | 2 | 0 | 1 | 3 | 0 | 0 | 0 | 0 |
| $\bar{X}$ | 92.3 | 52.7 | 23.0 | 35.6 | 6.7 | 3.1 | 4.9 | 2.7 | 1.9 | 0.9 | 0.5 | 0.3 | 0.1 |
| Canada Warbler | 85 | 95 | 55 | 71 | 45 | 6 | 6 | 9 | 5 | 4 | 0 | 0 | 1 |
| | 85 | 65 | 50 | 63 | 0 | 6 | 3 | 6 | 4 | 4 | 7 | 0 | 0 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 95 | 60 | 65 | 51 | 50 | 6 | 7 | 14 | 15 | 2 | 6 | 0 | 0 |
| | $\bar{X}$ | 88.3 | 73.3 | 56.7 | 61.7 | 33.3 | 6.0 | 5.3 | 9.7 | 8.0 | 3.7 | 4.3 | 0.0 | 0.3 |
| American Redstart | | 45 | 100 | 70 | 36 | 0 | 6 | 29 | 13 | 10 | 2 | 1 | 0 | 0 |
| | | 95 | 40 | 60 | 43 | 0 | 3 | 0 | 4 | 7 | 1 | 0 | 0 | 0 |
| | | 100 | 20 | 40 | 51 | 0 | 5 | 3 | 7 | 6 | 3 | 1 | 1 | 0 |
| | | 95 | 45 | 70 | 59 | 0 | 4 | 7 | 5 | 6 | 10 | 0 | 0 | 0 |
| | | 55 | 75 | 50 | 53 | 10 | 5 | 16 | 20 | 13 | 4 | 0 | 0 | 0 |
| | | 15 | 80 | 75 | 69 | 25 | 4 | 5 | 5 | 8 | 3 | 1 | 2 | 1 |
| | | 70 | 100 | 90 | 43 | 0 | 4 | 8 | 4 | 1 | 5 | 0 | 0 | 0 |
| | | 50 | 95 | 50 | 55 | 0 | 1 | 16 | 11 | 2 | 8 | 2 | 0 | 0 |
| | | 40 | 60 | 75 | 43 | 0 | 3 | 1 | 10 | 15 | 12 | 5 | 1 | 0 |
| | | 55 | 45 | 60 | 35 | 35 | 6 | 21 | 15 | 10 | 5 | 2 | 0 | 0 |
| | | 70 | 50 | 50 | 40 | 0 | 6 | 9 | 8 | 7 | 4 | 3 | 0 | 0 |
| | | 55 | 90 | 75 | 52 | 0 | 4 | 15 | 8 | 6 | 6 | 0 | 0 | 0 |
| | | 75 | 100 | 65 | 45 | 0 | 3 | 9 | 26 | 20 | 1 | 0 | 0 | 0 |
| | | 100 | 75 | 75 | 40 | 0 | 5 | 14 | 11 | 5 | 2 | 1 | 0 | 0 |
| | | 95 | 85 | 90 | 50 | 0 | 1 | 8 | 14 | 7 | 3 | 0 | 0 | 0 |
| | $\bar{X}$ | 67.7 | 70.7 | 66.3 | 47.6 | 4.7 | 4.0 | 10.7 | 10.7 | 8.2 | 4.6 | 1.1 | 0.3 | 0.1 |

[a]Explanation of code given in Chapter 3, Table 1.

[b]Indicates 0.04-ha plot centered around a nest.

Appendix II. Variables of the structure of the vegetation considered in the analysis of 0.04-ha circular plots for the Black-throated Green Warbler. Data from Minnesota are given in Appendix I.

| Location | | GC[a] | SC | CC | CH | CO | SPT | T1 | T2 | T3 | T4 | T5 | T6 | T7 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Franklin County, Maine | | 20 | 35 | 95 | 49 | 30 | 7 | 34 | 5 | 3 | 2 | 0 | 0 | 1 |
| | | 15 | 60 | 100 | 49 | 50 | 9 | 46 | 24 | 13 | 3 | 2 | 0 | 0 |
| | | 40 | 15 | 95 | 43 | 40 | 11 | 24 | 34 | 19 | 2 | 0 | 0 | 0 |
| | | 40 | 35 | 100 | 67 | 50 | 11 | 16 | 13 | 9 | 8 | 4 | 4 | 0 |
| | | 35 | 35 | 95 | 40 | 45 | 10 | 42 | 22 | 8 | 2 | 0 | 0 | 1 |
| | | 20 | 35 | 85 | 46 | 45 | 11 | 64 | 17 | 9 | 4 | 3 | 0 | 0 |
| | | 50 | 40 | 80 | 41 | 40 | 8 | 36 | 19 | 12 | 3 | 0 | 0 | 0 |
| | | 50 | 0 | 95 | 45 | 40 | 8 | 29 | 36 | 13 | 4 | 1 | 0 | 0 |
| | | 45 | 10 | 95 | 40 | 40 | 8 | 37 | 34 | 12 | 3 | 0 | 0 | 0 |
| | | 50 | 65 | 95 | 43 | 0 | 6 | 19 | 10 | 4 | 5 | 4 | 3 | 0 |
| | | 40 | 30 | 85 | 51 | 0 | 5 | 31 | 22 | 7 | 6 | 3 | 0 | 0 |
| | $\bar{X}$ | 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 |
| Mount Desert Island, Maine | | 85 | 45 | 80 | 48 | 75 | 5 | 38 | 33 | 20 | 7 | 1 | 0 | 0 |
| | | 85 | 25 | 80 | 35 | 75 | 5 | 98 | 67 | 8 | 1 | 0 | 0 | 0 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 70 | 15 | 75 | 42 | 75 | 6 | 30 | 46 | 15 | 3 | 1 | 0 | 0 |
| | 60 | 15 | 95 | 46 | 85 | 4 | 63 | 53 | 19 | 5 | 0 | 0 | 0 |
| | 60 | 45 | 65 | 40 | 50 | 3 | 39 | 32 | 8 | 2 | 0 | 0 | 0 |
| | 25 | 5 | 85 | 58 | 85 | 7 | 43 | 34 | 20 | 11 | 2 | 0 | 0 |
| | 40 | 15 | 100 | 51 | 90 | 8 | 33 | 45 | 16 | 4 | 9 | 0 | 0 |
| | 35 | 0 | 85 | 46 | 85 | 5 | 47 | 32 | 17 | 11 | 3 | 0 | 0 |
| | 40 | 25 | 85 | 46 | 80 | 7 | 34 | 42 | 13 | 7 | 4 | 0 | 0 |
| | 25 | 20 | 90 | 50 | 90 | 5 | 17 | 48 | 21 | 19 | 9 | 0 | 0 |
| $\bar{X}$ | 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 |
| White Mountain National | 45 | 60 | 90 | 56 | 0 | 5 | 34 | 19 | 13 | 2 | 5 | 2 | 0 |
| Forest, New Hampshire | 60 | 20 | 95 | 51 | 45 | 7 | 18 | 18 | 7 | 3 | 7 | 1 | 0 |
| | 30 | 60 | 95 | 49 | 30 | 4 | 41 | 24 | 13 | 8 | 2 | 2 | 0 |
| | 35 | 75 | 85 | 56 | 30 | 7 | 24 | 14 | 5 | 6 | 6 | 3 | 0 |
| | 65 | 15 | 95 | 46 | 5 | 7 | 22 | 15 | 7 | 3 | 2 | 2 | 0 |
| | 85 | 60 | 100 | 46 | 20 | 7 | 26 | 20 | 16 | 8 | 2 | 1 | 1 |
| | 40 | 80 | 85 | 53 | 40 | 8 | 35 | 29 | 15 | 5 | 3 | 1 | 0 |
| | 45 | 20 | 100 | 56 | 25 | 7 | 21 | 10 | 8 | 4 | 7 | 0 | 2 |
| | 30 | 20 | 100 | 46 | 40 | 10 | 44 | 31 | 10 | 3 | 2 | 1 | 0 |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 20 | 25 | 100 | 40 | 0 | 7 | 30 | 10 | 12 | 7 | 3 | 1 | 0 |
| | $\bar{X}$ | 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 |
| Southern Addirondack | | 10 | 70 | 85 | 69 | 25 | 6 | 28 | 3 | 3 | 5 | 7 | 2 | 3 |
| Mountains, New York | | 40 | 80 | 95 | 60 | 30 | 8 | 16 | 8 | 2 | 6 | 2 | 3 | 4 |
| | | 25 | 80 | 95 | 80 | 35 | 6 | 28 | 9 | 3 | 1 | 5 | 5 | 0 |
| | | 40 | 85 | 95 | 58 | 55 | 8 | 30 | 6 | 1 | 5 | 5 | 2 | 2 |
| | $\bar{X}$ | 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 |

[a]Explanation of variables is given in Chapter 3, Table 1.