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Habitat relationships of wood warblers (Parulidae) in northern central Minnesota

Scott L. Collins, Frances C. James and Paul G. Risser

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To analyze the habitat relationships of 16 species of wood warblers (Parulidae) breeding in northern 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 species identified three groups of species occupying (1) shrub-forest edge *(D. magnola, Mniotilta varia, Setophaga ruticilla, V. ruficilla, Wilsonia canadensis)*, (2) mature forest *(D. coronata, D. fusca, D. pinus, D. virens, Seiurus aurocapillus, Parula americana)*, and (3) open fields with shrubs *(Dendroica pensylvanica, D. petechia, Geothlypis trichas, Oporornis philadelphia, Vermivora chrysoptera)*. A reciprocal averaging ordination of the average habitat of each species produced a two-dimensional ordination. The first axis extends from forest vegetation to habitats with few trees and dense ground cover. A second axis separates areas of coniferous forest from those of younger deciduous and mixed forest. A principal components analysis of 199 samples permitted the construction of ellipses that reflect the variability and overlap in the habitat of each species.

The axes in these ordinations are multivariate resource axes, but we refrain from interpreting the results in terms of niche width and overlap. Instead we think the distribution of the species and the variation within the habitat of each are mainly attributable to affinities to biotic resources such as food, nest sites, and certain elements of the structure of the vegetation. To infer that these relationships represent the results of interspecific interactions is not justified.

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Для анализа соотношения местообитаний у 16 видов пеночек (*Parulidae*), гнездующихся на севере центральной Миннесоты, измеряли 13 переменных величин структуры биотопов на 207 округлых площадках площадью 0,04 га, расположенных на территориях гнездующихся самцов. Групповой анализ средних местообитаний отдельных видов выявил три группы видов, занимающие:
1. открытые поля с кустарником (*Dendroica pensylvanica, D. petechia, Geothlypis trichas, Oporornis philadelphia, Vermivora chrysoptera*) 2.опушки леса и кустарника (*D. magnolia, Mniotilta varia, Setophaga ruticilla, V. ruficilla, Wilsonia canadensis*), 3. зрелый лес (*D. coronata, D.fusca, D. pinus, D. virens, Seiurus aurocapillus, Parula americana*).
Реципрокная усредненная ординация среднего местообитания каждого вида дала двухмерную ординацию. Первая ось идет от лесной растительности к местообитаниям с редким древостоем и густым травяным покровом. Вторая ось отделяет территории с хвойным лесом от участков более молодых листопадных и смешанных лесов. Анализ главных компонентов 199 проб позволил сконструировать эллипсы, отражающие вариабельность и перекрывание биотопов для каждого вида. Оси этих ординат мультивариантны, но мы воздержимаемся от интерпретации результатов в отношении ширины и перекрывания ниш. Вместо этого мы полагаем, что распределение видов и различия внутри биотопов для каждого вида определяются в основном сходством биотопических ресурсов, таких, как пища, места для гнездования и некоторые элементы структуры растительного покрова. Заключение, что эти взаимоотношения представляют результаты межвидовых взаимодействий, не подтвердились.

1. Introduction

The birds inhabiting a study area are often considered to be interacting members of an avian community. Their differences in foraging behavior and their location within the vegetation are assumed to represent strategies that permit coexistence (MacArthur 1958, Morse 1967, 1976, Rabenold 1978, Holmes et al. 1979, Sabo 1980). But this community approach may overemphasize the role of interspecific interactions at the expense of direct adaptations to resources. Here we take a different approach and ask to what extent the distribution of birds in a region larger than the usual study plot can be explained on the basis of habitat affinities that are species specific. In the parlance of Hutchinson (1957) this would be interpreting distributions primarily in terms of the fundamental niche. In the absence of the results of removal experiments, it is not justified to interpret the magnitude of the differences between the fundamental and realized niches. Such differences would be a measure of the role of interspecific interactions in determining distributional patterns.

We compare the habitats of 14 sympatric species of breeding warblers in northern central Minnesota, asking 1) what is the typical habitat of each species? 2) how variable is it? 3) if the observed habitat relationships do not appear to be organized into communities dominated by interspecific associations, how can they be presented in an unbiased way? Because the concept of the niche, and associated terms such as niche breadth and overlap, are generally associated with the underlying but untested assumption of within-habitat resource limitation (Schoener 1974, Whittaker et al. 1973, Cody 1974, 1978) we will avoid these terms altogether. Our approach is to examine species-specific habitat relationships in the sense of Grinnell (1917) and James (1971), and to display their relationships in a habitat resource space without trying to assign untested mechanisms of coexistence or trying to define communities.

2. Methods

2.1. Study area

All field work was conducted within or near Itasca State Park in Becker, Clearwater, and Hubbard counties, northern central Minnesota. Within the park, 27 species of warblers have been reported, 13 of which are considered by Parmelee (1977) to be commonly nesting.

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, has created a diversity of vegetation types in the region.

The major 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.

2.2. Field methods

Thirteen structural characteristics of the habitat (Tab. 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 (Tab. 2). All habitat types were sampled, and the number of circular plots per species generally represents its relative abundance. 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 used in breeding territories is designed to determine the life form of vegetation where each species occurs (James 1971). It is an application of the individualistic approach to the distribution of organisms (Gleason 1926), in which species populations are treated independently. The technique permits analysis of the habitats of individual species and then comparisons among species not necessarily on the same study plot.

2.3. Data analysis

To obtain general habitat categories, 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,

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

Rohlf et al. 1974) based upon a 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 (PCA) 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 et al. 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 performed to assess variation in the habitat of each species as well as patterns among species. For 199 circular samples for 14 species of warblers (yellow-rumped 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. Correlations between the PC axes and standardized vegetation variables are presented. With PCA the eigenvalue expresses the variance of the component. To obtain the coefficient for a standardized variable for a component, divide its correlations with standardized vegetation variables by the square root of the eigenvalue for that component.

Interpretations of RA and PCA axes are somewhat different, even if the species relationships in the RA and PCA spaces are similar. RA ordinates the vegetation variables on a scale from 0 to 100; PCA provides equations for axes that express the maximum variance in the vegetation data.

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3. Results

3.1. Cluster analysis

Based on cluster analysis, the habitats of the 16 species of warblers can be divided into three general habitat types (Fig. 1). The cophenetic correlation coefficient ($r = 0.83$) indicates that the dendrogram adequately summarizes 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 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 of the American redstart in this region is aspen-birch or edges of other deciduous forests. Very little
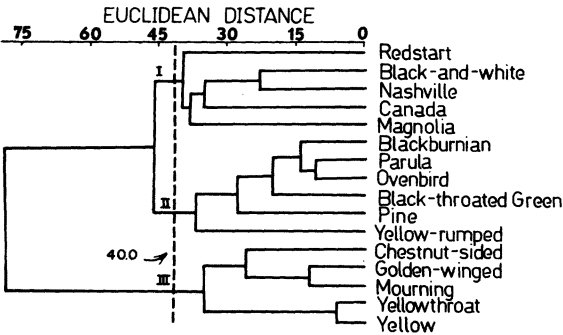

Fig. 1. A cluster analysis of average habitat variables for 16 species of warblers. The species fall into three habitat types: Group I contains shrub and forest edge species; Group II has mature forest species; and Group III contains open country birds.

coniferous vegetation occurs within its habitat (Tab. 3). The black-and-white and the Nashville warbler were found in forests similar to that of the American redstart but with more coniferous vegetation. Nashville warblers occupied densely vegetated bogs and swamps as well. A dense cover of bryophytes and grasses was usually present, providing high percent ground cover (Tab. 3). The Canada warbler was found in small forest openings with dense shrub and ground cover. The presence of small conifers 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 common in the Itasca region, but the yellow-rumped warbler was observed infrequently. Distinctive features of the habitat of the group are moderate ground and shrub cover and greater than 75% canopy cover (Tab. 3). 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 ovenbird and northern parula occurred in mixed coniferous-deciduous vegetation. Their association with conifers may be a secondary one.

The five species that prefer open habitats with dense ground cover and moderate shrub cover make up Group III. All are common and often co-occur. Within the group there is a gradient of shrub and canopy cover, the latter up to about 40% (Tab. 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

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

Vari-able[a]	AR[b] 1[c]	BW 1	NA 1	CA 1	MA 1	BB 2	NP 2	OV 2	BG 2	PI 2	YR 2	CS 3	GW 3	MO 3	CY 3	YE 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	14.5	14.8	14.8	18.8	16.9	16.1	16.8	15.5	20.2	22.0	16.2	13.1	10.5	10.8	5.2	6.0
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 Tab. 1.
[b] Bird species abbreviations are given in Tab. 2.
[c] Group numbers are given in Fig. 1.

Tab. 4. Correlation matrix of habitat characteristics. Data are from species averages. Abbreviations are explained in Tab. 1; n = 16.

	GC	SC	T1	T2	T3	T4	T5	T6	T7	CC	CH	CO
SC	−0.06											
T1	−0.46	0.01										
T2	−0.77	0.28	0.70									
T3	−0.76	0.34	0.54	0.90								
T4	−0.84	0.14	0.52	0.83	0.91							
T5	−0.61	−0.01	0.22	0.58	0.57	0.73						
T6	−0.54	−0.026	0.13	0.21	0.03	0.34	0.60					
T7	−0.43	−0.20	−0.08	0.18	0.01	0.29	0.70	0.92				
CC	−0.89	0.07	0.60	0.91	0.83	0.92	0.76	0.47	0.43			
CH	−0.70	0.22	0.51	0.79	0.66	0.76	0.85	0.61	0.62	0.88		
CO	−0.68	−0.22	0.61	0.73	0.56	0.66	0.81	0.55	0.54	0.81	0.82	
SPT	−0.75	0.20	0.44	0.81	0.84	0.87	0.77	0.30	0.33	0.90	0.85	0.72

deciduous edge vegetation with chestnut-sided and golden-winged warblers.

3.2. Correlation matrix

The correlation matrix of the 13 habitat variables (Tab. 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 further 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 the even-aged structure of many of the forests. This structure is the result of regeneration after fire.

3.3. Reciprocal averaging

A two-dimensional reciprocal averaging ordination of the bird species by their average habitat characteristics (Fig. 2, Tab. 5) shows relationships among the species in terms of two gradients in the vegetation of the Itasca region. The groups identified by the cluster analysis are labeled. Axis 1 is a gradient from large coniferous trees and little ground cover to increasing ground cover and low percent coniferous vegetation. Axis 2 extends from medium and small trees (T4, T3) to large trees (T7, T6). Thus, in the two-dimensional space (Fig. 2) there is a species-habitat continuum from coniferous forest inhabitants such as pine and yellow-rumped warblers to more mixed and deciduous forest species such as the
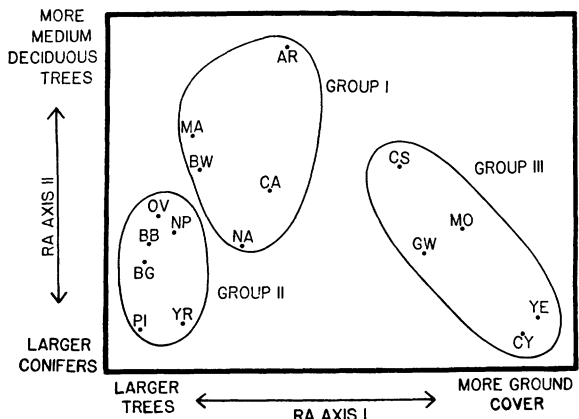

Fig. 2. A two-dimensional reciprocal averaging ordination of 16 species of warblers based upon average values of 13 structural variables of the vegetation. Axis 1 is a gradient from large trees to increasing ground cover. Axis 2 changes from medium and small deciduous trees to larger trees and higher percent of coniferous vegetation. The groups identified by cluster analysis are outlined. Species abbreviations are given in Tab. 2.

Tab. 5. Ordination statistics for reciprocal averaging (RA) and principal components analysis (PCA). RA scores for vegetation variables are scaled from 1 to 100 by the ordination program (Gauch 1977). PCA values are correlations of the principal components with standardized vegetation variables. See Tab. 1 for abbreviations.

Variable	RA		PC	
	I	II	I	II
GC	100.0	40.9	0.752	−0.020
SC	75.3	84.6	0.134	0.308
CC	23.8	69.6	−0.916	0.036
CH	41.4	60.6	−0.715	−0.433
CO	1.1	19.3	−0.720	−0.343
SPT	34.2	71.3	−0.801	0.081
T1	22.1	57.8	−0.450	0.266
T2	27.4	78.0	−0.660	0.326
T3	19.6	100.0	−0.662	0.476
T4	10.4	89.5	−0.636	0.340
T5	0.0	40.3	−0.519	−0.155
T6	5.5	7.4	−0.281	−0.691
T7	11.6	0.0	−0.218	−0.669
Eigenvalue	0.97	0.16	5.01	1.88
% Var[a]	73.8	12.3	38.5	14.5

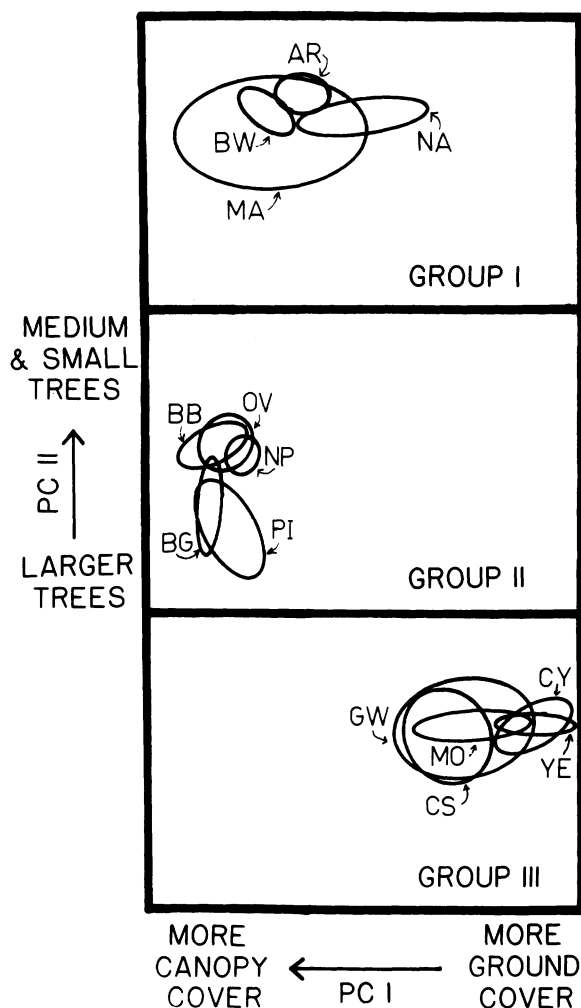[a] Percent of variance accounted for by each axis.

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Fig. 3. A two-dimensional principal components ordination of 199 circular samples for 14 species of warblers. The ordination space is repeated three times and the three groups of species identified by the cluster analysis are plotted separately. Ninety-five percent concentration ellipses (Sokal and Rohlf 1969) were drawn to show the variability of each species' habitat. Species abbreviations are given in Tab. 2.

the results for each species with 95% concentration ellipses (Fig. 3). Some distortion of the ellipses is introduced by the scaling of the PCA axes, and some of the differences among ellipses are attributable to differences in sample size. 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 the ellipses. The first PCA axis (38.5% of the variance, Tab. 5) is a gradient from forest to open field vegetation. Axis 2 (14.5% of the variance, Tab. 5) extends from large and coniferous trees to medium and small (T4, T3, T2) deciduous trees. Although the RA and PCA ordination procedures are different (see methods) the distributions of bird species in Figs 2 and 3 are similar.

The orientation and shape of the concentration ellipses in Fig. 3 provide a qualitative indication of the variability of a species' habitat structure. However, the size and orientation of each species' ellipse should not be used to determine whether or not a species is a habitat specialist or generalist, nor do the ellipses measure interspecific overlap of habitat preference. First, because of dimensionality problems, interspecific habitat overlap would be over-estimated by concentration ellipses in 2-dimensional PCA space, especially one that accounts for only 53% of the variance. As Major (1979) has indicated, overlapping curves along derived gradients imply that species co-occur at a given point when in fact they may not overlap in geographic space. Third, the species are not necessarily normally distributed around their means as confidence ellipses imply (Smith 1977). This distribution should be considered when evaluating measures of habitat breadth and 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 has the largest ellipse, always had some dense growth of spruce and fir saplings within its habitat. This is a good example of a species restricted to a narrow species-specific subset of habitat resources that appears to be a generalist in a multivariate resource space determined by the distribution of a set of species. This warbler occurred in open bogs and in coniferous forest. Other members of Group I, American redstart, black-and-white, and Nashville warblers, have equal-sized ellipses that are generally oriented along the first axis, indicating variability in canopy cover. Forest species (Group III) have small oval ellipses or are somewhat extended along the second axis suggesting variability in the number of large trees in their habitats. The black-throated green and pine warblers were in habitats with variable amounts of pine, whereas the blackburnian warbler, ovenbird, and northern parula habitats have at least some spruce and fir. Mourning, golden-winged, and chestnut-sided warblers, three secondary growth species, have large ellipses incorporating at least some edge habitat. The yellow warbler and common yellow-

northern parula and ovenbird (Group II). Next are species of secondary forest and edge habitats with abundant low vegetation (Group I). Of these the American redstart is the most dependent on small deciduous trees. At the extreme of RA I are the common yellowthroat and yellow warbler whose open habitats contain shrubs and high percent ground cover, but few trees (Group III). The mourning, golden-winged, and chestnut-sided warblers are in deciduous second growth.

3.4. Principal components analysis

The variability of each species' habitat can be visualized by ordinating all circular plots by PCA and summarizing

Fig. 4. A schematic diagram of the habitat gradient showing the regions along the gradient in which each species may be found. The gradient has been constructed from the ordinations. Horizontal lines represent the variability of each species along the gradient. Letters specify the species mode. Vertical arrangement is arbitrary. Species abbreviations are given in Tab. 2.
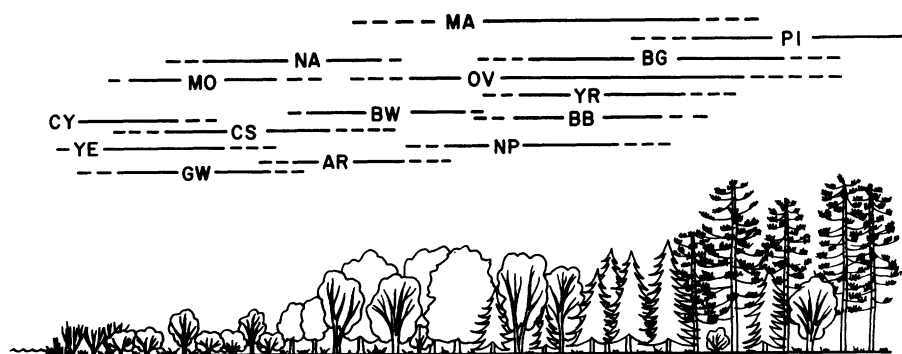
throat were found in structurally simple habitat containing patches of shrubs or scattered trees.

3.5. Synthesis

A schematic diagram summarizing the habitat use of each species along the major vegetational gradient is presented in Fig. 4. The species modes are taken from the reciprocal averaging ordination. The length of the line is based on RA and PCA results plus field observations. Each species occupies lengthy portions of the gradient and the habitats of many species overlap at any given point. These patterns emphasize both the high degree of interspecific overlap and the independent nature of the species distributions in this region.

4. Discussion

The selection of breeding territory is initiated at least partly by species-specific responses to elements of vegetation structure (Svärdson 1949, Hildén 1965, James 1971). This results in species-specific habitat distributions attributable to individualistic responses to various characteristics of the habitat. Rapid selection of optimal habitat based upon vegetation structure would seem advantageous because intraspecific competition for territories may be keen.

It is possible to arrange the habitats of the 16 species of warblers into three broad habitat groups: shrub-forest edge, mature forest, and open country, each of which contains about the same number of species (Fig. 1). However, habitat gradients in vegetation structure can also be identified for all 16 species as a set (Figs 2, 4). These gradients include all vegetation types present in the region: old fields and bogs, shrub thickets, forest edges, second growth forest, mature deciduous, and coniferous vegetation. Many of the open habitats are the result of either logging or fire. In either case, large trees, particularly pines, remain as a seed source for forest regeneration (Hansen et al. 1974). The large trees sometimes occur in the habitat of open

country species. This occurrence accounts for the location of the yellow warbler and common yellowthroat at the large tree end of the RA II gradient (Fig. 2). Thus although groups of species can be identified by cluster analysis, the gradients show that the 16 species do not form subsets.

An important construct in community ecology is the role of interspecific competition in determining species distributions. Previous authors (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 attributable to interspecific competition. The warblers in this study were distributed along a habitat gradient and this distribution could also be interpreted as conforming to this resource partitioning hypothesis. However, habitat structure data are probably neutral to this hypothesis. The variation in habitat structure noted for each species naturally results in interspecific overlap of habitat, a factor observed in the field. To assume that overlap implies either competition (Cody 1974, Schoener 1974) or lack of it (Colwell and Futuyma 1971) is not justified (Wiens 1977). An interpretation based on resource limitation from the observation of a pattern is unwarranted because no limitation has been demonstrated. Such an assumption confounds the observation of a pattern (even if it was predicted) with the testing of a hypothesis (Brady 1979). Klopfer and Hailman (1965) predicted that individuals living with many competitors should exhibit rigid habitat selection. Our results are counter to this prediction (Figs 3, 4) but we prefer to interpret the broad overlap as merely an indication of the presence of the resources required for these species.

If species overlap broadly along one resource dimension, such as habitat, they may show greater segregation and less overlap along another resource dimension such as foraging behavior (Cody 1974). The foraging behavior of several of these warblers has been intensively studied in Maine by Morse (1971, 1973). He concluded that the species were opportunistic foragers and that food was not a limiting resource to these birds. In fact, black-throated green warblers preferred to forage in red spruce (Picea rubens) even though more food could be

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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. Holmes et al. (1979) demonstrated that birds can depress the levels of defoliating insects, especially Lepidoptera, although 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 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. But high habitat variability and opportunistic feeding behavior are evidence that specialization by the warblers is not always evident. Also, single species populations occurring in a variety of habitats interact with a wide spectrum of other species (Ricklefs and Travis 1980). This complex and local nature of species associations makes fine tuning of species-specific behavior to that of other taxa unlikely because interactions are not consistent throughout each population. MacArthur's (1958) classic interpretation of the distribution of boreal forest warblers in New England, including several of the species in the present study, was that the birds used niche segregation to avoid interspecific competition, but Lister (1980) argued that it could have been an example of increased spatial similarity when there is abundant food!

We think that the distribution of warblers along habitat gradients is the result of individualistic responses by the species to characteristics of vegetation structure and we doubt 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 can be identified along a vegetation gradient. Overall, these relationships suggest 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 use patterns and these may be a result of interspecific interactions.

In conclusion, in northern central Minnesota, each species of wood warbler occurs in such a variety of habitats and displays such opportunistic foraging behavior that there is no need to invoke interspecific competition as a major force governing its distribution. The individualistic response of the species along gradients determined by vegetation structure suggests that a reasonable paradigm for examining the distributional relationships among the species is in terms of the structure of the habitat. These conclusions do not result from a test of competition theory (Wiens 1976). Experimental manipulation by adding or removing species or ele-

ments of the habitat will be required to truly test the validity of these conclusions. Until such studies are feasible, distributional observations should not be assumed to be mainly determined by interspecific relationships, and sets of species that co-occur on one's study plot should not be assumed to be communities in the sense of interacting units.

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