

DISPERSION PATTERNS AND HABITAT ASSOCIATIONS OF RUFOUS-SIDED TOWHEES, COMMON YELLOWTHROATS, AND PRAIRIE WARBLERS IN THE SOUTHEASTERN MASSACHUSETTS PINE BARRENS

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ABSTRACT.—We investigated dispersion patterns and habitat associations of Rufous-sided Towhees (*Pipilo erythrophthalmus*), Common Yellowthroats (*Geothlypis trichas*), and Prairie Warblers (*Dendroica discolor*) in the southeastern Massachusetts pine barrens. All three species were regularly dispersed within study sites and among study sites at fine grain sizes, apparently the result of intraspecific competition. At increasingly coarse levels of resolution, however, both Rufous-sided Towhees and Common Yellowthroats were dispersed randomly across successional stages, whereas Prairie Warblers exhibited a patchy dispersion. Prairie Warblers exhibited stronger relationships between density and habitat, and showed relatively strong habitat associations. They apparently responded to broad-scale patterns of habitat variation across successional stages. Rufous-sided Towhees and Common Yellowthroats had weaker associations at this scale. We suggest that the most abundant avian species in the pine barrens respond to habitat variation at different scales and point to the need for careful consideration of scale when investigating habitat relationships and interpreting patterns of community structure. Received 14 March 1990, accepted 1 October 1990.

DISPERSION patterns are the result of many factors operating at different spatial and temporal scales (Wiens 1984, Diamond and Case 1986, Holmes et al. 1986). These factors include habitat variation, biotic processes (such as intraspecific and interspecific competition), abiotic factors, landscape characteristics, and stochastic processes. Because dispersion patterns may vary with the scale at which they are viewed (Sherry and Holmes 1985), analyses of dispersion conducted at several levels of resolution (grain sizes) can provide insight into the factors (e.g. the scale of habitat selection) that influence individual distribution and abundance (O'Neill et al. 1986, Wiens 1989). However, knowledge of the ways in which dispersion patterns change with changing grain size by itself is not sufficient for drawing conclusions about how processes such as habitat selection influence the distribution and abundance of individuals. Therefore, analyses of dispersion must be accompanied by studies of habitat variation and habitat occupancy patterns in order to understand how and whether dispersion patterns can be accounted for by the responses of individuals to habitat variation.

Historically, quantitative analyses of dispersion have been restricted largely to plants (Greig-Smith 1961, Kershaw 1973, Phillips and

MacMahon 1981, Cox 1987, Getis and Franklin 1987; but see Simberloff 1979, Cox and Roig 1986). Few investigators have analyzed the dispersion patterns of territorial birds (Sherry and Holmes 1985). We studied the dispersion patterns of Rufous-sided Towhees (*Pipilo erythrophthalmus*), Common Yellowthroats (*Geothlypis trichas*), and Prairie Warblers (*Dendroica discolor*), the three most common breeding bird species in the southeastern Massachusetts pine barrens. For each species we tested the null hypothesis that individuals were dispersed randomly within (small extent) and among (large extent) study sites. We determined dispersion patterns among study sites at several levels of resolution, or grain sizes (Wiens 1989), to investigate the ways in which dispersion patterns changed with changing grain of investigation. We then examined the variation in vegetation structure and composition, and the habitat associations of each species. In this way we could interpret the scale-dependent dispersion patterns in light of the responses by individuals to habitat variation.

METHODS

This study was conducted in the pine barrens of Plymouth (Plymouth County), Bourne, and Mashpee

(Barnstable County) in southeastern Massachusetts. The pine barrens of Plymouth and Barnstable counties together represent the third largest (>20,000 ha) area of pine barrens remaining in North America (Cryan 1985), with the towns of Plymouth and Mashpee holding the largest tracts remaining in Massachusetts. These pine barrens occur on well-drained, sandy, glacial outwash soils and are subject to periodic burning. The land is topographically diverse (0–35% slope), with locally occurring boulders and occasional kettle depressions and ponds, and outwash plain valleys (Oldale 1976). The vegetation is simple both physiognomically and floristically. The dominant tree is pitch pine (*Pinus rigida*), which forms an open canopy. Black oak (*Quercus velutina*), white oak (*Q. alba*), and white pine (*P. strobus*) occur less frequently. The shrub layer is very dense and is dominated by scrub oak (*Q. ilicifolia*) and several ericaceous species, including black huckleberry (*Gaylussacia baccata*), sheep laurel (*Kalmia angustifolia*), late low blueberry (*Vaccinium vacillans*), and early low blueberry (*V. angustifolium*). The perennial herbs wintergreen (*Gaultheria procumbens*) and bearberry (*Arctostaphylos uva-ursi*) dominate the herb layer.

Eight 7–9 ha strip transects (100 m wide) that represented an array of successional stages from 5 yr to >30 yr postfire were established (Appendix 1). Each of these transects was located within at least 50 ha of pine barrens vegetation and at least 200 m from a border with dissimilar habitat. We used the plot-mapping technique (Emlen 1977, Christman 1984) to census breeding birds on each of the eight strip transects from late May to early July, 1985–1987. Plot sizes of 7–8 ha have been used extensively to census pine barrens birds (Lloyd-Evans 1973, 1974; Kerlinger 1984), and are adequate to estimate densities in this open habitat, particularly for the most abundant species. All censuses were conducted between 0500 and 0800 EST on days without rain or strong winds. The information recorded during the formal censuses was supplemented with extensive observations of individuals made during a study of foraging behavior. Thus we are confident that the locations and the estimates of abundance and territory boundaries are accurate. In the present analyses we concentrate on the three most abundant species—Rufous-sided Towhees, Common Yellowthroats, and Prairie Warblers—which comprised 49–70% of the breeding bird total density observed during the study.

The dispersion patterns of individuals are characterized as (1) *random*, in which the location of each individual is independent of the location of other individuals; (2) *clumped*, or *patchy*, in which individuals are located closer to one another than expected in a random distribution; or (3) *regular*, in which individuals are more evenly spaced than expected by chance.

To quantify dispersion patterns across transects we used the methods of Sherry and Holmes (1985), which

were adapted from techniques used in quantitative plant ecology (Kershaw 1973, Vandermeer 1981). For each transect, we superimposed a series of contiguous quadrats on the mapped territories of a given species, and we counted the number of territory centers per quadrat. The center of a territory was defined as the center of the smallest circle that enclosed that territory (Sherry and Holmes 1985). Because we were interested in how dispersion patterns changed with the spatial scale of resolution, or grain size (Kershaw 1973), we counted the number of territory centers in quadrats of five different sizes (representing different grain sizes): 0.25 ha (232 quadrats; 50 × 50 m), 0.50 ha (116 quadrats; 50 × 100 m), 1.0 ha (58 quadrats; 100 × 100 m), 3.5 ha (16 quadrats; 100 × 350 m), and 7.0 ha (8 quadrats; 100 × 700 m). The small quadrats of 0.25 ha and 0.50 ha corresponded to the mean (\pm SD) sizes of individual territories (Rufous-sided Towhees, 0.26 ± 0.06 ha, $n = 277$; Common Yellowthroats, 0.28 ± 0.06 ha, $n = 251$; Prairie Warblers, 0.36 ± 0.15 ha, $n = 187$), whereas the large quadrats of 7.0 ha corresponded to the size of individual transects. Therefore, at the largest grain size we were effectively measuring dispersion patterns across successional stages. Morisita's measure of dispersion (Vandermeer 1981), essentially a variance to mean ratio of the number of territory centers per quadrat, was calculated for each species and quadrat size; values of <1 indicated regular dispersion, values of 1 indicated random dispersion, and values of >1 indicated patchy dispersion. To determine the significance of deviations from random, Chi-square tests that compared the observed numbers of territory centers per quadrat with a Poisson distribution (Kershaw 1973) were performed for each year of the study. Thus, we were able to measure dispersion patterns at a relatively broad scale (including all transects; encompassing 58.5 ha) with varying degrees of resolution (from 0.25 to 7.0 ha).

In addition to these measures of dispersion across transects, dispersion was quantified within each transect by measuring intraspecific nearest-neighbor distances for each species. The distance between neighbors was defined as the distance between territory centers. In cases where nearest-neighbor distances between two individuals were reciprocal (22% of all cases), the distance to the second nearest-neighbor was used, which avoided statistical problems associated with such cases (Meagler and Burdick 1980, Sherry and Holmes 1985). We performed Student's *t*-tests to determine if the average nearest-neighbor distance was different from that predicted in a random distribution described using the formula of Clark and Evans (1954). The ratio of the observed average nearest-neighbor distance to the expected value was computed as an index of dispersion (Clark and Evans 1954); values of 1.0 indicated random dispersion, values of <1.0 indicated patchy dispersion, and values of >1.0 indicated regular dispersion. By narrowing the extent of the study to that of individual transects,

we reduced the spatial variation in habitat (Wiens 1989) and were thus able to understand more clearly, compared with the fine-grain analysis including all transects, the dispersion patterns of individuals and their causes at the scale of local populations.

We used a technique modified from James and Shugart (1970) to sample vegetation on 267 randomly located 0.04-ha circular plots from 1985–1987 (Appendix 1). In total, 22 variables (Appendix 2) that consisted of coverage estimates, measures of vertical and horizontal structure, and indices of vertical and horizontal heterogeneity were measured on each plot.

Coverage estimates were determined by recording the frequency of vegetation contacts per height interval (0–0.25 m, 0.25–0.5 m, 0.5–1.5 m, 1.5–3 m, 3–6 m, 6–8 m, >8 m) with a 5-m vegetation pole placed at 20 locations (every 2.25 m) along two perpendicular lines passing through the center of each plot. Litter depth was also measured at these 20 locations and averaged over the entire plot. Foliage height diversity (FHD), a measure of vertical heterogeneity, was calculated from the number of contacts per height interval using Hill's (1973) modification of Simpson's (1949) diversity index. At the 20 sampling points per plot, we determined the presence or absence of vegetation in each of the seven height intervals. This gave each point a characteristic foliage profile. Foliage profile diversity, a measure of horizontal heterogeneity, was calculated from the presence/absence information using the Shannon-Weaver index (Shannon and Weaver 1949, Ambuel and Temple 1983).

We performed principal components analysis (PCA) on the vegetation measures for the 267 plots to determine the major orthogonal patterns of variation in the vegetation across study sites. All variables expressed as proportions were arcsine-square root transformed (Sokal and Rohlf 1969). The factor scores for all components with eigenvalues of >1 were retained for analysis, and varimax rotation was employed to enhance their interpretability (Norusis 1985). Each principal component was named after the variable with the highest factor loading on that component. The factor scores for each principal component were averaged for each transect, and their means and standard deviations were plotted in multivariate space in order to depict graphically both the relative positions of transects along the vegetation gradients and the nature and extent of within-transect heterogeneity.

Relationships between bird densities and habitat characteristics were examined by linear regression. Separate regressions to relate the averaged PCA-derived habitat variables (independent variables) for each transect to bird densities (dependent variables) were performed for each species. Residuals were analyzed by examining normal probability plots and plots of unstandardized residuals with the independent variables. In addition, bird densities were plot-

ted with each independent variable to identify non-linear relationships.

We used discriminant function analysis (DFA) to determine patterns of habitat utilization (James 1971; Smith 1977; Noon 1981; Rice et al. 1981, 1983; Williams 1981, 1983; Conner et al. 1983; Adler 1985). Discriminant function analysis can be used to predict group membership by classifying cases based on values of the canonical variates and to interpret differences between groups by examining both the degree of statistical separation of group means and the variables contributing most to the discrimination between groups.

We recorded the presence or absence of individuals on each of the 267 vegetation plots. An individual was considered to be present if its territory overlapped at least 50% of a sampling plot. For each species we performed a two-group DFA using the PCA-derived habitat measures (factor scores) to discriminate plots where individuals of a given species were present from those where individuals were absent.

Both stepwise and direct DFAs were conducted for each species. Because the direct analyses yielded consistently lower Wilk's lambda values and consistently higher percentages of correctly classified cases, we used only the results of the direct analyses (Rice et al. 1983). Interpretation of discriminant functions was based on the correlations of the PCA-derived habitat measures with the canonical variates, a method preferable to the examination of discriminant function coefficients (Williams 1981, Conner et al. 1983, Morrison 1984). The results of the classification analyses were used to examine the habitat discrimination of species as reflected in the percentages of cases correctly classified. Classification of cases was based on prior probabilities of group membership that were determined by the proportion of occupied plots.

Several statistical problems associated with DFA may arise when groups differ substantially in sample size or when the assumption of homoscedasticity is violated (Williams 1981, 1983; Rice et al. 1983; Morrison 1984). In these cases the significance values associated with the Chi-square transformation of Wilk's lambda may be unreliable. In our work Rufous-sided Towhees and Common Yellowthroats were absent from relatively few plots. In addition, an examination of the results of Box's *M*-tests of homogeneity of variance-covariance matrices revealed that this assumption was violated in two of the three cases. Therefore, conclusions regarding habitat selectivity are based on the results of the classification procedure rather than on the potentially unreliable Wilk's lambda and associated significance values (Rice et al. 1981, 1983). The classification application of DFA can be useful and biologically valid despite the existence of biased significance values (Williams 1981, Rice et al. 1983).

To evaluate habitat selectivity we examined the percentages of plots correctly classified as occupied,

unoccupied, and the overall percentages of correctly classified plots. When examining classification results, it is important to take into account the classification rates expected by chance alone (Norusis 1985), particularly when group sample sizes are unequal (Titus et al. 1984), as was the case for Rufous-sided Towhees and Common Yellowthroats. Therefore, we calculated Cohen's (1960) kappa (K), representing the average proportion of cases correctly classified after removing the effects of chance, using the formula of Titus et al. (1984). The 95% confidence intervals (C.I.) for K were calculated and the null hypothesis that K was no different from chance was tested by calculating the z statistic.

These tests were performed for each of the three categories of classification. Kappa values and tests of significance allowed us to evaluate the relative strength of the habitat associations of each species and the extent to which habitat discrimination differed from chance expectations.

RESULTS

Rufous-sided Towhees were the most abundant species, followed by Common Yellowthroats and Prairie Warblers. In each year Prairie Warbler densities were considerably more variable among transects than Rufous-sided Towhees or Common Yellowthroats (Fig. 1).

Prairie Warbler dispersion patterns changed in different ways from those of Rufous-sided Towhees and Common Yellowthroats as grain size increased (Table 1). At the smallest quadrat size (0.25 ha), corresponding roughly to the territory sizes of these species in this habitat, all species had dispersion indices that indicated regular dispersion. Rufous-sided Towhees and Common Yellowthroats exhibited patterns of regular dispersion at quadrat sizes of 0.5 ha and random dispersion at quadrat sizes of 3.5 ha and 7 ha. In contrast to these two species, Prairie Warblers were randomly dispersed at quadrat sizes of 0.5 ha and tended to be patchily dispersed at quadrat sizes of 3.5 ha and, especially, 7.0 ha. Analyses of nearest-neighbor distances revealed that all three species were evenly dispersed within all transects in every year (Table 2). This indicates the importance of intraspecific competition in determining the dispersion of individuals.

The PCA of habitat measures for 267 vegetation plots extracted seven factors with eigenvalues of >1 (Table 3). Together these factors explained 71.5% of the variation in vegetation.

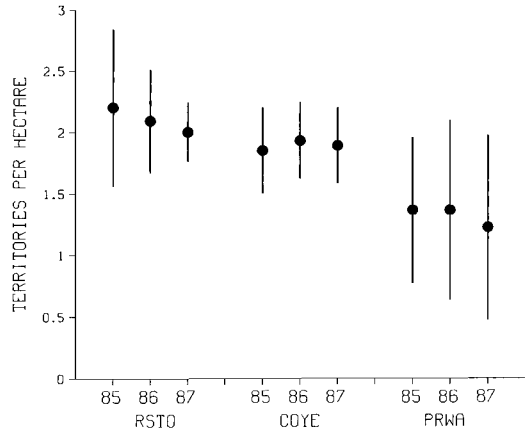


Fig. 1. Densities ($\bar{x} \pm SD$) of the three numerically dominant breeding bird species in the southeastern Massachusetts pine barrens, 1985–1987. Abbreviations: Rufous-sided Towhee (RSTO), Common Yellowthroat (COYE), and Prairie Warbler (PRWA).

The major component of variation (maximum height of vegetation, 25.8%) described a gradient of increasing coverage of pitch pines, associated with increasing height of vegetation, basal area, and heterogeneity. The second component (percentage cover of white oak, 12.1%) described a gradient of increasing coverage of oak trees. The remaining components each explained relatively little of the overall variation in vegetation and described independent gradients in the coverages of herbs, scrub oak, white pine, black huckleberry, and sheep laurel.

The two-dimensional ordination of average factor scores for each transect in the space described by the first two principal components (Fig. 2) revealed that maximum height, basal area, heterogeneity, and pitch-pine coverage (PC1) varied more or less continuously among sites. Transects loading high on this component also tended to be somewhat more heterogeneous. In contrast, oak tree coverage (PC2) did not vary continuously among transects. Oak coverage was very high and variable on MASH2, overlapping other transects only slightly. The remaining transects were clustered on this component.

It appears that the eight transects represented a rather shallow and nonlinear gradient with respect to oak coverage, with only MASH2 contributing substantially to the variation explained by this principal component. Further-

TABLE 1. Morisita's dispersion indices^a for the three dominant breeding bird species in the southeastern Massachusetts pine barrens (Rufous-sided Towhee [RSTO], Common Yellowthroat [COYE], Prairie Warbler [PRWA]). Values ≈ 1 indicate a random dispersion, values < 1 indicate a regular dispersion, and values > 1 indicate a patchy dispersion. Significant deviations from a random (Poisson) distribution are indicated (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

Species	Quadrat size (number of quadrats)								
	No. of territory centers			0.25 ha (232)			0.5 ha (116)		
	1985	1986	1987	1985	1986	1987	1985	1986	1987
RSTO	122	117	114	0.08***	0.03***	0.10***	0.53***	0.54***	0.49***
COYE	110	102	102	0.04***	0.09***	0.01***	0.52**	0.56**	0.43***
PRWA	69	66	59	0.19	0.01*	0.01*	0.76	0.65	0.69

^a $M = N \sum n_i(n_i - 1) / n(n - 1)$, where n_i = total number of territory centers in a quadrat, n = total number of territory centers, and N = number of quadrats (Vandermeer 1981).

more, although the transects fell along a rather continuous gradient on PC1, average pitch pine coverage never exceeded 17% on any transect or 45% on any sampling plot. Therefore, all transects had fairly open canopies.

The 21 linear regressions of the seven PCA-derived habitat measures on densities of the three bird species revealed three (14.3%) significant relationships (Table 4). The examination of residuals and density plots (Fig. 3) for the significant regression of maximum height of vegetation on Prairie Warbler densities re-

vealed that a linear model was not appropriate for describing this relationship. Rather, Prairie Warblers decreased in abundance in a curvilinear fashion with increasing height of vegetation, percent cover and basal area of pitch pines, and vertical and horizontal heterogeneity. Prairie Warblers were also less abundant on MASH2, which was characterized by high oak tree coverage. No other systematic linear or nonlinear relationships were apparent for Prairie Warblers. These habitat relationships are consistent with the findings of other studies of Prairie

TABLE 2. Ratios of observed to expected nearest-neighbor distances for each transect. All values are > 1 , indicating regular distributions. Significance values (all $P < 0.001$, except where indicated; * = $P < 0.05$, ** = $P < 0.01$) were determined using t -tests. Numbers of territories per 7.0 ha are in parentheses; see Appendix 2 for transect names and locations.

Transect	Rufous-sided Towhee			Common Yellowthroat			Prairie Warbler		
	1985	1986	1987	1985	1986	1987	1985	1986	1987
PCWT	1.73 (8)	1.74 (13)	2.05 (14)	2.04 (11)	1.64 (12)	1.89 (11)	2.09 (13)	2.15 (14)	1.73 (12)
MSSF1	1.82 (17)	1.87 (14)	1.97 (15)	2.05 (15)	2.09 (14)	1.80 (12)	2.09 (13)	1.85** (10)	2.10 (10)
MSSF2 ^a	1.78 (12)	1.77 (14)	1.94 (12)	2.17 (12)	1.84 (12)	1.88 (13)	— (3)	— (2)	— (2)
MSSF3	2.21 (20)	1.94 (15)	1.96 (13)	2.20 (15)	1.80 (13)	2.11 (15)	2.06 (15)	1.56** (17)	2.06 (15)
PLIM	2.00 (13)	1.81 (15)	1.89 (13)	1.95 (15)	1.59 (14)	1.96 (15)	1.95 (10)	1.45* (11)	1.85 (13)
OAFB	1.86 (15)	1.86 (13)	2.15 (15)	2.10 (13)	1.93 (12)	1.99 (12)	1.96** (6)	1.87 (11)	1.85 (11)
MASH1 ^a	1.97 (14)	1.70 (12)	1.88 (12)	1.84 (8)	1.40* (12)	1.86 (10)	2.02 (6)	— (4)	— (3)
MASH2 ^a	1.77 (22)	1.94 (21)	2.02 (17)	2.04 (14)	1.92 (18)	1.79 (16)	1.49* (8)	1.94* (5)	— (2)
Overall mean ±SE	59.59 1.19	59.77 1.21	70.01 1.34	68.26 1.40	63.09 1.60	65.40 1.03	73.79 2.23	74.34 3.04	75.08 1.75

^a Nearest-neighbor tests could not be performed for Prairie Warblers on transect 3 in all years and on transects 7 and 8 in some years because there were fewer than five territory centers in these cases.

TABLE 1. Extended.

Quadrat size (number of quadrats)								
1.0 ha (58)			3.5 ha (16)			7.0 ha (8)		
1985	1986	1987	1985	1986	1987	1985	1986	1987
0.80	0.79	0.70*	0.97	0.95	0.92	1.02	0.98	0.97
0.70***	0.82**	0.68	0.93	0.92	0.93	0.98	0.98	1.00
1.04	0.78	0.89	1.15	1.12	1.30*	1.16*	1.21	1.33**

Warblers (Lloyd-Evans 1973, Nolan 1978, Conner et al. 1983, Kerlinger 1984, Brush 1987).

The analyses of residuals for the regression of oak tree coverage (WOAK) on Rufous-sided Towhee and Common Yellowthroat densities revealed that linear models were not appropri-

ate for describing these positive relationships. An examination of the plots of bird densities with factor scores for oak tree coverage (Fig. 3) revealed that no systematic linear relationships were apparent and that the regression results were due to the high densities of these birds

TABLE 3. Principal components analysis of vegetation variables in the southeastern Massachusetts pine barrens. Only factor loadings >0.45 are shown, since others contribute <20% to a component. All *P* < 0.001; see Appendix 2 for variable descriptions.

Variable code	MAXHGT (PC1)	WOAK (PC2)	HERB (PC3)	SOAK2 (PC4)	WPINE (PC5)	BHUCK (PC6)	SLAUR (PC7)
Coverage							
SOAK1				0.758			
SOAK2				0.763			
BHUCK						0.764	
BLUEB			0.852				
SLAUR							0.720
SFERN							0.634
HERB			0.894				
SMIL	0.491						
PPINE1	0.799						
PPINE2	0.781						
WPINE					0.833		
BOAK		0.821					
WOAK		0.831					
Structure							
BASAL	0.758						
BASAL3	0.675						
DEADBAS				0.542			
HITS	0.565				0.492		
MAXHGT	0.834						
FALL				-0.468			
LITT						0.635	
Heterogeneity							
FHD	0.688						
FPD	0.625						
Eigenvalue	5.68	2.66	2.02	1.63	1.50	1.18	1.05
% variance	25.8	12.1	9.2	7.4	6.8	5.4	4.8
Cumulative %	25.8	37.9	47.1	54.5	61.4	66.7	71.5

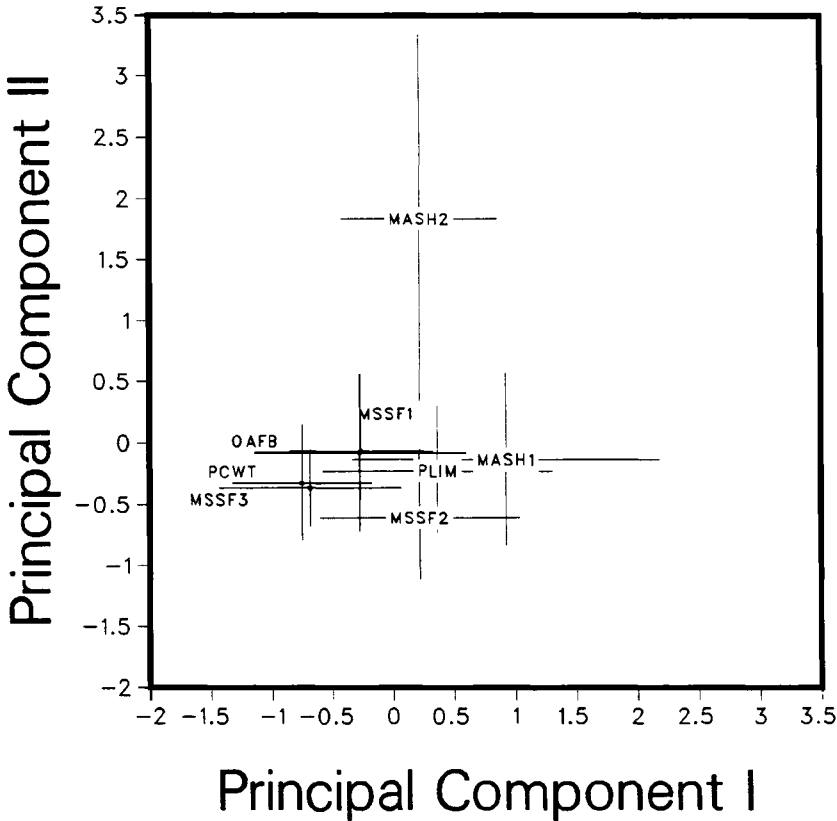


Fig. 2. Two-dimensional ordination of transects in the space described by the first two vegetation principal components. Average factor scores are plotted with standard deviations.

on MASH2. Although this transect had much higher average percent cover of white oaks (10.2%) and black oaks (9.8%) compared with other transects, oak coverage was extremely heterogeneous (Fig. 2; coefficients of variation equal 142% for white oak and 95% for black oak coverage). Rufous-sided Towhees and Common Yellowthroats exhibited no systematic linear or nonlinear relationships with any of the other PCA-derived habitat parameters.

The correlations of PCA-derived habitat mea-

asures with the discriminant axes derived from two-group DFAs are presented in Table 5. Only correlations > 0.45 (all $P < 0.001$) are given. The direction and relative magnitude of the correlations are more important considerations than significance levels when evaluating the importance of variables in discriminant analyses (Conner et al. 1983). The best separation of group means occurred for Prairie Warblers. Prairie Warblers avoided areas with high coverage, height, and basal area of pitch pines and high

TABLE 4. Significant ($P < 0.05$) linear regressions of PCA-derived habitat measures on bird densities ($n = 24$ for each species).

Dependent variable (density)	Independent variable ^a	Slope	Intercept	<i>t</i>	<i>P</i>	Adjusted <i>r</i> ²
Rufous-sided Towhees	WOAK	0.321	2.11	2.88	0.009	0.24
Common Yellowthroats	WOAK	0.209	1.90	2.65	0.015	0.21
Prairie Warbler	MAXHGT	-0.703	1.25	3.96	0.001	0.39

^a MAXHGT = maximum height of vegetation; WOAK = percentage cover of white oak.

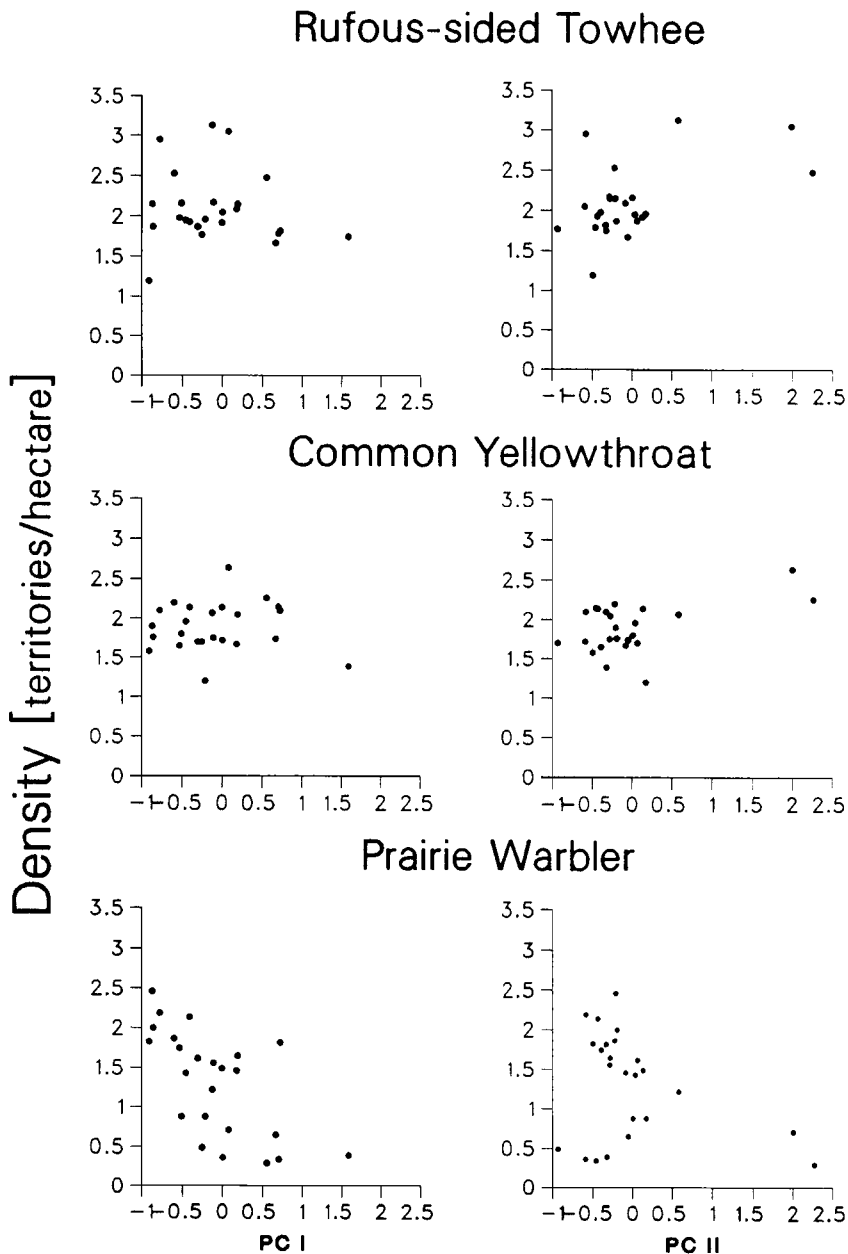


Fig. 3. Plots of bird densities with factor scores for the first two principal components of vegetation.

coverage of oak trees. These results were consistent with our density-habitat analysis. The DFAs revealed relationships for Rufous-sided Towhees and Common Yellowthroats that were not apparent from the density-habitat analysis. Rufous-sided Towhees occurred on plots with high coverage of herbs and black huckleberry, and with high litter depth; and Common Yel-

lowthroats occurred on plots with high coverage of scrub oak (Table 5). Despite these correlations, the associated PCA-derived habitat measures explained only a small percentage of the overall habitat variation compared with the variable with which Prairie Warbler densities were correlated (Table 4).

The classification (Table 6) of these DFAs re-

TABLE 5. Significant correlations ($r > 0.45$) of habitat measures with the canonical variates derived from two-group discriminant function analysis. Principal components are named after the variable with the highest factor loading. All $P < 0.001$; see Appendix 2 for variable descriptions.

	Rufous-sided Towhee	Common Yellowthroat	Prairie Warbler
Principal Component			
1 MAXHGT			0.65
2 WOAK			0.45
3 HERB	0.68		
4 SOAK2		0.68	
5 WPINE			
6 BHUCK	0.46		
7 SLAUR			
Group Means			
Present	0.07	0.21	-0.45
Absent	-0.17	-0.44	0.54
Wilk's Lambda	0.99	0.91	0.80
P	0.884	0.001	0.000
No. of plots occupied	191	180	145

vealed that the percentages of plots correctly classified as occupied were greater than expected by chance ($P < 0.01$) for Common Yellowthroats and Prairie Warblers in each category: occupied, unoccupied, and overall. The chance-corrected classification of occupied plots was generally high yet somewhat lower than non-chance-corrected values for all species except Rufous-sided Towhees (Table 6). However,

the K values for the classification of unoccupied plots and for overall classification were much lower for Rufous-sided Towhees and Common Yellowthroats compared with Prairie Warblers. In fact, the chance-corrected classification values for unoccupied plots and overall classification for Rufous-sided Towhees indicated that no improvement over chance was provided by the DFA. The considerable differences between observed overall classification rates and the corresponding chance-corrected K values suggest that the observed (non-chance-corrected) classification rates—and therefore group predictability—were highly inflated (Titus et al. 1984) for Rufous-sided Towhees and Common Yellowthroats compared with Prairie Warblers. Thus, while the chance-corrected classification results seem somewhat low, even for Prairie Warblers, they are not nearly as low as those for Rufous-sided Towhees and Common Yellowthroats.

DISCUSSION

Prairie Warblers exhibited more distinct habitat associations than Rufous-sided Towhees and Common Yellowthroats, as indicated by their patchy distribution among transects at the larger grain sizes considered, the one curvilinear relationship of density variation to habitat variation, and the relatively strong discrimination between occupied and unoccupied plots. In contrast, Rufous-sided Towhees and Common Yellowthroats exhibited relatively weak habitat

TABLE 6. Classification results for two-group discriminant function analyses of 267 vegetation plots. Expected values were estimated from classification tables based on prior probabilities. Kappa (K) values, representing chance-corrected proportions of correctly classified cases, are also given with 95% confidence intervals ($K \pm 1.96$ SE) and associated significance values derived from z-tests ($H_0: K = 0$; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

Species	No. of occupied plots	Percent correct classification					
		Observed			Expected		
		Absent	Present	Overall	Absent	Present	Overall
Rufous-sided Towhee	191	0.0 (0.0 \pm 0.00) ^a	100.0 (100.0 \pm 0.00) ***	71.5 (0.0 \pm 0.19) NS	0	71.5	71.5
Common Yellowthroat	180	19.5 (0.17 \pm 0.05) ***	93.9 (0.85 \pm 0.07) ***	69.7 (0.16 \pm 0.15) *	3.4	60.3	63.8
Prairie Warbler	145	59.0 (0.51 \pm 0.07) ***	81.4 (0.72 \pm 0.07) ***	71.2 (0.41 \pm 0.11) ***	16.9	34.2	51.1

^a We could not calculate z-statistic for Rufous-sided Towhees because division by 0 is impossible.

associations, as evidenced by their random dispersions among transects at larger grain sizes, the absence of systematic density-habitat relationships, and the overall lower habitat discriminability.

These findings are consistent with the natural histories of these species. Prairie Warblers have a smaller geographic range, are more locally distributed within this range, and have more restricted habitat preferences than either Rufous-sided Towhees or Common Yellowthroats. The overall extent of this study, encompassing an array of postfire successional stages in the pine barrens of southeastern Massachusetts, was adequate to capture broad-scale habitat variation to which Prairie Warblers responded. Prairie Warblers exhibited relatively clear patterns of habitat occupancy across transects. They responded to the major components of habitat variation: height, coverage, and basal area of pitch pines. This habitat variation occurred on a scale commensurate with the one at which Prairie Warblers exhibited a patchy dispersion (i.e. at the relatively coarse grain size of the 7.0-ha quadrats). With increasing grain size from the 0.25-ha quadrats to the 7.0-ha quadrats, much of the fine-scale between-quadrat variation in habitat was lost to resolution (Wiens 1989), and the relatively broad-scale habitat variation among transects that represented different successional stages emerged. Prairie Warblers appeared to be responding to this broad-scale habitat variation with patchy dispersions emerging at the 3.5-ha and 7.0-ha scales.

Although we did not determine habitat associations at the 3.5-ha scale of resolution, we can gain insight into the possibility of responses to habitat variation by Prairie Warblers at this grain size by considering the results of the within-transect dispersion analysis and by examining habitat variation within transects. Prairie Warbler density varied considerably among transects (Fig. 1). Because Prairie Warblers were dispersed regularly even in transects where they were less abundant (Table 2), they probably responded to within-transect heterogeneity, spacing themselves evenly within preferable areas. Indeed, the transects on which Prairie Warblers were least abundant (MASH1 and MASH2) were characterized by higher and more heterogeneous coverage of trees (Fig. 2). The Prairie Warblers' response to this within-transect heterogeneity is supported by the finding that the dispersion of Prairie Warblers at

grain sizes of the 3.5-ha quadrats was characterized by fewer quadrats with either 0, 1, 2, or 3 birds than expected in a random distribution. Thus, Prairie Warblers were responding to within-transect habitat heterogeneity by concentrating in preferred areas where they became evenly dispersed.

It is less clear if Rufous-sided Towhees and Common Yellowthroats responded in a systematic way to the major broad-scale patterns of habitat variation encompassed in our study. These two species presumably preferred a much greater array of pine barrens habitats and thus exhibited weaker patterns of habitat occupancy across successional stages. Correspondingly, they exhibited random dispersions at even the large grain sizes of the 3.5-ha quadrats and 7.0-ha quadrats. The failure to detect strong habitat relationships for Rufous-sided Towhees and Common Yellowthroats within the pine barrens does not mean that habitat preferences do not exist. For example, habitat preferences within the pine barrens might become apparent at smaller scales, expressed in patterns of behavior and prey selection (Eckhardt 1979, Robinson and Holmes 1984). Preferences could become apparent with an expanded spatial extent that included a greater variety of habitat types (Wiens and Rotenberry 1981). Patchy dispersion patterns and correspondingly strong habitat relationships would likely emerge as the extent was increased to include unfavorable habitat. In addition, more consistent indicators of habitat quality might be revealed by examining reproductive success (Van Horne 1983, Maurer 1986).

The regular dispersions of all three species within transects reflect the effects of intraspecific territoriality. This finding was not surprising given the high densities of these species within fairly homogeneous transects. Regular dispersion patterns also emerged among transects at fine grain sizes. The spatial (between-quadrat) variance in habitat at small grain sizes tends to be relatively large (Wiens 1989). Therefore, the broad-scale patterns of habitat variation were unresolved at the small grain sizes of the 0.25- and 0.5-ha quadrats. These small grain sizes roughly corresponded to the sizes of individual territories and, therefore, there was not much variation in the number of territory centers per quadrat. Low values of the dispersion indices reflect the regular dispersion patterns.

All three species were regularly dispersed at

the small extent of individual transects, presumably because of intraspecific competition. Prairie Warblers became first randomly and then patchily dispersed, whereas Rufous-sided Towhees and Common Yellowthroats became randomly dispersed, as the grain size increased to reflect dispersion in relation to broad-scale successional patterns within the southeastern Massachusetts pine barrens. These results, in combination with the analyses of habitat associations, imply that these three pine barrens species respond to habitat variation in different ways and at different scales, consistent with an individualistic view of communities. These results point to the importance of considering the possibility of scale-specific habitat selection and other scale-dependent processes when attempting to unravel complex patterns of co-occurrence (Holmes et al. 1986, Gutzwiller and Anderson 1987, Wiens et al. 1987).

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APPENDIX 1. Transect name, location, size (ha), number of years since last burned, and number of 0.04-ha vegetation plots sampled for eight strip transects in the southeastern Massachusetts pine barrens.

Transect	Location	Size	Years post-burn (to 1985)	No. of vegetation plots
1 PCWT	Plymouth	7.0	15	32
2 MSSF1	Plymouth	7.0	22	34
3 MSSF2	Plymouth	7.0	>30	32
4 MSSF3	Plymouth	7.0	10	32
5 PLIM	Plymouth	7.5	21	33
6 OAFB	Bourne	7.0	5	32
7 MASH1	Mashpee	9.0	>30	40
8 MASH2	Mashpee	7.0	>30	32

APPENDIX 2. Variables measured to characterize vegetation in the southeastern Massachusetts pine barrens.

Variable code	Description
Coverage	
SOAK1	% cover scrub oak <1 m
SOAK2	% cover scrub oak >1 m
BHUCK	% cover black huckleberry
BLUEB	% cover blueberry
SLAUR	% cover sheep laurel
SFERN	% cover sweet fern
HERB	% cover herbs
SMIL	% cover common greenbriar
PPINE1	% cover pitch pine <8 m
PPINE2	% cover pitch pine >8 m
WPINE	% cover white pine
BOAK	% cover black oak
WOAK	% cover white oak
Structure	
BASAL	Basal area of trees >5 cm DBH
BASAL3	Basal area of the 3 largest trees
DEADBAS	Basal area of standing dead trees
HITS	Total number of contacts with vegetation pole
MAXHGT	Maximum height of vegetation
FALL	Number of fallen trees >5 cm DBH
LITT	Average litter depth
Heterogeneity	
FHD	Foliage height diversity
FPD	Foliage profile diversity