HABITAT SELECTION BY PEATLAND BIRDS IN A CENTRAL MAINE BOG: THE EFFECTS OF SCALE AND YEAR

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Abstract.—To determine habitat preferences of peatland birds in a central Maine bog, spot-mapping was conducted in 1994 and 1995 on an 8-ha grid. Each 0.25-ha unit of the grid was characterized by various measurements of tree density, shrub density, and topographic relief. Multiple regression was used to identify habitat variables that best explained variation in bird occurrence. Contrary to expectation, the habitat selection of each species showed greater concordance within years at the two different scales than within scales in different years. The regression analysis was poor at predicting the abundance of Common Yellowthroats and Song Sparrows. Some of the regressions for Palm Warblers and White-throated Sparrows explained more than 70% of the variance in bird abundance. The results suggest that these peatland birds see their habitat as fine-grained environments. Therefore, habitat selection during the nesting season is likely made on some general perception of habitat rather than specific habitat features.

SELECCIÓN DE HÁBITAT POR AVES DE TURBERA EN UNA ANEGADO DE LA PARTE CENTRAL DE MAINE: EL EFECTO DE ESCALA Y AÑO

Sinopsis.—Durante 1994–1995 se llevó a cabo un censo de punto en una rejilla de 8 ha para determinar la preferencia de hábitat en aves de turbera en un anegado de la parte central de Maine. Cada punto tenía 0.25 ha, se caracterizó para varias medidas de densidad de árboles, densidad de arbustos y topografía del relieve. Se utilizó la regresión múltiple para identificar las variables del hábitat que mejor explicaban la variación de aves en la localidad. Contrario a lo esperado, la selección de hábitat de cada especie mostró mayor concordancia entre años, en dos escalas diferentes, que entre escalas en años diferentes. El análisis de regresión resultó pobre para predecir la abundancia de *Geothlypis trichas* y *Melospiza melodia.* Algunas de las regresiones para *Dendroica palmarum* y *Zonotrichia albicolis* explicaron el 70% de la varianza en la abundancia de aves. Los resultados sugieren que las aves de esta localidad ven sus hábitats como ambientes de gradientes finos. Por lo tanto, la selección durante la época de anidamiento posiblemente sea hecha bajo la persepción en general del hábitat en vez de características particulares del mismo.

Habitat selection is a critical determinant of avian distribution and abundance. Birds select habitats at different scales, requiring an investigator to match the scale of habitat description with the scale of bird distribution. For instance, birds may occur broadly in a biotic zone (e.g., Ponderosa Pine zone). Within such a zone, individual birds during the breeding season will choose particular portions of that broad habitat to establish territories. Even finer resolution of habitat is required to understand the components of habitat that influence the selection of sites for perching, foraging, and nest building (Collins 1981; Steele 1992, 1993).

A typical approach to understanding habitat selection at more local scales is to characterize the topographic and vegetative components of a given area and seek correlations of these variables with observed bird distributions (Parnell 1969, Franzreb 1978, Morrison 1981, Collins et al. 1982, Douglas et al. 1992). Interspecific differences in habitat may provide evidence of competition-driven resource partitioning (MacArthur 1958, Morse 1967, Sherry and Holmes 1988).

In northern New England, bog habitats are interspersed throughout the boreal forest around kettleholes and on the margins of lakes and ponds. Such habitats have predictable associations of birds, which differ from the surrounding uplands. These bogs have received little ornithological attention. In this paper, we quantify the features of a bog habitat at two scales and describe how these features are associated with the occurrence of the four most abundant breeding birds in a bog in central Maine.

STUDY SITE

The study area was located in Sidney Bog, Maine (44°23′N, 69°46′W). Sidney Bog is an ombrotrophic (rain-fed) bog of roughly rectangular shape, 4-km long from north to south and 2-km across from east to west.

Sidney Bog is open, with large trees sparsely scattered throughout. The most common trees are black spruce (*Picea mariana*), northern white pine (*Pinus strobus*), and tamarack (*Larix laricina*) with scattered black cherry (*Prunus serotina*) and gray birch (*Betula populifolia*) saplings. Heaths and related shrubs cover 100% of the bog; dominant species are rhodora (*Rhododendron canadense*), Labrador tea (*Ledum groenlandicum*), leatherleaf (*Chamaedaphne calyculata*), sheep laurel (*Kalmia angustifolia*), bog laurel (*K. polifolia*), bog rosemary (*Andromeda glaucophylla*), large-leaf cranberry (*Vaccinium oxycoccos*), and mountain holly (*Nemopanthus mucronatus*). The surface of the bog is covered by sphagnum mosses (*Sphagnum* spp.). In most places, the topographic relief is best described as a series of *Sphagnum*-covered hummocks, each about 50-cm high and 1-m or less across.

The adjacent upland area was dominated by red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), white ash (*Fraxinus pensylvanica*), and white birch (*Betula papyrifera*) with an understory dominated by serviceberries (*Amelanchier* spp.) and beaked hazelnut (*Corylus cornuta*). A lagg (moat) of approximately 20-m width encircled the bog. This wet area was dominated by thickets of mountain holly with an understory of cinnamon fern (*Osmunda cinnamomea*).

In April 1994, 8 ha of the bog were surveyed and marked with permanent stakes into 50 × 50-m sections. The grid was 400-m long and 200-

m wide. The grid was established at least 50 m from the lagg, in an attempt to minimize edge effects. The size of the study area was a compromise between size and ease of coverage. Because of the difficulty in traversing the habitat, areas larger than 8 ha could not be covered in a timely fashion during a morning census, particularly with only a single observer.

On 10 days in 1994 (31 May–12 July) and on 12 days in 1995 (29 May–8 July), spot-mapping surveys were conducted on the study grid using the techniques of Robbins (1970). On some censuses in 1994, two parties began at opposite ends of the grid. Proceeding from marker to marker, all birds heard or seen from each observation point were recorded on a map of the study area. In 1995, one observer (WHW) conducted all of the censuses. The censuses were begun at opposite ends of the study area in alternating fashion. Surveys began no later than 0630 h and were completed in most cases by 0900 h.

In July 1994, we quantified the vegetation of the study grid. In each 50 × 50-m section of the grid, all trees were counted. Each tree was identified and classified into a height class (<1 m, 1–2 m, 2–4 m, 4–8 m, and 8–16 m). Dead standing trees were also counted and classified by height but not identified to species.

To quantify the structure of the shrub component of the study area, the technique of Wiens and Rotenberry (1981) was used. A pole, 20 mm in diameter, and marked in 10-cm increments was randomly placed at 15 different locations within each 50 × 50-m section. The number of branches contacting the pole were noted. We also recorded the specific identity of each branch and the height at which the contact (hereafter, hits) occurred. The maximum height of the vegetation within 50 cm of the pole was measured. A measure of the topography was obtained by determining the vertical difference between the highest and lowest portion of the surface of the bog within a 50-cm radius of each pole.

These measures of the vegetational and topographic features of each block within the sampling grid produced a number of different measures of habitat structure: the number of the five different tree species and total dead trees in each of the five different height classes, the number of shrub hits in each of 10 increments of height (from the ground to a height of 1 m), maximum height of vegetation, and topographic relief (cm). Composite variables (e.g., all black spruce ≥2 m tall) were also calculated (see Table 1).

Finally, for each of the four common birds, the sighting frequencies (see below) of the three heterospecific bird species were entered into the analysis for each species for each year. Combining the simple and composite variables, 75 different measures of habitat variability were gathered for the 32 50 × 50-m sections of the study area.

For all habitat variables, we calculated the mean, standard deviation, range, and coefficient of variation within each sector. We did not use ANOVA to examine the patterns of variation along rows and columns of the grid because of autocorrelations of adjacent grid units.

Separate analyses were conducted for the 1994 and 1995 bird census

TABLE 1. Descriptive statistics for a number of vegetational and topographic features of the 8-ha study area in Sidney Bog. The grand mean of the 32 0.25-ha sectors is given along with the standard deviation, range, and coefficient of variation. The list includes all variables that are significant in multiple regressions analyzing bird habitat selection (Table 2).

Characteristic	Grand mean	Standard deviation	Range	Coefficient of variation
Hits—0–10 cm	1.6	0.52	1.0–2.7	0.32
Hits—10–20 cm	2.0	0.54	0.9–3.1	0.27
Hits—20–30 cm	1.8	1.89	0–10	1.03
Hits—80–90 cm	0.1	0.26	0–1.5	4.50
Hits—0–30 cm	5.4	1.12	3.4–7.5	0.21
Total hits	7.5	1.95	4.8–12.8	0.26
Hits/cm	0.16	0.028	0.11–0.24	0.176
Maximum height (cm)	50.2	13.78	35.2–87.5	0.27
Topographic relief (cm)	23.1	4.24	15.7–34.5	0.18
Black Spruce <1 m	3.3	4.84	0–19	1.46
Black Spruce 1–2 m	9.6	21.64	0–122	2.24
Black Spruce 2–4 m	7.0	11.44	0–58	1.63
Black Spruce 4–8 m	5.5	10.26	0–55	1.88
Black Spruce 8–16 m	1.7	6.01	0–34	3.50
Black Spruce <2 m	12.9	23.49	0–136	1.83
Black Spruce >2 m	14.4	26.07	0–147	1.81
Tamarack <1 m	0.2	1.19	0–7	5.21
Tamarack 1–2 m	0.6	2.00	0–11	3.36
Tamarack 2–4 m	0.31	0.74	0–3	2.36
Tamarack 4–8 m	0.3	1.04	0–5	3.01
Tamarack 8–16 m	0.6	0.84	0–3	1.49
Tamarack <2 m	0.8	3.19	0–18	3.78
Tamarack ≥2 m	1.2	2.03	0–10	1.66
White Pine 2–4 m	2.0	1.86	0–7	0.94
White Pine 4–8 m	4.5	3.44	0–12	0.76
White Pine 8–16 m	3.2	2.49	0–9	0.79
White Pine <2 m	0.9	1.27	0–4	1.35
White Pine ≥2 m	9.7	5.01	2–18	0.52
Gray Birch <1 m	0.1	0.42	0–2	3.37
Gray Birch 1–2 m	0.2	0.47	0–2	2.51
Black Cherry 1–2 m	0.3	0.73	0–3	2.59
Dead trees 2–4 m	0.2	0.40	0–1	2.12
Dead trees 4–8 m	0.1	0.39	0–2	4.16
Dead trees <2 m	0.2	0.45	0–2	2.87
Dead trees ≥2 m	0.3	0.70	0–3	2.04
Living trees <2 m	16.0	26.95	1–147	1.69
Living trees ≥2 m	25.2	27.58	4–156	1.10
Total trees ≥2 m	25.5	28.06	4–159	1.10

data. Rather than mapping the territories of the birds using all of the spot-maps for a season, we used the sum of individual sightings of birds for our analyses. Territorial males were probably detected and mapped on each census and it is possible that some birds were mapped more than once on a single survey. Therefore, the total of the sightings in a sector of the study area does not measure the actual abundance of a species.

However, the data do give a measure of the relative habitat use of each sector. Multiple step-wise regressions were performed using DataDesk 4.2© to regress the number of occurrences of each of the common species (Palm Warbler [*Dendroica palmarum hypochrysea*], Common Yellowthroat [*Geothlypis trichas*], Song Sparrow [*Melospiza melodia*] and White-throated Sparrow [*Zonotrichia albicollis*]) against the habitat variable with the highest correlation coefficient. Variables were added to the regression as long as each added variable produced a significant relationship with the density of a bird species. Although there is some concern about step-wise regression in that the sequence in which variables are entered can influence the results, we believe that this approach is the best analysis for our data (James and McCullough 1990).

The 32 0.25-ha sectors of the grid were then combined into eight 1-ha sectors. The numbers of trees in each of the four 0.25-ha sectors were added. Means of maximum height, topographic relief and the various hit data for the shrubs were calculated. The number of sightings of birds in the four 0.25-ha sectors within each 1-ha area were combined.

Although spot-mapping is typically used to map territories of breeding birds, we use the sum of the occurrence data from spot-mapping for a different end, the determination of relative use of a particular area of the bog habitat by a particular bird species. By dividing the study area into small sectors, we can judge habitat selection on a small scale and then combine adjacent areas to examine habitat selection at larger scales. The data collected are not truly independent as individuals may be repeatedly sighted on spot-maps, even on a single census. However, such an approach is necessary to allow us to examine the scale-dependence of habitat selection.

Other species present in the bog but not in sufficient numbers to analyze were Cedar Waxwing (*Bombycilla cedrorum*), Hermit Thrush (*Catharus guttata*), Eastern Towhee (*Pipilo erythrophthalmus*), Lincoln's Sparrow (*Melospiza lincolnii*), Purple Finch (*Carpodacus purpureus*) and American Goldfinch (*Carduelis tristis*). Species in the lagg and adjacent uplands (Nashville Warbler [*Vermivora ruficapilla*], Canada Warbler [*Wilsonia canadensis*] and Northern Waterthrush [*Seiurus novaeboracensis*]) did not venture into the study area.

RESULTS

The various habitat features showed strikingly different patterns of variation among 0.25-ha sectors. Some features varied along rows, some along columns and others varied along both rows and columns. Space does not permit summary of all the habitat variables here. However, Table 1 lists the grand mean, range, and coefficient of variation of selected variables to show the heterogeneous nature of the Sidney Bog habitat.

The results of the multiple regression analyses are given in Table 2. For Palm Warblers at the 0.25-ha level, the number of short gray birch and the number of tamarack ≥2 m tall were the best predictors of occurrence of Palm Warblers. However, at the 1.0-ha level, taller tamarack (4–8 m)

TABLE 2. Results of multiple regressions of habitat features for two wood warblers and two emberizid sparrows in Sidney Bog at two levels of scale. Variables are given in decreasing importance in each equation.

Palm Warbler
1994
0.25-ha scale: y = 2.211 + 0.509 (Tamarack ≥2 m) + 3.324 (Gray Birch 1–2 m), $R^2 = 0.483$
1.0-ha scale: y = 8.013 + 4.433 (Tamarack 4–8 m), $R^2 = 0.753$
1995
0.25-ha scale: y = 0.423 + 0.047 (Black Spruce 4–8 m) + 0.185 (8–16 m White Pine), $R^2 = 0.474$
1.0-ha scale: y = 2.061 + 0.085 (Black Spruce 2–4 m), $R^2 = 0.707$
Common Yellowthroat
1994
0.25-ha scale: no significant factors
1.0-ha scale: no significant factors
1995
0.25-ha scale: y = 3.616 + 0.426 (White Pine 4–8 m) + 1.911 (Gray Birch 1–2 m), $R^2 = 0.293$
1.0 scale: y = 15.976 + 0.498 (White Pine 4–8 m), $R^2 = 0.732$
Song Sparrow
1994
0.25-ha scale: y = 3.027 + 0.836 (Tamarack <1 m) − 0.960 (Black Cherry 1–2 m), $R^2 = 0.255$
1.0-ha scale: y = 3.109 + 1.273 (Tamarack 4–8 m) − 1.475 (Black Cherry 1–2 m), $R^2 = 0.294$
1995
0.25-ha scale: y = 13.117 − 0.082 (Black Spruce 2–4 m), $R^2 = 0.483$
1.0-ha scale: y = 2.286 − 1.678 (Dead Wood 2–4 m) + 0.36 (White Pine 2–4 m), $R^2 = 0.304$
White-throated Sparrow
1994
0.25-ha scale: y = 1.464 + 0.063 (Black Spruce 2–4 m) + 1.909 (Gray Birch <1 m), $R^2 = 0.321$
1.0-ha scale: y = 5.468 + 0.109 (Black Spruce 2–4 m), $R^2 = 0.524$
1995
0.25-ha scale: y = −0.362 + 0.157 (Black Spruce 2–4 m) + 0.541 (Hits 10–20 cm) − 0.069 (Living Trees <1 m) + 1.256 (Dead Wood <2 m) − 0.201 (Song Sparrow density), $R^2 = 0.741$
1.0-ha scale: y = −21.203 + 12.233 (Hits 20–30 cm), $R^2 = 0.785$

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was the best predictor. In 1995, the best predictors of habitat use were the number of 4–8-m black spruce and 8–16-m white pine were the best predictors at the 0.25-ha scale and number of 2–4-m black spruce at the 1.0-ha scale.

Common Yellowthroat occurrence showed poorer relationships with the habitat variables. No habitat variable was significantly correlated to Common Yellowthroat occurrence in 1994 at either level of area. In 1995, 4–8-m tall white pine density and 1–2-m gray birch were the only significant variables at the 0.25-ha level. At the 1.0-ha level, 4–8-m tall white pine was the only significant variable.

In 1994, Song Sparrow occurrence was positively related to the density of tamarack and negatively to the number of 1–2-m black cherry at both areal scales. In 1995, 2–4-m tall black spruce had a negative relationship to Song Sparrows. At the 1-ha scale, however, 2–4-m dead wood (negative relationship) and 2–4-m white pine (positive relationship) were the best predictors of habitat use.

For White-throated Sparrows, the number of 2–4-m tall black spruce was the best predictor of sparrow occurrence in three of four cases; 1–2-m gray birch was also significant at the 0.25-ha scale in 1994. At the 1-ha level, 2–4-m tall black spruce was the only significant predictor. In 1995, 2–4-m tall black spruce was a significant term in the multiple regression at the 0.25-ha level, together with four other variables (Table 2). At the 1-ha level, the best predictor was the number of shrub hits at the 20–30-cm height.

Pair-wise comparisons of the occurrence of each species in grid sections revealed that there were no significant negative correlations between species ($P > 0.20$ in all cases) in either year, suggesting that interspecific interactions played little role in habitat selection for each species. The lack of interspecific agonistic interactions observed during field work supports this inference.

DISCUSSION

The results of this study establish relationships between habitat characteristics and the occurrence of four species of peatland birds in 0.25-ha and 1-ha units of an 8-ha study grid (Tables 1, 2). These data represent the first analysis of habitat selection in North American peatland birds. However, of the four species analyzed, only the Palm Warbler is a specialist in bogs and fens in northern North America (Knight 1904, Welsh 1971, Wilson 1996).

Palm Warblers typically nest on the ground (Knight 1904, 1908; Walkinshaw and Olsen 1957; Welsh 1971). Males typically sing from high song posts, usually the top of one of the tallest trees in the territory (Welsh 1971). The lack of a positive relationship between the densities of tall trees and Palm Warbler abundance is not surprising because only a few trees are consistently used as song posts (Welsh 1971). The multiple regression analysis for the two years differ markedly and do not engender great confidence in the predictive value of these analyses for Palm Warblers (Table 2). In 1994, the birds seemed to respond primarily to tamarack, whereas in 1995, Palm Warblers responded mainly to the abundance of black spruce.

For Common Yellowthroats, no habitat preferences emerged at either the 0.25-ha or 1-ha scale in 1994. In 1995, white pines were the most important predictors at each of the two areal scales. Gray birch is probably less important than the regression indicates as the number of 1–2-m gray birch only varied between zero and two over all 32 0.25-ha areas.

Song Sparrow density is best explained by the density of short trees. However, the particular species and height of the trees varies between years and between areal scales (Table 2). The regressions are weak, explaining less than 31% of the variance in three of the four equations.

For White-throated Sparrows, three of the four regressions contain 2–4-m black spruce as the most important independent variable (Table 2). The regression for the 1-ha level in 1995 is strikingly discordant; only the density of the middle of the shrub layer has a significant effect in the regression.

For each species, we expected that there would be differences between the 0.25-ha and 1-ha scales of analysis but that similar relationships should emerge between years within each areal scale. The results reveal the opposite pattern; in general, there is far greater concordance within years between areal scales than concordance between years at either areal scale (Table 2). In some instances, different sizes of a particular tree species emerge in the regressions at different scales within a year (e.g., Palm Warbler in 1994 and 1995, Song Sparrow in 1994). The most striking discrepancy between areal scales within a year is for White-throated Sparrows in 1995. The two equations for Song Sparrow for 1995 involve different species, all of which are between 2–4-m tall.

Despite the 75 single and composite habitat variables which were tested for relationships with the abundance of each of the four bird species, the explanatory power of the regressions is frequently low (R^2 values in Table 2). The lack of any significant relationship for Common Yellowthroats in 1994 is particularly notable. Although obvious differences in habitat features across the study area are noticeable to a human observer, we argue that these four species of birds perceive the bog as a fine-grained habitat (With and Morrison 1990). In other words, habitat preferences of the four species of birds seem weakly affected by the range of variation of the habitat variables at the site. This inference is only made possible by performing our analyses at two different scales and in two different years.

The lack of strong relationships between habitat features and bird distribution in Sidney Bog are mirrored by results from a similar study of shrubsteppe bird communities (Wiens and Rotenberry 1981). These authors found that widely distributed species such as Western Meadowlarks (*Sturnella neglecta*) correlated very poorly with habitat variables. Three of the species studied in Sidney Bog (Common Yellowthroat, Song and White-throated Sparrows) occur widely in habitats other than bogs, perhaps explaining the lack of strong habitat preferences. Palm Warblers, bog specialists, consistently showed the strongest habitat preferences of the four species studied at both areal scales, suggesting Palm Warblers perceive Sidney Bog in a coarser grain.

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