1990

The Influence of Area and Habitat on the Avian Community in Red Maple Swamps of Southern Rhode Island

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THE INFLUENCE OF AREA AND HABITAT ON
THE AVIAN COMMUNITY IN RED MAPLE SWAMPS OF
SOUTHERN RHODE ISLAND

BY

JED S. MERROW

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
IN
NATURAL RESOURCES

UNIVERSITY OF RHODE ISLAND

1990

MASTER OF SCIENCE THESIS

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1990

ABSTRACT

Red maple swamps are common throughout the glaciated Northeast and, along with other wetland types, are protected for their wildlife habitat and other functions. Yet there are few descriptions of red maple swamp wildlife communities, and little research on how the wildlife are influenced by habitat features. Several states define jurisdictional wetlands on the basis of wetland size, but the influence of area on wetland wildlife communities is largely unknown.

Birds were censused in 12 mature, very poorly drained red maple swamps in southern Rhode Island. Swamps ranged from 0.49 to 19.24 ha and were placed in four size categories. Avian community composition was described and the influence of area and habitat on the avian community were examined.

Five species made up the majority (66%) of singing bird observations: Canada Warbler, Gray Catbird, Black-and-white Warbler, Veery, and Northern Waterthrush. The avian association was similar in composition to that observed by other researchers in red maple swamps in west-central Massachusetts.

Species richness at individual sites ranged from 3 to 15 singing bird species and from 7 to 24 total species. Richness was strongly ($P < 0.0001$) related to swamp area: for

singing birds, $R^2=0.81$, and for all species observed, $R^2=0.84$. Wetlands in either of the two larger size categories supported significantly more species than wetlands in either of the two smaller categories. Area did not relate significantly to avian relative abundance.

The smallest swamps studied, down to 0.5 ha, supported several breeding species, including the Northern Waterthrush, an obligate wetland species. Thus red maple swamps down to at least 0.5 ha have significant wildlife habitat value and support "wetland species." There was a rapid increase in the number of species in swamps up to about 6-8 ha in size, and a slower increase in species richness beyond this size.

In stepwise regression models, swamp area and measures of shrub structure were significantly related to species richness. Avian relative abundance was significantly related only to the thickness of the organic soil layer; the nature of the relationship between these variables is unknown.

ACKNOWLEDGEMENTS

I thank first and foremost my major professor, Dr. Frank Golet, for his selfless devotion of his time and energy to this thesis project. His high standards have certainly greatly improved the quality of this document and his student's skills.

There are many others who contributed a great deal to my work. Katie's seemingly boundless patience and understanding are beyond mere thanks. Aram Calhoun's cheerful assistance in adverse conditions was wonderful. And William DeRagon's constant help, expert advice, and friendship have been invaluable.

I also thank Tom Husband and Keith Killingbeck for their careful, thoughtful review and comments; Carol Baker for maps and moral support; Sarah Allen for all of her help; Pete August for being Pete August (keep it up); and Bill Wright for all of his assistance (and assistantships).

The landowners of my study sites were always supportive. I thank Edith Townsend, Irving Taylor, the Samsons, Lucy Tootell, the Kenyons, Mike Sullivan, Sandra Stewart, the DeCoppet Estate trustees, the state Division of Fish and Wildlife, and the U.S. Fish and Wildlife Service.

Finally, I thank my parents for encouraging me to explore and to learn, and for their unflagging support over the years.

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INTRODUCTION

Wetlands are common throughout the Northeastern United States and are considered one of the most valuable components of the landscape. The role of wetlands as valuable wildlife habitat is widely acknowledged and is frequently cited in wetlands protection legislation (e.g., Connecticut, Massachusetts, New York, New Jersey, Rhode Island). The habitat value of wetlands has been well documented in studies of certain habitat types (e.g., marshes) and certain species (principally waterfowl and furbearing mammals; Weller 1979). In other wetland types, including some of the most common types, there has been little research.

Red maple (Acer rubrum) swamp is the most abundant inland wetland type throughout most of the glaciated Northeast (Golet et al., in prep.). In Rhode Island, for example, there are nearly 18,000 ha of broad-leaved deciduous forested wetland (Tiner 1989), comprising 77% of the inland wetland area in the state and over 6% of the state's total land area; virtually all of this wetland is dominated by red maple. Despite the prevalence of red maple swamps, there has been little research on their fauna. Knowledge of faunal community composition and the key factors affecting the nature of this community is critical to the proper management of wetlands, including the

maintenance of viable wildlife populations, the protection of wetland-dependent species, and the assessment of potential impacts of human activities on wetland wildlife.

The avian community of red maple swamps has been described at only a few sites in the Northeast. Breeding Bird Census (BBC) results have been reported for three red maple swamps in New Jersey (Black and Seeley 1953; Seeley 1954, 1955, 1956, 1957, 1966; Meyers et al. 1981; Taylor 1984) and one in western New York (Slack et al. 1975). Golet et al. (in prep.) have summarized these results. Anderson and Maxfield (1962) used mist nets to census birds in a red maple-Atlantic white cedar (Chamaecyparis thyoides) swamp in southeastern Massachusetts as part of an encephalitis research project. Mist-netting samples a relatively small segment of the bird community and the results are comparable only to studies using similar netting techniques and sampling effort (Karr 1981). Swift et al. (1984) censused the breeding birds in eight large (30-45 ha) west-central Massachusetts red maple swamps. Their study sites were heterogeneous, including both forested swamp and shrub swamp, and both poorly drained and very poorly drained soils (see Wright and Sautter [1988] for drainage class definitions). Some of the sites also included features such as upland islands and powerline corridors.

Clearly, more studies are needed before the avian community of Northeastern red maple swamps can be

characterized definitively. Further, the effect of variations in geography, plant community structure and floristics, water regime, and other factors should be examined.

Many aspects of habitat influence the density or species richness of forest-dwelling breeding birds. Among these features are the relative length of habitat edge (Kroodsma 1984, Gotfryd and Hansell 1986); the types or diversity of surrounding habitat (Whitcomb et al. 1981, Gotfryd and Hansell 1986); the degree of isolation of the habitat patch from similar habitats (Lynch and Whigham 1984, Opdam et al. 1985); vegetation structure (MacArthur and MacArthur 1961, James and Wamer 1982); and the extent of surface water (Swift et al. 1984).

Only Swift et al. (1984) have investigated the effect of habitat on the avifauna of red maple swamps. Using multiple regression models, they found that the abundance of breeding birds was positively related to the stem density of shrubs 1-3 m tall, the percent cover of surface water, and the depth (thickness) of the organic soil layer. Bird species richness within census plots was positively related to stem density of shrubs 1-3 m tall and organic soil depth; it was negatively related to tall (3-5 m) shrub stem density and to lowest overstory branch height. As Swift et al. pointed out, however, there was extreme collinearity among their independent variables; this makes it difficult to

identify the most important variables in their regression models. The heterogeneity of their sites further complicates interpretation of the results. Additional research is needed to clarify how variables such as vegetation structure, surface water cover, and organic soil depth influence the avian community in red maple swamps.

Several states with legislation regulating wetland alteration protect only wetlands above a certain size. The minimum size of forested wetlands falling under the state's jurisdiction is 1.2 ha in Rhode Island (R.I.G.L., Sections 2-1-18 et seq.), 5 ha in New York (N.Y. Environmental Conservation Law, T. 3 of Art. 24), and 4 ha in Maine (Widoff 1988). However, it is not clear that the wildlife value of wetlands is a function of wetland size.

The area of a habitat patch strongly affects wildlife community composition (Lack 1942, Gottfried 1979, Lynch and Whigham 1984, King 1987). Larger blocks of habitat tend to support more species in greater numbers (Preston 1960, 1962; MacArthur and Wilson 1967; Simberloff 1972), provide a buffer against the influence of external factors such as parasitic edge species (Martin 1988), and reduce the rate of species extinction within a given patch (Simberloff 1976). On the other hand, several small habitat islands may collectively support more species than a single large island of equal size (MacArthur and Wilson 1967, Simberloff and Abele 1982). Clearly, the relationship between area and

wildlife community composition may have important implications for wildlife conservation and management.

significant avian species-area relationships have been found in forested habitats (e.g., Opdam et al. 1985, Gotfryd and Hansell 1986, Martin 1988) and in freshwater marshes (Brown and Dinsmore 1986, Tyser 1983). However, no species-area research has been done in forested wetlands.

Breeding bird density has been found to decrease as the area of an island or habitat patch increases (Oelke 1966, Martin 1980, Lynch and Whigham 1984). Peitzmeier (1950) proposed four rules on breeding bird density in woodland habitat, including a rule that density decreases as the area of uniform habitat increases. Oelke (1966) reviewed European Breeding Bird Census data and found that "small and moist" areas had higher breeding bird density than larger, drier ones. Linehan et al. (1967) studied 1- to 14-ha forest patches in Delaware and, although he found no clear relationship between area and density, he asserted that the densities found were higher than those from "interior" habitats (i.e., areas removed from habitat edges). Martin (1980) found a highly significant ($P < 0.001$) decrease in density with increasing area of shelterbelts in the U.S. Midwest. Lynch and Whigham (1984) studied a wide range of forest patch sizes in the U.S. Middle Atlantic States, and found patch area to be inversely related to the relative abundance of birds (the total number of pairs of birds

censused at a single point within each forest).

The influence of wetland size on the abundance and species richness of the avifauna of red maple swamps is unknown; investigation of that topic should provide some basis for judging whether the current size minima of wetland regulations are warranted.

The research reported on here addresses several of the above topics. Specific objectives of this research were:

1. To describe the breeding bird community of mature, very poorly drained red maple swamps, which predominate in much of southern New England.
2. To determine the influence of wetland size on the breeding bird community of these swamps.
3. To further elucidate the influence of habitat on breeding bird abundance and richness in red maple swamps.

METHODS

selection of Study Sites

Twelve red maple swamps in southern Rhode Island were selected for study. The criteria used in site selection, in approximate order of importance, were:

1. Size. Sites were selected to obtain a range of wetland sizes with at least three sites in each of four size categories. The minimum wetland size was based on the ability of a site to accommodate at least one 0.28-ha circular census plot.
2. Vegetation. Sites had to be mature wetland forests dominated by red maple, with at least 60% canopy cover throughout, and without any evidence of significant disturbance. In actuality, canopy cover exceeded 68% at every census plot and averaged over 80% for every site selected.
3. Soil drainage class. All sites had to have predominantly very poorly drained soils; the boundary between very poorly drained and drier soils was defined as the wetland edge.
4. Isolation. The study sites had to be continuous blocks of very poorly drained red maple swamp isolated from other maple swamps by dissimilar habitat. In some places, the study sites were separated from other

wetlands by only a narrow (<10 m) strip of upland habitat; in other cases, small patches of other wetland types occurred at the periphery of study wetlands.

5. Surrounding habitat. Surroundings were to be primarily upland deciduous forest.

Potential study sites were identified using the Soil Survey of Rhode Island (Rector 1981), wetland maps of the towns of Richmond (Golet and Davis 1982) and South Kingstown (Golet and Parkhurst, Dept. Forest Wildl. Manage., Univ. Rhode Island, Kingston), and National Wetlands Inventory maps (U.S. Fish and Wildlife Service) of southern Rhode Island. Sites meeting the above criteria were examined on large-scale aerial photographs and then field-checked. The sites selected (Figure 1 and Appendix A) ranged from 0.49 ha to 19.24 ha and were grouped in 4 size categories (Table 1).

Bird Censuses

Censusing birds in wooded swamps presents two major problems. First, the vegetation is dense, so that birds are difficult to see and must be censused primarily by vocalizations. This makes spot-mapping, which depends largely on visual observations, difficult. Second, in small swamps, the observer is often close to a habitat edge, so that unlimited-distance methods such as Emlen's variable-width transect (Emlen 1971, 1977) and the Indice

Figure 1. Location of study sites in southern Rhode Island.

Table 1. Area of study sites, number of census plots, and area sampled within each site.

Size category and site	Area (ha)	No. census plots	Sampled area (ha)	% of site sampled
<u><1 ha</u>				
Kenyon	0.49	1	0.28	57.7
Muddy Brook	0.64	1	0.28	44.2
Tuckertown	0.67	1	0.28	42.2
<u>1-5 ha</u>				
Tootell	1.60	2	0.57	35.3
Carolina	2.19	2	0.57	25.8
Turnpike	4.02	3	0.85	21.1
<u>6-8 ha</u>				
Fairgrounds	6.17	5	1.41	22.9
DeCoppet	6.33	5	1.41	22.3
Trustom	7.43	6	1.70	22.8
<u>13-20 ha</u>				
Narragansett	13.21	12	3.39	25.7
Townsend	13.49	10	2.83	21.0
Dead Swamp	19.24	14	3.96	20.6

ponctuel D'Abondance (IPA) point count (Blondel et al. 1981) are inappropriate. For these reasons, the fixed-radius circular plot technique was selected (Edwards et al. 1981, Swift et al. 1984, DeGraaf 1987, Morrison et al. 1987). This method is relatively simple, but requires that the observer accurately judge the location of singing birds with respect to plot boundaries. Most sources of error for this approach (such as the accuracy of distance estimates or variable weather conditions) also affect other census methods.

Censuses were carried out in 30-m radius (0.28-ha) circular plots located at the nodes of a 90-m grid established in each study area. A transparent representation of the grid was placed randomly over aerial photographs of the study sites, and then the grid was established in the field. All plots falling wholly within site boundaries were selected for sampling. To ensure that at least 20% of each site's area was sampled, a small number of plots which intersected the wetland edge were repositioned to lie entirely within the site. Plots were relocated following strict guidelines to ensure that (1) the minimum spacing of 30 m between plot edges was preserved, and (2) the randomness of plot placement was maintained insofar as possible. The number of plots within each site, the total area sampled, and the percentage of each site sampled are listed in Table 1.

Birds were censused six times at each plot center between 25 May and 2 July 1988. Each plot census consisted of a 1-min "settling" period followed by a 5-min observation period during which all bird observations within the plot were recorded. The bird species and type of observation--singing, calling, or visual--were noted. Only clearly identifiable territorial or mate-attraction vocalizations that are frequently repeated by birds on territories were considered "songs." All censuses were carried out within 4 hours after sunrise.

Each morning one group of sites was censused. Each group consisted of two or three sites. Groups were fixed throughout the census season and were based on site size categories and proximity: sites within a group were from different size categories and were as far apart geographically as feasible. The order of censusing of groups, sites within a group, and plots within a site was varied in the following systematic way in an effort to minimize the effects of time of day and season.

1. The order in which groups were censused was rotated after each complete round of sites, so that the group that was censused first in a given round was censused last in the following round.
2. The order in which sites within a group were censused was rotated each successive time, as with

groups.

3. The order of censusing of plots within a site was reversed for each successive census.

Species richness (the total number of species observed during all six censuses) and relative abundance (the average number of birds per plot per census) were calculated for both singing bird observations and all bird observations at each site.

Measurement of Independent Variables

Measurements of study-site area and surrounding habitat diversity were based on 1:4,800-scale panchromatic aerial photographs. Area measurements were made with a digital planimeter, and the length of wetland edge corresponding to each surrounding habitat type was determined with a map measurer. These edge lengths were then entered into the Shannon diversity formula (Shannon 1948) to obtain a measure of surrounding habitat diversity for each study site.

Patches of surrounding habitat had to be within 50 m of the wetland edge and at least 50 m long and wide to be measured.

Eight categories of habitat types were defined: developed

(e.g., residential) land; open upland (<10% tree canopy

cover); sparsely forested upland (10%-40% tree canopy

cover); open wetland (<40% canopy cover); and four other

types of forest land (>40% cover): deciduous upland forest,

coniferous upland forest, deciduous wetland forest, and coniferous wetland forest. Wetlands were defined as areas with very poorly drained soil.

Methods for sampling vegetation were adapted from Swift et al. (1984). Each census plot contained four 28-m transect lines oriented in the cardinal directions and originating 2 m from the plot center. Vegetation, surface water cover, and peat depth were sampled along these transects. The minimum acceptable sample size for each variable was determined in pilot studies prior to formal sampling. All variables and methods of measurement are described below and summarized in Table 2.

1. Tree canopy cover. A densiometer was used to estimate percent canopy cover. Four readings were taken, one 6 m from the plot center along each transect so that the canopy areas measured were centered over each transect. The total sample covered an estimated 800 m² or 28% of each bird census plot.
2. Tree density. The total number of trees, including dead trees (woody plants >3 m tall and >7.6 cm diameter at breast height [dbh]) and live trees (woody plants >6 m tall), was recorded in four 6- x 28-m belts centered on the line transects.
3. Tree diversity. Live trees were identified to species, and the Shannon index (Shannon 1948) was used

Table 2. Bird community and independent variables measured.

Variable	Measurement method
<u>Bird Community Variables</u>	
Species richness (no. species/site)	6 censuses in 1-14 plots/site*
Relative abundance (ave. no. individuals/ plot/census)	6 censuses
<u>Independent Variables</u>	
Area (ha)	Planimeter on aerial photos
Edge:area	Map measurer on aerial photos
Surrounding habitat diversity	Map measurer; Shannon diversity index
Live and dead tree density (stems/ha)	Counts in four 6- x 28-m belts/ census plot
Live and dead tree basal area (m ² /ha)	DBH tape on counted trees
Tree species diversity	Live tree data; Shannon diversity index
Tree height (m)	Altimeter on 5 trees/plot
Canopy cover (%)	Four densiometer readings/plot
Shrub cover (%)	Line-intercept (Canfield 1941) on 4 28-m transects/plot
Herb cover (%)	Line-intercept, as for shrubs
Surface water (%)	Presence/absence at 60 points/plot on 3 dates
Shrub foliage volume (%)	Subjective estimation at 56 locations/plot (14/transect)
Depth (thickness) of organic soil layer (m)	Probe at 5 points/plot
Foliage height diversity	Tree canopy, total shrub, and herb cover in Shannon index

* Plot refers to 30-m radius (0.28-ha area) circular bird census plot.

to calculate live tree species diversity.

4. Tree height. The heights of five live trees, one nearest the plot center and one nearest the distal end of each transect (within the plot), were measured with a Haga altimeter.

5. Tree basal area. The diameter at breast height of all live trees within the 6- x 28-m subplots was measured with a diameter tape and later converted to basal area.

6. Shrub cover. Percent cover of shrubs was measured along the four 28-m transect lines, using a modification of the line-intercept method (Canfield 1941). Shrubs were divided into four layers: low shrubs ($>0-0.9$ m), medium shrubs ($>1-1.9$ m), tall shrubs ($>2-3.9$ m), and saplings ($>4-5.9$ m). The minimum unit of measurement along the transect line, determined by pilot studies, was 0.5 m. Only the tallest (i.e., dominant) of the four layers was recorded at any point along the line.

7. Shrub foliage volume. Foliage volume was visually estimated for each of the four shrub layers described above. This method adopts the categorical approach found in two-dimensional cover estimators (Daubenmire 1959, Goldsmith et al. 1986), and is similar in concept to other recent efforts to quantify foliage volume in dense habitats (August 1983, Clark et al. 1983). The

volume of foliage and branches was estimated within three-dimensional, vertically stacked plots along each line transect. The low- and the medium-shrub plots each were 1 x 1 x 1 m in extent, and the tall shrub and sapling plots were 2 x 1 x 1 m each. Foliage volume for each of the four layers was estimated at 2-m intervals (14 locations) along each transect line. As with the Daubenmire (1959) method, the percentage estimates were assigned to one of six categories: 0-5%, 5-25%, 25-50%, 50-75%, 75-95%, or 95-100%. Statistics were calculated using category midpoints.

8. Herb cover. The percent cover of herbaceous vegetation was estimated, using the line-intercept method with a minimum unit of measurement of 0.5 m, on all four line transects. Herbs were defined as all nonwoody vascular plants over 2 cm tall.

9. Percent cover of surface water. The percent of the total surface area in each census plot that was covered with standing water was estimated by recording the presence or absence of water at 2-m intervals along each transect (i.e., 60 points/plot). Sampling was conducted at all sites on consecutive rainless days near the beginning, middle, and end of the 6-week bird census period. Results from these three samples were then averaged.

10. Depth of the organic soil layer. Total depth (thickness) of the organic horizons was measured in each plot by probing the organic layer down to refusal with a 1.25-cm diameter metal rod at five points: at the plot center and 20 m from the center on each of the four transect lines. The maximum depth of the probe was 3 m.

11. Foliage height diversity. To obtain a measure of foliage height diversity (MacArthur 1964), the percent cover of three vegetation layers (tree, shrub, and herb) were entered into the Shannon diversity formula.

Data Analysis

Regression analysis was used to describe the relationship between species richness or bird abundance and swamp area, and analysis of variance was used to determine whether differences between size categories of wetlands were significant. The significance of differences was determined using Duncan's New Multiple Range Test (Dowdy and Wearden 1983). The significance level for all tests was $P < 0.05$ unless otherwise noted.

Stepwise multiple linear regression (Dowdy and Wearden 1983) was used to determine which independent variables explained the most variation in bird species richness and relative abundance. Data collected for each habitat

variable were averaged across census plots to obtain a single value for each study site; in all of the above statistical analyses, therefore, each site represents one sample. Data from the sapling layer had insufficient information content (there was uniformly low sapling cover at all sites) and were omitted from the analyses.

RESULTS AND DISCUSSION

Characteristics of the Avian Community

Species composition.--The 62 plots were censused 6 times each, representing a total of 31 hours of census time. Over the 6-week census period, 350 singing bird observations, representing 25 species, and 758 bird observations of all kinds (singing and non-singing), totalling 39 species, were recorded. Two-thirds (66%) of the singing bird observations consisted of 5 species (Table 3): the Canada Warbler (21% of all singing observations), Gray Catbird (13%), Black-and-white Warbler (13%), Veery (9%), and Northern Waterthrush (9%). Five species made up just over half (53%) of all bird observations; the Black-capped Chickadee (16%) was most abundant, followed by the Canada Warbler (12%), Veery (10%), Gray Catbird (9%), and Black-and-white Warbler (6%). The few species making up the majority of observations might be considered the core of a red maple swamp bird association in Rhode Island. The relative abundance of each species within each site is listed in Appendix B.

The Gray Catbird was the only species observed singing at every site (Table 3). Other common singing birds included the Canada Warbler (10 sites), Veery (9), and Black-and-white Warbler (8). The results for all bird observations were similar: Gray Catbird (12 sites), Black-capped Chickadee (11), Veery (11), Canada Warbler (10), and

Table 3. Birds observed in 12 Rhode Island red maple swamps during the 1988 breeding season.^a

Species ^b	Total observations				No. sites	
	Singing birds		All birds		Singing	All
	n	%	n	%	birds	birds
Canada Warbler	75	21.4	89	11.7	10	10
Gray Catbird	46	13.1	66	8.7	12	12
Black-and-wh. Warbler	45	12.9	49	6.5	8	9
Veery	33	9.4	75	9.9	9	11
Northern Waterthrush	32	9.1	34	4.5	7	7
Common Yellowthroat	18	5.1	38	5.0	7	8
Great Cres. Flycatcher	16	4.6	18	2.4	7	7
Rufous-sided Towhee	13	3.7	23	3.0	3	7
Tufted Titmouse	11	3.1	45	5.9	6	8
Red-eyed Vireo	11	3.1	11	1.5	7	7
American Redstart	10	2.9	10	1.3	2	2
Wood Thrush	4	1.1	5	0.7	3	3
American Robin	4	1.1	26	3.4	2	4
Blue-winged Warbler	4	1.1	4	0.5	3	3
Northern Oriole	4	1.1	10	1.3	2	3
Carolina Wren	3	0.9	3	0.4	2	2
House Wren	3	0.9	3	0.4	2	2
White-eyed Vireo	3	0.9	3	0.4	2	2
Chestnut-sided Warbler	3	0.9	3	0.4	2	2
Scarlet Tanager	3	0.9	3	0.4	2	2
Rose-breasted Grosbeak	3	0.9	5	0.7	2	2
Black-th. Green Warbler	2	0.6	2	0.3	1	1
Black-capped Chickadee	1	0.3	122	16.1	1	11
Yellow-throated Vireo	1	0.3	1	0.1	1	1
Northern Cardinal	1	0.3	1	0.1	1	1
Blue Jay			32	4.2		6
White-breasted Nuthatch			8	1.1		3
Brown Creeper			7	0.9		5
Hairy Woodpecker			6	0.8		2
Northern Flicker			6	0.8		3
Song Sparrow			6	0.8		1
Blue-gray Gnatcatcher			5	0.7		2
Brown-headed Cowbird			5	0.7		3
Downy Woodpecker			4	0.5		2
Common Grackle			3	0.4		2
Ruffed Grouse			1	0.1		1
Eastern Phoebe			1	0.1		1
Prairie Warbler			1	0.1		1
Ovenbird			1	0.1		1
Unidentified species	1	0.3	23	3.0	1	10
All species	350		758			

^a Figures are based on 6 5-min censuses in 62 plots.

^b Species' scientific names are listed in Appendix C.

Black-and-white Warbler (9).

The most abundant species generally were found in the greatest number of study sites. Although most species observed were represented by only a few individuals, many were found at a relatively large number of study sites. Rufous-sided Towhees, Great Crested Flycatchers, and Red-eyed Vireos each accounted for 3% or less of all observations, yet were censused at seven sites. Brown Creepers were observed only seven times overall (1% of observations), but were found at five study sites.

In eight west-central Massachusetts red maple swamps studied by Swift (1980), the most abundant species were largely the same as those encountered in southern Rhode Island (Table 4). The minor differences may be attributable to differences in habitat complexity or geographic variation in species abundances or habitat use. It is apparent that the avian community of red maple swamps in southern New England is dominated by fewer than 10 common species.

Relative abundance.--Relative abundance (birds/plot/census) of singing birds ranged from 0.58 at the Narragansett site to 2.00 at Tuckertown (Table 5), with an average for all study sites of 1.05 ± 0.11 (SE). Relative abundance at most study sites (9 of 12) fell within the relatively narrow range of 0.80 to 1.08. The relative abundance of all birds observed ranged from 1.58 at Carolina

Table 4. Comparison of the most abundant birds in red maple swamps in southern Rhode Island (this study) and west-central Massachusetts (Swift 1980).^a

Species ^a	Southern Rhode Island				Massachusetts	
	Singing birds		All birds		Singing birds	
	% ^b	rank	% ^b	rank	% ^b	rank
Canada Warbler	21	1	12	2	12	3
Gray Catbird	13	2	9	4	7	6
Black-and-white Warbler	13	3	7	5	6	7
Veery	9	4	10	3	14	2
Northern Waterthrush	9	5	5	8	7	5
Common Yellowthroat	5	6	5	7	18	1
Tufted Titmouse	3	9	6	6	1	18
Black-capped Chickadee	<1	23	16	1	3	10
Ovenbird	<u>0</u>	-	<u><1</u>	34	<u>8</u>	4
Total	75		68		76	

^a Rhode Island figures are based on 6 5-min censuses in 62 plots in one year; Massachusetts figures are based on 12 5-min censuses in 80 plots over two years.

^b Percentage of all birds censused in the category (RI) or study (MA).

Table 5. Species richness and relative abundance of birds in 12 Rhode Island red maple swamps, based on 6 censuses during the 1988 breeding season.

Size category and site	Species richness		Relative abundance (birds/plot/census)	
	Singing birds	All birds	Singing birds	All birds
<u><1 ha</u>				
Kenyon	3	8	1.00	2.17
Muddy Brook	4	9	1.00	2.17
Tuckertown	6	7	2.00	2.33
<u>1-5 ha</u>				
Tootell	6	11	1.08	1.75
Carolina	5	9	0.83	1.58
Turnpike	7	11	0.83	2.11
<u>6-8 ha</u>				
Fairgrounds	8	14	0.87	1.80
DeCoppet	11	17	1.67	2.77
Trustom	13	18	0.94	2.03
<u>13-20 ha</u>				
Narragansett	11	15	0.58	1.68
Townsend	15	20	0.80	1.85
Dead Swamp	15	24	1.05	2.36

to 2.77 at DeCoppet, with an overall mean of 2.05 ± 0.10 .

Relative abundance estimates are directly influenced by the length of the census period and the size of the sample plot. This study used 5-min censuses; the popular Indice Ponctuel D'Abondance (IPA) point-count method (Blondel et al. 1981) utilizes 20-min censuses, and many other methods use censuses of unspecified or variable lengths. In each case, the result is an index of abundance which can only be compared to other indices derived in exactly the same manner.

Swift et al. (1984) also conducted six 5-minute censuses each year in roughly quarter-hectare census plots in red maple swamps in west-central Massachusetts. They censused birds in 80 0.25-ha plots at 8 sites over 2 years, compared to the 62 0.28-ha plots censused at 12 sites in this study. The overall relative abundance reported by Swift et al. (average, 2.79) is about 2.5 times as high as the present study's singing bird relative abundance (1.05) and about a third higher than the all-bird relative abundance (2.05) calculated here.

There are at least two possible explanations for these differences. First, Swift et al. (1984) used a broader definition of "singing" than was used here (B.L. Swift, NY Dept. Environ. Conserv., Albany; pers. comm., 1988), so that more species (for instance, Blue Jays and Brown-headed Cowbirds) were considered "singing" birds, and more kinds of

vocalizations were considered songs. Second, their study sites were more heterogeneous, often containing upland islands, powerline rights-of-way, large canopy openings, and areas of poorly drained soils. More diverse habitat and increased habitat edge may support a higher density and diversity of birds (Beecher 1940).

Species richness.--Species richness for singing birds ranged from three at Kenyon, the smallest site, to 15 at Townsend and Dead Swamp, the two largest (Table 5). For all birds, richness ranged from seven species at Tuckertown to 24 at Dead Swamp.

The Influence of Area

Area and species richness.--Regression analysis showed a highly significant relationship ($P < 0.0001$) between the species richness of both singing birds and all birds and red maple swamp area (Figure 2). Regressions based on log-transformed data explained slightly more of the variation in richness than those based on untransformed data (singing birds, $R^2 = 0.86$ vs. $R^2 = 0.81$; all birds, $R^2 = 0.86$ vs. $R^2 = 0.84$, respectively). The log-log regression equations are:

Singing birds: $\text{Log species richness} = 0.68 + 0.38(\text{log area})$

All birds: $\text{Log species richness} = 0.95 + 0.28(\text{log area})$

Figure 2. Bird species richness in 12 Rhode Island red maple swamps as a function of swamp area.

Analysis of variance revealed significant differences ($P < 0.05$) among the mean richness values of wetland size categories for both singing birds and all birds observed (Table 6). Species richness was not significantly different between the two smallest size categories or between the two largest size categories; however, wetlands in either of the two largest categories supported significantly more species than wetlands in either of the two smallest categories.

Although area explained the great majority of the variation in the singing bird species richness among study sites, the variation in richness can also be explained simply by the variation in sample area (i.e., number of census plots) among sites ($R^2 = 0.77$). However, because sample area and wetland area are very closely correlated ($r = 0.99$), the results are believed to accurately reflect the influence of wetland area on species richness.

The species-area analysis showed that (1) there were several species singing--and presumably breeding--in swamps less than 1 ha in size, (2) there was a rapid increase in the number of species in swamps up to about 6-8 ha in size, and (3) there was a slower increase in species richness beyond 6-8 ha.

The smallest sites, down to 0.5 ha, all supported several breeding species. One of these species, the Northern Waterthrush, was an obligate wetland species. Brown and Dinsmore (1986) and Tyser (1983) also found

Table 6. Average bird species richness and relative abundance for four size categories of red maple swamps based on six censuses during the 1988 breeding season.^a

Size category	No. sites	Ave. richness		Ave. rel. abundance	
		Singing birds	All birds	Singing birds	All birds
<1	3	4.33	8.00	1.33	2.22
1-5	3	6.00	10.33	0.91	1.81
6-8	3	10.67	16.33	1.16	2.20
13-20	3	13.67	19.67	0.81	1.96

^a Lines connect values that are not significantly different based on Duncan's test at $P < 0.05$.

wetland obligates in marshes less than 1 ha in size.

Robbins et al. (1989) recently compiled habitat area requirements of breeding birds in 279 forest patches, ranging from 0.1 ha to over 3,000 ha, in the U.S. Middle Atlantic States. For each area-sensitive species (i.e., species having a significantly greater probability of occurrence with increasing forest patch size), they calculated the forest area at which the species' probability of occurrence was 50% of that species' maximum probability of occurrence. Two of the most common species in Rhode Island red maple swamps, the Canada Warbler and Northern Waterthrush, had 50% probabilities of occurrence in forests 400 ha and 200 ha in size, respectively. In Rhode Island, however, both of these species occurred in the smallest swamp studied (0.5 ha). These results suggest that either (1) these species are responding to the larger forested landscape in which the swamps are located, or (2) they are not actually area-sensitive.

In this study, species richness increased at a relatively rapid rate until the wetlands exceeded about 6-8 ha in size. The same trend was apparent for singing birds and all birds observed (Figure 2). Richness continued to increase, but at a lower rate, in sites larger than 8 ha.

Swift (1980, Swift et al. 1984) reported bird species richness for west-central Massachusetts red maple swamps 30-45 ha in size. If species not considered as singing in the

present study (such as the Brown-headed Cowbird, Blue Jay, and woodpeckers) are excluded from his results, there were 20-23 singing species recorded in each of Swift's (1980) four forested, very poorly drained study sites. As noted above, there were some methodological differences between the two studies, but the results are consistent (Figure 3), and suggest that species richness may continue to increase gradually as swamp size increases beyond the size range sampled in the present study.

A frequently discussed aspect of the species-area relationship is the slope or z value of the regression equation (Connor and McCoy 1979). This parameter expresses the rate of increase in species richness, and may be influenced by many factors (e.g., the degree of isolation of the habitat patches; MacArthur and Wilson 1967). The z values calculated for singing birds (0.38) and all birds (0.28) in the present study are within the range of values reported in most other species-area research (0.20 to 0.40; MacArthur and Wilson 1967, Connor and McCoy 1979). Brown and Dinsmore (1986), in a study of species-area relationships in 30 marshes in Iowa ranging from 0.2 to 182 ha in size, calculated a z value of 0.23. Tyser (1983) studied 9 riverine marshes in Wisconsin ranging in size from 0.06 to 50 ha and found z to equal 0.42.

Connor and McCoy (1979) showed that the range of z values reported in species-area studies is more a function

Figure 3. Species richness of singing birds in red maple swamps of southern New England as a function of swamp area.

of the mathematics of the regression equation than the underlying data distribution, so the z value may not be biologically meaningful. Further clouding interpretation in the present study is the size range of study sites. While the range is probably representative of the majority of forested wetlands in southern New England (e.g., see Golet and Davis 1982), it is more limited than most other species-area studies. A larger size range could yield a different z value.

Area and relative abundance.--Regression analysis showed no significant relationships between the relative abundance of either singing birds or all birds and swamp area, and analysis of variance revealed no significant differences in the relative abundance of birds among the four site size categories (Table 6).

Previous research (Oelke 1966, Lynch and Whigham 1984, Martin 1980) has found bird density to decrease with increasing area; the higher density of animal populations near habitat edges (Forman and Godron 1986) may explain this relationship. The lack of a significant relationship between relative abundance and area in the present study may be due to any of several factors. The results from all sites may have been subject to edge effect, as no plot was more than 105 m from the wetland edge and all sites had plots within 10 m of an edge. Further, the degree of "edge

effect" in forested wetlands surrounded by predominately forested uplands is unknown. Changes in the composition of the avian community across the wetland/upland ecotone needs further research.

Implications for wetland protection and management.--The species-area relationship described above has important implications for wetland protection and management.

1. Red maple swamps as small as 0.5 ha supported several species of breeding birds, and the smallest site supported an obligate wetland species, the Northern Waterthrush. Thus, swamps which are much smaller than those currently protected by several states do appear to have significant habitat value. States with larger minimum sizes should consider reducing the minimum area required for protection.

2. Certain species were common and relatively abundant at most sites, suggesting that there is a characteristic association of avian species in red maple swamps. At least one of these species is a wetland obligate and several others (e.g., Canada Warbler, Veery) may prefer forested wetlands over other habitat types. If red maple swamp is the required or preferred habitat for these species, then protection of this habitat will be critical for the well-being of the species.

3. Bird species richness increases rapidly with the size of swamps up to about 6-8 ha, after which it continues to increase, but at a lower rate. It may be tempting to equate species richness with habitat value and to conclude that sites below a certain size (e.g., 6 ha) are of lower value, or that above 6 ha habitat value does not change significantly. However, other considerations, along with richness, also may be important in determining habitat "value," for example, the preservation of rare species, forest-interior species, species restricted to certain habitats, or species of special interest. In this study, the important conclusion is that all sites, regardless of size, display breeding bird habitat value, and that "wetland species" breed in even very small sites.

The Influence of Habitat

Habitat and species richness.--Habitat variables used in analyses are listed by site in Appendix D. In stepwise multiple regression models, swamp area accounted for the majority of the variation in species richness for both singing birds ($R^2=0.81$) and all birds ($R^2=0.84$; Tables 7 and 8). All other significant ($P<0.05$) independent variables were measures of shrub layer structure. For singing birds, significant variables included the combined foliage volume of medium and low (0-2 m) shrubs (+) and tall (2-4 m) shrub

Table 7. Summary of stepwise regression analysis, including significant ($P < 0.15$) independent variables explaining variation in bird species richness and relative abundance.

Independent variable	Order entered	Partial R^2	Model R^2	F	Prob>F
1. Species richness of singing birds (total per site)					
Area (+)	1	0.811	0.811	42.996	0.0001
Medium+low shrub vol. (+)	2	0.083	0.894	7.080	0.0260
Tall shrub cover (-)	3	0.049	0.943	6.971	0.0297
2. Species richness of all birds (total per site)					
Area (+)	1	0.839	0.839	52.199	0.0001
Total shrub volume (+)	2	0.079	0.918	8.599	0.0167
Tall shrub cover (-)	3	0.020	0.938	2.621	0.1441
Low shrub cover (+)	4	0.022	0.960	3.913	0.0884
3. Relative abundance of singing birds (ave./plot/census)					
Depth of peat (+)	1	0.375	0.375	6.009	0.0342
Tree basal area (-)	2	0.187	0.562	3.831	0.0820
% surface water (-)	3	0.110	0.672	2.684	0.1400
Surr. hab. divers. (+)	4	0.091	0.763	2.685	0.1453
4. Relative abundance of all birds (ave./plot/census)					
Depth of peat (+)	1	0.419	0.419	7.217	0.0228
Herb cover (+)	2	0.154	0.573	3.233	0.1057

Table 8. Stepwise regression models, including significant ($P < 0.05$) independent variables explaining variation in bird species richness and relative abundance.

Model	Model R^2
1. Species richness of singing birds = $0.82 + 0.51(\text{Area}) - 0.08(\text{Tall shrub cover}) +$ $0.28(\text{Medium and low shrub volume})$	0.94
2. Species richness of all birds observed = $1.72 + 0.79(\text{Area}) + 0.28(\text{Total shrub volume})$	0.92
3. Relative abundance of singing birds = $0.60 + 0.28(\text{Depth of peat})$	0.38
4. Relative abundance of all birds = $1.64 + 0.26(\text{Depth of peat})$	0.42

cover (-); for all birds, total shrub foliage volume (+) was significant. Simple correlations between species richness and individual habitat variables generally supported these results (Appendix E), as medium and low shrub variables were--besides area--the variables most strongly correlated with species richness.

The influence of shrub layer structure on avian species richness in red maple swamps has been documented by Swift et al. (1984). In a multiple regression analysis using 80 census plots (rather than study sites) as samples, they found significant relationships between avian richness and depth of peat (+), density of shrubs 1-3 m high (+), density of shrubs 3-5 m high (-), and lowest overstory branch height (-). Both this study and that of Swift et al. (1984) suggest that dense shrubs within 2-3 m of the ground, combined with a more open shrub layer above that level, support more avian species. Dense, low shrubs may provide escape cover and foraging and nesting substrates for a wide range of species. Other studies also have documented the importance of shrub layer structure, and foliage density in particular, to both bird species richness (Blake and Karr 1987, Martin 1988) and abundance (Best and Stauffer 1986). However, none of these studies distinguished between shrub height categories.

Habitat and relative abundance.--Peat depth was the only variable significantly related ($P < 0.05$) to avian relative abundance in stepwise multiple regression models. When peat depth was excluded from the analyses, no other variables were significant at $P < 0.05$, and only tree basal area was significant at the $P < 0.15$ level (and only for singing birds). Simple correlations (Appendix E) between relative abundance and most habitat variables also were very weak. Swift et al. (1984) found depth of peat to be highly significant ($P < 0.01$) in explaining bird relative abundance. Other significant variables in their model included surface water cover (+) and density of shrubs 1-3 m tall (+).

Depth of peat may influence the vegetational community which, in turn, influences avian abundance. Herb cover and foliage height diversity (which is partly a function of herb cover) were the only habitat variables with significant simple correlations (-) with depth of peat (Appendix E). More research is needed on the possible relationships between the avian community, soil characteristics, vegetation, and perhaps also invertebrate prey abundance.

Surface water cover, significantly related to bird abundance in the models of Swift et al. (1984), may also be a factor. While this was not a significant variable in Rhode Island, the census period in 1988 was relatively dry (precipitation in the area was 18% below normal during April-June; N.O.A.A. 1989), and many usually wet sites had

little or no surface water.

It should be noted that there was limited variation in avian relative abundance among study sites in the present study. More research is needed to determine whether other mature, very poorly drained red maple swamps exhibit the same limited variation in relative abundance, and what factors influence or limit abundance. Future research should examine the relationships between avian abundance and habitat in more detail, for example by describing bird use of specific vegetation strata or the habitat requirements of individual species.

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Appendix A. Location of study sites.

Site	USGS Quadrangle	Latitude	Longitude
Kenyon	Hope Valley	41°30'35"	71°39'20"
Muddy Brook	Carolina	41°28'30"	71°38'20"
Tuckertown	Kingston	41°25'48"	71°32'45"
Tootell	Hope Valley	41°30'15"	71°40'00"
Carolina	Carolina	41°29'10"	71°42'25"
Turnpike	Hope Valley	41°32'15"	71°40'15"
Fairgrounds	Kingston	41°29'45"	71°33'05"
DeCoppet	Hope Valley	41°31'08"	71°38'55"
Trustom	Kingston	41°22'35"	71°33'35"
Narragansett	Narragansett Pier	41°25'00"	71°28'15"
Townsend	Kingston	41°25'30"	71°32'00"
Dead Swamp	Slocum	41°36'50"	71°33'08"

Appendix B-1. Relative abundance of singing birds in 12 Rhode Island red maple swamps, based on 6 censuses during the 1988 breeding season. Relative abundance is expressed as birds per 0.28-ha plot per census.

Species	Study site ^a												No. n sites	
	KE	MB	TU	TO	CA	TP	FA	DE	TR	NA	TN	DS		
Canada Warbler	0.50	0.50			0.33	0.17	0.37	0.20	0.25	0.07	0.05	0.33	75	10
Gray Catbird	0.17	0.17	0.67	0.17	0.17	0.06	0.20	0.17	0.08	0.19	0.07	0.04	46	12
Black-and-white Warb.				0.17		0.17	0.07	0.27	0.14	0.03	0.12	0.19	45	8
Veery			0.33	0.42		0.06	0.03	0.17	0.08	0.06	0.10	0.07	33	9
No. Waterthrush	0.33			0.08	0.17	0.28		0.27			0.03	0.14	32	7
Common Yellowthroat		0.17		0.17		0.03		0.06	0.03	0.03	0.08	0.06	18	7
Great Cr. Flycatcher					0.08	0.06	0.03	0.17		0.07	0.02	0.02	16	7
Rufous-sided Towhee									0.03		0.13	0.05	13	3
Tufted Titmouse				0.08				0.03	0.03	0.01	0.05	0.05	11	6
Red-eyed Vireo			0.33		0.08	0.06	0.10	0.07		0.01		0.01	11	7
American Redstart								0.23	0.08				10	2
Wood Thrush			0.17						0.03			0.02	4	3
American Robin									0.03	0.04			4	2
Blue-winged Warbler							0.03				0.03	0.01	4	3
Northern Oriole										0.04		0.01	4	2
Carolina Wren									0.03		0.03		3	2
House Wren			0.33					0.03					3	2
White-eyed Vireo									0.06		0.02		3	2
Chestnut-sided Warbler								0.07	0.03				3	2
Scarlet Tanager											0.02	0.02	3	2
Rose-breasted Grosbeak		0.17								0.03			3	2
Black-thr. Green Warb.											0.03		2	1
Black-capped Chickadee											0.02		1	1
Yellow-throated Vireo												0.01	1	1
Northern Cardinal			0.17										1	1
Unidentified species									0.03				1	1
Total	1.00	1.00	2.00	1.08	0.83	0.83	0.87	1.67	0.94	0.58	0.80	1.05	350	
Species richness ^b	3	4	6	6	5	7	8	11	13	11	15	15		

^a Study sites: KE, Kenyon; MB, Muddy Brook; TU, Tuckertown; TO, Tootell; FA, Fairgrounds; DE, DeCoppet; TR, Trustom; NA, Narragansett; TN, Townsend; DS, Dead Swamp.

^b Unidentified species are not included in species richness totals.

Appendix B-2. Relative abundance of all birds observed in 12 Rhode Island red maple swamps, based on 6 censuses during the 1988 breeding season. Relative abundance is expressed as birds per 0.28-ha plot per census.

Species	Study site ^a												No. n sites
	KE	MB	TU	TO	CA	TP	FA	DE	TR	NA	TN	DS	
Black-cap. Chickadee	0.33	0.50		0.25	0.42	0.28	0.23	0.17	0.17	0.43	0.40	0.37	122 11
Canada Warbler	0.50	0.50			0.33	0.17	0.40	0.30	0.25	0.07	0.08	0.43	89 10
Veery		0.17	0.33	0.42	0.08	0.33	0.13	0.40	0.14	0.10	0.27	0.19	75 11
Gray Catbird	0.17	0.17	0.83	0.17	0.17	0.22	0.27	0.37	0.14	0.21	0.13	0.05	66 12
Black-and-wh. Warbler		0.17		0.17		0.17	0.07	0.27	0.14	0.06	0.12	0.20	49 9
Tufted Titmouse				0.08		0.22	0.03	0.20	0.33	0.04	0.07	0.17	45 8
Common Yellowthroat		0.17		0.17			0.10	0.03	0.14	0.06	0.13	0.17	38 8
No. Waterthrush	0.33			0.08	0.17	0.33		0.30			0.03	0.14	34 7
Blue Jay				0.08	0.08				0.03	0.17	0.12	0.12	32 6
American Robin			0.17						0.17	0.18		0.07	26 4
Rufous-sided Towhee	0.17			0.08				0.03	0.03	0.04	0.13	0.10	23 7
Great Cr. Flycatcher					0.08	0.06	0.03	0.17		0.10	0.02	0.02	18 7
Red-eyed Vireo			0.33		0.08	0.06	0.10	0.07		0.01		0.01	11 7
American Redstart								0.23	0.08				10 2
Northern Oriole		0.17								0.11		0.01	10 3
White-br. Nuthatch									0.06		0.07	0.02	8 3
Brown Creeper	0.17	0.17		0.17		0.06					0.03		7 5
Hairy Woodpecker										0.03		0.05	6 2
Northern Flicker	0.33						0.10					0.01	6 3
Song Sparrow							0.20						6 1
Blue-gray Gnatcatcher								0.03	0.11				5 2
Wood Thrush			0.17						0.03			0.04	5 3
Rose-breasted Grosbeak		0.17								0.06			5 2
Brown-headed Cowbird						0.06					0.05	0.01	5 3
Downy Woodpecker								0.03	0.08				4 2
Blue-winged Warbler							0.03				0.03	0.01	4 3
Carolina Wren									0.03		0.03		3 2
House Wren			0.33					0.03					3 2
White-eyed Vireo									0.06		0.02		3 2
Chestnut-sided Warbler								0.07	0.03				3 2
Scarlet Tanager											0.02	0.02	3 2
Common Grackle					0.08							0.02	3 2
Black-thr. Green Warbler											0.03		2 1
Ruffed Grouse							0.03						1 1
Eastern Phoebe							0.03						1 1
Yellow-throated Vireo												0.01	1 1
Prairie Warbler								0.03					1 1
Ovenbird												0.01	1 1
Northern Cardinal			0.17										1 1
Unident. woodpeckers	0.17			0.08							0.02		3 3
Unident. species					0.08	0.17	0.03	0.03	0.03	0.03	0.05	0.10	20 8
Total	2.17	2.17	2.33	1.75	1.58	2.11	1.80	2.77	2.03	1.68	1.85	2.36	758
Species richness ^b	8	9	7	11	9	11	14	17	18	15	20	24	39

^a See Appendix B-1 for full names of study sites.

^b Unidentified species are not included in species richness totals, except for unidentified woodpeckers (all *Picoides* species) in sites where these species did not otherwise occur.

Appendix C. Common and scientific names of bird species observed at 12 Rhode Island red maple swamps during the 1988 breeding season^a.

Common name	Scientific name
American Robin	<u>Turdus migratorius</u>
American Redstart	<u>Setophaga ruticilla</u>
Black-capped Chickadee	<u>Parus atricapillus</u>
Black-and-white Warbler	<u>Mniotilta varia</u>
Black-throated Green Warbler	<u>Dendroica virens</u>
Blue-gray Gnatcatcher	<u>Polioptila caerulea</u>
Blue-winged Warbler	<u>Vermivora pinus</u>
Blue Jay	<u>Cyanocitta cristata</u>
Brown-headed Cowbird	<u>Molothrus ater</u>
Brown Creeper	<u>Certhia americana</u>
Canada Warbler	<u>Wilsonia canadensis</u>
Carolina Wren	<u>Thryothorus ludovicianus</u>
Chestnut-sided Warbler	<u>Dendroica pensylvanica</u>
Common Grackle	<u>Quiscalus quiscula</u>
Common Yellowthroat	<u>Geothlypis trichas</u>
Downy Woodpecker	<u>Picoides pubescens</u>
Eastern Phoebe	<u>Sayornis phoebe</u>
Gray Catbird	<u>Dumetella carolinensis</u>
Great Crested Flycatcher	<u>Myiarchus crinitus</u>
Hairy Woodpecker	<u>Picoides villosus</u>
House Wren	<u>Troglodytes aedon</u>
Northern Waterthrush	<u>Seiurus noveboracensis</u>
Northern Cardinal	<u>Cardinalis cardinalis</u>
Northern Oriole	<u>Icterus galbula</u>
Northern Flicker (yellow-shafted)	<u>Colaptes auratus</u>
Ovenbird	<u>Seiurus aurocapillus</u>
Prairie Warbler	<u>Dendroica discolor</u>
Red-eyed Vireo	<u>Vireo olivaceus</u>
Rose-breasted Grosbeak	<u>Pheucticus ludovicianus</u>
Ruffed Grouse	<u>Bonasa umbellus</u>
Rufous-sided Towhee	<u>Pipilo erythrophthalmus</u>
Scarlet Tanager	<u>Piranga olivacea</u>
Song Sparrow	<u>Melospiza melodia</u>
Tufted Titmouse	<u>Parus bicolor</u>
Veery	<u>Catharus fuscescens</u>
White-eyed Vireo	<u>Vireo griseus</u>
White-breasted Nuthatch	<u>Sitta carolinensis</u>
Wood Thrush	<u>Hylocichla mustelina</u>
Yellow-throated Vireo	<u>Vireo flavifrons</u>

^a Taxonomic source: A.O.U. 1983.

Appendix D. Mean values for independent variables used in analyses, by site. Refer to Appendix E for variable names.

Site	No. plots	AREA (ha)	SHDV (*)	TDEN (stems/ha)	DDEN (stems/ha)	TBAS (m ² /ha)	DBAS (m ² /ha)	TDIV (*)	THGT (m)	CCOV (%)	TSCV (%)
Kenyon	1	0.49	0.00	476.19	29.76	19.65	2.94	0.28	15.91	89.68	59.38
Muddy Brook	1	0.64	0.67	416.67	14.88	22.23	0.39	0.71	15.91	85.84	81.70
Tuckertown	1	0.67	0.62	491.07	89.29	17.06	1.19	0.00	14.57	96.16	29.91
Tootell	2	1.6	0.69	513.39	119.05	17.19	1.88	0.28	13.50	82.96	42.41
Carolina	2	2.19	0.57	342.26	29.76	27.25	0.34	0.62	17.71	91.48	40.40
Turnpike	3	4.02	0.45	471.23	29.76	30.33	2.39	0.68	15.16	84.40	60.27
Fairgrounds	5	6.17	1.57	514.88	71.43	26.72	1.87	0.00	16.03	82.34	60.98
DeCoppet	5	6.33	0.64	592.26	47.62	23.83	1.25	0.49	13.90	91.31	51.16
Trustom	6	7.43	0.55	379.46	64.48	23.61	2.40	0.07	13.89	86.48	56.62
Narragansett	12	13.21	0.10	1001.98	100.45	23.22	1.10	0.49	13.61	98.92	37.05
Townsend	10	13.49	0.48	441.96	47.62	25.02	0.96	0.38	14.45	93.78	47.72
Dead Swamp	14	19.24	0.23	493.20	89.29	25.26	3.05	0.05	16.36	84.09	44.45
Mean		6.29	0.54	511.21	61.12	23.45	1.65	0.34	15.08	88.95	51.00
Stan. error		1.76	0.12	48.49	9.55	1.15	0.27	0.08	0.38	1.57	3.99
Minimum		0.49	0.00	342.26	14.88	17.06	0.34	0.00	13.50	82.34	29.91
Maximum		19.24	1.57	1001.98	119.05	30.33	3.05	0.71	17.71	98.92	81.70

Site	MSCV (%)	LSCV (%)	MLCV (%)	TOCV (%)	HECV (%)	WATR (%)	PEAT (m)	TSVL (%)	MLVL (%)	TOVL (%)	FHD (*)
Kenyon	17.86	2.68	20.54	79.91	0.00	33.33	2.5	22.72	26.72	24.72	0.69
Muddy Brook	10.27	3.13	13.39	95.09	51.34	17.78	0.8	28.30	33.04	30.67	1.07
Tuckertown	42.41	4.91	47.32	77.23	0.00	11.67	2.7	8.97	26.50	17.73	0.69
Tootell	30.13	7.37	37.50	79.91	0.45	67.50	1.4	14.58	28.06	21.32	0.71
Carolina	31.47	9.38	40.85	81.25	24.78	10.56	0.7	10.47	23.56	17.01	0.98
Turnpike	14.88	2.68	17.56	77.83	49.85	8.52	2.2	13.18	35.94	24.56	1.07
Fairgrounds	24.64	5.54	30.18	91.16	16.52	13.67	1.6	20.93	40.40	30.66	0.93
DeCoppet	28.66	6.70	35.36	86.52	12.23	4.56	2.5	21.21	37.27	29.24	0.89
Trustom	28.79	4.61	33.41	90.03	56.99	0.00	0.3	19.11	39.77	29.44	1.08
Narragansett	27.08	9.97	37.05	74.11	36.53	6.62	0.5	11.08	24.12	17.60	1.03
Townsend	45.22	4.91	50.13	97.86	4.73	3.11	1.8	16.63	42.70	29.67	0.79
Dead Swamp	30.58	15.34	45.92	90.37	16.23	2.30	2.2	15.72	29.05	22.39	0.92
Mean	27.67	6.43	34.10	85.11	22.47	14.97	1.60	16.91	32.26	24.58	0.90
Stan. error	2.92	1.06	3.42	2.23	6.13	5.42	0.24	1.66	1.95	1.54	0.04
Minimum	10.27	2.68	13.39	74.11	0.00	0.00	0.31	8.97	23.56	17.01	0.69
Maximum	45.22	15.34	50.13	97.86	56.99	67.50	2.66	28.30	42.70	30.67	1.08

* Shannon diversity index (Shannon 1948)

Appendix E. Pearson correlation coefficients and significance of correlations for all pairs of variables used in analyses.^a Refer to Appendix E for variable names.

	BRCHS	BRCHA	BDENS	BDENA	AREA	SHDV	TDEN	DDEN	TBAS	DBAS	TDIV	THGT
BRCHS		0.95 0.0001	-0.14 0.67	0.13 0.69	0.90 0.0001	-0.10 0.75	0.20 0.53	0.32 0.31	0.30 0.34	0.19 0.55	-0.30 0.34	-0.34 0.28
BRCHA			-0.21 0.50	0.17 0.60	0.92 0.0001	-0.08 0.81	0.14 0.66	0.26 0.41	0.35 0.26	0.31 0.33	-0.29 0.36	-0.19 0.55
BDENS				0.71 0.01	-0.33 0.30	0.12 0.70	-0.16 0.62	0.14 0.66	-0.52 0.08	-0.06 0.85	-0.32 0.30	-0.20 0.54
BDENA					0.01 0.97	-0.13 0.68	-0.09 0.78	-0.17 0.59	-0.14 0.66	0.26 0.42	-0.11 0.74	-0.14 0.66
AREA						-0.24 0.46	0.37 0.24	0.34 0.28	0.36 0.25	0.24 0.45	-0.23 0.46	-0.11 0.73
SHDV							-0.26 0.41	0.05 0.87	0.16 0.62	-0.23 0.47	-0.26 0.42	0.10 0.75
TDEN								0.49 0.11	-0.11 0.74	-0.06 0.85	0.07 0.82	-0.49 0.11
DDEN									-0.45 0.14	0.22 0.49	-0.59 0.04	-0.52 0.09
TBAS										0.01 0.97	0.36 0.26	0.41 0.18
DBAS											-0.51 0.09	-0.05 0.88
TDIV												0.13 0.69

	CCOV	TSCV	MSCV	LSCV	MLCV	TOCV	HECV	WATR	PEAT	TSVL	MLVL	TOVL	FHD
BRCHS	0.11 0.73	-0.26 0.42	0.50 0.10	0.48 0.11	0.58 0.05	0.43 0.17	0.07 0.83	-0.56 0.06	-0.06 0.84	-0.13 0.68	0.46 0.13	0.22 0.48	0.20 0.54
BRCHA	-0.10 0.75	-0.10 0.76	0.33 0.30	0.56 0.06	0.46 0.14	0.52 0.08	0.06 0.86	-0.47 0.13	-0.04 0.89	0.05 0.88	0.46 0.13	0.32 0.31	0.22 0.49
BDENS	0.18 0.58	-0.28 0.38	0.33 0.30	-0.10 0.75	0.25 0.44	-0.13 0.70	-0.43 0.16	0.03 0.94	0.61 0.03	-0.07 0.83	-0.08 0.82	-0.09 0.79	-0.50 0.10
BDENA	-0.03 0.92	0.16 0.62	-0.09 0.78	-0.07 0.83	-0.10 0.76	0.13 0.68	-0.11 0.74	-0.25 0.43	0.65 0.02	0.34 0.28	0.19 0.56	0.30 0.34	-0.13 0.69
AREA	0.11 0.74	-0.26 0.42	0.35 0.27	0.68 0.02	0.51 0.09	0.31 0.32	0.04 0.91	-0.51 0.09	-0.06 0.85	-0.16 0.61	0.20 0.53	0.04 0.90	0.22 0.49
SHDV	-0.44 0.15	0.23 0.46	0.03 0.94	-0.19 0.55	-0.04 0.91	0.36 0.25	-0.02 0.96	0.05 0.87	-0.07 0.83	0.20 0.53	0.49 0.11	0.42 0.18	0.07 0.82
TDEN	0.50 0.10	-0.33 0.29	-0.004 0.99	0.30 0.34	0.09 0.78	-0.46 0.13	-0.005 0.99	-0.05 0.88	-0.11 0.74	-0.25 0.44	-0.29 0.36	-0.32 0.31	0.07 0.83

(continued)

Appendix E. (concluded)

	CCOV	TSCV	MSCV	LSCV	MLCV	TOCV	HECV	WATR	PEAT	TSVL	MLVL	TOVL	FHD
DDEN	0.06 0.85	-0.65 0.02	0.47 0.12	0.52 0.08	0.56 0.06	-0.31 0.33	-0.34 0.27	0.31 0.32	-0.03 0.94	-0.49 0.11	-0.25 0.43	-0.42 0.17	-0.33 0.30
TBAS	-0.23 0.48	0.27 0.40	-0.23 0.48	0.11 0.74	-0.16 0.62	0.23 0.47	0.50 0.10	-0.60 0.04	-0.15 0.63	-0.03 0.93	0.40 0.20	0.24 0.46	0.70 0.01
DBAS	-0.48 0.12	0.06 0.87	-0.19 0.56	0.09 0.77	-0.13 0.68	-0.10 0.75	-0.09 0.79	0.12 0.71	0.37 0.23	0.08 0.81	0.09 0.79	0.10 0.77	-0.14 0.66
TDIV	0.14 0.66	0.33 0.29	-0.46 0.13	-0.21 0.51	-0.46 0.13	-0.11 0.74	0.41 0.19	-0.01 0.97	-0.24 0.45	0.11 0.74	-0.11 0.72	-0.02 0.96	0.43 0.17
THGT	-0.25 0.43	0.23 0.47	-0.25 0.43	0.17 0.60	-0.16 0.61	0.17 0.61	0.03 0.94	-0.16 0.62	0.02 0.95	0.10 0.76	-0.23 0.47	-0.10 0.77	0.16 0.62
CCOV		-0.56 0.06	0.48 0.12	0.05 0.88	0.43 0.17	-0.34 0.27	-0.19 0.56	-0.33 0.29	-0.01 0.98	-0.43 0.16	-0.34 0.28	-0.45 0.14	-0.19 0.56
TSCV			-0.78 0.003	-0.53 0.08	-0.83 0.0008	0.52 0.08	0.50 0.10	-0.01 0.99	-0.15 0.64	0.87 0.0002	0.47 0.12	0.77 0.004	0.43 0.16
MSCV				0.32 0.31	0.96 0.0001	0.07 0.83	-0.55 0.06	-0.17 0.61	0.16 0.62	-0.57 0.05	0.04 0.89	-0.28 0.38	-0.49 0.11
LSCV					0.59 0.05	-0.05 0.88	-0.15 0.63	-0.15 0.65	-0.11 0.74	-0.39 0.20	-0.40 0.20	-0.46 0.13	0.07 0.82
MLCV						0.04 0.89	-0.52 0.08	-0.19 0.56	0.10 0.75	-0.61 0.03	-0.09 0.79	-0.38 0.22	-0.39 0.20
TOCV							0.11 0.74	-0.30 0.35	-0.12 0.72	0.63 0.03	0.71 0.01	0.79 0.002	0.17 0.59
HECV								-0.42 0.18	-0.63 0.03	0.19 0.56	0.21 0.52	0.23 0.47	0.94 0.0001
WATR									0.05 0.87	0.07 0.84	-0.34 0.28	-0.18 0.58	-0.54 0.07
PEAT										-0.04 0.91	0.04 0.89	0.01 0.98	-0.62 0.03
TSVL											0.45 0.14	0.82 0.001	0.14 0.66
MLVL												0.88 0.0002	0.22 0.49
TOVL													0.22 0.50

^a Upper number is Pearson correlation coefficient, lower number is significance of correlation.

Appendix F. Variable codes.

Code	Variable
BRCHS	Species richness of singing birds
BRCHA	Species richness of all birds observed
BDENS	Relative abundance of singing birds
BDENA	Relative abundance of all birds
AREA	Area
SHDV	Surrounding habitat diversity
TDEN	Tree density
DDEN	Dead tree density
TBAS	Tree basal area
DBAS	Dead tree basal area
TDIV	Tree species diversity
THGT	Tree height
CCOV	Tree canopy cover
TSCV	Tall shrub cover
MSCV	Medium shrub cover
LSCV	Low shrub cover
MLCV	Medium and low shrub cover
TOCV	Total shrub cover
HECV	Herb cover
WATR	Surface water cover
PEAT	Depth (thickness) of peat
TSVL	Tall shrub foliage volume
MLVL	Medium and low shrub foliage volume
TOVL	Total shrub foliage volume
FHD	Foliage height diversity

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