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Seasonal dynamics of bird populations in small New England wetlands.—Wetlands are widely recognized as ecosystems with diverse attributes (Office of Technology Assessment 1984), including a distinctive avifauna (Burger 1985). Avian communities of herbaceous wetlands, although not as rich as upland forest systems, are nevertheless varied (Burger 1985) and include economically important species (Bellrose 1978, Weller 1981). Despite the perceived value of wetlands for birds, basic avian community parameters such as species richness, species composition, and population density are often poorly documented even for commonly occurring types of wetlands (but for prairie marshes see Weller and Spatcher 1965, Kantrud and Stewart 1984, Brown and Dinsmore 1986). Here we characterize the seasonal dynamics of these parameters for a northeastern wetland avifauna.

Study areas and methods.—We studied avian community dynamics from spring 1988 to winter 1989–1990 in Connecticut (8 seasons). Six sites were chosen to represent the range of small, typically human-impacted wetlands present in the state. Sites differed in extent of open water, vegetation type, surrounding habitat, and level of disturbance, but all were relatively small, dominated by herbaceous vegetation and bordered by thickets (i.e., areas dominated by shrubs). Subjectively ranked from most to least disturbed, they are (1) State Rt. 9 and Interstate 91 interchange, Cromwell (1.0 ha): This former streamside swamp, logged in 1987, became vegetated by herbaceous graminoids, annual weeds, stump sprouts, and patches of reed (*Phragmites communis*) and cattail (*Typha latifolia*). Two shallow (1–2 m deep) ponds bordering it were constructed in 1988, increasing the total area to about 3 ha. (2) Horsebarn Hill, Storrs (0.4 ha): This marsh, with little open water, was situated in a damp, heavily grazed cow pasture. Cattail and reed canary grass (*Phalaris arundinacea*) dominated the marsh, and a copse of boxelder (*Acer negundo*), ash (*Fraxinus americana*), and multiflora rose (*Rosa multiflora*) bordered its north side. (3) Rt. 178 and 187, Bloomfield (1.1 ha): Created by bulldozers ca 1978, this marsh was traversed by a stream that was nearly dry by mid-summer. It was vegetated by reed canary grass, cattail, and purple loosestrife (*Lythrum salicaria*) and bordered by old fields and thickets of spiraea (*Spiraea* spp.), dogwoods (*Cornus* spp.), and multiflora rose. (4) Piper Brook, Newington (2.5 ha): This floodplain marsh along Piper Brook was dominated by cattail, reed canary grass, tussock sedge (*Carex stricta*), and pickerelweed (*Pontederia cordata*). It was edged by a railroad bed and recently (ca 3 yr) cutover forest dominated by tree sprouts, weedy herbs, speckled alder (*Alnus rugosa*), spiraea, and willow (*Salix* spp.). (5) Cedar Swamp, Mansfield (3.7 ha): This streamside swamp became a herbaceous marsh when road construction raised its water level in 1965. Common herbaceous plants included bulrush (*Scirpus atrovirens*), burreed (*Sparganium eurycarpum*), sedges, and cattail. It was bordered by forest, old fields, and thickets of buttonbush (*Cephalanthus occidentalis*) and speckled alder. (6) Schoolhouse Brook Park, Mansfield (0.9 ha): This 19th-century millpond, although still with open water, was silted and vegetated by cattail, reed, and tussock sedge. It was bordered by a forest and shrubby thickets of buttonbush, spiraea, and speckled alder.

Birds were studied at these sites twice each season (8 visits/site/year) on days when weather was relatively calm and there was little or no precipitation. Although logistical difficulties (e.g., construction and heavy traffic) prevented a uniform starting time, observations began 1–2 h after sunrise. During each visit, Craig counted bird species by recording all those encountered for 6 h. By counting for 6 h, locating all species present at these relatively small sites was virtually assured. Data from both counts/season were combined to produce one species list, from which we computed seasonal species richness for each site. The seasonal frequency of occurrence of individual species was computed by dividing the number of counts on which a species occurred by the total number of censuses/season (24 over 2 years).

The relative densities of small passerines, the predominant members of the avian communities at these sites, were concurrently assessed by mist netting with two pairs of ATX nets. The inner member of the pair was placed at the thicket border, and the outer member extended into the marsh interior. Net locations were changed between visits to obtain a more representative view of avian density. Density sampling lasted 5 h/visit (20 total net h/visit), and all birds captured for the first time were banded. Capture data for any particular day consisted of birds banded plus birds recaptured from a previous visit's banding but did not include same-day recaptures. Because capture rates were low, data from all four nets for both seasonal visits to a site were combined in analyses.

Based on field observations and on habitat summaries provided by DeGraff and Rudis (1987), species were categorized by principal habitat association: (1) herbaceous marsh and associated open water and mud, (2) adjacent wetland thicket, (3) upland edge or edge thicket to upland habitats, (4) interior forest, (5) field or agricultural land, (6) mosaics of the above habitats. Analyses primarily concern birds in the first two categories, i.e., those species most closely associated with wetlands.

Factorial analyses of variance were performed on species richness data. Variables entered

TABLE 1

PERCENT SEASONAL OCCURRENCE FOR THE THREE MOST COMMON MARSH AND THICKET SPECIES

Species	Winter	Spring	Summer	Fall	Mean
Marsh:					
Red-winged Blackbird (*Agelaius phoeniceus*)	29.2 (7)[a]	100 (24)	91.6 (22)	45.8 (11)	65.6 (63)
Swamp Sparrow (*Melospiza georgiana*)	8.3 (2)	54.2 (13)	58.3 (14)	83.3 (20)	51.0 (49)
Cedar Waxwing (*Bombycilla cedrorum*)	4.2 (1)	45.8 (11)	70.8 (17)	62.5 (15)	45.8 (44)
Thicket:					
Song Sparrow (*M. melodia*)	79.2 (19)	95.8 (23)	95.8 (23)	100 (24)	92.7 (89)
American Goldfinch (*Carduelis tristis*)	50.0 (12)	79.2 (19)	87.5 (21)	95.8 (23)	78.1 (75)
Common Yellowthroat (*Geothlypis trichas*)	0	75.0 (18)	75.0 (18)	37.5 (9)	47.9 (46)

[a] Percents computed by dividing censuses on which a species occurred (N, in parentheses) by the total censuses (24/season) (× 100).

into the ANOVA model were sites, seasons, and habitats (marsh and thicket). For capture data, variables entered into the factorial ANOVA model were sites and seasons. In both analyses, data from the four 1988–1989 and four 1989–1990 seasons served as replicates. Before analyzing species richness and capture data, they were square root transformed to normalize distributions and stabilize variances. Comparisons between significantly different means were made with the Bonferroni test which Day and Quinn (1989) recommended as a superior multiple comparison procedure.

Results and discussion.—During eight seasons, we encountered 121 bird species at the six wetlands. Species (N) were distributed among the six categories of habitat association as follows: marsh (31), adjacent thicket (22), edge (44), forest (17), field (13), and mosaic (6). Twelve species changed their habitat association between seasons (e.g., the Canada Goose [*Branta canadensis*] nested in marshes in spring but used agricultural land in winter).

The Red-winged Blackbird (*Agelaius phoeniceus*) was the marsh species most frequent on censuses and most often netted. It was nearly ubiquitous in spring and summer, but occurred on $<50\%$ of censuses in fall and winter (Tables 1, 2). The Song Sparrow (*Melospiza melodia*) was the thicket species most often present on censuses (Table 1) and most often netted (Table 2), with a density peak occurring in fall. It was also the most abundant species in any habitat. The seasonal occurrence of predominant species in marshes and thickets is summarized in Tables 1 and 2.

Analysis of variance revealed that species richness varied between seasons ($F = 71.0$, df $= 3, 48$, $P < 0.001$), although spring, summer, and fall showed little difference. Winter differed significantly from all other seasons (minimum Bonferroni difference between transformed means = 0.23; Fig. 1a). Richness also differed among the six sites ($F = 18.7$, df $= 5, 48$, $P < 0.0001$). The minimum Bonferroni difference (0.31) showed that Horsebarn Hill had significantly fewer species than all other sites, and Cromwell was lower in richness than

TABLE 2

PERCENT CAPTURES FOR THE THREE MOST COMMONLY NETTED MARSH AND THICKET SPECIES

Species	Winter	Spring	Summer	Fall	Total
Marsh:					
Red-winged Blackbird (*Agelaius phoeniceus*)	0	13.9 (35)[a]	10.7 (27)	0	7.4 (62)
Swamp Sparrow (*Melospiza georgiana*)	0	4.8 (12)	5.9 (15)	9.9 (28)	6.6 (55)
Common Grackle (*Quiscalus quiscula*)	0	4.0 (10)	0.8 (2)	0	1.4 (12)
Thicket:					
Song Sparrow (*M. melodia*)	25.5 (12)	22.7 (57)	32.0 (81)	45.0 (127)	33.3 (277)
Gray Catbird (*Dumetella carolinensis*)	0	6.4 (16)	13.8 (35)	3.2 (9)	7.2 (60)
American Goldfinch (*Carduelis tristis*)	0	10.8 (27)	5.1 (13)	6.4 (18)	7.0 (58)
Total captures:	47	251	253	282	833

[a] Percents computed by dividing captures/season (N, in parentheses) by total captures (× 100).

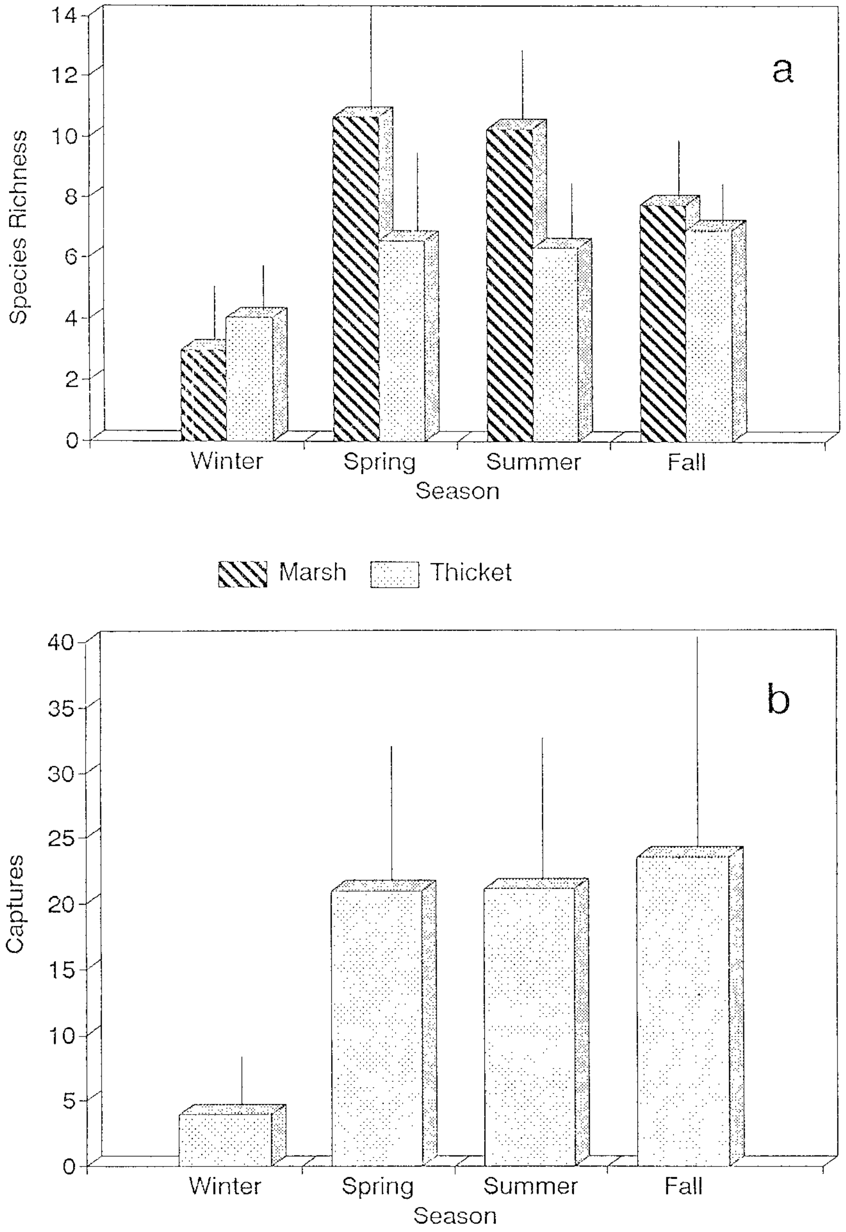

FIG. 1. Seasonal comparisons ($\bar{x}$ ± SD) of (a) species richness, and (b) captures. N = 12 counts/season.

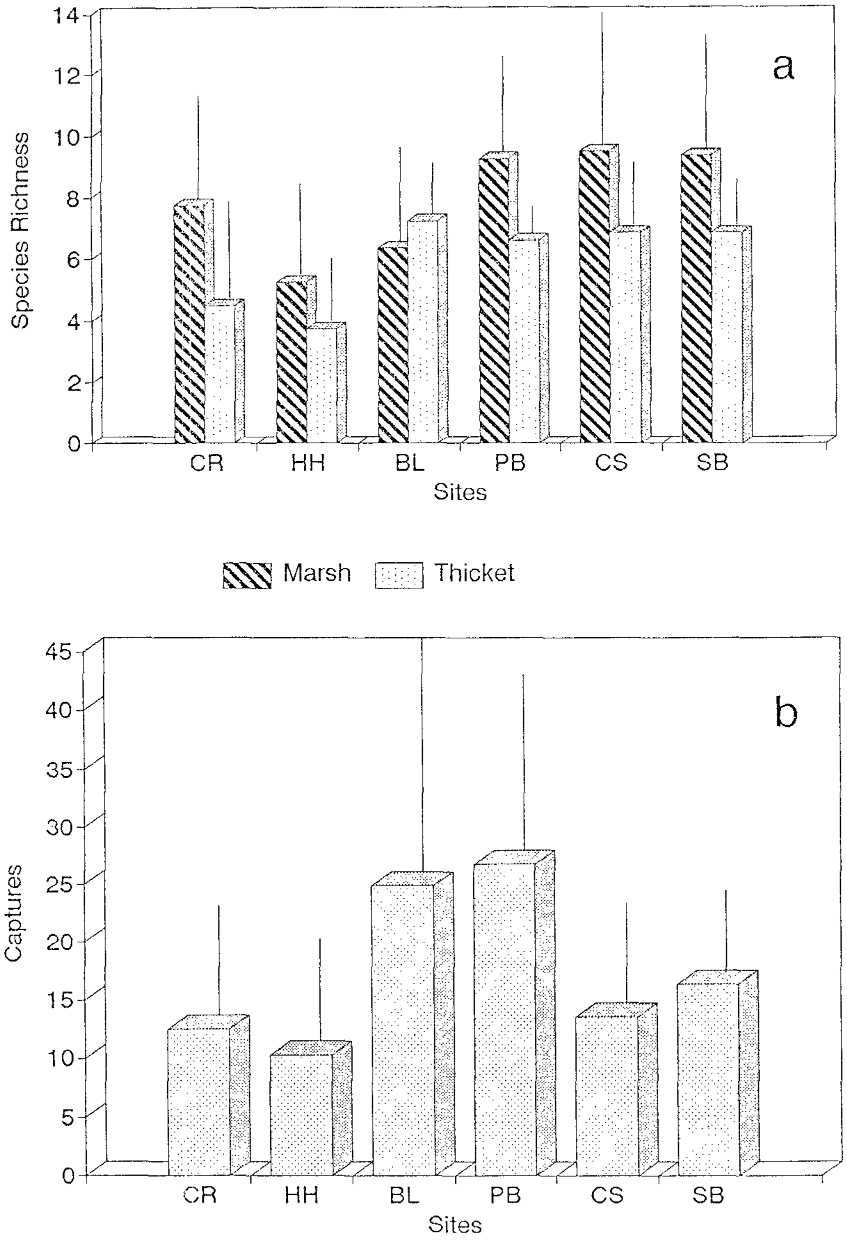

FIG. 2. Comparisons ($\bar{x}$ ± SD) of sites and (a) species richness and (b) captures. N = 8 counts/site.

Piper Brook, Cedar Swamp, and Schoolhouse Brook, which had similarly high richness (Fig. 2a). Species richness in marshes ($\bar{x} = 7.9 \pm 3.9$) also differed from that in thickets ($\bar{x} = 6.0 \pm 2.2$; $F = 28.6$, df = 1, 48, $P < 0.0001$).

Seasonal patterns of species richness were not significantly different among sites ($F = 1.8$, df = 15, 48, $P > 0.06$) nor was the interaction of seasons, sites and habitats ($F = 0.9$, df = 15, 48, $P > 0.52$). However, sites differed between habitats in species richness ($F = 3.9$, df = 5, 48, $P < 0.005$). Marsh species were least abundant at Horsebarn Hill and Bloomfield, although Cromwell also averaged lower than the remaining three sites which were nearly uniform in marsh species richness. Horsebarn Hill and Cromwell also had relatively few thicket species, whereas the other sites were similarly high in thicket species richness (Fig. 2a).

Marshes and thickets differed among seasons in species richness ($F = 18.1$, df = 3, 48, $P < 0.001$). Although both habitats showed steep declines during winter, thickets were more uniform in richness than marshes. Marsh species outnumbered those in thickets during spring and summer, but declined to about the same number in fall. During winter, fewer species inhabited marshes than thickets (Fig. 1a).

Analysis of density data showed seasonal differences in netting frequency ($F = 23.4$, df = 3, 24, $P < 0.0001$). As with species richness, netting frequency did not differ between spring, summer, and fall, but winter was significantly lower in captures than all other seasons (minimum Bonferroni difference = 1.2; Fig. 1b). The six sites also differed in netting frequency ($F = 5.0$, df = 5, 24, $P < 0.003$); the minimum Bonferroni difference (1.6) showed that Horsebarn Hill had significantly fewer captures than Bloomfield and Piper Brook, which had the highest capture rates. Moreover, Cromwell had significantly fewer captures than Piper Brook (Fig. 2b). There was no interaction between sites and seasons ($F = 1.6$, df = 15, 24, $P > 0.15$).

Sharp declines in species richness during winter are consistent with patterns typically observed among bird communities of temperate forests (e.g., Morrison et al. 1986, Yahner 1986). However, divergent patterns of species richness for marshes and thickets indicate that these habitats function differently in their seasonal capacity to support species. Marshes reached their peak species richness in spring, when local water levels are typically high and food organisms like aquatic invertebrates are at their peak abundance (Craig 1984). As water and food levels decline through late summer (Craig 1984), progressively fewer species use this habitat. The relatively uniform species richness of thickets from spring to fall may be related to more continuously available food and cover in thickets compared to marshes.

Comparatively high capture rates from spring to fall, followed by a sharp decline in winter, further reflects seasonal patterns typically observed in temperate bird density (e.g., Morrison et al. 1986, Yahner 1986). The winter drop in species richness and density traditionally has been ascribed to the comparative environmental harshness and lack of food at this season (e.g., Welty 1982).

Although we did not attempt to quantify all physical and biotic habitat differences among sites, there was a tendency for the most disturbed sites, Cromwell and Horsebarn Hill, to have low richness and density. This suggests that disturbance negatively impacted these community parameters and points out that the role of disturbance in affecting wetland bird communities deserves further study.

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Habitat and reproductive success of Piping Plovers nesting on Great Lakes islands.— Piping Plovers (*Charadrius melodus*) historically nested along the Great Lakes. Russell (1983) estimated there may have been up to 802 breeding pairs in the Great Lakes region. In the 1940s and 1950s the Great Lakes Piping Plover population declined dramatically following shoreline development and subsequent loss of nesting habitat (Russell 1983). By 1979 the population had decreased to 38 pairs (Lambert and Ratcliff 1981). The Great Lakes Piping Plover population was listed as federally endangered in 1986 (U.S. Fish and Wildlife Service 1985). At the time of listing, only 17 breeding pairs remained in the Great Lakes population, and viable breeding areas were reduced from locations in eight Great Lakes states to sites entirely within the state of Michigan (Haig et al. 1988). The Great Lakes Piping Plover population has remained relatively stable since 1986, but in 1990 the population decreased by 35% to only 11 breeding pairs (Powell, in press). Although habitat loss may have been the primary cause of the decline in Piping Plover populations in the Great Lakes region thirty years ago, current sites used by breeding plovers are protected, and reasons for the decline in recent years are difficult to elucidate (Haig et al. 1988). The population is now extremely vulnerable and may have reached a size where natural recovery is unlikely.

Islands have historically been an important component of breeding habitat for the Great Lakes Piping Plover population. In Michigan, Piping Plovers once nested on North and South Manitou islands, North and South Fox islands, and Beaver Island (Hatt et al. 1948, Cotrille 1957). In the past decade, Piping Plovers have nested only on Beaver and High