

BIRD POPULATIONS OF BOGS

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BOGS throughout the glaciated region of the northern hemisphere show considerable uniformity in structure and composition (Curtis, 1959). In the southern portion of this region, bogs form "boreal islands" with a high percentage of species of northern affinities and are regarded as relicts of former conditions associated with Pleistocene glaciation (Bailey, 1896; Transeau, 1903). These statements are fair conclusions based on numerous floristic and vegetational studies. Faunal studies are fewer and, as a consequence, such questions as the degree of uniformity of species composition and geographical affinities among bog animals are unresolved. As a contribution toward answering such questions, bird populations in two bogs in southwestern Michigan were studied and analyzed in conjunction with the existing published information on avian populations of eastern North American bogs.

STUDY AREAS

One study area (Portage Bog) consisted of a 16.5-acre tract of sphagnum-leatherleaf-tamarack bog with sides of 600 and 1200 feet. Located south of Portage in Kalamazoo County (NE $\frac{1}{4}$, Sec. 28, R 11 W, T 3 S), it is part of a much larger area of similar peatland about one-quarter-mile wide and one and one-half miles long. The study area is surrounded on all sides by similar vegetation but about 150 feet to the southwest and roughly parallel to one side runs a drainage ditch 12 feet wide. Beyond the ditch is deciduous thicket or forest on thin peat or mineral soil. The study area was located wholly on deep peat (17 feet). Six physiognomic vegetation types occurred in a fairly complex mosaic. Open wet bog made up about 0.3 acre; open dry bog (Fig. 1), 8.7; low thicket, 0.9; high thicket (Fig. 2), 4.7; parkland, 0.8; and tamarack forest, 0.9.

The second study area (Sugarloaf Bog, Fig. 3) consisted of a strip 100×1000 feet (2.3 acres) in 1965 and 200×1000 feet (4.6 acres) in 1966 running down the center of a red maple-yellow birch-white pine bog forest fringing Sugarloaf Lake southwest of Portage in Kalamazoo County (Sec. 32, R 11 W, T 3 S). The bog forest was 300–600 feet wide and lay between an upland oak-pine forest and an expanse of open bog 100–300 feet wide adjacent to the lake.

Elevation of both study areas was 850–60 feet above mean sea level. Botanical features of both areas and a vegetation map of Portage Bog are given in Brewer (1966).

METHODS

Breeding bird populations were studied by the standard spot-map method (Williams, 1947). Establishment of census plots was careful, using a Brunton pocket transit and steel tape. Because of the strip-like nature of the Sugarloaf Bog plot, virtually no territories lay wholly within it and, therefore, estimation of the fraction included was



FIG. 1. General view in Portage Bog showing expanse of open bog with a narrow zone of high tamarack thicket fringing a strip of tamarack forest (canopy height 20-40 feet). The only noticeable plants are leatherleaf and tamarack. (Sept. 1965)

one source of error. This error is also present when using plots of more standard dimensions because, except when plots are very large, most territories include some area beyond the boundaries. At Portage Bog, for example, only about one-third of the total number of Song Sparrow territories touching the plot lay wholly within the 16.5 acres.

Coverage of Portage Bog included six breeding seasons as follows: 1961 (9 trips, 1 May-21 August; total hours 17), 1962 (4, 10 April-24 July; 8.5), 1963 (7, 4 May-17 August; 15), 1964 (7, 20 May-22 July; 10.5), 1965 (9, 22 April-24 August; 17), and 1966 (12, 11 April-30 July; 37). Most censuses were in the forenoon, usually beginning after 6 and before 9 and lasting about two hours. Visits to the tract for other purposes provided corroborative observations beyond the time spent in formal censusing. Although the results for 1962 are believed to be generally correct, less confidence can be placed in them compared with other years because of the sparseness of coverage.

Less attention was paid to the area outside the breeding season, but 20 additional trips totaling 55 hours were made (September, 5; October, 2; November, 3; December, 6; January, 2; February, 1; March, 1), and the same field procedures of mapping locations of birds were followed.

Sugarloaf Bog was censused the summers of 1965 (15 trips, 7 June-23 August; total hours 29.5) and 1966 (8, 13 May-30 June; 23.5).



FIG. 2. The denseness of the extensive high thickets is indicated by this photograph taken just outside one. The pale spot to the left of center is the jacket worn by a person standing about six feet inside the thicket. (Sept. 1965)

BREEDING BIRD POPULATIONS AT PORTAGE BOG

Twenty-four species occurred regularly during at least one of the six breeding seasons; however, the average annual number of breeding species was only about 16 (Table 1). Density was about 170 pairs per hundred acres. In interpreting this and other estimates of density, the limits to the precision of the spot map method (see, e.g., Breckenridge, 1955:410), especially for species not showing Type A territories (Nice, 1941) and those with very large territories need to be borne in mind. The only species in these groups which seemed of moderately high density here was the Brown-headed Cowbird.¹ For this species the largest number of males seen together in June was assumed to represent the number frequenting the area; density was taken as one-half this number on the assumption that most of the cowbirds had some portion of their home range outside the tract. The reader may decide for himself the limits of precision of this estimate.

Song Sparrows were by far the most abundant species, having an average density of 9.4 territorial males (57 per 100 acres). The only other species

¹ Scientific names of birds are given in Table 3 or, for species not in Table 3, where they are first mentioned.



FIG 3. Sugarloaf Bog, looking toward the lake. Canopy height is 65-80 feet. Cinnamon fern is noticeable on the hummocky surface. The shrub at left is spice bush. (Sept. 1965)

having an average density greater than 10 per 100 acres were Yellowthroat, Field Sparrow, Rufous-sided Towhee and, perhaps, Brown-headed Cowbird.

The Yellow Warbler was present the first two years and virtually absent thereafter (although it continued to occur elsewhere in the bog). The Traill's Flycatcher (evidently *Empidonax brewsteri* Oberholser, according to Stein's diagnosis, 1963) was absent the first two years and present three of the last four. Both species were birds of the thicket areas, and it may be that between 1961 and 1963 conditions became unfavorable for the warblers and favorable for the flycatchers. The most prominent change was an increase in high thicket at the expense of low thicket. Possibly the same successional trend was responsible for the appearance in 1965 of the Nashville Warbler, a northern species not previously known to nest in southwestern Michigan (Brewer and Raim, 1966).

Neither Black-capped Chickadees nor Yellow-shafted Flickers had a nest on the study area. Tamaracks were the only dead trees of any size, and they seemed not to decay in a way that rendered them suitable for excavation by cavity-nesting birds. The scarcity of such species is evident. Both chickadees and flickers may have nested in hardwoods adjacent to the bog and used

TABLE 1
BREEDING BIRD POPULATIONS OF PORTAGE BOG (MALES)

Species	1961	1962	1963	1964	1965	1966	Mean, all years	Males/100 acres
Song Sparrow	9.5	8.0	10.1	9.8	10.2	8.5	9.4	57
Yellowthroat	3.8	5.6	3.8	5.3	3.4	4.9	4.5	27
Field Sparrow (<i>Spizella pusilla</i>)	1.1	4.0	2.4	3.0	2.4	1.2	2.4	14
Rufous-sided Towhee	2.2	2.1	1.7	4.1	1.6	3.0	2.4	14
Brown-headed Cowbird	+	+	+	+	+	+	2.4	14
Catbird	1.0	1.2	1.2	2.1	2.0	1.5	1.5	9
Am. Goldfinch	+	+	+	+	1	1	>0.3	6
Traill's Flycatcher	0	0	2.0	1.4	1.1	0	0.8	5
Yellow Warbler	2.3	0.8	0	0	0	+	>0.5	3
Black-capped Chickadee	+	+	+	+	+	0.9	>0.2	3
Mourning Dove	+	0	+	+	+	+	+	3
Cedar Waxwing	+	+	+	+	+	+	+	3
Yellow-shafted Flicker	+	+	+	+	+	+	+	2
Cardinal	0	0	0	0.8	0.9	0.9	0.4	2
Brown Thrasher	0	0.9	0	+	0.5	0.6	>0.3	2
Ruby-throated Hummingbird (<i>Archilochus colubris</i>)	0	0	0	1 ♀	0	0	0.2	1
Nashville Warbler	0	0	0	0	0.9	0	0.2	1
Mallard (<i>Anas platyrhynchos</i>)	1 nest	0	1 nest	+	1 nest	+	+	+
Marsh Hawk	+	+	0	0	0	+	+	+
Eastern Bluebird (<i>Sialia sialis</i>)	+	0	0	0	0	0	+	+
Tree Swallow	+	0	0	0	0	0	+	+
Robin	0	0	0	0	+	+	+	+
Whip-poor-will (<i>Caprimulgus vociferus</i>)	?	?	?	?	+	?	+	+
Veery	0	0	0	0	0	+	+	+
No. species	16	13	13	16	18	18	16	
No. males							>25.1	>166

+ indicates present on tract but density low or difficult to assess.

the tract only as a part of their feeding range. A possible indication of the rarity of suitable nest holes within the bog was the use of the same cavity in a dead pine just off the tract by bluebirds in May 1961 and Tree Swallows in June. I believe that Robins also placed their nests in deciduous areas and came into the bog only for feeding.

There were substantial differences in the utilization of different vegetation types by certain species. To place this on a quantitative basis, numbers of territories were calculated for the eastern portion of the bog (8.7 acres) which was predominantly open and for the western portion (5.1 acres) which was predominantly low and high thicket. The year 1962 was omitted because

the small number of sightings for each territory made approximation of percentages in different vegetation types impossible. The average figures for five years indicate slight preferences by Field Sparrow for open bog and Song Sparrow for thicket and rather strong preferences by towhee, Yellowthroat, and Catbird, for thicket. The number of species occurring regularly during at least one year in open bog was about 13 and in thicket about 21; densities were less than 100 males per 100 acres in open bog and well over 200 males per 100 acres in thicket.

Several differences between 1964 and other years appeared related to a fire which that spring burned areas on each side of the drainage ditch along one edge of the tract, although not reaching the tract itself. The immediate result of the fire was a reduction in woody growth followed by plentiful root sprouting of aspens. Changes in density considering the whole tract between 1963 and 1964 were not particularly striking, but the distribution of territories was. Song Sparrows were virtually absent from the areas (open bog) adjacent to the burn, with the result that the number of territories in open bog dropped from 6.4 in 1963 to 3.4 in 1964. An increase from 1.2 to 4.0 in thicket compensated for the decrease in open bog. Towhees used the burnt area much more extensively than in other years, so that portions of 3 territories included open bog whereas only the edge of 1 territory did so in most years. Similar trends of increased density in open bog for 1964 were seen in Yellowthroat and Field Sparrow.

Breeding season visitors to the bog were infrequent. Probably most represent birds making an occasional trip beyond their usual limits or adults, young, or family groups that moved away from their nest area following nesting. The only species that visited the bog in numbers were the Blue Jay and the Robin. Blue Jays were frequently seen in the bog until late May; then they were almost entirely absent until early August at which time they again began to visit the bog regularly. Robins were essentially absent from the bog during winter and also during the peak of the breeding season (except in 1965 and 1966, when one pair included a part of the bog in its breeding territory). They were occasionally seen during spring, but it was only during blueberry season that they were common. With ripening of the berries, both adults and young swarmed into the area. On 11 July 1964, I plotted 18 individuals and twice that number would be a conservative estimate of the birds present during the two-hour census.

It is my impression that some of the visitors were surplus single birds seeking to set up territories or pairs searching for a suitable area for nesting, possibly following a nest failure. In the latter category might fall Eastern Meadowlarks which I three times saw in the open portion of the bog. On 25 June 1963, I saw two meadowlarks, one with what I took to be nesting

TABLE 2
BREEDING BIRD POPULATIONS OF SUGARLOAF BOG
(Males per 100 acres)

Species	1965	1966	Mean
Black-capped Chickadee	39	41	40
Ovenbird	4	72	38
Wood Pewee	24	28	26
Blue Jay	28	15	22
Cardinal	28	13	20
Scarlet Tanager	24	11	18
Downy Woodpecker	22	11	16
Red-eyed Vireo	17	15	16
Great Crested Flycatcher	13	17	15
Song Sparrow	26	0	13
Tufted Titmouse	4	13	8
Rufous-sided Towhee	17	+	>8
Wood Thrush	13	0	6
Yellow-throated Vireo (<i>Vireo flavifrons</i>)	0	11	6
Hairy Woodpecker	9	0	4
Yellow-shafted Flicker	6	2	4
White-breasted Nuthatch	+	6	>3
Black-throated Green Warbler	6	0	3
Catbird	4	0	2
Common Grackle	+	0	+
Veery	+	+	+
Ruffed Grouse	+	+	+
Yellowthroat	+	0	+
Owl (Barred?) (<i>Strix varia?</i>)	+	0	+
Wood Duck (<i>Aix sponsa</i>)	0	+	+
Brown-headed Cowbird	0	+	+
Number of species	23	18	20
Number of males	>284	>255	>270

+ indicates present on tract but density low or difficult to assess.

material in its beak, sit for more than 20 minutes on a dead tamarack. The speculation is worth entertaining that the physiognomy of open bog is close enough to that of open fields that in hunting for nest-sites the species may occasionally be misled.

It is evident that the avifauna of Portage Bog has little of a boreal nature about it. To provide an objective standard for determining geographical affinities here and in subsequent sections, I have used the analysis of Udvardy (1963) in which he erects 17 faunal groups each composed of North American passerine species "whose ranges are similar and more or less overlapping. Most of them also stand well as ecological entities." In making

use of Udvardy's analysis, two additional categories were necessary: an unanalyzed element, consisting of several species of wide geographical range which Udvardy did not assign to faunal groups and non-passerine species, which also tend to have extensive geographical ranges and which Udvardy did not treat.

For Portage Bog, the unanalyzed element was by far the most important, making up 42 per cent of the species; next most important were non-passerine species (25 per cent). This agrees with the frequent observation (e.g., Odum, 1945:198) that geographically wide-ranging species are important in early seral stages. Species of the eastern deciduous forest, boreal forest, and eastern ecotone faunas were all about equally well represented (12, 12, and 8 per cent).

In terms of vegetational affinities, the avifauna is forest edge. The species list is scarcely different from that to be expected on a southwestern Michigan moist thicket area having a wholly different flora of, for example, willows, brambles, and goldenrod. This conclusion supports the view that physiognomy or structure of vegetation is important in the community distribution of birds (Odum, 1945; Kendeigh, 1948).

BREEDING BIRD POPULATIONS AT SUGARLOAF BOG

Twenty-six species occurred as breeding birds during one of the two summers. The average number of species per year was about 20, or four more than at the 16.5-acre Portage Bog, and the density was about 270 males per 100 acres. The Black-capped Chickadee was the most abundant species, with an average of 40 males per 100 acres (Table 2). Ten species occurred at densities greater than 10 males per 100 acres compared with four such species at Portage Bog. Nine species (22 per cent) were common to the two tracts.

Thirty-eight per cent of the species, including five of the 10 most common, were members of the eastern deciduous forest fauna. Unanalyzed and non-passerine species together made up 46 per cent, eastern ecotone species 12 per cent, and boreal forest species 4 per cent.

There were notable changes in abundance between the two years. Partly this was because the tract was small; a territory shifted 200 feet could make a difference of 20 males in the calculations for 100 acres. Two changes were certainly real; these were the decrease of Song Sparrows and the increase of Ovenbirds. In 1965, the territories of five Song Sparrows lay partly on the 4.6-acre strip, mainly centered toward open bog; in 1966 no territories reached the strip. In 1965 territories of four Ovenbirds just touched the strip; in 1966 three territories were centered on the strip and three others included sizable portions of it. There was an interesting dif-

ference in behavior of the Song Sparrows in Sugarloaf Bog compared with their usual habitats; they were little in evidence past late June. In such areas as Portage Bog, singing and nesting activities continue far into July and beyond. The latest nesting record for Kalamazoo County is 8 September (Batts, 1957). Most of the extension of Ovenbird territories onto the census strip occurred in the latter part of the summer after Song Sparrows had largely disappeared.

An explanation for these changes lies in two possible directions: (1) the environment may have changed so that Song Sparrows were favored in 1965 and Ovenbirds in 1966, or (2) a competitive situation may exist in which the presence of Song Sparrows prevented the occupation of the area by Ovenbirds in 1965 (the reverse, that Ovenbirds in 1966 prevented utilization by Song Sparrows, is also conceivable). In favor of the first hypothesis is the fact that the other forest edge species in Sugarloaf Bog were also scarcer in 1966 than 1965. Individually all of the declines were slight (Cardinal, 1.3 to 0.6 males on the 4.6-acre strip; towhee, 0.8 to 0; and Catbird, 0.2 to 0), but the decline of the whole group possibly has significance. There was, however, no evident change in the habitat except that the peat surface was slightly wetter in 1966. This would seem to favor Song Sparrows over Ovenbirds because Song Sparrows do not avoid hydric habitats, whereas Ovenbirds tend to be more common in mesic situations. Standing water also decreases the area available for nests of the exclusively ground-nesting Ovenbird.

Relevant to hypothesis 2 are the following points: (a) The two species are similar enough in feeding, nesting, and singing sites that they could be competitors if they occurred together; (b) Their ecological distribution is such that only in a few communities, somewhat marginal for both, are they likely to come into contact; (c) Spring territory establishment of Song Sparrows precedes that of Ovenbirds (in southwestern Michigan mid-April or earlier compared with early May). If interspecific territoriality existed, Song Sparrows would have the advantage of possession; (d) Interspecific territoriality is prominent in Song Sparrows (Nice, 1943:158-161; Tompa, 1964), although I am not aware of any instances involving Ovenbirds; (e) Bog forest is probably used by both species mainly by overflow populations from more nearly optimal vegetation. The open bog and thicket areas of Portage Bog, two miles from Sugarloaf, represent nearly optimal conditions for Song Sparrows. In 1965 numbers were the highest in six years and in 1966, the second lowest (Table 1). It is possible that population changes in optimum habitats are only a very subdued reflection of actual population

changes (Brewer, 1963; Kluyver and Tinbergen, 1953); it is perfectly feasible that there were substantial surplus sparrows in 1965 and few or none in 1966.

It is hoped that observations during territorial establishment will allow a choice between the two hypotheses.

In a sense the presence of Ovenbirds and Song Sparrows in Sugarloaf Bog depends on adjacent vegetation types. This was also true of Yellowthroats, which had high populations on the bog mat and occasionally extended their activities as far as the census strip. The Acadian Flycatcher (*Empidonax virescens*) was an interesting contrast. Although quite common in upland forest, including the part immediately adjoining the bog forest, it seemed never to penetrate the bog forest more than five or ten feet, and that only rarely.

Estimation of population size was difficult for the Veery. It sang steadily on the border between bog forest and open bog (about three males), rarely on the border between bog forest and upland forest, and almost never within the bog forest. I suppose that territories may extend across the bog forest, but I have not tried to estimate density.

About one-third of the breeding species and individuals were hole-nesters. This is probably related to the large number of dead elms (of Dutch elm disease) and yellow birch suitable for excavation.

OBSERVATIONS AT PORTAGE BOG OUTSIDE THE BREEDING SEASON

The mean number of species recorded per visit during June and July was 10. For August it was slightly less, 9; but about the end of August there appears to be a rapid exodus from the bog so that the mean number for September and October is 5. The sparseness of the bird population in the bog at this time compared with the deciduous areas near it is quite noticeable. Most of the prominent birds of the bog, towhee, Song Sparrow, Yellowthroat, Catbird, are still to be found in numbers in the aspens and bog birches along the drainage ditch when they are virtually absent from the census tract. Of several possible explanations, a post-breeding emigration into different vegetation types seems most likely; why this would occur is not evident.

Winter populations were low; on two December trips of about an hour each, no birds were seen on the census plot. The average number of species seen per trip was 2 for November, less than 1 for December, and slightly more than 1 for January–March. Only Blue Jay (seen on 5 trips), Black-capped Chickadee (4), and Eastern Goldfinch (2) occurred on more than one of the 13 winter trips.

The extreme sparseness of the bird population in winter is probably related to a poor food supply, although the flatness of the peatland, resulting in lack of protection from wind, may also be involved. It is evident from an examination of the list of plant species present in Portage Bog (Brewer, 1966) that fruits and seeds are not likely to be in good supply in the winter. Tamarack, which might be thought to provide a fairly rich supply, sheds its seeds in the autumn. Duncan (1954) found that in Minnesota about 97 per cent of tamarack seeds had fallen before 31 October. I have no direct evidence that invertebrates are scarcer in bogs than elsewhere in winter, but in view of the substantial amount of energy that becomes tied up in peat and thus does not become available to other trophic levels, this seems a reasonable possibility.

BREEDING BIRD POPULATIONS OF EASTERN NORTH AMERICAN BOGS

Ecological and zoogeographic relationships of bogs were studied by means of compilations including previous studies. Both censuses and studies giving lists of characteristic species for a particular area were used. All such studies that I am aware of were included except those conducted on areas of heterogeneous vegetation or on excessively small and isolated areas.

The study areas were grouped into open bog (8 areas), thicket (8), and forest (17) using physiognomic criteria. Forests were further classified into those of pure or nearly pure tamarack, those with spruce as a dominant or co-dominant, those with cedar as a dominant or co-dominant, and those with both coniferous and broad-leaved trees important.

The specific areas used were as follows:

Open Bog—Martin (1959, 1960), wet bog and dry bog; Jackson (1914), sedge and cassandra associations; LeFebvre (1959), open sedge mat; Root (1942), bog mat association; Aldrich (1943), *Chamaedaphne calyculata* consocieties; and open wet and dry areas of Portage Bog.

Thicket—Buckner and Turnock (1965), Plot II; LeFebvre (1959), bog birch; Root (1942), lowland thicket and dead tree associations; Aldrich (1943), *Nemopanthus-Alnus* association; Stewart and Aldrich (1952), scrub black spruce bog and bog shrubs; Robbins and Stewart (1951), scrub spruce bog; and high and low thickets of Portage Bog.

Tamarack Forest—Buckner and Turnock (1965), Plot I; LeFebvre (1959), tamarack; Goodwin and Jarvis (1964), Fairfield, Jarvis, and Woodford (1960), tamarack swamp; and tamarack forest of Portage Bog.

Spruce Forest—Jackson (1914), tamarack-black spruce association; Walkinshaw (1949), black spruce-tamarack bog; Martin (1959, 1960, and pers. comm.), *Picea mariana* and *P. mariana-Thuja* forests; Stewart and Robbins (1951), virgin spruce-hemlock bog forest.

Cedar Forest—Breckenridge (1955), bog forest habitat; Jackson (1914), cedar-balsam-hemlock association; Root (1942), cedar bog association; Kendeigh (1948),

TABLE 3
PERCENTAGE FREQUENCY OF OCCURRENCE (AND MAXIMUM DENSITY) IN BOG VEGETATION
TYPES

Species	Open bog	Thicket	Tamarack forest	Spruce forest	Cedar forest	Mixed forest
American Bittern (<i>Botaurus lentiginosus</i>)	38	25	0	0	0	0
Marsh Hawk (<i>Circus cyaneus</i>)	38	12	25	0	0	0
Ruffed Grouse (<i>Bonasa umbellus</i>)	0	0	25	20	67	40
Virginia Rail (<i>Rallus limicola</i>)	25	0	0	0	0	0
Sora (<i>Porzana carolina</i>)	38	0	0	0	0	0
Mourning Dove (<i>Zenaidura macroura</i>)	12	25	50	20	33(11)	20
Yellow-shafted Flicker (<i>Colaptes auratus</i>)	25	62	50	80	50	80
Pileated Woodpecker (<i>Dryocopus pileatus</i>)	0	0	0	20	50	40
Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>)	0	12	25	20	17	20
Hairy Woodpecker (<i>Dendrocopos villosus</i>)	0	38	0	20	67	60
Downy Woodpecker (<i>D. pubescens</i>)	0	38	0	0	17	60(16)
Eastern Kingbird (<i>Tyrannus tyrannus</i>)	50	25	25	0	33	0
Great Crested Flycatcher (<i>Myiarchus crinitus</i>)	0	25	25	20	50(14)	80(15)
Eastern Phoebe (<i>Sayornis phoebe</i>)	0	25	50	0	0	0
Yellow-bellied Flycatcher (<i>Empidonax flaviventris</i>)	0	25	25	60(22)	33(22)	0
Traill's Flycatcher (<i>E. traillii</i>)	12	50	50	20	0	0
Least Flycatcher (<i>E. minimus</i>)	0	25	25	0	50	20
Eastern Wood Pewee (<i>Contopus virens</i>)	0	0	25	0	33	60(26)
Olive-sided Flycatcher (<i>Nuttallornis borealis</i>)	12	25	25	40	33	0
Tree Swallow (<i>Iridoprocne bicolor</i>)	38	25	0	0	0	0
Barn Swallow (<i>Hirundo rustica</i>)	25	0	0	0	0	0
Blue Jay (<i>Cyanocitta cristata</i>)	12	25	25	60	67	80(22)
Common Crow (<i>Corvus brachyrhynchos</i>)	0	0	0	40	17	60
Black-capped Chickadee (<i>Parus atricapillus</i>)	25	75	75(13)	60	100(19)	100(40)
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	0	0	0	0	33	40
Red-breasted Nuthatch (<i>S. canadensis</i>)	0	0	25	60	84	20(12)
Brown Creeper (<i>Certhia familiaris</i>)	0	0	25	40	33	20(12)
House Wren (<i>Troglodytes aedon</i>)	0	25	0	0	17	20

TABLE 3 (*Cont'd*)

Species	Open bog	Thicket	Tamarack forest	Spruce forest	Cedar forest	Mixed forest
Winter Wren (<i>T. troglodytes</i>)	0	0	25	80	50	20
Catbird (<i>Dumetella carolinensis</i>)	12	50(11)	50	20	17	60
Brown Thrasher (<i>Toxostoma rufum</i>)	0	25	25	0	17	0
Robin (<i>Turdus migratorius</i>)	0	38(11)	75	0	33	40(14)
Wood Thrush (<i>Hylocichla mustelina</i>)	0	0	0	20	33	80(13)
Hermit Thrush (<i>H. guttata</i>)	0	38(19)	25	40	17	20(21)
Swainson's Thrush (<i>H. ustulata</i>)	0	25(14)	25	60	17	20
Veery (<i>H. fuscescens</i>)	0	25	25(18)	20	84(18)	80
Golden-crowned Kinglet (<i>Regulus satrapa</i>)	0	12	25	100(32)	50(15)	40(32)
Cedar Waxwing (<i>Bombycilla cedrorum</i>)	38	62(11)	75(27)	60	67	20
Red-eyed Vireo (<i>Vireo olivaceus</i>)	12	12(42)	50(16)	0	50	60(16)
Black-and-white Warbler (<i>Mniotilta varia</i>)	12	25(11)	50	60	67(19)	60
Tennessee Warbler (<i>Vermivora peregrina</i>)	0	25(22)	25	0	17	20
Nashville Warbler (<i>V. ruficapilla</i>)	0	62(39)	100(55)	60(28)	100(28)	40
Parula Warbler (<i>Parula americana</i>)	0	0	25	0	50	40
Yellow Warbler (<i>Dendroica petechia</i>)	0	50(10)	25	20	0	0
Magnolia Warbler (<i>D. magnolia</i>)	0	38(33)	25	100(40)	50(27)	60(40)
Myrtle Warbler (<i>D. coronata</i>)	12	38	25	60	50	20
Black-throated Green Warbler (<i>D. virens</i>)	0	0	0	20	33(18)	40(26)
Blackburnian Warbler (<i>D. fusca</i>)	0	38(39)	25	60(96)	67(13)	60(96)
Chestnut-sided Warbler (<i>D. pensylvanica</i>)	12	38	0	20	33	0
Ovenbird (<i>Seiurus aurocapillus</i>)	12	0	0	0	50	60(38)
Northern Waterthrush (<i>S. noveboracensis</i>)	0	25(33)	25	60(64)	33	60(64)
Yellowthroat (<i>Geothlypis trichas</i>)	75(134)	100(55)	100(32)	60(26)	50(29)	60(13)
Canada Warbler (<i>Wilsonia canadensis</i>)	0	38(22)	50	60(44)	50(12)	60(44)
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	75(12)	12	25	0	0	0
Common Grackle (<i>Quiscalus quiscula</i>)	25	0	0	0	0	20
Brown-headed Cowbird (<i>Molothrus ater</i>)	25	25(25)	50	0	17(13)	40
Scarlet Tanager (<i>Piranga olivacea</i>)	0	12	25	40	67	80(18)
Cardinal (<i>Richmondia cardinalis</i>)	12	12	50	0	0	40(20)

TABLE 3 (*Cont'd*)

Species	Open bog	Thicket	Tamarack forest	Spruce forest	Cedar forest	Mixed forest
Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>)	0	12	50	0	17	20
Purple Finch (<i>Carpodacus purpureus</i>)	25	50	50(15)	60	50	20
American Goldfinch (<i>Spinus tristis</i>)	25	12	50	20	17	20
Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>)	25	50(24)	25	0	17	20
Slate-colored Junco (<i>Junco hyemalis</i>)	0	38(13)	0	80	50	20(14)
White-throated Sparrow (<i>Zonotrichia albicollis</i>)	0	38(61)	50(39)	80(62)	100(48)	40(14)
Swamp Sparrow (<i>Melospiza georgiana</i>)	75(176)	50	50	20	17	20
Song Sparrow (<i>M. melodia</i>)	75(51)	88(63)	75	20	50	40(13)

cedar-balsam forest; Martin (1959, 1960, and pers. comm.), *P. mariana*-*Thuja* forest; Stewart and Aldrich (1952), white cedar-tamarack-black ash bog forest.

Mixed Coniferous-Deciduous Forest—Sugarloaf Bog; Aldrich (1943, also 1939), *Larix*-*Acer*-*Betula* association; Stewart and Aldrich (1952), white cedar-tamarack-black ash bog forest; Smith (1938, 1941, 1943, 1944, and 1945), balsam-black ash bog; Stewart and Robbins (1951), virgin spruce-hemlock bog forest.

Community relationships.—The categories given above (and in Table 3) are of descriptive value but otherwise have no fundamental significance. The breeding birds of one open bog are not greatly like those of another; the avifauna of one spruce forest is rather like that of another, but it may be equally similar to that of a cedar forest or a spruce thicket.

If we attempt to determine in what vegetation types the peaks of occurrence for various species fall, they appear to be equally scattered through the whole series from open bog to mixed forest (Table 3). If we pursue the matter, however, by preparing other lists for pure deciduous forest in the same geographical areas, non-bog spruce-fir forest, etc., it becomes evident that the peaks of occurrence tend to fall into four groups corresponding to marsh, thicket or forest edge, spruce-fir forest, and deciduous forest. The species which seemingly peak at tamarack forest, between spruce and cedar bog, etc., virtually all have still higher peaks in one of these four types. If we recognize these four ecological groups (which appear to correspond to the biociations and biocies of Kendeigh, 1948) we can make the following statements:

(1) The avifauna of open wet bogs is not closely related to other bog types, being made up of wide-ranging marsh species such as rails, American bittern, Red-winged Blackbird, and Swamp Sparrow.

(2) Open dry bogs are depauperate forest-edge communities possessing those species able to exist with a minimum of taller woody growth (e.g., Song Sparrow, Yellowthroat).

(3) The avifauna of thickets is a conglomeration of species, mainly forest-edge (such as Yellow Warbler, Traill's Flycatcher, Rufous-sided Towhee) but also with species from adjacent forests (e.g., Downy and Hairy woodpeckers, Hermit Thrush, and several warblers).

(4) Bird populations of tamarack forests are likewise conglomerations of thicket and forest species. The species that within the bog sequence reach their peak of frequency in tamarack forest (e.g., Phoebe, Brown-headed Cowbird, Rose-breasted Grosbeak, American Goldfinch) are probably all still more frequent in some non-bog vegetation.

(5) Spruce bog populations are composed primarily of spruce-fir forest species such as Yellow-bellied Flycatcher, Swainson's Thrush, Golden-crowned Kinglet, Hermit Thrush, Myrtle Warbler, Winter Wren, Magnolia Warbler, Brown Creeper, Purple Finch, and Slate-colored Junco. There are few very striking differences in species composition between spruce bogs and mature spruce-fir forests on non-peat sites. The Olive-sided Flycatcher is perhaps more apt to occur in spruce bogs, and the Solitary Vireo (*Vireo solitarius*), Cape May Warbler (*Dendroica tigrina*), and Bay-breasted Warbler (*D. castanea*) are probably more frequent in spruce-fir forests.

(6) Cedar forests share species of spruce-fir forest (e.g., Winter Wren, Yellow-bellied Flycatcher, Slate-colored Junco, Purple Finch) and deciduous forest (e.g., Hairy Woodpecker, Wood Pewee, White-breasted Nuthatch, Red-eyed Vireo).

(7) Mixed forests likewise have birds both of spruce-fir and deciduous forest, with the latter more prominent than in cedar forest. Virtually all of the species in the bog sequence reaching their highest frequency in mixed forest (e.g., Wood Pewee, Ovenbird, Scarlet Tanager) have still higher peaks in pure deciduous forest. Mixed bog forests and pure deciduous, non-bog forests differ in three ways: (a) The spruce-fir species that persist at varying frequencies in mixed forest are generally absent in deciduous forest. (b) Several forest-edge species have rather high frequencies in mixed bog forest but are scarce in pure deciduous forest. I suspect that this is related to the presence of a dense shrubby and herbaceous cover through the summer in mixed bog forest (see Brewer, 1966:44). (c) Many deciduous forest species have higher frequencies in pure deciduous forest than in mixed forest.

(8) A few species have rather obvious peaks in cedar or cedar-mixed forest and do not seem still more characteristic of pure deciduous forest or pure spruce-fir forest. These include Red-breasted Nuthatch, Black-throated Green Warbler, Parula Warbler, Black-and-white Warbler, and Veery. The first three of these Martin (1960) assigns to a hemlock forest community. This may be correct; nevertheless, in comparing species lists for pure hemlock forests and hemlock-white pine-northern hardwoods forests, I see few differences other than the absence of a few species from pure hemlock. Such species as Black-and-white Warbler, Black-throated Green Warbler, Black-throated Blue Warbler, and Yellow-bellied Sapsucker appear to reach their peak frequencies in hemlock-pine-hardwood forests. This may also be the case for the Veery. The Red-breasted Nuthatch does not seem to be a member of this group; Fawver (cited in Kendeigh, 1961), in contrast to Martin (1960), found the species to be more common in spruce-fir than in hemlock. Possibly the answer is that this species is, in fact, most characteristic of neither of these, but cedar forest instead.

A second way of looking at the community relationships of bog bird populations is this: the species present in any given stand of bog vegetation depend not only on the vegetation of that stand but also upon the geographical ranges of species able to utilize the vegetation and further upon adjacent vegetation and the birds occurring there. The latter point is particularly important in bog communities because they generally occur in relatively small patches surrounded by dissimilar vegetation. Examples have already been given in the occurrence of Yellowthroats, Ovenbirds, and Song Sparrows in Sugarloaf Bog and in the effect of a fire in adjacent vegetation at Portage Bog. To illustrate the geographic effect, the southwestern Michigan bogs have no White-throated Sparrows for the simple reason that the southern limit of this species lies well to the north (however complicated the interactions of climate, physiology, etc. that set this limit).

Furthermore, when it is stated that the species present in a given stand are, in part, determined by the vegetation of that stand, it is not meant that the birds select marsh, thicket, spruce-fir forest, or deciduous forest as such. Presumably they behave in habitat selection as they do in other areas of their life and tend to establish themselves in areas possessing features that act as a series of releasers for, perhaps, investigation of an area, establishment of a territory, etc. (Svärdson, 1949). Doubtless these features are those generally associated with the presence of certain environmental factors required for the birds' existence. In some cases we may see some fairly obvious feature such as the presence of dead trees suitable for nesting cavities with which the occurrence of certain species is correlated. Given this factor, the species may occur in stands of otherwise greatly variable vegetation.

Such observable features may be the releaser or the requisite, or both, or neither but merely some additional features associated with one or the other.

The "typical" birds of a given kind of vegetation are not all of a piece. No two show exactly the same distribution when examined stand by stand. "Deciduous forest species," for example, may be such for quite dissimilar reasons. Ovenbirds, Kendeigh (1945:428) suggests, may require broad leaves for use in nest building. Scarlet Tanagers, on the other hand, appear to require "deciduousness" rather than "broad-leavedness." They tend to be present in bog forests with a deciduous element whether provided by broad-leaved trees or by the needle-leaved but deciduous tamarack. Their dependence on deciduousness may be related to illumination in the spring. Prescott (1965) has described courtship activities involving display of the red back by males perched near the ground to females in the canopy that seem to demand good light penetration.

Because the bird population of a given stand of vegetation is a product of so many factors—the geographical location of the stand, the surrounding vegetation, and a great variety of structural features of the vegetation—we cannot expect to find a given community displaying much unity. This lack of unity is both geographical, in that a given spruce bog is likely to have fewer and fewer species in common with other spruce bogs located at greater and greater distances, and vegetational, in that there is no tendency for "spruce bog" to have a well-defined group of species occurring in about the same relative numbers over the whole variety of vegetational conditions that can be contained in the term "spruce bog." Rather we find the avian composition shifts as we move from tamarack-spruce to pure spruce to spruce-cedar or from spruce forest with small trees and openings to spruce forest of large trees and a closed canopy.

The two foregoing discussions represent, I believe, the organismic and the individualistic views of communities as they can be applied to bog bird populations. Briefly, for those unfamiliar with this controversy (Curtis, 1959; Goodall, 1963; Daubenmire, 1966), the concepts differ as follows: Given a region occupied by biota, the individualistic view holds that each species occurs independently of others in those spots it is able to disperse to and survive in. Further, the conditions under which each species survives and prospers differ from those of every other species. As a consequence, the biota of a given piece of ground is simply a gathering of those species finding it within their tolerances. A usual corollary to the individualistic view is the continuum approach to describing biota: the biota is supposed to vary continuously in time and space, and each point of the continuum is equally probable. In other words, if a certain combination of species is

termed oak-hickory forest and another combination, beech-maple forest, every intermediate between these two combinations is possible and, in fact, just as likely to occur as oak-hickory or beech-maple forest.

The organismic concept regards the biota as being integrated. The emphasis is upon interactions among community associates rather than upon the responses of a single individual to its environment. As a consequence, proponents of the organismic concept generally adopt a classificatory approach to the description of biota, regarding various combinations of species as being more probable than others, the "others" representing transitions. The greater probability of certain combinations is viewed as the result of activities of the community, such as production of a mature soil, development of a certain level of shading, establishment of food chains, etc.

If these are fair statements of the two positions, I believe that both are, to a degree, correct. One possible area of reconciliation in the interpretation of bog bird populations is that of paleoecological history.

The broad-leaved deciduous forests of eastern North America are the product of a long period of development, largely from the temperate portion of the Arcto-Tertiary Geoflora (Braun, 1950). The now extensive boreal forest is probably a product of the Pleistocene (Braun, 1950:511; Mengel, 1964:10); at least, there are no known Tertiary floras so heavily dominated by spruce, fir, and similar coniferous forms. The bog sere of glaciated North America is also doubtless a product of the Pleistocene, constituted of plants from a variety of pre-glacial sources.

I shall suggest that the number of species typical of a certain kind of vegetation (i.e., having their peak of occurrence there) is strongly dependent on the opportunity for species to adapt to this vegetation. Three prime considerations in this opportunity are (1) time of existence of the vegetation; (2) area occupied by the vegetation; and (3) the number of species already able to use the vegetation. The opportunity for adaptation to eastern deciduous forests has been extensive because of the long period of their existence and the rather large area occupied. The opportunity for adaptation to spruce-fir forest has also been of large magnitude (as Mengel (1964) has pointed out), representing as it did a large area of vegetation of a kind previously unavailable. The bog communities of open wet bog, open dry bog, bog thicket, tamarack forest, and cedar forest offered much less of an opportunity for several reasons: bog communities tend to occur as small patches surrounded by different kinds of vegetation. They tend also to be short-lived in any one place, disappearing through successional processes. Finally, open wet bog duplicates in many structural features the ancient marsh vegetation type, and open dry bog, thicket, and tamarack duplicate in many features

forest-edge vegetation such as occurred along streams, cliff-edges, etc. throughout the history of the eastern deciduous forest. Thus, many species were probably already available to occupy these types.

It seems entirely reasonable then that we may recognize four "clumps" of species corresponding to conditions of the ancient communities of marsh, deciduous forest, and deciduous forest edge and to the new spruce-fir forest community. It seems possible that a few species might find themselves pre-adapted for success in tamarack or cedar forest or in coniferous forest edge (largely provided by bogs) and might fairly rapidly become adjusted in their habitat selection and life history to these communities. The Nashville Warbler appears to come close to such a species for coniferous forest edge-tamarack, and the Olive-sided Flycatcher may represent another coniferous edge species. Possibly the Red-breasted Nuthatch is such a cedar forest species.

I suspect that the hemlock-white pine-hardwood forests represent another community to which adaptation of several species has occurred and which has supplied species to mixed bog forests; however, the history of the former vegetation type is not clear (Braun, 1950:528).

Both the organismic and individualistic concepts, in their usual practice, have failed to take adequate account of historical and evolutionary factors in community organization. The organismic concept seems to consider all communities as equally well integrated and, by implication, equally ancient. The individualistic concept seems to ignore history, except that of the individual stand, altogether.

It is scarcely possible to deny the existence of biotic continua, in the sense that when the abundance of species is plotted against a real or hypothetical environmental gradient a series of curves with differing modes and amplitudes is produced. The existence of continua, however, seems to favor the organismic concept. Given an area of deciduous forest for existence and adaptation, there seems every reason to believe that different species, as they experienced differential success resulting from competition, would become adapted to somewhat different conditions. I see little difference between this form of organization and such forms as stratification and aspection. In all three cases, the environment is divided up in a manner suggesting that the presence of other species has been important in the evolutionary processes producing such partitioning. The view that such organization depends solely on the combination at a particular time and place of species having tolerances and life histories that happen to fit one another and the physical environment is almost perfectly correct if all we are interested in is the instantaneous description of an individual stand; but it is incomplete.

TABLE 4
ZOOGEOGRAPHIC RELATIONS OF THE BREEDING BIRDS OF VARIOUS BOG VEGETATION
TYPES (PERCENT OF SPECIES IN EACH FAUNAL GROUP)

Vegetation	Unanalyzed	Non-passerine	Boreal	Eastern ecotone	Eastern deciduous forest
Open	50	30	20	0	0
Thicket	26	13	35	22	4
Tamarack Forest	36	9	22.5	22.5	9
Spruce Forest	11	7	54	21	7
Cedar Forest	14	14	31	25	16
Mixed Forest	18	15	12	27	27

Zoogeographic relationships.—All species of at least 33 per cent frequency in each vegetation type (Table 3) were assigned to faunal groups (Udvardy, 1964). (Complete species lists for each vegetation type were not used because many species of low frequency may be represented for some nearly accidental reason, such as the presence of some favorable vegetation adjacent to a single study area.) This analysis supports the conclusions drawn in preceding sections. The early successional stages of open bog, thicket, and tamarack forest show high percentages of the wide-ranging species of the unanalyzed element (Table 4). Open bog, by virtue of its marsh birds, has a high percentage of non-passerine species. Spruce bogs are heavily dominated by boreal forest species; cedar forest has fewer boreal species and mixed forest still fewer. Eastern deciduous forest species show the reverse trend, increasing from boreal through cedar to mixed forest.

To return to the question of bogs as boreal islands, we may examine the percentages of boreal species occurring on the individual study areas. Given in Figure 4, these show a strong latitudinal trend, northern bogs having high percentages and southern bogs low.² At the latitude of northern Michigan it is reasonable to regard bog forests as boreal islands because both the actual and the presumed potential general vegetation of the region has a substantially lower percentage of boreal birds. For example, the beech-maple-pine forest in Cheboygan County (45.5° N. lat.) reported on by Kendeigh (1948) had only 12.5 per cent boreal species compared with values from 16 to 37 per cent for bog thickets and forests in the area. Farther north, however, the concept has less validity because the region in general is rather strongly boreal. For Aroostook County, Maine, Stewart and Aldrich

² Some of Udvardy's eastern ecotone species could be considered "boreal." I have preferred to use Udvardy's groups rather than risk the possible circularity involved in constructing my own. In any case, expansion of the boreal category to include group 1 of Udvardy's eastern ecotone fauna would not change the trends described.

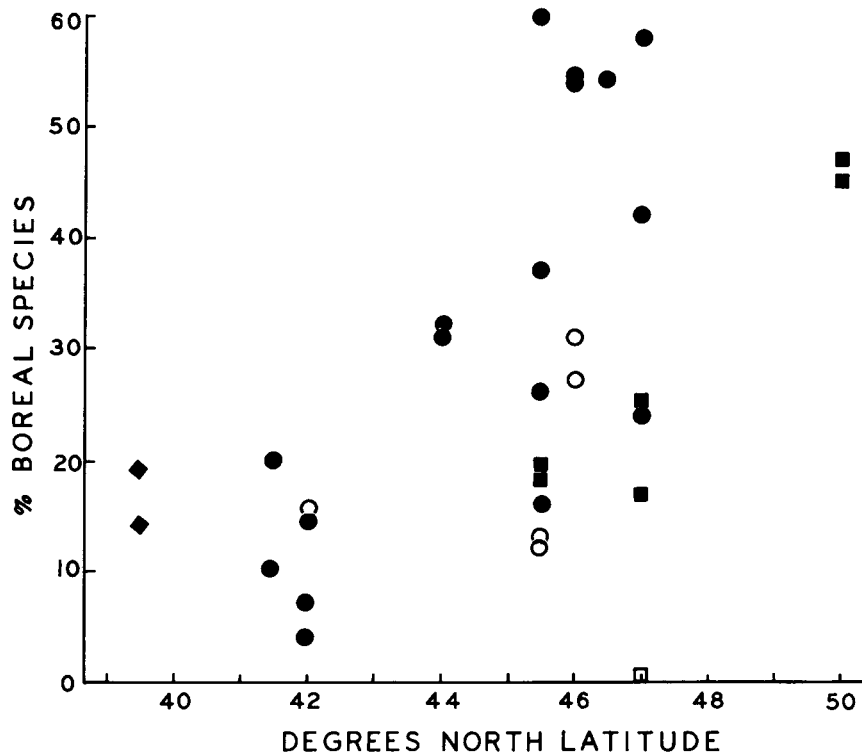


FIG. 4. Relationship between percentage of boreal species in the avifauna of 31 bog areas and latitude. Open symbols represent open bog, squares represent western areas (Minnesota and Manitoba), and diamonds, Appalachian areas (Maryland).

(1952) state that a mixed hemlock-hardwood-spruce-fir forest is probably the climax vegetation. One such forest for which they give census data had 33 per cent boreal species compared with values from 24 to 58 for bog thickets and forests of the area. In Ontario, if hemlock forest is indeed climax (as Martin, 1959, states), the percentage of boreal species in the potential prevailing vegetation of the area is 50 per cent compared with 54 per cent for spruce and spruce-cedar bog forests (Martin, 1960).

As one proceeds south from northern Michigan, the percentage of northern species declines. A comparison between Portage Bog and a tamarack bog in Ontario (Goodwin and Jarvis, 1964) illustrates this. The Ontario area has a much higher percentage of tamarack forest and much less open bog, but having allowed for these differences, the dissimilarity of avian populations is still striking. The two areas have 12 species (out of 40; 30

per cent) in common. Present on the Ontario area but absent from Portage Bog are such northern species as White-throated Sparrow, Canada Warbler, Red-breasted Nuthatch, Brown Creeper, Winter Wren, and Purple Finch. No similar array of species replaces these in the south, and as a result Portage Bog has a much less diverse avifauna (mean number of species per year about 16 compared with about 20 for the Ontario area).

The entire boreal element of the two southwestern Michigan areas consists of Tree Swallow, Black-capped Chickadee, and Traill's Flycatcher. All three are widely distributed in non-bog vegetation in southwestern Michigan and farther south. More to the point as boreal, or at least northern species, are the Nashville Warbler at Portage Bog and the Black-throated Green Warbler at Sugarloaf Bog. Both are rare in southwestern Michigan, and the Nashville Warbler probably would not be present if bog vegetation were not present. Black-throated Green Warblers, however, have been reported as summer residents elsewhere in the region in non-bog forests (e.g., MacArthur, 1964). And finally, such good boreal species as the Brown Creeper (Walkinshaw, 1948) and the Winter Wren (Wallace, 1944) have spent the summer (and nested in the case of the creeper) in two Michigan localities of about the same latitude as Kalamazoo County. Neither record was from a bog. In sum, the concept of bogs as boreal islands seems to have no validity when applied to bird populations of southwestern Michigan.

A few other trends in the percentage of boreal species are also present. Open bogs are not particularly boreal in character whether located north or south. It must be remembered that open bogs have a high proportion of non-passerine and thus unclassified species; however, I do not think the conclusion would be substantially altered if the non-passerines were assigned to faunal groups. There appears also to be a trend toward increased numbers of boreal species in the Appalachians, as might be expected, and a decrease westward such that the Minnesota bogs and even those of Manitoba rate rather low in comparison with others of the same latitude.

Succession.—Table 3 lists all species occurring in at least two open bogs, two bog thickets, and four bog forests (i.e., all species having about a 25 per cent frequency or greater in one of the three types). Frequency and maximum reported density (mean number of males per 100 acres; only values over 10 included) for each species in each of the six vegetational categories are given. This compilation is of descriptive value for two reasons. First, it is often handy to categorize bog vegetation into these six types and, within the already stated limitations of geographic and local variation, the lists indicate the prevailing avifauna of these vegetational categories. Second, the sequence open bog to mixed forest is a frequent successional pathway in northern Michigan (Gates, 1942). The table may be taken as a generalized

summary of bird succession in bogs if it is borne in mind that no real bog in northern Michigan or elsewhere is likely to exhibit just such a sequence of species. This is true because (a) succession of bird species in a given bog will have a strong local character because of differing geographical ranges of species, the influence of surrounding vegetation, and peculiarities of particular situations as they influence the structure of the vegetation, and (b) vegetational succession is itself highly variable both between and within regions. The sequence given is frequent in northern Michigan, but it often happens that spruce enters without an intervening tamarack stage. In southwestern Michigan spruce and cedar are essentially absent and here the succession may be from open bog to tamarack thicket to tamarack forest to mixed forest.

Within a restricted geographical area, there appears to be a decrease in number of species from open wet bog to open dry bog and then an increase from open dry bog through thicket and forest. Probably these trends are related to a loss of marsh growth forms followed by the addition of low and then high woody strata. When numbers of species for given vegetation types are examined over larger geographical areas, however, these trends largely disappear; open dry bog is consistently low in species, but otherwise numbers overlap widely. This situation appears to result from the differing distributions of species able to make use of the various vegetation types. Specifically, it seems to be related to the decrease of boreal and eastern ecotone species southward and westward and the extent to which deciduous forest and forest-edge species enter the various vegetation types.

Although densities as reported here for southwestern Michigan increased directly from open bog to thicket to mixed forest, this trend was not general. In Ontario, for example, open bogs had 50–100 more males per 100 acres than bog forests (Martin, 1960). Neither were there obvious geographical trends in population size.

SUMMARY

Bird populations were studied on two bog areas in southwestern Michigan. One, a sphagnum-leatherleaf-tamarack bog, had an average of about 16 breeding species per year and an average density of about 170 males per 100 acres. Song Sparrow was by far the most abundant species; Yellowthroat, Rufous-sided Towhee, and Field Sparrow were also numerically important. All but the last showed higher densities in thicket compared with open parts of the bog. Most of the birds were forest-edge species of wide geographical range. Populations were sparse outside the breeding season, probably because of a poor food supply.

The second area, a yellow birch-red maple-white pine bog forest, had about 20 breeding species a year. Density was about 270 males per 100 acres. Black-capped Chickadee, Ovenbird, Wood Pewee, Blue Jay, Cardinal, Scarlet Tanager, and four other species had densities greater than 10 per 100 acres. Between 1965 and 1966, the number of Ovenbirds greatly increased and Song Sparrows greatly declined.

Two ways of viewing bog bird communities are set forth. The first, classificatory or organismic, recognizes four main ecological groups of birds occurring in bogs (marsh, thicket or forest edge, spruce-fir forest, and deciduous forest), while acknowledging that any given stand may contain elements of more than one group. The second, individualistic, view emphasizes the tendency for each species to be distributed accordingly as it encounters suitable habitat within its range of geographic occurrence. The second view is essentially correct for the instantaneous description of a stand, but it seems not to give sufficient weight to historical and evolutionary factors.

The concept of bogs as boreal islands is valid for a certain range of latitudes. North of this, bogs are not much more boreal than surrounding vegetation and southward the number of boreal species rapidly diminishes until in southwestern Michigan there is practically no boreal character to the bird population.

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