

BREEDING BIRDS OF TWO FLORIDA WOODLANDS: COMPARISONS WITH AREAS NORTH OF FLORIDA

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Florida has witnessed the forays of ornithologists since the times of Bartram and Audubon, but few investigators have remained in one locality long enough to gain a detailed knowledge of its avifauna. Consequently the distribution of the breeding birds of Florida, and especially the landbirds, is poorly known, and measurements of their densities are almost entirely lacking. This report describes the results of censuses of two deciduous woodland habitats in Florida. We know of only two other censuses in broad-leaved forests within the state. Since it has been suggested that the breeding landbird fauna of peninsular Florida is impoverished compared with that of continental eastern North America (Robertson 1955), in the second part of this paper we compare the Florida censuses with certain ones made farther north in the eastern United States.

PART I: THE SAWGRASS LAKE STUDY AREA

Sawgrass Lake lies in the southern third of Pinellas County, 4.8 miles north and 1.9 miles west of the city hall of St. Petersburg. It is the only extensive fresh-water swamp and wet woods near the city. The area is bounded to the north and northeast by pine flatwoods and pasture, and on the other sides by encroaching suburbs. Our two study plots of 96 and 30 acres lay in the main body of woods northeast of the lake; they were bounded to the west by the interior edge of the lake ecotone and on the other three sides by canals.

Study of the breeding avifauna of the Sawgrass Lake deciduous woodlands was conducted as a part of a larger investigation of the ecologies of arbovirus in the Tampa Bay region of Florida. Pinellas County forms the

western boundary of this bay. The Tampa Bay region has been the scene of three outbreaks of human St. Louis encephalitis since 1959, the last and major epidemic of 1962 being the second largest recorded in the United States. Virtually all of the approximately 60 square miles of Pinellas County south of Sawgrass Lake are occupied by the suburbs of St. Petersburg, an area from which numerous cases of encephalitis were reported in the epidemic year of 1962. Since the Sawgrass Lake swamp and wet woods support a high population of mosquitoes, studies of both vector and vertebrate populations were conducted here in an attempt to link the life histories of arboviruses with their hosts.

PROCEDURES

Censusing began on 21 January and terminated on 19 September 1964. During this period 48 visits during which both of us were usually present were made at no greater than weekly intervals; altogether these totaled approximately 250 man-hours. Several additional visits were made in 1965.

In 1964 densities of breeding species were estimated by systematically traversing our two plots (though they could not be thoroughly worked on any one visit) and recording the number and location of individuals on Xerox copies of aerial photographs. Impressions of density gained in this manner for the 96-acre tract were checked by intensive study of two quadrats wherein all individual birds were counted on every visit.

VEGETATION

Two major habitats occur in the Sawgrass Lake study area, including a red maple (*Acer rubrum trilobum*) wet woods of 96 acres and a mixed oak ridge of 30 acres. The maple woods can be subdivided by its vegetation into three habitats: 6 acres of large maples, 71 acres of small maples, and 19 acres of mixed small maples and coastal plain willows (*Salix caroliniana*). One of our quadrats, 5 acres in

TABLE 1. Trees and shrubs recorded in the three subdivisions of the 96-acre maple wet woods.

	Number of trees	Size range in inches	Average DBH in inches	Modal size in inches
<i>Large Maple Area</i> (359 transect yards)	24 Red maple (<i>Acer rubrum trilobum</i>)	2 -16.5	9.3	10 (4 individuals)
	2 Dahoon (<i>Ilex cassine</i>)	4 - 6	-	-
<i>Small Maple Area</i> (834 transect yards)	192 Red maple (<i>Acer rubrum trilobum</i>)	0.5-14	3.6	2 (35 individuals)
	9 Swampbay (<i>Persea palustris</i>)	1 -10	4.5	4 (3 individuals)
	4 Dahoon (<i>Ilex cassine</i>)	1 - 3.5	-	-
<i>Mixed Small Maple and Willow Area</i> (398 transect yards)	134 Red maple (<i>Acer rubrum trilobum</i>)	0.5-12	2.2	2 (28 individuals) 1 (29 individuals)
	85 Coastal plain willow (<i>Salix carolinana</i>)	1.5- 8.5	3.5	3 (35 individuals)
	16 Buttonwood (<i>Cephalanthus occidentalis</i>)	0.5- 3	1.1	1 (11 individuals)

area, was within the 71 acres of small maples, the other of 3 acres was within the 6 acres of large maples. The 30-acre ridge was dominated by oaks, but contained a small, centrally located, open sand crest. The areas of these subdivisions were calculated from aerial photographs.

The vegetation of each of the four habitats was assessed by yard-wide parallel transects totaling 1989 yards. We recorded the diameter at breast height (DBH) of every tree or shrub within the strip. In the frequent cases of multiple-trunked willows or maples, each trunk was individually recorded. Other than counting the clumps of elderberry (*Sambucus simpsonii*) we made no attempt to record quantitatively the herbaceous vegetation.

The maples in the Sawgrass Lake area grow in low-lying muck soils that were formerly flooded during the summer rainy season. Canals, which were dug as a part of a mosquito control program, presently prevent flooding of much of the maple habitat. The trees and shrubs recorded on the 1591 yards of transect passing through these maple-dominated portions of our plot are summarized in table 1. The dominant undergrowth of these muck-lands was elderberry, 264 clumps of which were recorded. Individuals 10 to 12 feet high were abundant along the well-illuminated canal banks where the maples had been cleared to permit excavation; those of the shaded interior were much smaller and usually bore no fruit. Primrose-willow (*Jussiaea peruviana*) and Caesar weed (*Urena lobata*) were also common on the canal banks but were not found in the shaded interior of the lowlands.

In addition to elderberry the low-growing vegetation of the interior of the maple woods consisted of Virginia willow (*Itea virginica*), pokeberry (*Phytolacca rigida*), wild coffee (*Psycotria nervosa*), and babypepper (*Rivina humilis*). These plants were common but their numbers were not recorded since they were either much smaller or less abundant than the elderberry.

In the area of mixed willows and small maples the willows are being replaced by the maples. Forty-one dead willow trunks (not included in table 1) were recorded on the transect of maple-willow habitat, and all of the living willows were scraggly, having leaves only at their tops. Willows were abundant near the lake (outside of our study area) and apparently are one of the first woody plants to succeed the aquatic herbs; however, as the rotting vegetation turns to muck, maples establish themselves and appear to shade out the willows.

The maples, though apparently healthy, are probably not reproducing themselves. We found no saplings in the large maple quadrat and no seedlings in the entire study area. No bald-cypress (*Taxodium disticum*) or stumps thereof were found in the woodland. Sawgrass (*Mariscus jamaicensis*) was present only in the wetter areas. It appears to have been more widespread in the past, but is being eliminated by the drainage program and the shade of the maples.

In order of decreasing abundance the ground ferns of the muck soils were: royal fern (*Osmunda regalis*), cinnamon fern (*Osmunda cinnamomea*), and giant fern (*Acrosticum*

TABLE 2. Vegetation recorded in the 398 yards of transect crossing the mixed oak ridge.

Plant	Number of individuals	Size range in inches	Average size in inches	Modal size in inches
Saw-palmetto (<i>Serenoa repens</i>)	31	—	—	—
Grape vines (<i>Vitis</i> sp.)	20	1- 4	1.9	1 (12 individuals)
Sweetbay (<i>Magnolia virginiana</i>)	16	1- 8	3.1	3 (4 individuals)
Live oak (<i>Quercus virginiana</i>)	13	2-25	8.0	3 (5 individuals)
Laurel oak (<i>Quercus hemisphaerica</i>)	4	(DBHs 14, 3, 2, and 2 inches)		
Possum-haw (<i>Ilex decidua</i>)	3	(all about 1 inch DBH)		
Black gum (<i>Nyssa biflora</i>) (sp.?)	1	(DBH 16 inches)		

danaefolium); all formed large, elevated racine tussocks.

The mixed oak ridge was surrounded by the maple wet woods. The vegetation of its sandy soils was different and much more complex than that of the muck-lands. Table 2 summarizes its vegetation as recorded in 398 yards of transect. This transect did not cross the white sand crest which was dominated by sand-live oak (*Quercus geminata*). Other plants present on the mixed oak ridge but not in our transect included common persimmon (*Diospyros virginiana*), cabbage palmetto (*Sabal palmetto*), pignut hickory (*Carya glabra*), cherrylaurel (*Prunus caroliniana*), red mulberry (*Morus ruber*), tree sparkleberry (*Vaccinium arboreum*), citrus (*Citrus* sp.), sumac (*Rhus copallium*) greenbriar (*Smilax* sp.), blackberry (*Rubus* sp.), and beautyberry (*Callicarpa americana*). Some Caesar weed also grew around the edge of the ridge but it was more abundant along the canals. One area of the ridge, slightly more than an acre in extent, consisted of a tangle of buckthorn (*Sageretia minutiflora*). The predominant fern was sword fern (*Nephrolepis cordifolia*) which did not form elevated tussocks characteristic of the ferns growing in the muck areas.

Plant identifications and names follow Small (1933, 1938) and Kurz and Godfrey (1962).

RESULTS

Only 12 species of birds bred in the entire Sawgrass Lake area. Estimates of their densities in the two study plots are listed in table 3. Carolina Wrens (*Thryothorus ludovicianus*), Cardinals (*Richmondia cardinalis*), and Yellow-billed Cuckoos (*Coccyzus americanus*) nested in the maple wet woods as well as on the oak ridge. Blue Jays (*Cyanocitta cristata*) and Brown Thrashers

(*Toxostoma rufum*) confined most of their activities to the ridge, as did Screech Owls (*Otus asio*), although in the latter case we have fewer supporting observations. The one pair of Red-shouldered Hawks (*Buteo lineatus*) and their young foraged throughout the woods surrounding the lake. They were never seen in the nearby open country frequented by several Red-tailed Hawks (*Buteo jamaicensis*). The one pair of Green Herons (*Butorides virescens*) regularly seen in the study area spent considerable time elsewhere; the pair of Mourning Doves (*Zenaidura macroura*) also foraged outside of the area but fledged at least one young from a nest on the ridge. The few pairs of White-eyed Vireos (*Vireo griseus*) and Yellowthroats (*Geothlypis trichas*) we recorded confined most of their activities to the canal borders.

Pairs of three species had territories entirely within the maple wet woods. In the three-acre large maple quadrat their densities were: Carolina Wren, two pairs; Cardinal, less than two pairs; Yellow-billed Cuckoo, one pair. In the five-acre small maple quadrat the densities were: Carolina Wren, two and one half pairs; Cardinal, just under two pairs; Yellow-billed Cuckoo, one pair. Thus the small maple habitat had lower densities per unit area.

Cardinals were somewhat more common on the oak ridge than in the maple-dominated wet woods; the densities of cuckoos and wrens were not perceptibly different in the two major habitats. For all 126 acres of the Sawgrass Lake study area cuckoos, wrens, and Cardinals comprised 93 per cent of the breeding birds. Active nests of the Mourning Dove, Carolina Wren, and Cardinal were found. Wrens built nests in fern tussocks in the small maple area. Although no active nest of the

TABLE 3. Breeding birds of the two broad-leaved woodlands in the Sawgrass Lake study area in 1964.*

Species	30-acre mixed oak ridge		96-acre maple wet woods	
	actual density	pairs per 100 acres	actual density	pairs per 100 acres
Green Heron (<i>Butorides virescens</i>)	0	—	+	—
Red-shouldered Hawk (<i>Buteo lineatus</i>)	+	—	+	—
Mourning Dove (<i>Zenaidura macroura</i>)	+	—	0	—
Yellow-billed Cuckoo (<i>Coccyzus americanus</i>)	6	20	19	20
Screech Owl (<i>Otus asio</i>)	2	7	v	—
Great Horned Owl (<i>Bubo virginianus</i>)	+	—	+	—
Blue Jay (<i>Cyanocitta cristata</i>)	5	17	v	—
Carolina Wren (<i>Thryothorus ludovicianus</i>)	15	50	49	51
Brown Thrasher (<i>Toxostoma rufum</i>)	3	10	v	—
White-eyed Vireo (<i>Vireo griseus</i>)	0	—	canal ecotone only	
Yellowthroat (<i>Geothlypis trichas</i>)	0	—	canal ecotone only	
Cardinal (<i>Richmondena cardinalis</i>)	15	50	38	40
total density	46	154	106	111
number of species		9		6

* v = visitor; + = ranged outside of study area.

Yellow-billed Cuckoo was observed, a female collected on 27 April 1964 contained a fully formed egg, and we found several old nests and shells from hatched cuckoo eggs. Other old nests, apparently those of Brown Thrashers were located in the shrubs on the mixed oak ridge.

A number of local species regularly visited the study area. They may be treated best under two categories, including species for which adults were visitors, and species for which juveniles were visitors. Few adult birds visited the study area during the breeding season, and only four species were recorded on more than 5 of the 17 trips made between 15 May and 15 June. These were the Purple Martin (*Progne subis*), five to ten of which regularly fed low over the trees around the edge of the ridge; Great Crested Flycatcher (*Myiarchus crinitus*), several of which hawked insects on the ridge and early in the season appeared to be seeking nest sites thereon; Red-winged Blackbird (*Agelaius phoeniceus*), a dozen or more females of which obtained food in the vegetation along the canals; and Red-bellied Woodpecker (*Centurus carolinus*), two or three of which foraged in all habitats of the study area. Pairs of the latter three species nested nearby along the edge of the deciduous woods. Adults of several other species (including herons, charadriiforms, icterids, and the Fish Crow, *Corvus ossifragus*) were frequently recorded overhead but never, or rarely, fed in the plot.

In the late summer a remarkable number of young birds invaded the Sawgrass Lake area from other habitats. None was seen to be cared for by an adult, and, except for family groups of Eastern Kingbirds (*Tyrannus*

tyrannus), Boat-tailed Grackles (*Cassidix mexicanus*), and Common Grackles (*Quiscalus quiscula*), they were unaccompanied. Juvenile Mockingbirds (*Mimus polyglottos*) made the most dramatic invasion. Our first record was for 17 June, when we counted 8; on 29 June we recorded 45 along one canal bordering the plot. Over 25 Mockingbirds were identified on every trip thereafter until early August, and additional individuals were overlooked, undoubtedly, since we spent little time along the canals where they congregated to feed on the abundant ripening elderberries. Between 7 July and 5 August 187 fledgling Mockingbirds (plus only two adults) were netted and color-marked to gain information on their dispersal from the Sawgrass Lake area. Over 35 sightings of marked individuals were later reported from nearby residential areas (Kale and Jennings 1966). Many young Blue Jays also invaded the Sawgrass area. Six unattended juveniles were observed on 15 June and, because they were independent, both of us felt that they had not been produced in the study plot. By 14 July the number had increased to 50, and over 15 were recorded on each trip thereafter until the end of August.

Most of Pinellas County south of the Sawgrass Lake area is either residential or commercial, and the remaining natural habitats are rapidly disappearing. In the residential areas total breeding-bird densities are as high as 500–600 pairs per 100 acres, with the densities of Blue Jays and Mockingbirds being exceeded only by House Sparrows (*Passer domesticus*) and Mourning Doves. For a few species these residential areas offer great expanses of ideal habitat, and the suburbs are

virtually blanketed by their adjacent territories. In two years of censusing in study plots in these suburbs, we saw no independent fledgling Blue Jay or Mockingbird, and we frequently saw young birds being driven away by adults (Woolfenden and Rohwer, unpublished data). Because breeding densities are high and suitable refugia for young birds are scarce, it seems that fledglings upon becoming independent are literally driven out of the city as subsequent nesting is begun. The Sawgrass Lake wet woods with its low breeding bird density and abundant food sources serves as a refuge for these juveniles.

In late June and throughout July a few juveniles were recorded for the following 10 species (the largest number of individuals recorded on any one visit follows the name): Yellow-crowned Night Heron (*Nyctanassa violacea*), 1; Red-bellied Woodpecker, 1; Downy Woodpecker (*Dendrocopos pubescens*), 1; Eastern Kingbird, 1; Loggerhead Shrike (*Lanius ludovicianus*), 1; Starling (*Sturnus vulgaris*), 5; Red-winged Blackbird, 60; Boat-tailed Grackle, 2; Common Grackle, 3; and Rufous-sided Towhee (*Pipilo erythrophthalmus*), 5. Young Red-winged Blackbirds were recorded only once, on 6 August, when a flock of over 60 individuals, plus a few adult females, was seen feeding along one of the canals. Concentrations of fledgling Brown Thrashers (6+) and Cardinals (10+) were observed on the ridge, but in neither case did we feel that they came from areas outside the plot.

PART II: COMPARISONS WITH AREAS NORTH OF FLORIDA

Robertson (1955) was the first to discuss the impoverished nature of the breeding landbird fauna of Florida. He found support for his contention in a general comparison of several regional studies. In seven areas in the northeastern United States and Ontario an average of 73 passerine species was recorded breeding, whereas only 56 species were listed for the entire state of Florida (Howell 1932). Robertson also noted that the number of breeding passerine species decreases as one proceeds south on the Florida peninsula, passing in its central region the southern terminus of the breeding range of a number of widespread northeastern species. In extreme southern Florida (Dade and Monroe Counties) Robertson found breeding records for only 29 passerine species, 9 of which are either no longer present, extremely rare, or confined to isolated segments of suitable habitat.

More detailed quantitative analyses of the breeding birds of any portion of the eastern deciduous forests are difficult to make. The region is geologically old, and clearly delimiting physiographic features are absent. Thus the different types of forests grade gradually into one another. Correspondingly, the breeding densities of many individual bird species vary between forest types, with most not simply being present or absent, but instead being more or less abundant as one changes forest types. Bond (1957) has ably demonstrated this phenomenon in southern Wisconsin by using 64 forest stands for which vegetational descriptions had been carefully quantified. These stands formed a gradient from xeric oak forests to mesic sugar maple (*Acer saccharinum*) climaxes, and the densities of most bird species were found to vary continually along this gradient of forest types. Furthermore, the density of many species followed normal curves or what appeared to be parts of normal curves. For species where an entire curve was present, the range of Bond's forest types apparently contained both their xeric and mesic tolerance limits (at least for southern Wisconsin). The American Redstart (*Setophaga ruticilla*) for example, was nearly absent in the most xeric stands but as the forests became increasingly mesic they increased in abundance to a maximum in mixed mesophytic stands. Then, as the forests became even more moist, their densities began to decline until, in the most mesic climax forests, they were again almost absent.

In discussing Bond's paper, Mengel (1965: 97) points out that "many species tend to 'slide' up and down the forest continuum" as one changes geographic localities. Thus, a species' point of maximum abundance on the continuum of forest types may be expected to shift as one moves from one region to another. It becomes evident that a detailed analysis of bird distribution in the eastern deciduous forests must take densities of individual species into account. Unfortunately the vegetational descriptions accompanying most censuses are not adequate for a faunal analysis which could include densities.

In the southeastern United States two major physiographic provinces, the Piedmont and the Coastal Plain, occur south and east of the Blue Ridge Mountains (Fenneman 1938). The latter includes all of peninsular Florida. Since Norris (1958) found some differences in the avifauna of the Piedmont and the Coastal Plain in his study of the distribution of birds in Georgia, our analysis of the breed-

TABLE 4. Pairs per hundred acres followed by percentage of the total avifauna for the most common breeding birds of thirteen study areas in southeastern United States.*

Species	I Upland oak-pine woodland, 25 acres Birmingham, Ala. 1949-1950, 1954	II Second growth oak-gum forest, 30.4 a. Birmingham, Ala. 1948	III Swampy and upland mixed woods, 49.5 a. Hurricane, Ala. 1960	IV Chimney oak-hickory forest, 20 a. Athens, Geo. 1947	V Woodland swamp, 27 a. Athens, Geo. 1966	VI Beech-magnolia hammock, Damascus, Geo. 1951	VII Mixed hardwood climax forest, 20 a. Geo. 1963-1965	VIII Hammock type forest, Bill's Island, S. C. 1948	IX Broadleaf forest on stream floodplain, 12.3 a. Savannah River Plant, S. C. 1957	X Live oak-cabbage palm hammock, 33.3 a. Hillsborough River State Park 1967	XIA Mixed oak ridge, 30 a. Sawgrass Lake, Fla. 1964	XIB Maple wet woods, 96 a. Sawgrass Lake, Fla. 1964	XII Tropical hammock, 25 a. Florida Keys 1951-1952														
Red-eyed Vireo (<i>Vireo olivaceus</i>)	57	21	28	17	60	16	40	16	19	7	70	9	30	9	14	6	45	17	27	15	0	0	0	0			
Blue Jay (<i>Cyanocitta cristata</i>)	22	8	20	12	7	2	23	9	15	6	12	6	15	4	0	0	0	0	0	3	2	0	0	0	0		
Cardinal (<i>Richmondia cardinalis</i>)	19	7	18	11	25	7	9	15	6	102	14	40	12	40	12	29	13	20	7	27	15	50	32	40	36	5	
Pine Warbler (<i>Dendroica pinus</i>)	17	6	0	0	3	-	0	0	0	0	12	2	11	3	0	0	0	0	0	0	0	0	0	0	0	0	
Kentucky Warbler (<i>Oporornis formosus</i>)	17	6	9	6	4	1	5	2	15	6	20	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Blue-gray Gnatcatcher (<i>Poliophtila caerulea</i>)	17	6	0	0	14	4	13	5	15	6	16	2	4	1	9	4	16	6	15	8	0	0	0	0	0	0	
Tufted Titmouse (<i>Parus bicolor</i>)	17	6	8	5	15	4	15	6	11	4	27	4	17	5	0	0	0	0	6	3	0	0	0	0	0	0	
Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>)	17	6	29	18	7	-	0	0	19	7	8	1	29	8	2	-	0	0	0	0	0	0	0	0	0	0	
Carolina Wren (<i>Thryothorus ludovicianus</i>)	13	5	3	2	17	5	13	5	15	6	47	6	15	4	26	12	16	6	6	51	28	50	32	51	46	0	
Wood Thrush (<i>Hylocichla mustelina</i>)	11	4	9	6	6	2	30	12	19	7	35	5	0	0	0	0	4	1	0	0	0	0	0	0	0	0	
Summer Tanager (<i>Piranga rubra</i>)	9	3	3	2	5	1	15	6	7	3	8	1	13	4	3	1	8	3	0	0	0	0	0	0	0	0	
Downy Woodpecker (<i>Dendrocopos pubescens</i>)	7	3	3	2	4	1	5	2	7	3	8	1	0	0	0	0	16	6	0	0	0	0	0	0	0	0	
Acadian Flycatcher (<i>Empidonax vireescens</i>)	4	2	0	0	9	2	5	2	7	3	23	3	1	-	3	1	33	12	0	0	0	0	0	0	0	0	
Yellow-billed Cuckoo (<i>Coccyzus americanus</i>)	3	1	0	0	14	4	13	5	7	3	51	7	13	4	3	1	8	3	6	3	6	3	20	13	20	18	0
Great Crested Flycatcher (<i>Myiarchus crinitus</i>)	3	1	3	2	11	3	13	5	7	3	39	5	4	1	18	8	0	0	0	3	2	0	0	0	2	11	
White-eyed Vireo (<i>Vireo griseus</i>)	0	0	0	0	31	8	0	0	11	4	86	12	21	6	10	4	20	7	0	0	0	0	0	0	0	0	
Hooded Warbler (<i>Wilsonia citrina</i>)	0	0	0	0	8	13	5	4	1	74	10	35	10	0	0	0	28	11	0	0	0	0	0	0	0	0	
Prothonotary Warbler (<i>Protonotaria citrea</i>)	0	0	0	0	29	8	0	0	7	3	4	-	0	0	0	0	8	3	0	0	0	0	0	0	0	0	
Parula Warbler (<i>Parula americana</i>)	0	0	0	0	40	11	0	0	0	0	47	6	35	10	28	13	12	4	33	18	0	0	0	0	0	0	
Yellow-throated Warbler (<i>Dendroica dominica</i>)	0	0	0	0	0	0	0	0	0	0	0	0	9	3	25	11	0	0	0	0	0	0	0	0	0	0	
Painted Bunting (<i>Passerina ciris</i>)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	5	0	0	0	0	0	0	0	0	0	0	
Brown Thrasher (<i>Toxostoma rufum</i>)	0	0	0	0	0	0	0	0	7	3	16	2	0	0	0	0	0	0	0	0	0	10	7	0	0	0	
Black-whiskered Vireo (<i>Vireo altiloquus</i>)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	61
pairs per hundred acres*	271	162	368	249	256	746	343	224	268	183	154	111	18														
total number of species recorded on count*	22	15	32	21	29	22	21	23	24	16	9	6	3														

a v = visitor in study area; * = averages used if area censused more than one year.
 References: I, Audubon Field Notes (A.F.N.), 3:267, census no. 20, 4:300-301, census no. 12, 8:368, census no. 10; II, A.F.N., 2:238, census no. 17; III, A.F.N., 14:498, census no. 19; IV, A.F.N., 1:213-214, census no. 24; V, A.F.N., 20:609-610, census no. 6; VI, Norris, 1951; VII, A.F.N., 17:502-503, census no. 20, 18:555, census no. 19, 19:602, census no. 22; VIII, A.F.N., 2:240, census no. 20; IX, A.F.N., 11:437-438, census no. 4; X, A.F.N., 21:635-637, census no. 34; XI and XII, Robertson 1955.

TABLE 5. Matched-pairs comparisons of species composition (above diagonal) and faunal size (below diagonal) for nine censuses from the Coastal Plain of mainland United States (I-IX) and four from peninsular Florida (X-XII), made from data given in table 4. See text for explanation.

	I	II	III	IV	V	VI	VII	VIII	IX	X	XIA	XIB	XII
I													
II	80	83	87	92	80	93	73	69	71	89	80	100	67
III	88	71		100	88	88	80	77	100	100	80	100	67
IV	87	92	76		85	92	69	62	85	78	60	100	67
V	94	75	94	81		88	73	62	79	78	80	67	67
VI	83	67	94	72	89		87	77	86	100	100	100	67
VII	100	80	88	87	94	83		85	64	100	80	100	67
VIII	87	92	76	100	81	72	87		69	78	60	100	67
IX	93	86	82	93	88	78	93	93		67	60	100	33
X	60	75	53	69	56	50	60	69	64		80	100	67
XIA	33	42	29	38	31	28	33	38	36	56		100	33
XIB	20	25	18	23	19	17	20	23	21	33	60		33
XII	20	25	18	23	19	17	20	23	21	33	60	100	

ing birds of peninsular Florida will make comparisons with censuses taken only on or near the Coastal Plain in Alabama, Georgia, and South Carolina.

PROCEDURES

Breeding-bird censuses were available for only five deciduous forests on the Coastal Plain of these neighboring states. In order to increase our comparative sample we included censuses from four areas that lie just above the Fall Line in the Piedmont, two each from Birmingham, Alabama, and Athens, Georgia. All of these censuses were composed entirely of species typically found on the Coastal Plain, so our comparisons are not biased by introducing elements of the Appalachian avifauna.

Table 4 summarizes the data obtained from the nine censuses of areas lying north of Florida and the four censuses from peninsular Florida. Following Norris's procedure (1951) we have included in table 4 only those species that constitute five per cent or more of any one fauna. Once a species qualified for the list its percentage was given for all censuses on which it accounted for one per cent or more of the fauna. In addition to presenting percentage compositions, table 4 gives the number of pairs per 100 acres for each species from which the percentages were derived, and the total density and total number of species recorded for each locality. (In cases where plots were censused more than once we used averages, and all figures were rounded to whole numbers.)

The census data presented in table 4 have been analyzed in detail by two comparisons designed to quantify the degree of similarity between faunas. (Species recorded in very low densities, less than one per cent in table 4, were excluded from these comparisons.) The first comparison expresses the degree of similarity in the species composition of two faunas. The method has been discussed in detail by Simpson (1947), and applied to bird distribution by Miller (1951) and Mengel (1965). In this comparison the number of species common to two faunas is divided by the total number in the smaller fauna. The quotient is then converted to a percentage, so that results may range from 0 to 100. Similarity of faunal composition is indicated by higher percentages and dissimilarity by lower percentages. The comparison of species composition gives high values when the smaller of two faunas is composed primarily of

species found in the larger; however, the two faunas may be quite different because of a reduced number of species in the smaller fauna.

Our second procedure is designed to quantify differences in the size of two faunas. This is accomplished by dividing the number of species in the smaller of two faunas by the number in the larger. Again the quotient is converted to a percentage, and results may range from 0 to 100, with similarity in faunal size being indicated by higher percentages and dissimilarity by lower percentages.

RESULTS

Inspection of table 4 discloses significant differences between the censuses made on the Coastal Plain north of Florida and those taken on the peninsula. The average number of species recorded on the censuses in Alabama, Georgia, and South Carolina was 23; for peninsular Florida the *maximum* was only 16, and the average was a mere 9. Pairs per 100 acres averaged 320 for the localities north of Florida (or 268 if the extraordinarily high hammock census from Damascus, Georgia, is deleted); for Florida the *maximum* was 183, and the average was only 117. In numbers of species and total density the nine areas north of Florida are similar to other eastern hardwood forests. Kendeigh (1944) reviewed a large number of breeding-bird censuses, primarily from the north-central portion of eastern United States, and concluded that eastern forests are typically inhabited by 20 to 30 species, and have densities of 200 to 300 pairs per 100 acres. In both respects Florida is depauperate. Further comparisons of total densities are not made because so few censuses with detailed descriptions of vegetation are available for the southeastern Coastal Plain.

The results of our analyses of the data shown in table 4, using the two methods explained above, are given in table 5. In this table the measurements of species composition lie above the diagonal and the measurements

of faunal size lie below the diagonal. The intra- and inter-regional comparisons of Florida and the three states to the north are separated by a horizontal and a vertical line. We verified our conclusions with the Mann-Whitney *U* test, a nonparametric test for determining whether or not two samples represent populations of different central tendency. Intra-regional differences for Florida (lower right rectangle) will not be discussed because the number of censuses available is too small.

The upper left rectangle contains the intra-regional measurements of species composition (above the diagonal) and faunal size (below the diagonal) for the three states north of Florida. These measures establish bases with which the Florida censuses are compared. Variation in these intra-regional measures primarily comes from comparing different types of broad-leafed forests, which was necessary because of the scarcity of census data.

Indexes of species composition within the northern states ranged from 62 to 100 (with one exception of 50), with a mean of 80. The censuses taken in central Florida are similar (columns X, XIA, XIB), with a range from 60 to 100 and a mean of 83, indicating the two regions are not significantly different from each other in species composition ($P = 0.4472$). The one census from southern Florida with eight inter-regional measures of 67 and one of 33 (column XII) is significantly different from the more northern states ($P < 0.00046$) because it had a total of only three species, one of which was the Black-whiskered Vireo (*Vireo altiloquus*), a colonizer from the West Indies.

Intra-regional comparisons of faunal size for the states north of Florida range from 67 to 100, with a mean of 85. When compared with these northern censuses the oak-palm hammock (row X) shows a significantly reduced fauna with a range from 50 to 75 and a mean of 62 ($P < 0.00006$). The Sawgrass Lake censuses (rows XIA, XIB) and the south Florida tropical hammock (row XII) have even smaller faunas with their comparisons ranging from 17 to 42 with a mean of 25 ($P < 0.00006$). In these comparisons with northern areas the two Sawgrass Lake censuses are significantly different from each other because Blue Jays and Brown Thrashers nested on the mixed oak ridge but not in the adjacent maple woods in 1964, a fact made less significant by Rohwer's discovery in 1967 of an active jay nest in the small maple portion of the maple wet woods.

In these comparisons of faunal size, the mid-

peninsular coastal Sawgrass Lake study plots are more similar to the south Florida hammock, whereas the mid-peninsular oak-palm hammock, which lies farther inland, is more similar to the census areas to the north. The dissimilarity of these two mid-peninsular study areas is explained by the breeding distributions of many continental forms in Florida, which typically breed farther south in interior Florida than along the coast. Thus the oak-palm hammock which was located 27 miles inland from Sawgrass Lake had breeding Tufted Titmice (*Parus bicolor*), Blue-gray Gnatcatchers (*Poliophtila caerulea*), Red-eyed Vireos (*Vireo olivaceus*), and Parula Warblers (*Parula americana*), all of which breed south of both areas, but only in the interior of the state.

We intentionally excluded from the foregoing analyses certain censuses of the southern Coastal Plain north of Florida because either the habitats were not dominated by broad-leafed trees (e.g. Audubon Field Notes 20: 629, census no. 33) or the study plots were too small (e.g., op. cit., 20: 609, census no. 5). One additional study is available from Florida, that of a 25-acre longleaf pine (*Pinus palustris*)-turkey oak (*Quercus laevis*) habitat near Gainesville, which we excluded because the plot was dominated by pines. In five consecutive years of censusing, this plot had only 6 to 10 breeding species and 54 to 96 pairs per hundred acres. Six species accounted for five per cent or more of the total breeding density during the five years, two of which are not listed in table 4, the Yellow-throated Vireo (*Vireo flavifrons*) and Mourning Dove (op. cit., 12: 450, census no. 15; 13: 466, census no. 14; 14: 497-498, census no. 18; 15: 524, census no. 43; 16: 527-528, census no. 19).

DISCUSSION

The preceding data and analysis exemplify the depauperate nature of the breeding land-bird fauna of peninsular Florida. These facts lead naturally to the question of why an impoverished fauna occurs on a subtropical peninsula of a temperate land mass. Robertson (1955) considered the question and presented a twofold explanation. First, he suggested that many of the species breeding in eastern North America are not adapted to the climate of peninsular Florida. Second, he suspected that natural colonization of the peninsula by tropical species, which should be adapted to the climate, has been deterred by physiographic barriers. In support of his first

supposition he pointed out that the southern breeding limits of many northeastern species lie in north-central Florida, although present-day physiographic features that might prevent them from ranging farther south appear to be absent. Furthermore, he noted that at least four birds, the Sparrow Hawk (*Falco sparverius*), Red-cockaded Woodpecker (*Dendrocopos borealis*), Brown-headed Nuthatch (*Sitta pusilla*), and Summer Tanager (*Piranga rubra*), which once bred in the pine lands of southern Florida, on Long Pine Key for example, are no longer found there. In addition, Robertson has called attention to the scarcity of recent records for the Hairy Woodpecker (*Dendrocopos villosus*) in southern Florida (pers. comm.) and for the White-breasted Nuthatch (*Sitta carolinensis*) in the entire state (Robertson 1967). Today apparently both are either extremely rare or absent as breeders on the peninsula of Florida. Robertson (1955: 473) suggested that "since the height of the Wisconsin glaciation the climate of peninsular Florida has become progressively more unfavorable for northern species and that they represent a receding element in the avifauna."

The breeding schedule of the Bald Eagle (*Haliaeetus leucocephalus*) and the history of the Starling (*Sturnus vulgaris*) lend support to Robertson's first hypothesis. Florida Bald Eagles nest in the winter and migrate north for the summer, and this has been attributed to the summer heat by Van Tyne and Berger (1959).

Starlings were released in New York City in the early 1890s, and by 1952 their range included southern Canada and the entire United States except southern Florida (Kessel 1953). Even though rural and urban habitats had long been abundant in Florida, Starlings did not nest on the peninsula until the late 1930s, at which time they were breeding as far west as Kansas (Johnston 1960). By the mid 1950s Starlings had bred in Arizona (Phillips et al. 1964), New Mexico (Ligon 1961), and Washington (Jewett et al. 1953), and had been recorded from Alaska (Gabrielson and Lincoln 1959). In peninsular Florida Starlings first bred in Tampa in 1942 (Nicholson 1964), at Kissimmee in 1946, at Miami in 1956, and at Cocoa in 1961 (Sprunt 1954, with addendum, 1963). The low breeding densities of Starlings in residential St. Petersburg of 2 to 6 pairs per hundred acres (Woolfenden and Rohwer, unpublished data), as compared with a density of 26 pairs per hundred acres in Ithaca, New York (Simmers 1965), and 60

to 90 pairs per hundred acres in urban Illinois (Graber and Graber 1963) perhaps reflect their recent arrival in peninsular Florida. Thus, despite a lack of significant geographic barriers and a general north-south migratory pattern, features which might have encouraged a more rapid southward range expansion, Starlings extended their breeding ranges across the entire western half of the continent with its mountain and plain barriers before they bred in the southern half of the Florida peninsula.

Only seven natural colonizers from the West Indies now breed in Florida, and the invasions of two of these, the Cuban Nighthawk (*Chordeiles gundlachi*, *sensu* Eisenmann 1962) and the West Indian race of the Yellow Warbler (*Dendroica petechia gundlachi*), have occurred recently. The Florida ranges of five species, the Smooth-billed Ani (*Crotophaga ani*), Gray Kingbird (*Tyrannus dominicensis*), Black-whiskered Vireo, and the nighthawk and warbler, are expanding, indicating that at least some West Indian birds are adapted to the climate of peninsular Florida. Conditions for colonization of Florida by tropical birds may be near optimum today. Both the cooler climates of glacial times and the smaller land areas and larger water barriers of interglacial times would reduce the probability of colonization from the West Indies and, in the past, have perhaps eliminated some species that were successful in earlier times.

If, as seems to be the case, it is the summer climate that retards colonization of peninsular Florida by widespread continental forms, one might expect some of them to be adapting gradually and thereby extending their ranges southward. The Red-eyed Vireo seems to be an example. Baynard (1942) considered the species "a regular summer visitor," but only "an occasional nester" in Hillsborough River State Park from 1919 to 1942. In 1967 we found this vireo to be a common breeder in an oak-palm hammock in this park (Woolfenden 1967). In 1964 a singing Red-eyed Vireo restricted itself to a small area in the mixed oak woods near Sawgrass Lake beginning on 5 April. No mate was ever observed and the bird disappeared after 5 May.

The depauperate condition of the landbird fauna of south coastal and tropical Florida should leave a number of unfilled niches. Of the 12 species recorded breeding in the Sawgrass Lake area, only the Yellow-billed Cuckoo is found in closed hardwood forests. No forest vireo or warbler bred there, although, with only slight range expansions, certain mem-

bers of both groups might do so. Red-eyed Vireos, Parula Warblers, and Yellow-throated Warblers (*Dendroica dominica*) breed 15 to 20 miles north in Pinellas County, and Black-whiskered Vireos breed within four miles in mangrove habitat bordering Tampa Bay. Twice in 1964 we recorded this tropical vireo in the Sawgrass Lake area; on 14 May two birds, one of which was singing, were observed, and on 8 June one singing bird was noted. In Florida the Black-whiskered Vireo is generally confined to coastal areas, although it is gradually expanding its range inland. In Pinellas County we found a nest near the fresh-water Lake Maggiore in St. Petersburg; it fledged young on about 27 June 1963. Numerous singing males have been recorded in Brevard and Dade Counties away from mangrove habitat and as much as 15 to 20 miles inland (Robertson 1962). Robertson recorded 10 and 11 pairs per 100 acres in the two years that he censused the south Florida tropical hammock, part of which was a canopied forest and which contained no mangroves. In the West Indies, in addition to inhabiting mangroves, the species lives in forests, occurring up to 5000 feet above sea level (Robertson, pers. comm.).

The abundance of Carolina Wrens and Cardinals in the Sawgrass Lake study area may in part be a response to the absence of true forest passerines. This possibility seems supported by the lower average densities of these two species on 16 censuses of breeding birds taken within their ranges in deciduous forests which did not include pines (see Audubon Field Notes 1962-1966). On these censuses the average density of Carolina Wrens was 17 pairs (range 0-42) per 100 acres. We recorded 50 and 51 pairs per 100 acres in the two Sawgrass Lake study plots. For these same extralimital censuses the average density of Cardinals was 35 pairs (range 7-88) per 100 acres; in the Sawgrass Lake study plots 40 and 50 pairs per 100 acres were recorded. In the oak-palm hammock census where four additional forest passerines were present, the density of Cardinals was but 27 pairs per 100 acres. Carolina Wrens, however, were as abundant here as in the Sawgrass Lake study areas, with a density of 51 pairs per 100 acres. Cardinals feed their young insects, and it was our impression that these were frequently taken well above the forest floor in our census areas; thus in the oak-palm hammock the presence of four other forest passerines may account for their lower density. Wrens seemed to feed close to the

ground in our census areas and they probably had no other avian competitors. Their densities are much lower in more northern forests, perhaps because of the presence of thrushes and warblers which also feed on or near the forest floor.

SUMMARY

Part I of this paper describes the procedures and habitats and gives the results for two breeding-bird censuses conducted in Pinellas County on the Gulf coast of Florida. Including these, a total of four breeding-bird censuses of deciduous forest habitats are now available for the state. The two additional censuses were taken in a hammock in the Florida Keys and in an oak-palm hammock in mid-peninsular Hillsborough County. In Part II we compare the four Florida censuses with nine taken on or near the Coastal Plain to the north in Alabama, Georgia, and South Carolina. The Florida censuses show significantly lower total densities and fewer species. Further comparisons of the species composition and the faunal sizes of the peninsular Florida and mainland Coastal Plain areas were made using two formulas designed to quantify degrees of similarity between matched pairs of faunas. From these comparisons we conclude that the hardwood forests of Florida have mostly the same species of breeding land birds as the hardwood forests of continental United States, but fewer of them. Further evidence supporting Robertson's hypothesis that Florida's depauperate breeding landbird fauna is the result of present-day climate and persisting geographical barriers is presented and discussed.

ACKNOWLEDGMENTS

We wish to thank Olga Lakela and Robert W. Long for their assistance with botanical problems encountered in the Sawgrass Lake habitats, and Richard A. Hutzler who helped us make the transects. We greatly appreciate the constructive comments of Robert M. Mengel, and the support given us throughout the project by William L. Jennings and James O. Bond of the Encephalitis Research Center, Tampa, Florida. The field work was supported by grant no. AI-05504-02 from the National Institute of Allergy and Infectious Diseases, National Institutes of Health.

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Accepted for publication 23 October 1967.