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BREEDING BIRD POPULATIONS OF THE OKEFENOKEE SWAMP IN GEORGIA: BASELINE FOR ASSESSING FUTURE AVIFAUNAL CHANGES

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Abstract.—Breeding birds were surveyed using the spot-mapping method in 17, 16-ha sites representative of major successional stages in both the uplands and wetlands of the Okefenokee Swamp, Georgia, 1979–1980. Population density ranged from 120 to 875 pairs/km^2. Both density and diversity increased with successional age in both upland and wetland series with peaks in the middle to late stages rather than in the oldest forests. Although there were fewer species than in more northern localities, high diversity and low dominance characterized Okefenokee bird populations (Overall Shannon index 3.2, evenness index 0.89 based on importance values that combine numbers, frequency and biomass). More than 50% of breeding species and 75% of individual land birds were migrants, many wintering in the tropics. Since the Okefenokee is preserved and managed to remain more or less as it is now, our surveys provide a baseline for assessing future avifaunal changes that might result from changes beyond the Okefenokee boundaries (tropical forest destruction and climate change, for example). Several hypotheses advanced to predict bird species diversity were tested, and we conclude that in a complex landscape such as the Okefenokee no one habitat feature or index will likely account for the avian community structure.

REPRODUCION DE AVES EN EL PANTANO OKEFENOKEE DE GEORGIA: LÍNEA DE BASE PARA MEDIR CAMBIOS FUTUROS EN ELLAS

Sinopsis.—En este estudio se examinaron pajaros con cria usando el metodo de "spot-mapping" en 17 localidades de 16-ha representativos de las mayores etapas sucesionales en las tierras altas y humedas del cenegal de Okefenokee, Georgia, 1979–1980. La densidad de poblacion oscilo de 120 a 875 parejas con cria/km^2. Tanto la densidad como la diversidad incrementaron segun las etapas sucesionales en las tierras altas y humedas con puntos maximos en las etapas de posicion intermedia a ultima en vez de puntos maximos en los bosques mas antiguos. Aunque hubo menos especies que en las localidades situadas mas al norte, la avifauna del Okefenokee se caracterizo por una alta diversidad con pocos dominantes (El indice Shannon global es 3.2, el indice de uniformidad es 0.89 basado en valores de importancia que combinan numeros, frequencia, y biomasa). Mas de 50% de los pajaros con cria y 75% de los pajaros terrestres solitarios fueron migratorios y muchos invernan en los tropicos. Puesto que el Okefenokee esta protegido y administrado para mantenerlo mas o menos en las condiciones actuales, nuestro estudio proporciona una base de comparacion para evaluar cambios futuros en la avifauna que podrian resultar de cambios fuera de los limites del Okefenokee (destrucion de bosques tropicales y cambios en el clima global, por ejemplo). Se examinaron varias hipotesis formuladas para predecir la diversidad de especies y llegamos a la conclusion que en un terreno tan complejo como el Okefenokee ninguna caracteristica del ambiente o indice podra explicar la structura de la comunidad de aves.

The Okefenokee Swamp is the largest freshwater wetland in the eastern United States, encompassing about 1700 km^2 on the lower coastal plain of southeastern Georgia. About 1600 km^2 of the swamp is protected and managed as a National Wildlife Refuge and National Wilderness Area

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by the U.S. Fish and Wildlife Service. The upland watershed, 2000 km^2 according to Blood (1980), that drains into the swamp is state owned or privately owned largely by timber companies.

A large number of Okefenokee's land birds are neotropical migrants, which along with some of the water birds are endangered by human global developments and pollution (Terborgh 1989). Since the Okefenokee is a large area that will remain relatively free of human disturbance and presumably will be managed to remain more or less as it is now, the area is ideal for assessing future changes. For example, a future decline in neotropical migrant species within the Okefenokee would indicate that the cause is to be found on the migration or winter grounds. And, of course, a good baseline will be useful in assessing changes should the regional climate change.

In this study we document the relationships between bird density and diversity to ecological succession in both upland and wetland series, and test several hypotheses that have been advanced to account for avian community structure. These hypotheses include, (1) MacArthur and MacArthur's (1961) hypothesis that bird species diversity (BSD) is correlated with foliage height diversity (FHD); (2) Roth's (1976) suggestion that BSD is influenced by horizontal heterogeneity of vegetation; and (3) the concept that functional attributes such as trophic structure and primary production influence community structure (Wiens 1975, Willson 1974).

THE OKEFENOKEE ENVIRONMENT

Climate of the Okefenokee region is influenced by a tropical maritime air mass and occasional intrusions of the continental polar air mass in winter. It is hot and wet in summer, warm and dry in autumn, cool and moist in winter and warm and moist in spring (Trewartha 1968). Mean annual temperature is 19.6°C with 7 mo or more of growing season. Monthly precipitation varies from 4.8 cm in November to 18.5 cm in July with a mean annual total of 128.5 cm (Rykiel 1977).

The Okefenokee is a forested peat-forming bog with extensive open water and marshes (locally called "prairies") maintained by periodic droughts and fires. The Okefenokee has had a recent history of drought and fires on about a 25-yr cycle. Up to 80% of the swamp was burned during fires of 1932 and 1954–1955 (Cypert 1961a,b). In the open-water areas, layers of peat periodically rise to the surface due to accumulation of methane gas to form floating islands (thus the "land of the trembling earth" as the Indians called it). These islands quickly undergo succession to swamp forests. The current vegetation and successional trends have been described by Hamilton (1982) and mapped by McCaffrey and Hamilton (1982).

Relative areas in major habitats within the swamp itself (not including the watershed) are as follows (Blood 1980): marshes, 21%; shrub swamp, 34%; swamp forest, 29%; upland islands, 8%; and open water, 7%.

Major marsh species in the deeper water are white water lily (*Nymphaea*

oderata), neverwet (*Orontium aquaticum*), bladderwort (*Utricularia* spp.), haptin (*Eriocaulon compressum*) and spike rush (*Eleocharis elongata*). At shallow-water sites panic grass (*Panicum* spp.), sedge (*Carex* spp.), beak rush (*Rhynchospora* spp.), chain fern (*Woodwardia virginica*), red root (*Lachnanthes caroliniana*) and *Sphagnum* moss may be found.

Major species in the shrub swamp habitat are: hurrah bush (*Lyonia lucida*), titi (*Cyrilla racemiflora*), greenbrier (*Smilax laurifolia*), pepper bush (*Clethra alnifolia*) and fetter bush (*Leucothoe racemosa*).

Okefenokee forest wetlands are dominated by pond cypress (*Taxodium ascendens*), three species of bays (*Gordonia lasianthus, Magnolia virginiana* and *Persea palustris*) or black gum (*Nyssa sylvatica biflora*). Lumbering activities in the 1920s prior to the establishment of the Swamp as a National Wildlife Refuge, especially that involving removal of mature cypress, has affected about 40% of the forested area in that the virgin old growth has been replaced by younger second growth (Hamilton 1982, Izlar 1972).

Predominant upland forest types are longleaf and slash pine (*Pinus palustris* and *P. elliotii*). Southern oaks and other hardwoods (*Quercus virginiana, Q. nigra, Q. laurifolia, Q. phellos* and *Magnolia virginiana*) become established in the absence of fire. The larger pine stands within the Okefenokee refuge as well as outside are currently managed with prescribed burning to maintain pine dominance.

METHODS

Seventeen study sites were randomly selected from 17 vegetation types, as listed in Table 1. An effort was made to select vegetation types representative of the major successional stages as shown in Figure 1. Square 16-ha study areas were surveyed with a Suunto liquid-filled compass (½°) and tape. Minor adjustments in configurations were made on a few sites because of stand shape or vegetation density, and three of the sites were less than 15–16 ha. There was evidence of selective logging dating from the 1920s in wetland sites 7, 8, 15, 16 and 17. Cypress stumps were present in all of these sites. Detail description, including exact location and a photograph of each study site, are included in Meyers (1982).

For each study area bird populations were censused four or five times at approximately 2-wk intervals from mid April to early June 1979 or 1980. The spot-mapping method was used to estimate the number of breeding males of each species (International Bird Census Committee 1970). Each census began 30 min before sunrise and ended between 4 and 4.5 h after sunrise. Survey routes were reversed every other census to reduce bias caused by time of day. All upland and shallow-water sites were walked with standardized stops uniformly distributed within the site. Deep-water habitats were censused from a camouflaged boat. Site 12 at Grand Prairie was censused from a blind 7 m above the swamp surface.

Since each singing male recorded in successive visits is presumed to represent a breeding pair, population density is expressed as pairs/km^2.

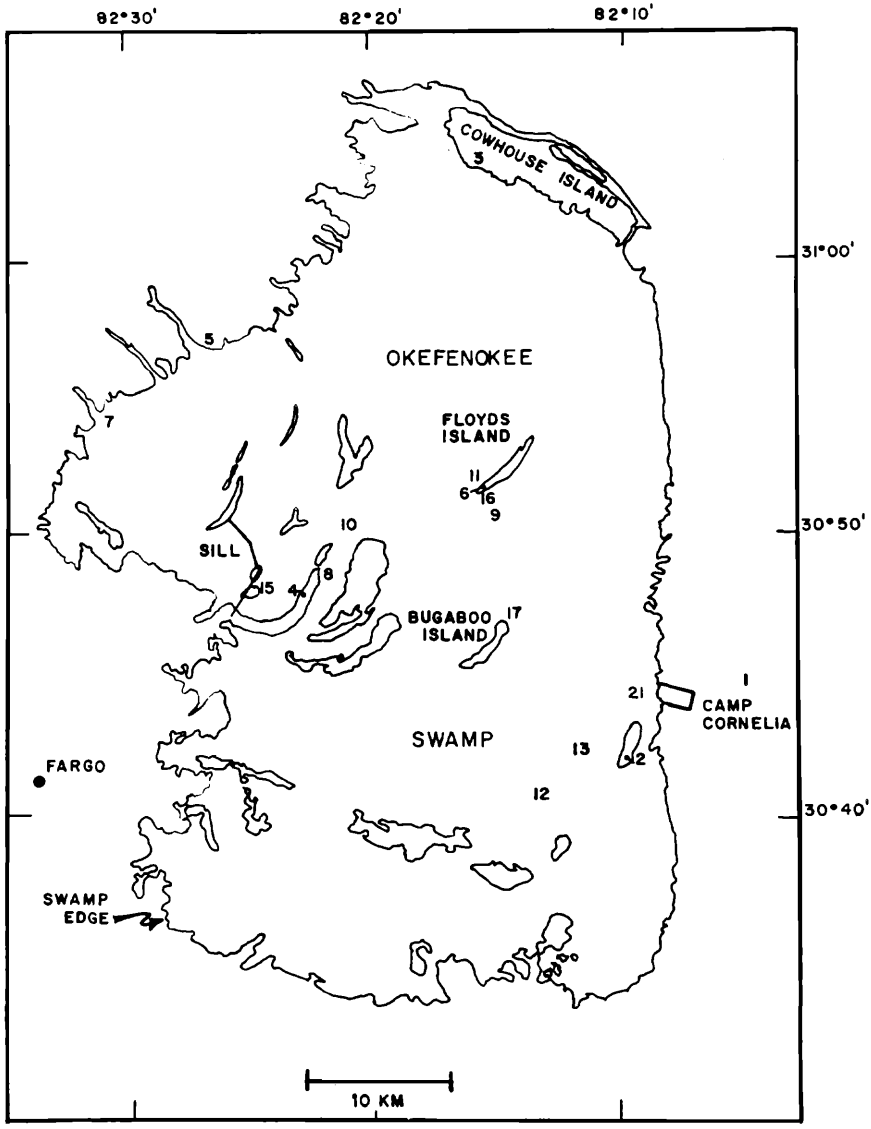

FIGURE 1. The Okefenokee Swamp avian study sites 1979–1980.

Species diversity was calculated by Shannon's formula (Shannon and Weaver 1949):

$$H' = -\sum (n_i/N)\log_e(n_i/N),$$

where n_i is the number of individuals of each species (twice the number of singing males) and N the total number of individuals. Since there is

TABLE 1. Descriptions of avian study sites, Okefenokee Swamp 1979–1980.

Site	Area (ha)	Site name†	Habitat
1	16.0	Union Camp	5-yr-old slash pine
2	16.0	Chesser Island	15-yr-old slash and longleaf pine
3	16.0	Cowhouse Island	30-yr-old slash and longleaf pine
4	16.0	The Pocket	45 to 60-yr-old slash pine
5	16.0	Smokehouse Jam	80-yr-old longleaf pine
6	15.3	Floyd's Island	virgin mixed hardwoods (40%), second growth pine-hardwoods (60%)
7	16.0	Surveyor's Creek	mature black gum swamp
8	8.8	The Pocket Gum	young black gum swamp
9	16.0	Chase Cypress	virgin, shallow-water cypress swamp
10	16.0	Billy's Lake	virgin, deep-water cypress swamp
11	16.0	Floyd's Prairie	herbaceous prairie with scattered young bay trees
12	16.0	Grand Prairie	aquatic macrophyte prairie
13	18.0	Chesser Prairie	mixed shallow-water swamp
15	18.0	The Sill	mixed deep-water swamp
16	15.0	Jackson Bay	mature bay swamp
17	5.5	Bugaboo Boat Run	shrub swamp with scattered pines
21	4.6	Suwannee Canal	shrub swamp with scattered dead cypress

† All names except sites 1 and 15 were derived from USGS 7½′ topographic maps.

a large variation in size of bird species, diversity was also calculated by a weighted version of Shannon's formula as developed by Lyons (1981) as follows:

$$H'' = -\sum (w_i p_i/W)\log_e(w_i p_i/W),$$

where w_i is the fixed weight assigned to each individual of a species i, p_i is the sampled proportion of individuals, n_i, of sample N and $W = \sum w_i p_i$. We rescaled H″ as an exponential function so that it is proportional to the number of species rather than the logarithm of the number of species (Ricklefs 1979). Comparison of species diversity between study areas and habitat was done using this scaled H″. Differences between habitats were analyzed by *t*-tests using Hutcheson's (1970) approximation for the variance modified by Lyons (1981).

The evenness index for both diversity indices was calculated by:

$$J = H/\log_e s,$$

where H is the diversity index, s the number of species in the sample and $\log_e s$ is the maximum possible H.

Foliage height diversity (FHD) was calculated from three vertical layers of vegetation (measured at 0–1.5, 1.6–5 and >5 m from the ground) at 50 random locations in each of 12 plots in a study site, according to the method used by MacArthur and MacArthur (1961). Relationship of bird species diversity (BSD) and FHD for each habitat (or study site) was analyzed by simple linear regression.

The relationship of H′ and horizontal spatial heterogeneity was ana-

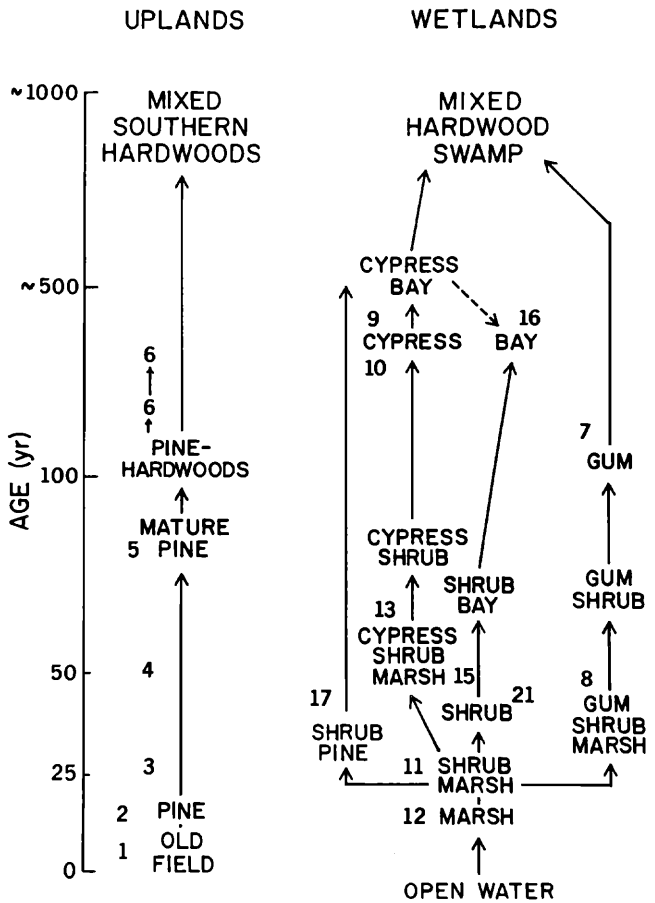

FIGURE 2. Avian study sites and theoretical successional patterns (Hamilton 1982). Numbered sites placed by approximate age of vegetation. Dashed line indicates successional set-back due to lumbering of the cypress-bay forests.

lyzed by simple linear regression of H′ and the coefficient of variation of point to center of shrub clump or center of overlapping canopy for each quadrat (Roth 1976).

Species importance values (I) for the upland and wetland sites as a whole were calculated by giving equal weight to density, frequency and biomass as follows:

$$I = 100(\text{relative density} + \text{relative frequency} + \text{relative biomass})/3.$$

A check-list of all avian species that have been recorded for the Okefenokee is included in Laerm et al. (1980). Colonially nesting water birds are not included in this study except as they were encountered consistently feeding in the study areas.

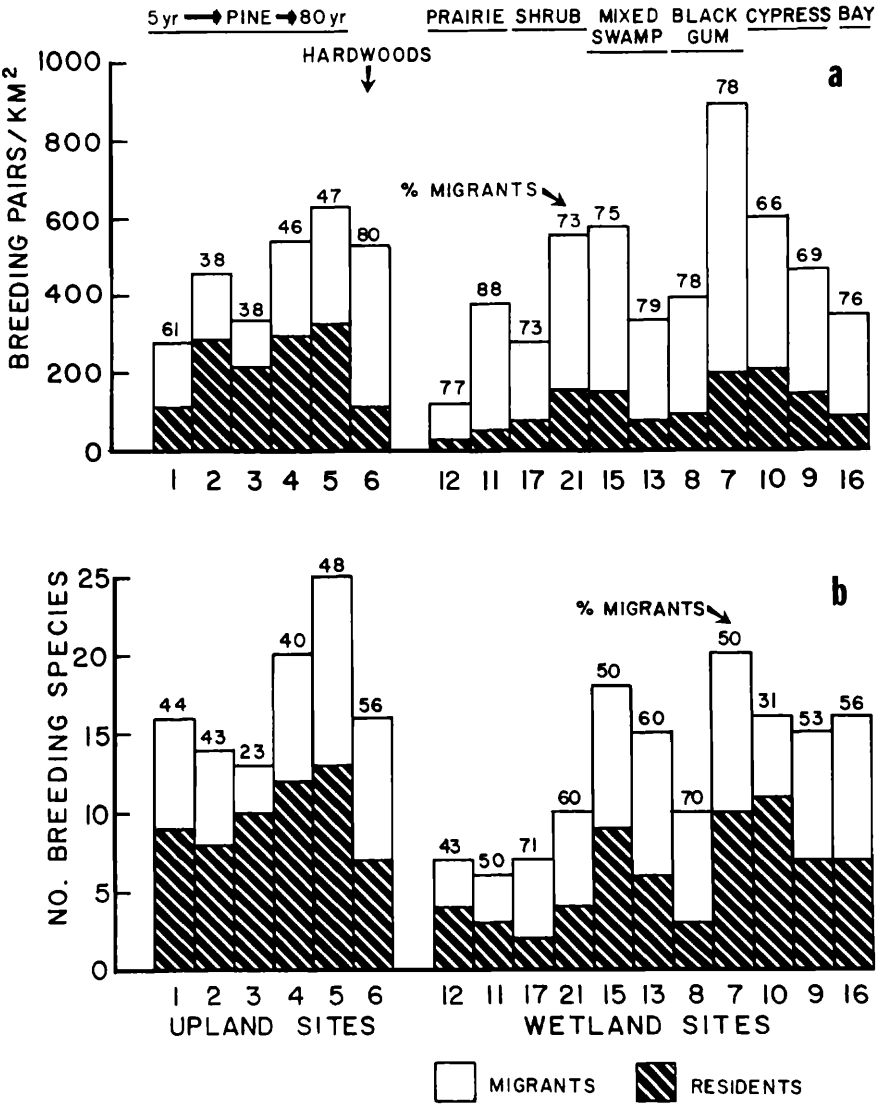

FIGURE 3. Density (a) and species richness (b) of breeding birds by study sites which are arranged in sequence from young to mature communities.

RESULTS AND DISCUSSION

Successional trends.—Both number of species and density increased with successional age and increased vegetative volume (Tables 2, 3), but peaks in density, biomass and species diversity occurred in the middle to late stages rather than in the oldest forests (Figs. 3, 4). This pattern is similar

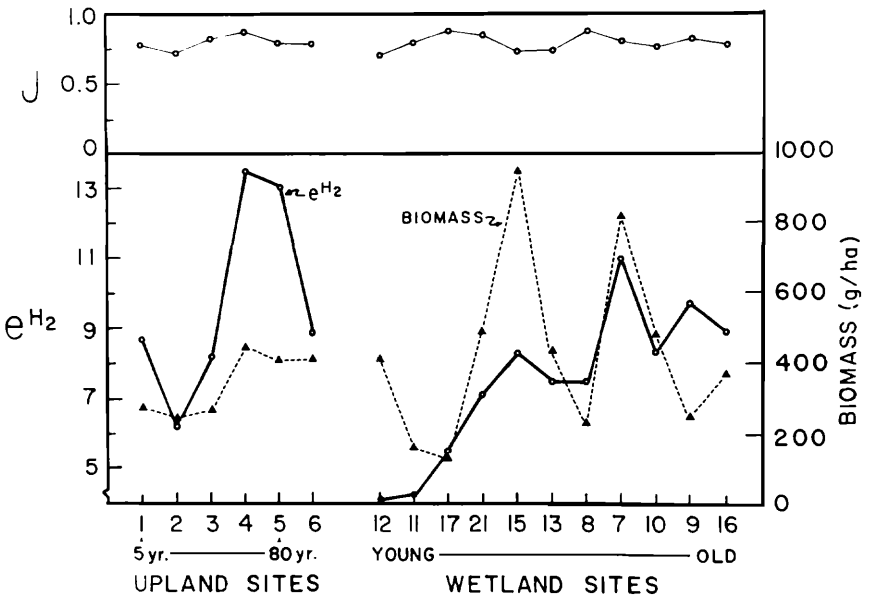

FIGURE 4. Species diversity ($e^{H'}$ and J) and biomass of breeding bird populations at study sites arranged in sequence from young to mature vegetation.

to that reported for upland series in other areas of the southeastern United States (Johnston and Odum 1956, Meyers and Johnson 1978). We suggest an energetic explanation for this pattern. In mature forests almost all photosynthetic production goes into maintenance (respiration) reducing net primary production and thereby bird food production.

Forests had higher diversity (H″) than some early successional stages; however, paired comparisons of H″ by habitat were not significantly different in many cases ($P < 0.05$). For example, H″ in shrub habitats did not differ from that in mature hardwoods or cypress swamp. These results suggest that BSD is not necessarily increased with maturation of vegetation or increased vegetation height.

Species composition.—The most common species in pine forests were Common Yellowthroat (*Geothlypis trichas*), Rufous-sided Towhee (*Pipilo erythrophthalmus*), Carolina Wren (*Thyrothorus ludovicianus*) and Pine Warbler (*Dendroica pinus*). In old growth pine and pine-hardwood forests (sites 5 and 6) Northern Cardinal (*Cardinalis cardinalis*), Great Crested Flycatcher (*Myiarchus crinitus*), Northern Parula (*Parula americana*), Hooded Warbler (*Wilsonia citrina*) and Red-eyed Vireo (*Vireo olivaceus*) had estimated densities greater than 50 pairs/km^2 (Table 2). The abundance of ground-story birds such as Rufous-sided Towhee and Common Yellowthroat in pine forests we judge to result from the prescribed burning that maintains an open, parklike forest with extensive shrub and ground cover.

TABLE 2. Breeding bird populations in pairs/km² upland sites, Okefenokee Swamp 1979–1980. Species ranked according to mean density, all sites. Sites (each 16 ha) arranged in successional order (young to old-growth). See Table 1 for description of sites.

Species	Sites						Mean
	1	2	3	4	5	6	
Common Yellowthroat	90	141	69	166	153	+	103.2
Rufous-sided Towhee	35	128	72	72	131	+	73.0
Carolina Wren	16	88	63	44	59	33	50.5
Northern Parula	+		28	19	6	140	32.2
Pine Warbler	3	50	19	50	44		27.7
Great Crested Flycatcher	13	9	31	25	38	49	27.5
Northern Cardinal	6	3		19	13	49	15.0
Acadian Flycatcher				+	+	68	11.3
Red-eyed Vireo						62	10.3
Hooded Warbler					+	62	10.3
Red-bellied Woodpecker	+	3	6	22	19	3	8.8
Brown-headed Nuthatch			6	31	6		7.2
Gray Catbird	6	6	+	6	13	6	6.2
Pileated Woodpecker		3	13	13	3	6	6.3
Yellow-throated Warbler				6	19	7	5.3
Prairie Warbler	31						5.2
Blue Jay			9	13	6		5.2
Eastern Meadowlark	25						4.2
Common Grackle				6	19		4.2
Prothonotary Warbler				19	6	+	4.2
Downy Woodpecker				6	13	6	4.2
Bobwhite	9		9		6		4.0
Mourning Dove	16	6					3.7
White-eyed Vireo		6			6	10	3.7
Carolina Chickadee	6		+	+	13		3.2
Bachman's Sparrow					19		3.2
Eastern Kingbird	6	6			6		3.0
Wood Pewee				6	9		2.5
Red-cockaded Woodpecker					13		2.2
Summer Tanager					13		2.2
Yellow-billed Cuckoo						13	2.2
Barred Owl				3		10	2.2
Brown Thrasher	+	+	6				2.0
Tufted Titmouse	3	3				3	1.5
Red-shouldered Hawk		+	+	3			1.0
Common Nighthawk					6		1.0
Fish Crow				6			1.0
Orchard Oriole	6						1.0
Red-tailed Hawk	3						0.5
Wild Turkey			3				0.5
Total breeding species	16	14	13	20	25	16	
Pairs/km²	275	456	328	541	631	526	

In the wetlands, Red-winged Blackbird (*Agelaius phoeniceus*) and Common Yellowthroat were the most common species in the marshes (sites 11 and 12, Table 3). Gray Catbird (*Dumetella carolinensis*), Carolina Wren, Common Yellowthroat and Great Crested Flycatcher were the

TABLE 3. Breeding bird populations in pairs/km² wetland sites Okefenokee swamp, 1979–1980. Species ranked according to mean density, all sites. Sites arranged in successional order (prairies to old-growth swamp forests). See Table 1 for descriptions of sites.

Species	Sites											Mean
	12	11	13	15	17	21	8	7	16	9	10	
Prothonotary Warbler			83	122	+	55	154	256	90	138	190	99.8
Common Yellowthroat	6	288	33		82	76	74			6		51.4
Northern Parula	+		83	122	+	65	17	169	37	91	100	49.5
Carolina Wren	6	13	28	25	55	76	63	59	27	79	44	43.2
Great Crested Flycatcher		+	19	64	27	87	11	19	23	34	52	30.6
Red-winged Blackbird	78	28	36	78	+							20.0
Red-bellied Woodpecker		+	19	19	19	22	11	31	10	31	38	18.2
Gray Catbird	6		28		55		108	+		+	9	17.9
Common Grackle	+	+	3	50		65	23	6	7	+	+	14.0
Yellow-throated Warbler			17	39						22	44	11.1
Hooded Warbler								59	47			9.6
Red-eyed Vireo							11	72	23			9.6
Acadian Flycatcher								75	17		6	8.9
Northern Cardinal		3	11	3	+	33		13	13	9	13	8.9
Green Heron	+		+	42	+	22	11	+		+		6.8
Tufted Titmouse				6				25		6	25	5.6
Yellow-billed Cuckoo		13	8	+			11	13	7	6		5.3
Downy Woodpecker				11	+			16	7	+	19	4.8
Pileated Woodpecker		+	6	+	+		+	13	10	6	13	4.4
White-eyed Vireo	+				9		+	19	7	13		4.4
Carolina Chickadee				17						6	19	3.8
Wood Duck	+	+	+	17							13	2.7
Red-shouldered Hawk		3	3					6	7	3		2.0
White Ibis	6		+					13				1.7
Barred Owl								9	7	+	+	1.4
Eastern Kingbird			+	11								1.0

TABLE 3. Continued.

Species	Sites											Mean
	12	11	13	15	17	21	8	7	16	9	10	
Eastern Kingbird			+	11								1.0
Osprey			6	6								1.1
Great Egret	9		+									0.8
Little Blue Heron	6		+	+		+						0.5
Purple Gallinule				6								0.5
Common Flicker			+	+							6	0.5
White-breasted Nuthatch											6	0.5
Wood Thrush								6				0.5
Blue-gray Gnatcatcher				6								0.5
Chimney Swift										6		0.5
Total breeding species	7	6	15	18	7	10	10	20	15	16	16	
Pairs/km^2	119	347	336	575	273	563	389	875	337	450	603	

most common in shrub swamps (sites 17 and 21, Table 3), while Prothonotary and Northern Parula Warblers dominated gum and cypress swamp forests (sites 7, 9, 10 and 16, Table 3). Greater than 50% of species and 75% of individual land birds in the wetland series were migrants, many wintering in the tropics (Fig. 3).

Rufous-sided Towhee in the uplands and Prothonotary Warbler in the wetlands rated highest in importance value, while Common Yellowthroat and Carolina Wren were "important" in both series (Table 4). Since biomass was included in the index, larger species such as Pileated Woodpecker (*Dryocopus pileatus*) and Barred Owl (*Strix varia*) were ranked higher than when numbers only are considered (compare Table 4 with Tables 2 and 3). Standing crop biomass was not highly correlated with H′ or species richness ($r < 0.5$); large birds accounted for high biomass at site 12, but not at sites 7 and 15, which were populated by many small birds.

A factor that affects species richness is the "reversed latitudinal gradient," that is, the tendency in eastern North America for the number of species of breeding land birds to decrease from north to south (Cook 1969, Tramer 1974). For example, only 65 species of land birds are known to breed in the south Georgia Okefenokee region (Laerm et al. 1980) as compared with 90 in the north Georgia Athens area, a well studied region of comparable size (Tramer 1968) and 150 or more in New England (Cook 1969). In theory, fewer species result in increased niche width for those present, which, we judge, helps to explain the wide range of habitats occupied by the common Okefenokee birds, especially the parulids.

Despite the reduced number of species, Shannon diversity (H′) and evenness indices (J) calculated on the basis of importance values were relatively high and almost identical for both the upland and wetland series (Table 4). Accordingly, the Okefenokee bird populations comprise fewer species than more northern regions but are characterized by high relative abundance diversity and low dominance.

Comparison with other wetlands.—Terwilliger and Rose (1984) found a mean density of 303 pairs/km^2 for red maple-gum habitats and 589 pairs/km^2 in the Atlantic white cedar stands in the Dismal Swamp on the eastern Virginia-North Carolina border, a range comparable to our estimates of 337–875 pairs/km^2 for gum and cypress swamp forests of the Okefenokee. In the forested parts of both the great swamps, warblers comprised more than half the numbers, and Prothonotary Warbler and Common Yellowthroat were the most abundant species.

Based on data compiled from Audubon Breeding Bird Censuses, northern marshes appear to support a greater density of breeding birds than do southern marshes, but northern and southern swamp forests are not significantly different (Table 5). For forested wetlands then, fewer species southward is not associated with lower densities.

Community structure and BSD.—Since breeding birds tend to be segregated by vegetation layers, species richness and diversity often increase

TABLE 4. Importance values (I[a]) of birds by upland and wetland habitats, Okefenokee Swamp, 1979–1980.

Upland		Wetland	
Species	I	Species	I
Rufous-sided Towhee	12.3	Prothonotary Warbler	11.5
Common Yellowthroat	11.2	Carolina Wren	7.1
Carolina Wren	6.9	Northern Parula	6.4
Great Crested Flycatcher	5.4	Common Yellowthroat	6.4
Wild Turkey	4.9	Great Crested Flycatcher	6.0
Pileated Woodpecker	4.8	Red-bellied Woodpecker	5.4
Pine Warbler	4.1	Common Grackle	4.7
Northern Parula	3.9	Red-winged Blackbird	4.0
Northern Cardinal	3.6	Green Heron	3.6
Barred Owl	3.4	Osprey	3.5
Red-bellied Woodpecker	3.2	Wood Duck	3.5
Bobwhite	2.5	Red-shouldered Hawk	3.3
Gray Catbird	2.4	Pileated Woodpecker	3.3
Blue Jay	1.9	Gray Catbird	3.3
Red-shouldered Hawk	1.8	Cardinal	3.1
Mourning Dove	1.7	White Ibis	2.9
Brown-headed Nuthatch	1.6	Yellow-billed Cuckoo	2.3
Common Grackle	1.6	Barred Owl	2.2
Downy Woodpecker	1.4	Yellow-throated Warbler	1.9
Yellow-throated Warbler	1.4	Red-eyed Vireo	1.7
Red-tailed Hawk	1.3	Tufted Titmouse	1.5
Acadian Flycatcher	1.3	Acadian Flycatcher	1.5
Eastern Kingbird	1.3	Downy Woodpecker	1.4
Red-eyed Vireo	1.3	Great Egret	1.4
Eastern Meadowlark	1.3	White-eyed Vireo	1.3
White-eyed Vireo	1.2	Hooded Warbler	1.3
Hooded Warbler	1.2	Carolina Chickadee	1.0
Tufted Titmouse	1.1	Blue Jay	0.6
Prothonotary Warbler	1.0	Little Blue Heron	0.5
Carolina Chickadee	0.9	Purple Gallinule	0.4
Fish Crow	0.9	Common Flicker	0.3
Eastern Wood Pewee	0.8	Eastern Kingbird	0.3
Yellow-billed Cuckoo	0.7	Chimney Swift	0.3
Prairie Warbler	0.7	Wood Thrush	0.3
Bachman's Sparrow	0.6	Blue-gray Gnatcatcher	0.2
Red-cockaded Woodpecker	0.6	White-breasted Nuthatch	0.2
Common Nighthawk	0.5		
Brown Thrasher	0.5		
Summer Tanager	0.5		
Orchard Oriole	0.4		
Species diversity (H′)	3.275		3.214
Evenness	0.888		0.897
Total area (ha) censused	95.3		149.9

[a] I = 100(relative density + relative frequency + relative biomass)/3.

TABLE 5. Breeding bird density (mean pairs/km^2 ± SD) in four wetland habitats in the Okefenokee compared with densities in comparable wetlands in northeastern (Virginia north) and southeastern (North Carolina south) regions.

Habitat	Okefenokee		Northeastern U.S. and Canada		Southeastern U.S.	
	N	Mean	*N*	Mean	*N*	Mean
Marshes and wet prairies	2	223	22	871 ± 153	3	187 ± 80
Shrub swamps	2	418	2	847 ± 383	2	417 ± 145
Young swamp forests	3	433	12	622 ± 49	4	483 ± 71
Mature swamp forests	4	566	7	705 ± 137	11	975 ± 124

N = number of censuses.

Data on northeastern and southeastern regions from Breeding Bird Censuses (see Meyers 1982).

with additional layers of vegetation (Tramer 1969). However, this relationship was only partially substantiated in this study since the highest diversity was not found in habitats with the most layers, such as the 3–4 layered upland hardwoods (site 6) or mature cypress swamps (site 9). Sites were compared by using FHD to predict BSD with MacArthur and MacArthur's (1961) regression model. The predicted BSD (H′) was 1.69 for site 5 (actual 2.56); 2.45 for site 6 (actual 2.29); 2.58 for site 9 (actual 2.11). No relation between H″ and FHD was evident (linear regression analysis of H″ versus FHD, $r^2 = 0.106$. $P = 0.22$). H′ and FHD also were poorly correlated, $r^2 = 0.143$, $P = 0.15$. Consequently, increased FHD or number of vegetation layers did not correlate with BSD as suggested by MacArthur et al. (1962).

Horizontal spatial heterogeneity also failed to account for increases in BSD as was hypothesized by Roth (1976). Linear regression analysis predicted no relationship of spatial heterogeneity in the shrub, understory and overstory layers of vegetation (shrub, $r^2 = 0.10$, $P = 0.70$; understory, $r^2 = 0.03$, $P = 0.92$; overstory, $r^2 = 0.27$, $P = 0.31$). Any combination of the three layers was also poorly correlated with BSD. Szaro and Balda (1979) also found no relationship between Roth's heterogeneity index and BSD in ponderosa pine forests of Arizona.

As is the case in many forested wetlands the presence of dead trees and snags has major effects on breeding bird populations since woodpeckers, Great Crested Flycatchers, Prothonotary Warblers and other cavity nesters are important members of the breeding bird populations.

We conclude that no one habitat feature or index will likely account for avian density or diversity in a complex and dynamic landscape such as the Okefenokee. Accordingly, factor analysis was undertaken as an exploratory technique to classify numbers of significant variables into groups of biologically interpretable factors (Meyers 1982). Results of these analyses will be reported in a subsequent paper.

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TIOF ENDOWMENT FUND PROPOSAL

The International Osprey Foundation (TIOF) is seeking applications for its second grant to support research activities of a graduate student primarily focusing on ospreys. Work with other raptor species may be considered, however. The award recipient will be expected to provide a report on his or her research and use of the funds within a year of receiving the grant.

Gustavo D. Danemann, a graduate student with the Seabird Program at the Universidad Autonoma de Baja California Sur, Marina Biology Departmento in La Paz, Mexico was awarded the first grant. He is studying the breeding ecology, philopatry and dispersion of ospreys in the coastal lagoons of Baja California and the effect of nest density on breeding performance.

Applicants should submit a proposal outlining their project and the intended use of the funds by April 15, 1991. The grant will be awarded on June 1, 1991. Send applications to: TIOF, Endowment Fund, P.O. Box 250, Sanibel, Florida 33957-0250, USA.