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AVIAN COMMUNITY DYNAMICS IN A PENINSULAR FLORIDA LONGLEAF PINE FOREST

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Abstract.—The bird community of a mature longleaf pine (*Pinus palustris*) forest in central Florida was studied seasonally over a four-year period. Seventy-seven species were observed on the study area, with the highest seasonal average (36) in the spring. Permanent residents represented the majority of species (about 70%) and individuals (about 80%) in all seasons. Bird density (562/km^2) and biomass (29.2 kg/km^2) in summer were more than twice those of the winter. Insectivores were the dominant trophic group in all seasons except fall, when omnivores were most common. Virtually all seasonal turnover occurred within the insectivore group. The longleaf pine community supported more birds and bird species in summer than in winter, suggesting that natural longleaf pine forests do not serve as major wintering areas for migrants. In this respect they are very different from southern bottomland forests and certain other pine forests.

A continental gradient of decreasing breeding bird species richness from northwest to southeast continuing down the Florida peninsula seems well established (MacArthur and Wilson 1967, Cook 1969, Robertson and Kushlan 1974). This gradient is counter to the conventional increase in diversity with decreasing latitude. Tramer (1974) and Rabenold (1979) have focused attention on this reverse latitudinal diversity gradient, which is observed to start with a "tropical threshold" at about 25° in Florida and proceed north to 45-50° N in New England. However, several complications to the above generality exist. Short (1979) presented the case that "within-habitat" species richness (alpha diversity) does not follow the same pattern, and Wiens (1975: 228) observed that, "mature northeastern forests, southeastern pine forests, and forests in the Sierra Nevada of California all support relatively large numbers of breeding species."

Whereas a gradient may exist for breeding birds, the same gradient clearly does not apply to wintering birds, at least not in certain habitats (Dickson 1978, Hirth and Marion 1979, Harris and Vickers 1984). Neither does the gradient apply to non-passerine breeding land birds (Robertson and Kushlan 1974). A multi-season study of bird community dynamics in a low-latitude North American setting would help to shed light on these issues.

Of equal relevance to the gradient issue is whether the data considered in analyses are derived from natural or secondary habitats. Open-spaced longleaf pine (*Pinus palustris*) originally dominated some 24 million hectares, over 60% of the southeastern coastal plain (Croker 1979, Ware et al. in press). Yet, only one thorough, multi-seasonal study of this vegetation type has been reported (Repenning and Labisky 1985). Norris (1951) described qualitative characteristics of the summer avifauna but established no quantitative reference point. Harris et al. (1974) compared seasonal abundance and richness in young pine plantations to a mature longleaf control stand, but no emphasis was given to community characteristics. Engstrom (1981) reported on data collected in a small (58 ha), mature longleaf stand in southern Georgia. Only Repenning and Labisky (1985), working in the Florida Panhandle, have provided data on birds from large natural longleaf pine stands.

The objective of our study was to establish the nature of seasonal avian community dynamics in a natural longleaf pine forest of the deep southeastern coastal plain. With a second reference point from a natural forest community and one nearer the "tropical threshold," greater significance can be attached to more northern studies and to those in managed and/or second-growth forests.

Study Area

This study was conducted on a 162 ha tract of mature longleaf pine 10 km north of Brooksville, Hernando County, Florida at 28° N (Fig. 1). Although many of the trees were "turpentined" early in this century, the stand is believed to be the only sizeable tract of old-growth "virgin" pine in Florida. The forest was subjected to controlled burning and cattle grazing until 1960, when cattle were fenced out and fire was excluded (Beckwith 1967). In 1977 winter burning was reintroduced. Because of the 17-year period without fire, a hardwood midstory and brushy understory proliferated. In this respect the study area differed from a "natural" longleaf pine stand, which would have had little or no midstory.

The dominant trees on the study area were mature longleaf pines (dbh $\bar{x} \pm SD = 26.1 \pm 11.8$ cm; density $\bar{x} \pm SD = 194.6 \pm 52.6$/ha), water oak (*Quercus nigra*) (dbh $\bar{x} \pm SD = 16.8 \pm 5.6$ cm; density $\bar{x} \pm SD = 25.2 \pm 23.8$/ha) and laurel oak (*Q. hemisphaerica*) (dbh $\bar{x} \pm SD = 19.1 \pm 8.1$ cm; density $\bar{x} \pm SD = 9.2 \pm 5.5$/ha); the oaks are fast-growing invaders (Table 1). That the latter two species also were the most important midstory species, and ranked second and third as understory species, portrays the speed with which these hardwoods become established in the absence of fire. The dominant understory shrub was runner oak (*Q. pumila*). Wire grasses (*Aristida* spp. and *Sporobolus* spp.) were the most prevalent herbaceous species, constituting 27.8% of the ground cover.

METHODS

The bird population on the study area was estimated by walking the center line of 20 x 500 m (1 ha) quadrats, a fixed-width transect technique (Type D in Emlen 1971). Five east-west quadrats were randomly chosen on the study area with the only constraint that they be a minimum of 100 m apart. Because of a dense hardwood midstory, narrow transects were specifically chosen to reduce the seasonal bias inherent in all bird population estimates in which breeding season data are compared with non-breeding season data.

Birds were counted during four seasonal sampling periods each year from February 1976 to June 1979. Sampling periods were as follows: winter, Feb. 12 to Feb. 27; spring, Mar. 26 to Apr. 30; summer, June 1 to July 16; fall, Oct. 17 to Oct. 27. During each sampling period, quadrats were counted on four or five usually consecutive days starting about 0.5 hr after sunrise. It took about 2 hrs to count all five quadrats with quadrats being covered in a different sequence each day to reduce temporal bias. All birds seen or heard were recorded, but only those within 10 m of the center line were noted as on the quadrat. Estimates of avian biomass were based on data from specimens in the Florida Museum of Natural History collection and information from J. B. Dunning, Jr. (pers. comm.).

We calculated avian species diversity in two ways. Both were measures of alpha diversity (Whittaker 1960). The first was derived from just those birds that occurred directly on quadrats, whereas the second was derived from the frequencies of all birds seen or heard while walking the transects.

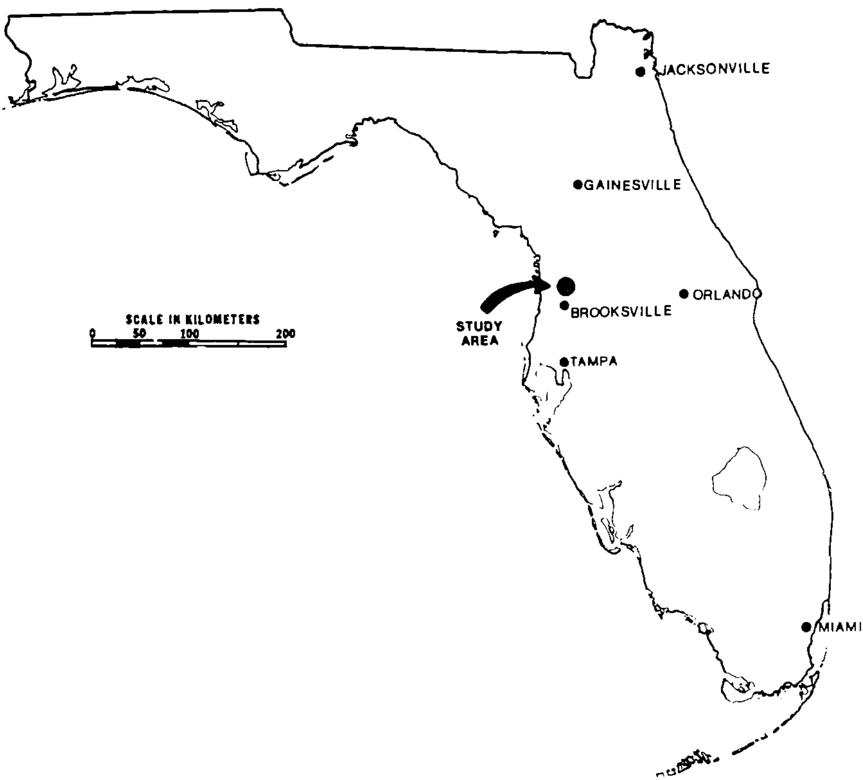

Figure 1. Location of study area in Hernando County, Florida.

Table 1. Percent cover of the 10 most important woody species in 3 strata. Note that only nine species occurred in the canopy stratum.

	Understory 0-2 m		Midstory 2-8 m		Canopy >8 m	
Rank 1	*Quercus pumila*	(4.6)	*Quercus nigra*	(12.9)	*Pinus palustris*	(37.5)
Rank 2	*Q. nigra*	(4.1)	*Q. hemisphaerica*	(12.2)	*Quercus nigra*	(4.1)
Rank 3	*Q. hemisphaerica*	(2.5)	*Q. margaretta*	(9.1)	*Q. hemisphaerica*	(4.0)
Rank 4	*Myrica cerifera*	(2.4)	*Pinus palustris*	(6.4)	*Carya glabra*	(1.4)
Rank 5	*Q. margaretta*	(1.9)	*Q. laevis*	(4.8)	*Prunus serotina*	(1.0)
Rank 6	*Smilax* spp.	(1.9)	*Prunus serotina*	(2.1)	*Q. virginianus*	(0.4)
Rank 7	*Vaccinium arboreum*	(1.1)	*Q. virginianus*	(2.0)	*Liquidambar styraciflua*	(0.4)
Rank 8	*Viburnum dentatum*	(0.9)	*Liquidambar styraciflua*	(1.9)	*Myrica cerifera*	(0.3)
Rank 9	*Gelsemium sempervirens*	(0.6)	*Carya glabra*	(1.6)	*Magnolia grandiflora*	(0.2)
Rank 10	*Q. laevis*	(0.5)	*Smilax* spp.	(1.3)	—	
Total		20.5		54.3		49.3
% cover all species $\bar{x} \pm$ SD		22.5 ± 7.3		58.9 ± 26.4		49.3 ± 8.0

To analyze trophic relations of the community, we categorized species as granivores, carnivores (predominantly insectivores), and omnivores. Although assignments to these categories involved some arbitrary decisions because of seasonal shifts in food habits, placment of the great majority of species was straight-forward (Martin et al. 1951, Hamel et al. 1982).

There were two small (< 1 ha) ponds on and adjacent to the study area. Because we were interested in the birds of the longleaf pine community, we have deleted from consideration in this paper those species associated with the aquatic ecosystems. These included Wood Duck (*Aix sponsa*), Anhinga (*Anhinga anhinga*), Wood Stork (*Mycteria americana*), Belted Kingfisher (*Megaceryle alcyon*), and a variety of herons and egrets. Cattle Egrets (*Bubulcus ibis*) passing over from nearby pastures were not considered. Scientific names of other avian species in the text are listed in Table 2 and follow AOU (1983) checklist.

Habitat measurements were taken on a 0.5-ha quadrat located on each of the bird sampling quadrats (50 x 100 m). Density and dbh of trees > 10 cm were tallied by a total quadrat count on the five quadrats. Percent cover and species composition (both woody and herbaceous) were estimated by the line intercept method along three 30 m lines on each quadrat.

RESULTS

There were no significant differences in number of birds seen among the five transects during any season (ANOVA, df = 4, 236, F = 0.2975, P = 0.88), and thus we pooled the data from all transects for further analysis. A total of 77 species was seen from January 1976 to June 1979 (Table 2). The highest seasonal average of 36 species occurred during spring (total for 4 springs = 53) when both permanent residents and migrants were present, and the lowest seasonal average of 33 species (total = 50 species) was for winter (Table 3).

Permanent residents constituted the majority of species and the majority of individuals on the study area during all seasons (Tables 2 and 3). Of the 77 species seen, 38 were permanent residents, 23 were winter-only residents, 11 were summer-only residents, and 5 were transients. Permanent residents constituted 58% of the species recorded during winter and 68% of the species recorded during summer. The proportion of total individuals contributed by permanent resident species in summer and winter was 82% and 79%, respectively.

Only 45 of the 77 species observed on the study area occurred on the sample quadrats (Table 2). The 17 permanent resident species observed on the quadrats during summer were complemented by 7 summer-only species, whereas 18 permanent resident species observed during winter were complemented by 9 winter-only species. Thus, permanent residents represented about 70% of the total species array during summer and winter. Only five species classified as transients were seen on the study area, and only three of these appeared on our quadrats (Table 2).

The summer bird density (as opposed to breeding bird density) was more than twice the winter bird density (Table 3). The density of individuals in species classified as permanent residents more than doubled

Table 2. Mean density (± SD), residency status, and foraging groups of birds occurring on the study area, Hernando County, Florida, February 1976 to June 1979.

Species	Residency status*	Foraging group**	Density (birds/km²)***			
			Win.	Spr.	Sum.	Fall
Black Vulture *Coragyps atratus*	P	C	x	x	x	x
Turkey Vulture *Cathartes aura*	P	C	x	x	x	x
Sharp-shinned Hawk *Accipiter striatus*	W	C	—	—	—	3.3 (26.0)
Cooper's Hawk *Accipiter cooperii*	P	C	—	—	—	x
Red-shouldered Hawk *Buteo lineatus*	P	C	x	x	x	x
Red-tailed Hawk *Buteo jamaicensis*	P	C	x	x	x	—
American Kestrel *Falco sparverius*	P	C	—	—	—	x
Northern Bobwhite *Colinus virginianus*	P	G	37.7 (155.5)	18.8 (98.7)	63.3 (259.0)	48.3 (202.1)
American Woodcock *Scolopax minor*	W	C	1.6 (12.9)	—	—	—
Mourning Dove *Zenaida macroura*	P	G	x	1.3 (11.3)	4.4 (26.0)	x
Common Ground-Dove *Columbina passerina*	P	G	—	x	x	x
Yellow-billed Cuckoo *Coccyzus americanus*	S	I	—	x	x	x
Eastern Screech Owl *Otus asio*	P	C	—	—	—	x
Great Horned Owl *Bubo virginianus*	P	C	x	—	—	x
Barred Owl *Strix varia*	P	C	1.6 (12.9)	—	x	1.7 (13.0)
Chuck-will's-widow *Caprimulgus carolinensis*	S	I	—	1.3 (11.3)	8.9 (36.7)	—
Whip-poor-will *Caprimulgus vociferus*	W	I	3.3 (18.3)	—	—	—
Chimney Swift *Chaetura pelagica*	S	I	—	—	x	x
Ruby-throated Hummingbird *Archilochus colubris*	S	N	—	1.3 (11.3)	2.2 (15.0)	—
Red-headed Woodpecker *Melanerpes erythrocephalus*	P	I	—	x	—	—
Red-bellied Woodpecker *Melanerpes carolinus*	P	O	4.9 (22.4)	23.8 (65.6)	14.4 (43.7)	10.0 (31.9)
Yellow-bellied Sapsucker *Sphyrapicus varius*	W	O	x	—	—	—

Table 2. (continued)

Species	Residency status*	Foraging group**	Density (birds/km²)*** Win.	Spr.	Sum.	Fall
Downy Woodpecker *Picoides pubescens*	P	I	1.6 (12.9)	3.8 (19.5)	22.2 (58.1)	5.0 (22.5)
Northern Flicker *Colaptes auratus*	P	I	1.6 (12.9)	x	x	1.7 (13.0)
Pileated Woodpecker *Dryocopus pileatus*	P	I	1.6 (12.9)	3.8 (25.2)	7.8 (35.2)	3.3 (18.4)
Eastern Wood Pewee *Contopus virens*	S	I	—	—	—	x
Eastern Phoebe *Sayornis phoebe*	W	I	6.6 (31.6)	—	—	x
Great-crested Flycatcher *Myiarchus crinitus*	S	I	—	31.3 (75.5)	36.7 (95.4)	x
Purple Martin *Progne subis*	S	I	—	x	x	—
Tree Swallow *Tachycineta bicolor*	W	I	x	x	—	x
Barn Swallow *Hirundo rustica*	T	I	—	—	—	x
Blue Jay *Cyanocitta cristata*	P	O	3.3 (31.6)	15.0 (55.1)	27.8 (71.1)	26.7 (68.9)
Fish Crow *Corvus ossifragus*	P	O	1.6 (12.9)	x	x	x
Carolina Chickadee *Parus carolinensis*	P	O	24.6 (61.9)	11.3 (43.6)	26.7 (76.4)	11.7 (43.2)
Tufted Titmouse *Parus bicolor*	P	O	18.0 (67.1)	52.5 (107.9)	85.6 (156.1)	93.3 (209.1)
Red-breasted Nuthatch *Sitta canadensis*	W	I	—	—	—	x
White-breasted Nuthatch *Sitta carolinensis*	P	I	—	x	—	—
Carolina Wren *Thryothorus ludovicianus*	P	I	8.2 (28.9)	17.5 (57.4)	27.8 (84.1)	10.0 (36.8)
House Wren *Troglodytes aedon*	W	I	—	1.3 (11.3)	—	3.3 (26.6)
Golden-crowned Kinglet *Regulus satrapa*	W	I	3.3 (25.8)	—	—	—
Ruby-crowned Kinglet *Regulus calendula*	W	I	23.0 (79.6)	12.5 (45.0)	x	1.7 (13.0)
Blue-gray Gnatcatcher *Polioptila caerulea*	P	I	3.3 (25.8)	43.8 (101.3)	35.6 (88.7)	28.3 (89.3)
Eastern Bluebird *Sialia sialis*	P	I	—	—	—	x
Veery *Catharus fuscescens*	T	I	x	—	—	1.7 (13.0)
Hermit Thrush *Catharus guttatus*	W	I	4.9 (28.9)	5.0 (22.5)	—	—

Table 2. (continued)

Species	Residency status*	Foraging group**	Density (birds/km²)*** Win.	Spr.	Sum.	Fall
Wood Thrush *Hylocichla mustelina*	T	I	—	x	—	1.7 (13.0)
American Robin *Turdus migratorius*	W	O	x	1.3 (11.3)	—	—
Gray Catbird *Dumetella carolinensis*	W	O	x	x	—	15.0 (50.4)
Northern Mockingbird *Mimus polyglottus*	P	O	—	x	x	—
Brown Thrasher *Toxostoma rufum*	P	O	x	x	5.6 (28.0)	1.7 (13.0)
Cedar Waxwing *Bombycilla cedrorum*	W	O	—	x	—	—
White-eyed Vireo *Vireo griseus*	P	I	11.5 (48.3)	10.0 (35.6)	25.6 (84.1)	6.7 (31.9)
Yellow-throated Vireo *Vireo flavifrons*	S	I	—	10.0 (55.1)	7.8 (31.8)	x
Red-eyed Vireo *Vireo olivaceus*	S	I	—	x	6.7 (36.7)	—
Northern Parula *Parula americana*	S	I	—	16.3 (60.6)	13.3 (42.4)	—
Magnolia Warbler *Dendroica magnolia*	T	I	—	—	—	5.0 (29.1)
Yellow-rumped Warbler *Dendroica coronata*	W	I	x	31.3 (148.8)	—	6.7 (52.1)
Black-throated Green Warbler *Dendroica virens*	T	I	x	—	—	—
Yellow-throated Warbler *Dendroica dominica*	P	I	3.3 (18.3)	1.3 (11.3)	—	3.3 (18.4)
Pine Warbler *Dendroica pinus*	P	I	42.6 (108.0)	25.0 (76.3)	54.4 (119.5)	35.0 (115.7)
Prairie Warbler *Dendroica discolor*	P	I	—	x	—	—
Palm Warbler *Dendroica palmarum*	W	I	3.3 (25.8)	1.3 (11.3)	—	1.7 (13.0)
Black and White Warbler *Mniotilta varia*	W	I	3.3 (25.8)	1.3 (11.3)	—	6.7 (31.9)
Ovenbird *Seiurus aurocapillus*	W	I	3.3 (18.3)	5.0 (27.6)	—	—
Common Yellowthroat *Geothlypis trichas*	P	I	1.6 (12.9)	7.5 (35.6)	1.1 (10.6)	6.7 (31.9)
Summer Tanager *Piranga rubra*	S	I	—	6.3 (29.8)	14.4 (43.7)	—
Northern Cardinal *Cardinalis cardinalis*	P	G	21.3 (51.6)	50.0 (88.6)	48.9 (99.4)	26.7 (63.8)

Table 2. (continued)

Species	Residency status*	Foraging group**	Density (birds/km²)***			
			Win.	Spr.	Sum.	Fall
Rufous-sided Towhee *Pipilo erythrophthalmus*	P	G	1.6 (12.9)	13.8 (46.4)	28.9 (70.3)	11.7 (46.9)
White-throated Sparrow *Zonotrichia albicollis*	W	G	x	—	—	—
Dark-eyed Junco *Junco hyemalis*	W	G	x	—	—	—
Red-winged Blackbird *Agelaius phoenicus*	P	O	1.6 (12.9)	x	x	38.3 (221.3)
Eastern Meadowlark *Sturnella magna*	P	I	—	x	—	—
Boat-tailed Grackle *Quiscalus major*	P	O	x	—	x	—
Common Grackle *Quiscalus quiscula*	P	O	x	x	—	x
Brown-headed Cowbird *Molothrus ater*	W	O	—	x	—	—
Pine Siskin *Carduelis pinus*	W	G	x	—	—	—
American Goldfinch *Carduelis tristis*	W	G	x	—	—	—

*Seasonal status designated: P, permanent resident; W, winter resident; S, summer resident; T, transient.
**Foraging group designated: C, carnivorous; I, insectivorous; O, omnivorous; G, granivorous; N, other.
***x denotes bird present on study area during season but not on a quadrat.

from 215/km² in winter to 315/km² in spring and 472/km² during summer sampling periods. The spring increase occurred prior to the nesting season and clearly represented an influx of migrants from farther south. Downy Woodpecker, Tufted Titmouse, Blue Jay, and Carolina Wren were examples of permanent resident species that increased markedly from winter to spring; populations of Pine Warblers and Carolina Chickadees declined during the same period (Table 2). The increase in summer density presumably resulted from production of young.

Summer biomass of the avian community exceeded the winter biomass by the same magnitude (29.2 kg/km² versus 13.6 kg/km²) as summer density exceeded winter density. Biomass of permanent resident species represented 90% of the total avian community during summer, and 91% during winter. Even though the density of Northern Bobwhites was exceeded by Pine Warblers in winter and by Tufted Titmice in summer, large body size caused bobwhites to represent 51% of the avian biomass during winter, and 38% during summer. When we deleted Northern Bobwhites from this analysis, permanent residents were less

Table 3. Mean density (± SD), species number, and species diversity by season over four years on the study area, Hernando County, Florida, February 1976 to June 1979.

	Season			
	Winter	Spring	Summer	Fall
Mean density (birds/km^2)	246	424	570	417
Standard deviation	(303)	(456)	(468)	(557)
Percent permanent residents	78	71	84	88
Species on quadrats ($\bar{x}$)	14.0	18.5	19.5	8.0
Diversity (H')*	2.19	2.61	2.64	2.37
Equitability (J')**	0.83	0.89	0.89	0.82
Total species on study area ($\bar{x}$)	33.0	36.0	29.5	35.0
Diversity (H')*	2.81	3.00	2.86	2.85
Equitability (J')**	0.80	0.84	0.85	0.80

*$H' = -\Sigma p_i \log_e p_i$
**$J' = H'/\log_e S$

dominant in the avian community, but they still represented 83% of the total biomass in both summer and winter.

"Quadrat-only" diversity, the more conservative and restrictive diversity measure, showed greater seasonal changes than "total-count" diversity, being lowest in winter and highest in summer (Table 3). Total-count diversity was higher than quadrat-only diversity at all seasons, largely because it was based on more species, but it showed little seasonal fluctuation, except for a peak in spring.

The bird community was dominated by insectivores at all seasons except fall when omnivores, such as Red-winged Blackbirds, Tufted Titmice, Red-bellied Woodpeckers, Blue Jays, and Carolina Chickadees predominated (Fig. 2). Insectivore populations were highest in spring and summer when insect abundance was presumed to be highest. The granivore group was dominated by Northern Bobwhites, and during summer when they were most abundant, the combination of their high numbers and large size amplified their biomass density (Fig. 2).

Since all summer-only and winter-only residents except the Ruby-throated Hummingbird were carnivores (includes raptors, insectivores, and American Woodcock), the greatest seasonal dynamics occurred within the carnivore guild. During summer, 35% of the insectivore population consisted of summer-only residents; during winter, 42% were winter-only residents. Thus, eight winter-only, insectivorous migrants from the north (plus the American Woodcock) replaced six summer-only, insectivorous species that migrated farther south (plus the Ruby-throated Hummingbird). In some cases, winter-only immigrants served as ecological equivalents to summer-only emigrants. For instance, Whip-poor-will replaced Chuck-will's-widow, and Red-eyed Vireo and Yellow-throated Vireo, both midstory gleaners, left in late summer and were

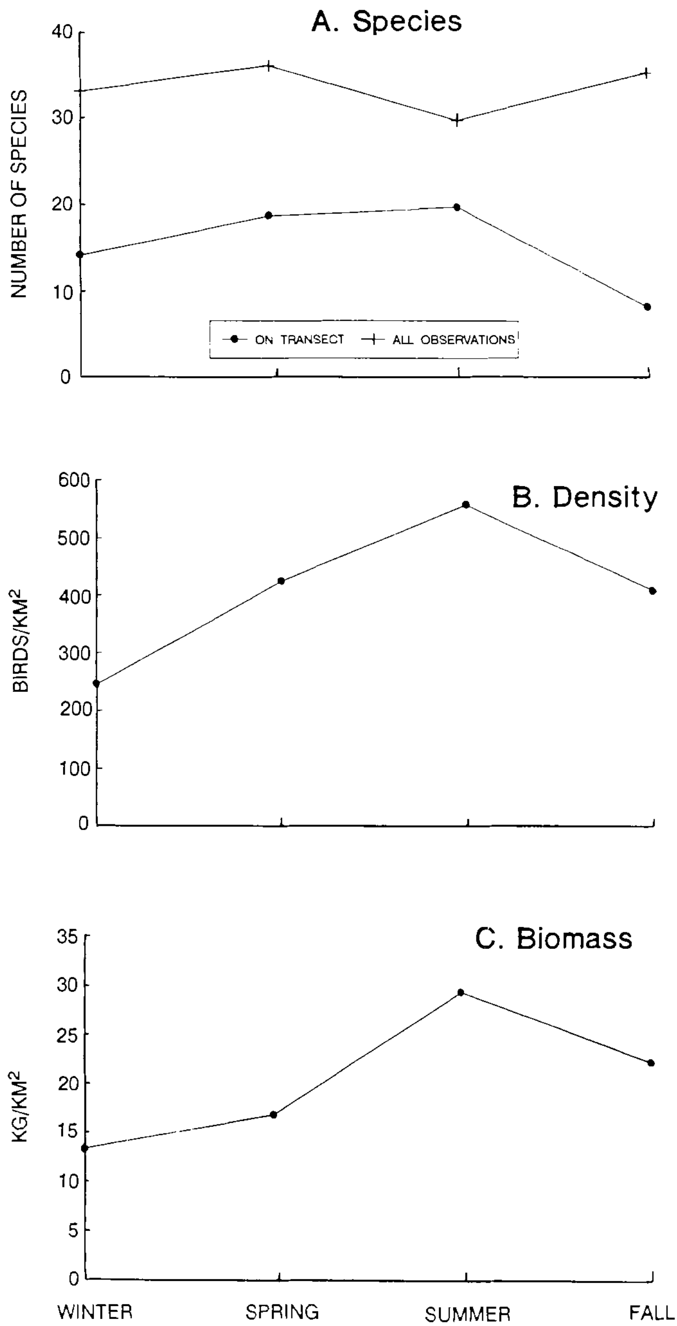

Figure 2. Seasonal changes in numbers of species (A), density (B), and biomass (C) of a longleaf pine bird community in peninsular Florida.

replaced by the Ruby-crowned Kinglet in winter. In other cases there was no apparent correspondence between species leaving and those arriving. For example, the ground foraging Ovenbird and Hermit Thrush occurred during winter when food resources might be more abundant near the ground, but there were no apparent ecological counterparts on the area during summer.

In addition, to the species replacement described above, considerable seasonal turnover occurred within species that were classified as permanent residents. The most dramatic case of this seasonal dynamic occurred within the omnivore trophic group. Red-winged Blackbirds increased from very low numbers during summer to the second most abundant species during fall and declined to modest densities during winter (Table 2). Red-bellied Woodpeckers increased from 5/km^2 during winter to 24/km^2 during spring, then declined to 14/km^2 during summer. Blue Jay numbers followed a similar pattern. Thus, seasonal shifts within these "permanent-resident" species also constituted an important aspect of overall community dynamics.

Thirteen cavity-nesting species were present on the study area as either permanent or summer residents. Tufted Titmice and Great-crested Flycatchers were the most common cavity nesters during summer. Summer densities of primary and secondary cavity nesters were almost the same (100.6/km^2 and 92.9/km^2, respectively) if numbers of chickadees and titmice were divided equally between the two categories. It should be kept in mind, however, that these data (Table 2) were collected in summer after at least first broods had fledged and that these densities can not be translated to numbers of breeding pairs.

Discussion

Longleaf pine communities formerly dominated the lower coastal plain but have now been reduced to a trivial amount in states such as Florida. The overall decline of longleaf pine communities may be over 98%, and the remaining stands are mostly of poor quality (Noss 1988, Ware et al. in press). This leaves us in the unenviable position of attempting to manage second growth stands for biotic diversity without a reference point. This and a study by Repenning and Labisky (1985) help to establish that reference point. In addition, this site is at 28° N, just north of the "tropical threshold" described by Rabenold (1979) and sufficiently far down the Florida peninsula to manifest the "peninsula effect."

Our density estimate of 570 birds/km^2 during summer fell within the range of reported values (Short 1979, Engstrom 1981, Repenning and Labisky 1985) and thus neither supports nor detracts from the notion that old-growth longleaf pine supports notably high densities of birds. The winter density of 246 birds/km^2 was lower than we had anticipated and deserves further verification. The fact that our winter density was significantly ($P < 0.05$) less than the density during other seasons shows that not all southeastern coastal plain community types support higher bird densities during the winter. We believe this is because longleaf pine characteristically occurs on drier sites than other common pine species (excluding *P. clausa*). Although all southeastern "piney woods" are fire-maintained communities, longleaf is best adapted to frequent fire (Stoddard 1962). In combination, the drier sites and more frequent fire generally result in a less shrubby understory than occurs in slash pine (*P. elliottii*) or loblolly pine (*P. taeda*) stands. It is the broad-leaved evergreen shrubs and vines (e.g., *Ilex* spp., *Lyonia* spp., *Smilax* spp.) that produce large quantities of fruit and support arthropod populations during late fall and winter (Harris et al. 1974, Rowse 1980). Thus, without an abundance of these plant species in the understory (Table 1), and without abundant seeds and arthropods provided by a dense forb layer, there is little food available during winter. This contrasts distinctly with other southeastern community types, such as bottomland hardwoods, where winter bird densities far exceed breeding bird densities (Dickson 1978, Harris and Vickers 1984).

Unlike the bird communities of temperate North America where winter species represent a small subset of the breeding bird community, the long-leaf pine bird community is seasonally more balanced. On our study area, 23 winter-only species joined 38 permanent-resident species, while 11 summer-only species migrated to Central and South America. As noted above, a number of obvious cognate pairs exists (Tree Swallow/Purple Martin, Whip-poor-will/Chuck-will's-widow, Ruby-crowned Kinglet/Red-eyed Vireo and/or Yellow-throated Vireo, and maybe others), which fill apparently similar foraging guilds in the community. Other species including the Ovenbird, American Woodcock, Hermit Thrush, and American Robin forage on or near the ground at a time when deciduous trees such as turkey oaks have lost their foliage, and food resources occur closer to the ground.

These results are somewhat different, though not unexpected from the pattern reported for a mature longleaf pine forest in southwest Georgia (Engstrom 1981). Being nearly 250 km farther north, that area supported fewer (8 vs. 14) winter-only species and slightly more (10 vs. 7) summer-only species than our plots.

Species richness and diversity calculated from our data were slightly higher than generalizations published elsewhere (Tramer 1974, Bock and Lepthien 1975, Peterson 1975, Short 1979). We recorded more breeding species (23 vs. 20) and fewer wintering species (27 vs. 32) than Tramer (1974) predicted, but we presume these discrepancies to be non-significant. Rabenold (1979) also has examined patterns of alpha diversity with respect to latitude, although he considered only deciduous forests. Our longleaf pine community had more breeding passerine species (16) than Rabenold (1979) predicted (< 11), and higher H′ (2.48) than he predicted (< 2.2) considering only passerines. The greater species diversity of our study area was perhaps surprising in light of the prevailing view that southeastern pine forests have little habitat diversity compared to deciduous forests. Engstrom et al. (1984), however, found higher breeding bird species richness in a structurally simple longleaf pine forest in the Florida Panhandle than in a more complex beech-magnolia forest. They explained this by noting that longleaf pine, until recently, was the dominant vegetation of this region; more birds could have adapted to this habitat due to its extensive area. The apparent increased diversity on our study area compared with other pine forests is perhaps explained by our having worked in a natural old-growth stand rather than in planted or second-growth stands.

Permanent residents dominated the avian community on our study area summer and winter. It appears, therefore, that the avian community of the longleaf pine ecosystem is far more self-contained than those of other southeastern forest types. Possibly the food resources in the longleaf pine forest do not fluctuate as much seasonally as those in other southeastern forest types, and the permanent resident bird population is better able to track the available food supply than birds of slash and loblolly pine and hardwood forest communities, leaving less resource space for winter residents.

Our study helps to establish the nature of the avifauna characteristic of old-growth longleaf pine for future reference. However, the fact that three of four species, Red-cockaded Woodpecker (*Picoides borealis*), Brown-headed Nuthatch (*Sitta pusilla*), Bachman's Sparrow (*Aimophila aestivalis*) and Pine Warbler, characteristic of mature, open pinelands were not observed on our study area deserves comment. Red-cockaded Woodpeckers would normally be expected to occur in a 160 ha tract of old-growth longleaf pine, were it surrounded by adequate foraging area and other colony sites. However, this tract was isolated and vast distances separated it from the nearest known clan. Fire suppression and the resulting increase in understory vegetation are probably responsible for the absence of Bachman's Sparrow, a ground-nesting species, and may have contributed also to the absence of the Brown-headed Nuthatch and Red-cockaded Woodpecker.

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