

Comparison of breeding bird communities in bottomland hardwood forests of different successional stages.—The area of bottomland hardwood forests, an important habitat for many birds, is declining (Harris and O'Meara 1989, Hefner et al. 1994). From the mid-1970s to mid-1980s, forested wetlands in the southeast U.S. declined by 1.3 million ha (Hefner et al. 1994) and are expected to decrease into the year 2030 (USDA Forest Service 1988). An estimated 13.3 million ha of forested wetlands remain in the southeastern U.S. (Hefner et al. 1994). These forests are important for several species of birds, particularly Neotropical migrants with diminishing populations. However, bottomlands in different successional stages have different habitat qualities. Late-successional habitats exhibit greater vegetative diversity, including multiple vegetation layers, high vegetation density, edges, snags, and interspersed habitats (Bull and Skovlin 1982) which provide more potential nesting and foraging sites. Bird density and species diversity parallel structural diversity in riparian habitats (Swift et al. 1984) and generally are greatest in late-successional habitats such as mature bottomland forests (Zimmerman and Tatschl 1975, Dickson 1978). We compared avian abundance, species richness, and species diversity among bottomland hardwood forests of three successional stages.

Study area and methods.—We conducted this study on the U.S. Dept. of Energy's Savannah River Site (SRS). This 78,000-ha facility in Aiken, Allendale, and Barnwell counties, South Carolina, is composed of pine stands of various ages in the uplands and bottomland hardwoods associated with the numerous creeks that traverse the site. Study plots were located in three bottomland corridors, representing early-, mid-, and late-successional bottomland hardwood forests, respectively. Pen Branch, an early-successional bottomland corridor, received regular influxes of thermal effluent from the SRS's K Reactor beginning in 1954. The original bottomland hardwood vegetation was destroyed by elevated water levels and sediment loads, and water temperatures in excess of 45°C (Sharitz et al. 1974). Thermal input ceased in 1988, but high flow rates continued until August 1993. The creek currently is dominated by black willow (*Salix nigra*) and smooth alder (*Alnus serrulata*), interspersed with grassy openings. The mid-successional bottomland, Steel Creek, received thermal effluent until 1968 when the last reactor on the creek was closed. It is dominated by large black willow and smooth alder. Red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), and sycamore (*Platanus occidentalis*) also are present. The late-successional bottomland, Tinker Creek, never received thermal effluent. Timber harvest and other disturbances in the creek have been minimal for over 60 years (Workman and McLeod 1990). Swamp tupelo (*Nyssa sylvatica* var. *biflora*), red maple, and tulip poplar (*Liriodendron tulipifera*) dominate the overstory. Midstory species include red maple, American holly (*Ilex opaca*), sweetbay (*Magnolia virginiana*), and wax myrtle (*Myrica cerifera*).

In each corridor, we sampled 12 randomly located habitat plots. Percent green ground cover, percent water cover, shrub density, canopy height, percent canopy closure, and basal area were measured according to James and Shugart (1970). Vegetative profile was estimated using a 3-m density board (Nudds 1977). Estimated avian community parameters were correlated with habitat variables using Pearson's correlation coefficient. Avian censuses were conducted along each creek five times per year from mid-May to late June, 1994–1995. The fixed-radius (50 m) point count method (Ralph et al. 1993) was used to estimate avian abundance, species richness, and species diversity. Six census points were located at least 50 m from the edge of each bottomland and were separated by 200 m. Censusing began at

TABLE 1
VEGETATIVE CHARACTERISTICS OF THE THREE BOTTOMLANDS SURVEYED ON THE SAVANNAH RIVER SITE, 1994–1995

	Pen Branch	Steel Creek	Tinker Creek
Years since disturbance	7	27	60+
Canopy height (m)	8.3 ± 0.9	12.2 ± 0.8	18.3 ± 0.8
Canopy closure (%)	52.3 ± 5.4	83.4 ± 2.6	92.5 ± 0.8
Green ground cover (%)	61.7 ± 4.3	46.3 ± 4.9	36.0 ± 4.1
Water cover (%)	17.3 ± 2.7	9.6 ± 2.3	35.8 ± 6.4
Shrubs per ha (×10 ³)	119.0 ± 0.4	159.0 ± 1.2	139.0 ± 1.3
Basal area (m ² ha ⁻¹)	8.0	20.6	43.7
Basal area by species (%)			
<i>Salix nigra</i>	76.3	33.6	0.0
<i>Alnus serrulata</i>	3.3	19.1	2.5
<i>Acer rubrum</i>	1.7	12.0	17.4
<i>Liquidambar styraciflua</i>	0.0	19.4	4.8
<i>Liriodendron tulipifera</i>	0.0	0.0	7.6
<i>Nyssa sylvatica</i> var. <i>biflora</i>	0.0	1.0	49.9

sunrise and was completed within 3.5 h. All visual and auditory detections of birds, except those flying over the site, were recorded for 5 min. Species detected ±3 min of each point count period while en route to census points and species detected outside the census plot were recorded for inclusion in the species list for each site. No censusing was done during high wind or rain.

Abundance is reported as mean number of birds per census point. Species richness is mean number of species per creek. Bird species diversity, reported as mean diversity per creek, was computed using the Shannon-Weaver formula (Shannon and Weaver 1949). Among creeks, comparisons of avian abundance by habitat preference and migratory strategy (Whitcomb et al. 1981), species richness, and diversity were tested with one-way analysis of variance and Tukey's test was used to compare means for differences ($\alpha = 0.05$). Comparisons within species among sites were made if sample sizes were large ($N \geq 30$).

Results.—There were pronounced differences in the vegetation among the three bottomlands (Table 1). As expected, canopy height, canopy closure, and basal area, increased with age of the stand. The early-successional site was dominated by black willow and smooth alder of relatively uniform height. Early-successional shrubs, including wax myrtle and buttonbush (*Cephalanthus occidentalis*), were common. The mid-successional bottomland was a mix of large black willow and smooth alder and some later successional species.

Avian abundance was negatively correlated with canopy closure ($r = -0.25$, $P = 0.02$). Richness was negatively correlated with ground cover ($r = -0.56$, $P = 0.02$) and coverage of the two lower sections of the profile board ($r = -0.69$, $P = 0.001$; $r = -0.59$, $P = 0.01$) and positively correlated with canopy height ($r = 0.57$, $P = 0.01$), canopy closure ($r = 0.63$, $P = 0.01$), and basal area ($r = 0.70$, $P = 0.001$). There were no significant differences in abundance, richness, or diversity within treatments between years, so data were pooled. Avian abundance was greater in the early-successional bottomland than in the mid-successional bottomland (Table 2). Species richness increased as successional stage increased among the three bottomlands. Diversity was greater in the late-successional creek

TABLE 2

MEAN ABUNDANCE, RICHNESS, AND DIVERSITY OF BIRD SPECIES IN BOTTOMLAND HARDWOOD FORESTS IN DIFFERENT STAGES OF SUCCESSION ON THE SAVANNAH RIVER SITE, 1994-1995

Site	Abundance		Richness		Diversity ^a	
	Mean	SE	Mean	SE	Mean	SE
Pen Branch	5.08	0.23 A ^b	11.6	0.5 C	1.89	0.05 B
Steel Creek	3.72	0.25 B	16.3	0.6 B	2.11	0.07 AB
Tinker Creek	4.20	0.37 AB	19.1	0.8 A	2.34	0.09 A

^a Bird species diversity computed using information theory formula: $-\sum p_i \log_2 p_i$.

^b Means followed by the same letter, within the same column, are not significantly different at $\alpha = 0.05$ (Tukey's Studentized Range Test).

compared to the early-successional. Forest interior species were most common in the late-successional bottomland (Table 3). The early-successional creek contained more forest edge/scrub species than the other creeks. No forest edge/scrub species were recorded in the late-successional creek over the two years. Abundance of forest interior/edge species and field/edge species did not differ among the creeks.

Short-distance migrants, defined as species that move a few hundred km to wintering grounds (Whitcomb et al. 1981), were more than twice as abundant in the early-successional creek than in the other creeks (Table 3). Several Neotropical migrant species were detected in Pen Branch, including Ruby-throated Hummingbird (*Archilochus colubris*), Yellow-billed Cuckoo (*Coccyzus americanus*), Red-eyed Vireo (*Vireo olivaceus*), Northern Parula (*Parula americana*), Hooded Warbler (*Wilsonia citrina*), and Indigo Bunting (*Passerina cyanea*). Two species were found only in Pen Branch, Yellow-breasted Chat (*Icteria virens*) and Blue

TABLE 3

MEAN ABUNDANCE BY HABITAT CATEGORY AND MIGRATION CATEGORY OF BIRD SPECIES IN EARLY- (PEN BRANCH), MID- (STEEL CREEK), AND LATE-SUCCESSIONAL (TINKER CREEK) BOTTOMLAND HARDWOOD FORESTS ON THE SAVANNAH RIVER SITE, 1994-1995

	Pen Branch		Steel Creek		Tinker Creek	
	Mean	SE	Mean	SE	Mean	SE
Habitat category ^a						
Interior	0.3	0.5 B ^b	0.6	0.2 B	5.5	0.5 A
Interior/edge	21.5	1.2 A	19.8	1.8 A	18.9	1.4 A
Edge/scrub	6.2	1.1 A	0.3	0.2 B	0.0	0.0 B
Field/edge	2.2	0.5 A	1.1	0.3 A	0.8	0.4 A
Migration category						
Resident	3.3	0.8 A	5.9	1.1 A	3.9	0.7 A
Short-distance	17.4	1.3 A	7.6	0.9 B	7.4	1.0 B
Neotropical migrant	9.5	1.5 B	8.3	0.9 B	13.5	0.7 A

^a Habitat and migration categories after Whitcomb et al. (1981).

^b Means followed by the same letter, within the same row, are not significantly different at $\alpha = 0.05$ (Tukey's Studentized Range Test).

Grosbeak (*Guiraca caerulea*). Of these species, only the Northern Parula had a sample size large enough to compare among sites, and its abundance was not different among the three creeks. However, the Hooded Warbler, Northern Parula, Red-eyed Vireo, and Yellow-billed Cuckoo generally were detected more often in the late-successional creek and in similar numbers in the mid-successional creek compared to the early-successional creek.

The abundance of Neotropical migrants was greatest in the late-successional site. Swainson's Warbler (*Limnothlypis swainsonii*), Summer Tanager (*Piranga rubra*), and Eastern Wood-Pewee (*Contopus virens*) were found only in the late-successional creek, and Acadian Flycatcher (*Empidonax virens*), Louisiana Waterthrush (*Seiurus motacilla*), and Wood Thrush (*Hylocichla mustelina*) were found almost exclusively in that site. The American Crow (*Corvus brachyrhynchos*) and Brown-headed Nuthatch (*Sitta pusilla*) also were found only in Tinker Creek. Prothonotary Warblers (*Protonotaria citrea*) were equally abundant in the mid- and late-successional bottomlands but were not seen in Pen Branch. The mid- and late-successional creeks contained similar numbers of the three woodpecker species detected: Pileated (*Dryocopus pileatus*), Red-bellied (*Melanerpes carolinus*), and Downy (*Picoides pubescens*). In the early-successional creek, only the Downy Woodpecker was observed.

Discussion.—Most researchers who have related avian community parameters to forest successional stage have reported increasing abundance, species richness, and diversity with increasing successional stage (Karr 1968). However, Shugart and James (1973) reported a drop in richness and diversity at the "climax" stage. In our study, richness and diversity values were comparable to previous studies (Karr 1968, Zimmerman and Tatschl 1975), although there was no drop in either value in the late-successional creek. Zimmerman and Tatschl (1975) observed greater breeding bird abundance but lower richness and diversity in a young forest than in a mature hardwood stand in a Kansas floodplain. Similarly, our early-successional creek had greater avian abundance than the other creeks, significantly greater than the mid-successional bottomland. Richness and diversity generally were greater in the two later successional bottomlands. The greater abundance in Pen Branch compared to Steel Creek was unexpected because avian density and species diversity usually parallel structural diversity (Swift et al. 1984). Pen Branch was characterized by three habitat types: short willow/alder, herbaceous cover 2–3 m high, and patchy grassy openings. Steel Creek, the mid-successional bottomland, appeared to have a greater degree of vegetative heterogeneity than Pen Branch, and this can be inferred by its greater canopy height, more shrubs per ha, greater basal area, and greater variety of tree species compared to Pen Branch. Nonetheless, Steel Creek had the lowest abundance of birds among the creeks.

The change in community composition was well-defined. Late-successional bottomlands generally contain a high variety and abundance of Neotropical migratory species (Karr 1968), some of which are almost solely associated with this habitat type (Dickson 1991). In our study, the late-seral stage contained a greater abundance of Neotropical migrants and forest interior birds than the other two sites. Most species in Tinker Creek were either forest interior or forest interior/edge species. The high abundance of short-distance migrants in the early-successional bottomland largely is the result of the creek being dominated by a few short-distance migratory species. Common Yellowthroats (*Geothlypis trichas*), White-eyed Vireos (*Vireo griseus*), and Red-winged Blackbirds (*Agelaius phoeniceus*), plus one Neotropical migrant, the Indigo Bunting, comprised 70% of the birds detected in Pen Branch and contributed to the low diversity value. As a group, these four species were more abundant ($P < 0.05$) in Pen Branch than in the other creeks. Although not significant, Steel Creek contained the greatest number of resident birds, primarily Northern Cardinals (*Cardinalis cardinalis*).

Results of this study emphasize the importance of mature bottomlands as habitat for a number of interior Neotropical migrant species. Similar results have been reported for bottomland habitats elsewhere in the southeastern U.S. (Hamel 1989, Harris 1989) and other

regions of the country (Knopf et al. 1988). Maintenance of these habitats is important because the populations of many interior species and Neotropical migrants likely are declining. These results also demonstrate the changes in the avian community along a successional gradient. Maximizing avian species composition may require maintenance of a diversity of habitat types and successional stages. This will require proper design and management of forested bottomlands to secure the future for species currently losing habitat.

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