Importance of Carolina Bays to the Avifauna of Pinelands in the Southeastern United States

Stephen J. Czapka[1,2,*] and John C. Kilgo[1]

Abstract - Past anthropogenic activity has led to the destruction or alteration of Carolina bay wetlands throughout the southeastern United States. Presently, urban development, combined with a 2001 ruling by the US Supreme Court relaxing protection of isolated wetlands, poses an increasing threat to these and other isolated wetland systems; however, little information exists on the importance of these wetland systems to birds. We compared breeding and wintering bird communities of upland pine (*Pinus* spp.) forests with and without Carolina bays. Estimated species richness was greater in pine forests with Carolina bays than without during the winter (31.7 ± 1.3 [mean ± SE] vs. 26.9 ± 1.2; $P = 0.027$), but not in the breeding season (27.9 ± 2.2 vs. 26.3 ± 2.2; $P = 0.644$). Total relative abundance did not differ between pine forests with Carolina bays and those without in either the breeding (148.0 ± 16.0 vs. 129.4 ± 10.4 birds/40 ha; $P = 0.675$) or winter (253.0 ± 36.4 vs. 148.8 ± 15.1 birds/40 ha; $P = 0.100$) seasons. However, 23 species, 43% of which were wetland-dependent, were observed only in pine forests with bays during the breeding season, and 20 species, 30% of which were wetland-dependent, were observed only in such sites during winter. In contrast, only 6 and 1 species were observed only in pine forests without bays during the breeding and winter seasons, respectively, indicating that few species were negatively affected by the presence of bays. Thus, Carolina bays appear to enrich the avifauna of pine forests in the southeastern United States.

Introduction

The pre-settlement landscape of the South Atlantic Coastal Plain was dominated by *Pinus palustris* Mill (Longleaf Pine) and *P. taeda* L. (Loblolly Pine) forests (White and Gaines 2000). Embedded within this pine matrix were Carolina bays, geographically isolated depression wetlands that occur on the Atlantic Coastal Plain from New Jersey to northern Florida, with the greatest concentration in the Carolinas (Sharitz 2003, Tiner 2003). Carolina bays are characterized by their unique elliptical shape, the northwest to southeast orientation of their long axis, and the presence of a sand rim on the southeast side. Sizes of Carolina bays range from <1 to >3600 ha (Sharitz and Gibbons 1982), but most are small; of 371 Carolina bays identified on the Savannah River Site in South Carolina, 46.4% were ≤1.2 ha and 87.3% were ≤4.0 ha (Kirkman et al. 1996, Schalles et al. 1989). The principle hydrologic input is direct precipitation. Large bays may be permanently flooded while smaller bays are ephemeral wetlands, drying completely during periods of low precipitation (Lide et al. 1995).

Anthropogenic activity has dramatically altered most Carolina bays (Bennett and Nelson 1991). From the early 1800s until the mid-1900s, bays were frequently

[1]USDA Forest Service Southern Research Station, PO Box 700, New Ellenton, SC 29809. [2]Current address - Ecology and Environment, Inc., 348 Southport Circle, Suite 100, Virginia Beach, VA 23452. [*]Corresponding author - sczapka@ene.com.

ditched and drained for agricultural purposes. Of 2651 Carolina bays examined in South Carolina, 65% had drainage ditches (Bennett and Nelson 1991). Kirkman et al. (1996) similarly reported, based on 1951 aerial photography, that 66% of 299 bays studied in South Carolina appeared to be ditched. Urban development now poses an increasing threat to these wetlands as the human population of the southeastern Coastal Plain grows (Sharitz 2003).

A 2001 ruling by the US Supreme Court has changed the protection status of Carolina bays, particularly those of small size, under Section 404 of the Clean Water Act. In that decision (Solid Waste Agency of Northern Cook County vs. US Army Corps of Engineers, 531 US 159; Sharitz 2003) the Supreme Court ruled that the US Army Corps of Engineers' authority to issue permits for the discharge of dredge or fill material into waters of the United States is restricted to navigable waterways and their tributaries (Semlitsch and Bodie 1998, Sharitz 2003). Because small isolated wetlands like Carolina bays, by definition, do not have natural connections to other bodies of water, they are not likely to be protected under this ruling (Sharitz 2003, Sharitz and Gresham 1998).

Little quantitative information exists on avian use of Carolina bays, and what is available is often in the form of species lists from a few large bays (Lee 1987, Norris 1957, Post 1969). Knowledge of the ecology of particular species provides some insight on the importance of bays as avian habitat. For example, Carolina bays are used for foraging and nesting by *Aix sponsa* L. (Wood Duck; Kennamer and Hepp 2000), *Mycteria americana* L. (Wood Stork; Bryan 2005), and other wading birds (Kilgo and Bryan 2005). Mamo and Bolen (1999) used mist nets to sample small Passerines in forested Carolina bays and found their sites to serve as breeding habitat for several Neotropical migrants experiencing population declines. However, more comprehensive information is needed on the influence of small Carolina bays on the avian communities of pine landscapes of the southeastern United States. Here we examine the contribution of Carolina bay habitat to the avifauna of Southeastern pine forests by comparing breeding and wintering bird communities found in upland pine forests with and without small Carolina bays.

Field Site Description

We conducted this study at the US Department of Energy's Savannah River Site (SRS), a 78,000-ha National Environmental Research Park in Aiken, Barnwell, and Allendale counties, SC. The SRS is in the Upper Coastal Plain physiographic province. Its landscape is dominated by pine forests on the uplands and bottomland hardwood forests along riparian zones. Approximately 350 Carolina bays occur within the upland pine forest matrix (Barton et al. 2005).

Pine forests at SRS are managed on relatively long rotations (50–120 yrs), primarily for the endangered *Picoides borealis* Vieillot (Red-cockaded Woodpecker*)* recovery program. More than half of the forested area of the SRS is pine forest, with two-thirds of the pines being between 40 and 70 years old (Imm and McLeod 2005). Forest management activities at SRS included thinning and prescribed burning (approximate 5-yr rotation). Canopies of SRS pine forests were

dominated by Loblolly and Longleaf Pine. Midstories, where present, included pines, *Liquidamber styraciflua* L. (Sweetgum), *Quercus* spp. (oaks), and various hardwoods. Understories were highly variable, ranging from scattered herbs to a nearly continuous shrub and sapling layer. Common understory species included *Andropogon virginicus* L. (Broomsedge), *Pteridium aquilinum* (L.) Kuhn (Bracken Fern), *Rhus toxicodendron* L. (Poison Oak), *Vaccinium stamineum* L. (Deerberry), *Vaccinium arboreum* Marsh (Sparkleberry), *Myrica cerifera* L. (Wax Myrtle), and *Rubus* spp. (blackberry) (Imm and McLeod 2005).

We surveyed birds in eight 300- x 300-m (9-ha) study areas within mature (>40 yrs old) upland pine forests (hereafter, non-wetland areas) and in 15 pine forest study areas that each contained a Carolina bay (hereafter, wetland areas) ranging in size from 0.5–1.7 ha. Wetland study areas were delineated by a 100-m radius extending from the bay margin into the surrounding upland pine forest, such that the total area surveyed averaged 7.1 ha (range = 4.7–10.6), of which 84% was upland and 16% was bay (Fig. 1). The pine forests of both wetland and non-wetland study areas were generally similar, but for the presence of the bays; overstories were dominated by Loblolly Pine, midstories were sparse, and understories ranged from open to dense within both study area types. Basal area of the non-wetland study areas averaged 12.0 m^2/ha, and that of the wetland study areas averaged 14.6 m^2/ha. The slight difference was attributable to a greater hardwood component in the wetland study areas, primarily at the margins of bays; pine basal area in the two types was similar (10.6 m^2/ha in wetland, 10.7 m^2/ha in non-wetland), but hardwood basal area was greater in wetland (4.0 m^2/ha) than in non-wetland (1.4 m^2/ha) study areas (US Forest Service - Savannah River, New Ellenton, SC, unpubl. data). The pine forest component of the wetland areas was more variable in age than that of the non-wetland areas. Three bays were surrounded by pole-sized pine forest (8–25 yr old), but of the remainder (n = 12), 3 had >40-yr-old pine forest around 30–75% of their margins and 9 were completely surrounded by >40-yr-old pine forest. Thus, although the pine forests surrounding the wetland areas encompassed a somewhat wider range of conditions within the pine forest type, all were pine forest and most were similar in age and habitat structure (canopy height, canopy cover, basal area) to those in the non-wetland areas.

The bays studied were wet meadow emergent wetlands dominated by grasses and sedges, including *Panicum verrucosum* Muhl. (Warty Panic-grass), *Panicum* spp. (witch-grasses), *Cyperus* and *Rhynchospora* spp. (sedges), and *Juncus* spp. (rushes). Extended drought prior to initiation of this study permitted the encroachment of upland species, particularly seedlings and saplings of Loblolly Pine and Sweetgum, into the bay interiors.

Methods

We sampled breeding-season bird communities between 5 May and 26 June 2003 and winter bird communities between 6 December 2003 and 5 March 2004. We surveyed birds during both seasons using 100-m wide, parallel strip-transects

(Bibby and Burgess 1991, Verner 1985). We used transect rather than point-count surveys because we felt it important to maximize the number of detections per study area, given the limited number of our study areas. The length of each transect and number of transects per area was determined by the dimensions of each area. In non-wetland areas, three adjacent transects, totaling 900 m in length, sampled the entire 9.3 ha (Fig. 1). In wetland areas, we used two or three adjacent transects, totaling 700–1050 m in length and oriented parallel to the long axis of the bay, to sample the entire areas (Fig. 1). At both non-wetland and wetland areas, an observer traversed the center line of each transect, pausing every 50 m to record all birds seen or heard within 50 m of the center line. The observer mapped bird locations and noted movement of individuals to minimize double counting. We conducted surveys between sunrise and 3.5 h post sunrise during the breeding season (Ralph et al. 1995) and between sunrise and 1400 during winter (Kolb 1965). We surveyed each area three times during the breeding season and five times during the winter. We conducted more surveys during winter than summer due to the length of season (approximately 3 months in winter vs. 1.5 months in the breeding season) and the greater variance typically associated with winter bird surveys. Start times were rotated among areas to control for diurnal variations in bird activity. We did not include transient species and flyovers in analyses. We averaged total bird numbers across visits to determine relative abundance for each study area. Because of variation in size of sampling areas, we standardized each study area to number of birds per 40 ha by multiplying relative abundance × (40 ha / area surveyed [ha]). We estimated species richness for each individual study area using the software EstimateS (Colwell 2004).

For both seasons, we used one-way analysis of variance (ANOVA; SAS Institute 2000) to test for differences in species richness, total bird abundance, and relative abundance of individual species (those with at least 40 total observations)

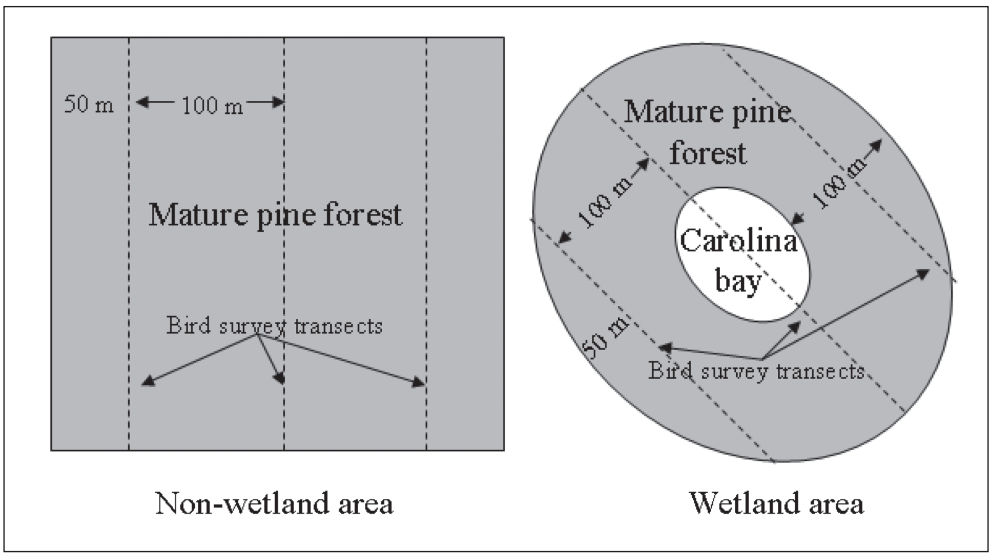

Figure 1. Schematic diagram showing arrangement of wetland and non-wetland study areas and bird survey transects within each.

between wetland and non-wetland areas. When the assumptions of ANOVA were not met (i.e., normal distribution and homogeneous variance), we used a Wilcoxon rank-sum test (SAS Institute 2000). As an additional comparison of the communities between wetland and non-wetland areas, we calculated Morisita's index of community similarity (Morisita 1959). This index accounts for presence and absence as well as abundance of species within the community and ranges from 0 (no similarity) to 1 (complete similarity), with 0.40 considered low and 0.74 high (Krebs 1989).

Results

Breeding season

In all areas combined, we observed 64 species, 58 in wetland areas and 41 in non-wetland areas. We detected 23 species only in wetland areas, whereas we detected 6 species only in non-wetland areas (Table 1). Mean estimated species richness did not differ between wetland and non-wetland areas (27.9 ± 2.2 [mean ± SE] vs. 26.3 ± 2.2, respectively; $F_{1,21} = 0.22$, $P = 0.64$).

Total relative abundance did not differ between wetland and non-wetland areas (148.0 ± 16.0 vs. 129.4 ± 10.4 birds/40 ha, respectively; $Z = -0.42$, $P = 0.68$). We had sufficient detections of 15 species to compare relative abundance

Table 1. Breeding bird densities (birds/40 ha [mean ± SE]) at upland pine forests with (wetland areas) and without (non-wetland areas) Carolina bays. Statistical comparisons are presented for species with at least 40 observations.

Species	Non-wetland areas ($n = 8$)	Wetland areas ($n = 15$)	P
Greater than 40 observations			
Melanerpes erythrocephalus L. (Red-headed Woodpecker)[A]	10.7 ± 2.0	3.9 ± 1.1	0.008
Contopus virens L. (Eastern Wood-Peewee)[A]	7.6 ± 1.0	2.5 ± 0.8	0.003
Myiarchus crinitus L. (Great-crested Flycatcher)[A]	5.4 ± 1.3	7.6 ± 1.9	0.872
Poecile carolinensis Audubon (Carolina Chickadee)[B]	5.9 ± 1.3	4.6 ± 1.1	0.559
Baeolophus bicolor L. (Eastern Tufted Titmouse)[B]	5.7 ± 1.1	5.8 ± 0.9	0.958
Sitta pusilla Latham (Brown-headed Nuthatch)[A]	6.1 ± 1.6	3.9 ± 1.2	0.204
Thryothorus ludovicianus Latham (Carolina Wren)[B]	7.2 ± 1.5	9.7 ± 1.3	0.266
Polioptila caerulea L. (Blue-gray Gnatcatcher)[A]	3.3 ± 1.5	3.0 ± 0.7	0.768
Dendroica pinus A. Wilson (Pine Warbler)[A]	22.0 ± 4.1	8.9 ± 1.2	0.006
Piranga rubra L. (Summer Tanager)[A]	1.7 ± 0.7	5.5 ± 0.9	0.015
Pipilo erythrophthalmus L. (Eastern Towhee)[A]	8.2 ± 2.6	3.0 ± 0.7	0.064
Cardinalis cardinalis L. (Northern Cardinal)[B]	7.4 ± 1.8	9.9 ± 1.0	0.203
Passerina cyanea L. (Indigo Bunting)[B]	12.8 ± 2.4	12.1 ± 2.6	0.869
Agelaius phoeniceus L. (Red-winged Blackbird)[A]	0.0	5.0 ± 1.3	0.009
Quiscalus quiscula L. (Common Grackle)[A]	0.0	6.3 ± 2.5	0.029
Wetland areas only			
Aix sponsa L. (Wood Duck)	0.0	3.0 ± 2.2	n/a
Ardea herodias L. (Great Blue Heron)	0.0	0.2 ± 0.1	n/a
Ardea alba L. (Great Egret)	0.0	0.5 ± 0.3	n/a
Egretta caerulea L. (Little Blue Heron)	0.0	0.2 ± 0.2	n/a
Bubulcus ibis L. (Cattle Egret)	0.0	0.1 ± 0.1	n/a

Table 1, continued.

Species	Non-wetland areas (n = 8)	Wetland areas (n = 15)	P
Butorides virescens L. (Green Heron)	0.0	1.8 ± 0.7	n/a
Buteo jamaicensis J.F. Gmelin (Red-tailed Hawk)	0.0	0.1 ± 0.1	n/a
Falco sparverius L. (American Kestrel)	0.0	0.1 ± 0.1	n/a
Ceryle alcyon L. (Belted Kingfisher)	0.0	0.2 ± 0.2	n/a
Empidonax virescens Vieillot (Acadian Flycatcher)	0.0	0.3 ± 0.3	n/a
Tyrannus tyrannus L. (Eastern Kingbird)	0.0	2.8 ± 1.0	n/a
Hirundo rustica L. (Barn Swallow)	0.0	0.4 ± 0.4	n/a
Hylocichla mustelina J.F. Gmelin (Wood Thrush)	0.0	0.1 ± 0.1	n/a
Dumetella carolinensis L. (Gray Catbird)	0.0	0.1 ± 0.1	n/a
Mimus polyglottos L. (Northern Mockingbird)	0.0	0.7 ± 0.4	n/a
Parula americana L. (Northern Parula)	0.0	1.0 ± 0.5	n/a
Setophaga ruticilla L. (American Redstart)	0.0	0.5 ± 0.2	n/a
Seiurus aurocapillus L. (Ovenbird)	0.0	0.4 ± 0.4	n/a
Seiurus motacilla Vieillot (Louisiana Waterthrush)	0.0	0.1 ± 0.1	n/a
Wilsonia citrina Boddaert (Hooded Warbler)	0.0	0.5 ± 0.5	n/a
Icterus spurius L. (Orchard Oriole)	0.0	1.9 ± 0.8	n/a
Non-wetland areas only			
Colinus virginianus L. (Northern Bobwhite)	0.4 ± 0.2	0.0	n/a
Archilochus colubris L. (Ruby-throated Hummingbird)	0.4 ± 0.2	0.0	n/a
Vireo flavifrons Vieillot (Yellow-throated Vireo)	0.7 ± 0.5	0.0	n/a
Vireo solitarius Wilson (Blue-headed Vireo)	0.2 ± 0.2	0.0	n/a
Aimophila aestivalis Lichtenstein (Bachman's Sparrow)	1.9 ± 1.3	0.0	n/a
Carduelis tristis L. (American Goldfinch)	0.7 ± 0.4	0.0	n/a
Wetland and non-wetland areas			
Meleagris gallopavo L. (Wild Turkey)	0.4 ± 0.4	1.5 ± 1.4	n/a
Zenaida macroura L. (Mourning Dove)	0.7 ± 0.4	1.7 ± 0.9	n/a
Coccyzus americanus L. (Yellow-billed Cuckoo)	0.2 ± 0.2	1.6 ± 0.6	n/a
Melanerpes carolinus L. (Red-bellied Woodpecker)	1.9 ± 0.6	3.6 ± 1.0	n/a
Picoides villosus L. (Hairy Woodpecker)	0.6 ± 0.6	0.2 ± 0.2	n/a
Picoides pubescens L. (Downy Woodpecker)	2.4 ± 1.1	1.8 ± 0.7	n/a
Colaptes auratus L. (Northern Flicker)	1.3 ± 0.5	1.1 ± 0.5	n/a
Dryocopus pileatus L. (Pileated Woodpecker)	0.7 ± 0.4	1.6 ± 0.5	n/a
Vireo griseus Boddaert (White-eyed Vireo)	0.2 ± 0.2	2.5 ± 1.2	n/a
Vireo olivaceus L. (Red-eyed Vireo)	1.1 ± 0.5	3.3 ± 1.1	n/a
Cyanocitta cristata L. (Blue Jay)	0.6 ± 0.4	1.7 ± 0.5	n/a
Corvus brachyrhynchos Brehm (American Crow)	0.7 ± 0.4	1.0 ± 0.4	n/a
Corvus ossifragus Wilson (Fish Crow)	0.2 ± 0.2	0.1 ± 0.1	n/a
Sitta carolinensis Latham (White-breasted Nuthatch)	0.7 ± 0.7	0.2 ± 0.2	n/a
Sialia sialis L. (Eastern Bluebird)	0.2 ± 0.2	2.2 ± 1.3	n/a
Toxostoma rufum L. (Brown Thrasher)	3.0 ± 1.4	0.7 ± 0.7	n/a
Dendroica discolor Vieillot (Prairie Warbler)	1.3 ± 0.8	1.3 ± 0.9	n/a
Geothlypis trichas L. (Common Yellowthroat)	0.4 ± 0.2	3.0 ± 0.9	n/a
Icteria virens L. (Yellow-breasted Chat)	0.9 ± 0.6	3.7 ± 2.1	n/a
Spizella passerina Bechstein (Chipping Sparrow)	1.1 ± 0.8	0.3 ± 0.3	n/a
Guiraca caerulea L. (Blue Grosbeak)	1.9 ± 0.8	1.5 ± 0.6	n/a
Molothrus ater Boddaert (Brown-headed Cowbird)	1.1 ± 0.4	1.1 ± 0.6	n/a

[A]Wilcoxon rank-sum test.
[B]One-way ANOVA.

between wetland and non-wetland areas (Table 1). *Melanerpes erythrocephalus* L. (Red-headed Woodpecker), *Contopus virens* L. (Eastern Wood-peewee), and *Dendroica pinus* A. Wilson (Pine Warbler) were more abundant in non-wetland than wetland areas ($P \leq 0.05$). By comparison, *Piranga rubra* L. (Summer Tanager), *Agelaius phoeniceus* L. (Red-winged Blackbird), and *Quiscalus quiscula* L. (Common Grackle) were more abundant in wetland than non-wetland areas, the latter two being unique to wetland areas. Morisita's index of community similarity between wetland and non-wetland areas was high (0.78).

Winter

In all areas combined, we observed 55 species, 54 in wetland areas and 35 in non-wetland areas. We detected 20 species only in wetland areas, whereas only one species was unique to non-wetland areas (Table 2). Mean estimated species richness was greater in wetland than non-wetland areas (31.7 ± 1.3 vs. 26.9 ± 1.2, respectively; $F_{1, 21} = 5.69$, $P = 0.027$).

Total relative abundance did not differ between wetland and non-wetland areas (253.0 ± 36.4 vs. 148.8 ± 15.1 birds/40 ha, respectively; $Z = -1.65$, $P = 0.100$). We detected 24 species in sufficient numbers to compare relative abundance between areas (Table 2). One species (*Spizella passerina* Bechstein [Chipping Sparrow]) was more abundant in non-wetland than wetland areas ($P = 0.002$). In contrast, 6 species were more abundant in wetland than non-wetland areas (Wood Duck, *Melanerpes carolinus* L. [Red-bellied Woodpecker], *Thryothorus ludovicianus* Latham [Carolina Wren], *Regulus calendula* L. [Ruby-crowned Kinglet], *Melospiza melodia* Wilson [Song Sparrow], and *Melospiza georgiana* Latham [Swamp Sparrow]). Of these, Wood Duck and Swamp Sparrow were detected only in wetland areas (Table 2). Morisita's index of community similarity between wetland and non-wetland areas in winter also was high (0.79).

Table 2. Winter bird densities (birds/40 ha [mean ± SE]) at upland pine forests with (wetland areas) and without (non-wetland areas) Carolina bays. Statistical comparisons are presented for species with at least 40 observations.

Species	Non-wetland areas ($n = 8$)	Wetland areas ($n = 15$)	P
Greater than 40 observations			
Aix sponsa L. (Wood Duck)[A]	0.0	3.6 ± 1.4	0.029
Melanerpes carolinus L. (Red-bellied Woodpecker)[A]	2.0 ± 0.2	5.0 ± 1.0	0.047
Picoides pubescens L. (Downy Woodpecker)[A]	1.4 ± 0.6	3.1 ± 0.8	0.163
Sayornis phoebe Latham (Eastern Phoebe)[A]	2.3 ± 0.6	3.5 ± 0.5	0.086
Poecile carolinensis Audubon (Carolina Chickadee)[A]	3.9 ± 1.3	3.7 ± 0.9	0.897
Baeolophus bicolor L. (Eastern Tufted Titmouse)[B]	4.4 ± 1.0	4.8 ± 1.0	0.809
Sitta pusilla Latham (Brown-headed Nuthatch)[A]	6.5 ± 1.1	5.7 ± 1.5	0.538
Thryothorus ludovicianus Latham (Carolina Wren)[A]	5.4 ± 0.7	11.3 ± 1.9	0.042
Regulus satrapa Lichtenstein (Golden-crowned Kinglet)[A]	2.3 ± 1.9	1.4 ± 0.6	0.942
Regulus calendula L. (Ruby-crowned Kinglet)[A]	10.3 ± 2.8	21.4 ± 3.6	0.026
Sialia sialis L. (Eastern Bluebird)[A]	0.3 ± 0.3	2.9 ± 1.4	0.226
Turdus migratorius L. (American Robin)[A]	8.6 ± 6.7	10.0 ± 5.5	0.232

Table 2, continued.

Species	Non-wetland areas (n = 8)	Wetland areas (n = 15)	P
Dendroica coronata L. (Yellow-rumped Warbler)[A]	15.6 ± 5.4	38.7 ± 11.9	0.146
Dendroica pinus Wilson (Pine Warbler)[A]	20.6 ± 5.1	13.3 ± 2.4	0.420
Pipilo erythrophthalmus L. (Eastern Towhee)[A]	9.1 ± 2.4	26.6 ± 7.5	0.518
Spizella passerina Bechstein (Chipping Sparrow)[A]	15.1 ± 4.6	4.5 ± 3.3	0.002
Passerella iliaca Merrem (Fox Sparrow)[A]	11.0 ± 8.4	4.8 ± 2.3	0.197
Melospiza melodia Wilson (Song Sparrow)[A]	0.4 ± 0.3	12.1 ± 6.9	0.044
Melospiza georgiana Latham (Swamp Sparrow)[A]	0.0	9.1 ± 5.7	0.005
Zonotrichia albicollis Gmelin (White-throated Sparrow)[A]	1.8 ± 1.1	11.1 ± 3.8	0.265
Junco hyemalis L. (Dark-eyed Junco)[A]	3.9 ± 2.4	9.1 ± 4.0	0.714
Cardinalis cardinalis L. (Northern Cardinal)[A]	20.6 ± 5.1	13.3 ± 2.4	0.420
Quiscalus quiscula L. (Common Grackle)[A]	0.0	2.4 ± 2.4	0.523
Carduelis tristis L. (American Goldfinch)[A]	1.3 ± 1.1	7.8 ± 2.2	0.094
Wetland areas only			
Lophodytes cucullatus L. (Hooded Merganser)	0.0	0.7 ± 0.3	n/a
Ardea herodias L. (Great Blue Heron)	0.0	0.1 ± 0.1	n/a
Coragyps atratus Bechstein (Black Vulture)	0.0	0.2 ± 0.2	n/a
Accipiter striatus Vieillot (Sharp-shinned Hawk)	0.0	0.1 ± 0.1	n/a
Buteo lineatus Gmelin (Red-shouldered Hawk)	0.0	0.2 ± 0.1	n/a
Buteo jamaicensis Gmelin (Red-tailed Hawk)	0.0	0.2 ± 0.1	n/a
Scolopax minor Gmelin (American Woodcock)	0.0	0.3 ± 0.2	n/a
Ceryle alcyon L. (Belted Kingfisher)	0.0	0.4 ± 0.2	n/a
Colaptes auratus L. (Northern Flicker)	0.0	1.0 ± 0.3	n/a
Vireo griseus Boddaert (White-eyed Vireo)	0.0	0.1 ± 0.1	n/a
Corvus brachyrhynchos Brehm (American Crow)	0.0	1.6 ± 0.6	n/a
Sitta carolinensis Latham (White-breasted Nuthatch)	0.0	0.1 ± 0.1	n/a
Troglodytes aedon Vieillot (House Wren)	0.0	0.8 ± 0.4	n/a
Dumetella carolinensis L. (Gray Catbird)	0.0	0.8 ± 0.5	n/a
Mimus polyglottos L. (Northern Mockingbird)	0.0	0.1 ± 0.1	n/a
Geothlypis trichas L. (Common Yellowthroat)	0.0	2.2 ± 0.7	n/a
Spizella pusilla Wilson (Field Sparrow)	0.0	1.3 ± 0.7	n/a
Non-wetland areas only			
Aimophila aestivalis Lichtenstein (Bachman's Sparrow)	0.4 ± 0.4	0.0	n/a
Wetland and non-wetland areas			
Meleagris gallopavo L. (Wild Turkey)	0.1 ± 0.1	0.2 ± 0.2	n/a
Zenaida macroura L. (Mourning Dove)	0.5 ± 0.3	0.6 ± 0.4	n/a
Melanerpes erythrocephalus L. (Red-headed Woodpecker)	0.6 ± 0.6	0.3 ± 0.3	n/a
Sphyrapicus varius L. (Yellow-bellied Sapsucker)	0.6 ± 0.2	1.4 ± 0.5	n/a
Picoides villosus L. (Hairy Woodpecker)	0.3 ± 0.2	0.2 ± 0.1	n/a
Dryocopus pileatus L. (Pileated Woodpecker)	0.8 ± 0.3	1.0 ± 0.2	n/a
Vireo solitarius Wilson (Blue-headed Vireo)	0.8 ± 0.2	0.6 ± 0.2	n/a
Cyanocitta cristata L. (Blue Jay)	0.1 ± 0.1	2.2 ± 0.8	n/a
Certhia americana Bonaparte (Brown Creeper)	0.8 ± 0.3	0.1 ± 0.1	n/a
Troglodytes troglodytes L. (Winter Wren)	0.1 ± 0.1	1.5 ± 0.5	n/a
Catharus guttatus Pallas (Hermit Thrush)	1.2 ± 0.7	0.9 ± 0.3	n/a
Toxostoma rufum L. (Brown Thrasher)	0.5 ± 0.3	0.7 ± 0.4	n/a
Agelaius phoeniceus L. (Red-winged Blackbird)	0.4 ± 0.4	1.8 ± 0.7	n/a

[A]Wilcoxon rank-sum test.
[B]One-way ANOVA.

Discussion

The presence of Carolina bays enhanced the avian community of the pine forests in which they were embedded, as evidenced by higher winter species richness in areas containing bays, higher relative abundance of several species in both seasons, and the high number of species unique to wetland areas in both seasons. The avian community of our pine forests without bays was comprised of species characteristic of mature pine forests of the southeastern United States (Childers et al. 1986, White and Kepler 1996). Our pine forests containing bays supported most of these species in similar abundance, as reflected by the high value of Morisita's index of community similarity, but also supported several additional wetland- and edge-dependent species. This finding may be attributed not only to the presence of the wetlands, but also to the habitat structure created by the forest openings they represent, and to the edge habitat at the upland-wetland interface.

Even small wetlands embedded in a pine forest matrix apparently provide suitable foraging habitat for many wetland birds. Of the 23 species detected only in wetland areas during the breeding season, 10 are considered wetland-dependent species (Brooks and Cronquist 1990). Similarly, in winter, six of the 20 species observed only in wetland areas were wetland-dependent species. Only four wetland species (Wood Duck, *Butorides virescens* [Green Heron], Red-winged Blackbird, and Common Grackle) were actually observed nesting in the bays. That relatively few wetland birds nested in the bays is not surprising given the small size and isolated nature of Carolina bays; such sites likely do not provide all resources necessary to support a nesting territory for most wetland birds. However, the number of wetland birds that used the bays for other purposes highlights the importance of bays as resting and foraging habitat for this group.

Other species apparently benefited from the forest openings that the bays represented. During the breeding season, birds of prey (e.g., *Buteo jamaicensis* [Red-tailed Hawk] and *Falco sparverius* [American Kestrel]) and aerial insectivores (e.g., *Tyrannus tyrannus* [Eastern Kingbird] and *Hirundo rustica* [Barn Swallow]) were observed only in wetland areas. Likewise, during the winter, *Accipiter striatus* (Sharp-shinned Hawk), *Buteo lineatus* (Red-shouldered Hawk), and Red-tailed Hawk where observed only in wetland areas. Johnson and Landers (1982) noted that fallow areas near *Pinus elliottii* Engelm. (Slash Pine) stands in Georgia, which often contained standing water, were used by aerial-feeding and aquatic birds and were frequented by hawks when these areas were adjacent to mature forests.

The transition zones between Carolina bays and pine uplands, which contain extremely high plant species richness (Kirkman et al. 1998), appeared to benefit a number of bird species. This was apparent during the breeding season by the presence of edge specialists such as *Icterus spurius* (Orchard Oriole), *Dumetella carolinensis* (Gray Catbird), and *Mimus polyglottos* (Northern Mockingbird) in wetland areas. This zone was temporarily expanded during our study by drought conditions that permitted the encroachment of Loblolly Pine and Sweetgum into the bays. These saplings provided nesting substrates for Red-winged Blackbird

and Common Grackle (S.J. Czapka, pers. observ.). The transition zone also apparently affected several wintering species; Carolina Wren, *Troglodytes aedon* (House Wren), Gray Catbird, Northern Mockingbird, *Vireo griseus* (White-eyed Vireo), and Song Sparrow were edge species that were either more abundant or occurred only in wetland areas. Finally, although pine dominated the overstory in all areas, the wet conditions around the immediate margins of some Carolina bays supported more hardwood trees. During the breeding season, these hardwoods supported species such as Summer Tanager, *Hylocichla mustelina* (Wood Thrush), *Parula americana* (Northern Parula), *Setophaga ruticilla* (American Redstart), *Seiurus aurocapillus* (Ovenbird), and *Wilsonia citrina* (Hooded Warbler). Johnson and Landers (1982) noted that wet Slash Pine forests with mixed hardwoods supported 17 species absent from sites composed mainly of pine.

Despite the positive impacts of bays on bird communities, seven species that occurred in non-wetland areas were absent from wetland areas (over both seasons combined) and four were less abundant in wetland areas. Two factors may explain the abundance patterns of these species. First, wetland areas had less upland habitat available compared to non-wetland areas. Second, the presence of hardwood trees around the margins of some bays, which benefited many species, likely explains the absence or lower abundance of five species characteristic of pine savanna habitat: *Colinus virginianus* (Northern Bobwhite), Red-headed Woodpecker, Eastern Wood-pewee, Pine Warbler, and *Aimophila aestivalis* (Bachman's Sparrow). Although these five include species of continental conservation importance (Rich et al. 2004), suitable pine habitat for these species is not limited on SRS; with the exception of Northern Bobwhite and Bachman's Sparrow, all are common in SRS pine forests (Kilgo and Bryan 2005).

As the human population of the southeastern United States continues to grow, urban development poses an increasing threat to small isolated wetlands. The recent ruling by the US Supreme Court has made protection of these wetland systems less certain, yet they play an important ecological role in pine forest ecosystems of the Southeast. Our data demonstrate that the presence of Carolina bays increases the richness of bird communities in pine-dominated landscapes. Carolina bays not only support wetland dependent bird species, but also provide habitat for a number of upland species, particularly species requiring hardwoods and open areas, not otherwise common in continuous pine forest.

Acknowledgments

This research was funded by the US Department of Energy—Savannah River Operations Office through the US Forest Service—Savannah River under Interagency Agreement No. DE-AI09-00SR22188 and by the US Forest Service Southern Research Station. We thank P.J. Champlin for assistance with data collection. A. Brinton, R.K. Kolka, and D.W. Imm assisted with site selection, and C.D. Barton, J.I. Blake, and E. Olson assisted with logistics. H. Li, S.M. Lohr, T.J. Underwood, and M. Vukovich provided helpful comments on the manuscript.

Literature Cited

Barton, C.D., J.I. Blake, and D.W, Imm. 2005. Ecological restoration. Pp. 84–102, *In* J.C. Kilgo and J.I. Blake (Eds.). Ecology and Management of a Forested Landscape: Fifty Years on the Savannah River Site. Island Press, Washington, DC.

Bennett, S.H., and J.B. Nelson. 1991. Distribution and status of Carolina bays in South Carolina. Nongame and Heritage Trust Publication Number 1, South Carolina Wildlife and Marine Resources Department, Columbia, SC.

Bibby, C.J., and N.D. Burgess. 1991. Bird census techniques. Academic Press, London, UK.

Bryan, A.L., Jr. 2005. Wood stork. Pp. 289–294, *In* J.C. Kilgo and J.I. Blake (Eds.). Ecology and Management of a Forested Landscape: Fifty Years on the Savannah River Site. Island Press, Washington, DC.

Brooks, R.P., and M.J. Cronquist. 1990. Research note: Wetland, habitat, and trophic response guilds for wildlife species in Pennsylvania. Journal of the Pennsylvania Academy of Science 64:93–102.

Childers, E.L., T.L. Sharik, and C.S. Adkisson. 1986. Effects of Loblolly Pine plantations on songbird dynamics in the Virginia piedmont. Journal of Wildlife Management 50:406–413.

Colwell, R.K. 2004. EstimateS: Statistical estimation of species richness and shared species from samples, Version 7, User's guide and application. Available online at http://purl.oclc.org/estimates. Accessed June 30, 2009.

Imm, D.W., and K.W. McLeod. 2005. Vegetation types. Pp. 106–161, *In* J.C. Kilgo and J.I. Blake (Eds.). Ecology and Management of a Forested Landscape: Fifty Years on the Savannah River Site. Island Press, Washington, DC.

Johnson, A.S., and J.L. Landers. 1982. Habitat relationships of summer resident birds in Slash Pine flatwoods. Journal of Wildlife Management 46:416–428.

Kennamer, R.A., and G.R. Hepp. 2000. Integration of research with long-term monitoring: Breeding Wood Ducks on the Savannah River Site. Studies in Avian Biology 21:39–49.

Kilgo, J.C., and A.L. Bryan, Jr. 2005. Nongame birds. Pp. 223–252, *In* J.C. Kilgo and J.I. Blake (Eds.). Ecology and Management of a Forested Landscape: Fifty Years on the Savannah River Site. Island Press, Washington, DC, USA.

Kirkman, L.K., R.F. Lide, G. Wein, and R.R. Sharitz. 1996. Vegetation changes and land-use legacies of depression wetlands of the western Coastal Plain of South Carolina: 1951–1992. Wetlands 16:564–576.

Kirkman, L.K., M.B. Drew, L.T. West, and E.R. Blood. 1998. Ecotone characterization between non-wetland Longleaf Pine/Wiregrass stands and seasonally ponded isolated wetlands. Wetlands 18:346–364.

Kolb, H. 1965. The Audubon winter bird-population study. Audubon Field Notes 19:432–434.

Krebs, C.J. 1989. Ecological Methodology. Harper and Row, New York, NY.

Lee, D.S. 1987. Breeding birds of Carolina bays: Succession-related density and diversification on ecological islands. Chat 51:85–102.

Lide, R.F., V.G. Meentemeyer, J.E. Pinder, III, and L.M. Beatty. 1995. Hydrology of a Carolina bay located on the Upper Coastal Plain of western South Carolina. Wetlands 15:47–57.

Mamo, L.B., and E.G. Bolen. 1999. Effects of area, isolation, and landscape on the avifauna of Carolina bays. Journal of Field Ornithology 70:310–320.

Morisita, M. 1959. Measuring the interspecific association of and similarity between communities. Memoirs Faculty Kyusu University, Series E 3:65–80.

Norris, R.A. 1957. Breeding bird census no. 23: Three Carolina bays. Audubon Field Notes 11:451–452.

Post, W. 1969. Breeding birds of Williston Bay. Chat 33:83–84.

Ralph, C.J., J.R. Sauer, and C.S. Robbins. 1995. Managing and monitoring birds using point counts: Standards and applications. Pp. 161–168, *In* C.J. Ralph, J.R. Sauer, and S. Droege (Eds.). Monitoring Bird Populations by Point Counts. General Technical Report PSW-GTR-149, USDA Forest Service Pacific Southwest Research Station, Albany, CA.

Rich, T.D., C.J. Beardmore, H. Berlanga, P.J. Blancher, M.S.W. Bradstreet, G.S. Butcher, D.W. Demarest, E.H. Dunn, W.C. Hunter, E.E. Iñigo-Elias, J.A Kennedy, A.M. Martell, A.O. Panjabi, D.N. Pashley, K.V. Rosenberg, C.M. Rustay, J.S. Wendt, and T.C. Will. 2004. Partners in Flight North American landbird conservation plan. Cornell Laboratory of Ornithology, Ithaca, NY.

SAS Institute, Inc. 2000. SAS user's guide: statistics, Version 8.1. SAS Institute Inc., Cary, NC.

Schalles, J.F., R.R. Sharitz, J.W. Gibbons, G.J. Leversee, and J.N. Knox. 1989. Carolina bays of the Savannah River Plant. National Environmental Research Park Publication SRO-NERP-18, Savannah River Ecology Laboratory, Aiken, SC.

Semlitsch, R.D., and J.R. Bodie. 1998. Are small, isolated wetlands expendable? Conservation Biology 12:1129–1133.

Sharitz, R.R. 2003. Carolina bay wetlands: Unique habitats of the southeastern United States. Wetlands 23:550–562.

Sharitz, R.R., and J.W. Gibbons. 1982. The ecology of southeastern shrub bogs (pocosins) and Carolina bays: A community profile. FWS/OBS-82/04, US Fish and Wildlife Service Biological Services Program, Slidell, LA.

Sharitz, R.R., and C.A. Gresham. 1998. Pocosins and Carolina bays. Pp. 343–377, *In* M.G. Messina and W.H. Conner (Eds.). Southern Forested Wetlands: Ecology and Management. Lewis Publishers, Boca Raton, FL.

Tiner, R.W. 2003. Geographically isolated wetlands of the United States. Wetlands 23:494–516.

Verner, J. 1985. Assessment of counting techniques. Current Ornithology 2:247–303.

White, D.H., and C.B. Kepler. 1996. Habitat associations of birds in the Georgia piedmont during winter. Journal of Field Ornithology 67:159–166.

White, D.L., and K.F. Gaines. 2000. The Savannah River Site: Site description, land use, and management history. Studies in Avian Biology 21:8–17.