

A COMPARISON OF BREEDING BIRD COMMUNITIES AND HABITAT FEATURES BETWEEN OLD-GROWTH AND SECOND-GROWTH BOTTOMLAND HARDWOOD FOREST

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Abstract—To characterize bird species composition, relative abundance, and habitat affinities, spot-mapping and strip-count censuses were conducted in an old-growth stand and adjacent second-growth tracts in Moro Bottoms Natural Area, Arkansas, during 1991 and 1992. More species were recorded on the old-growth site ($S = 35$) as compared to the second-growth grid ($S = 32$). Similarly, the old-growth grid had a larger Shannon-Weaver diversity index than the second-growth site. Territories of several species coincided with specific habitat features: white-eyed vireo (*Vireo griseus*), Carolina wren (*Thryothorus ludovicianus*), Kentucky warbler (*Oporornis formosus*), and prothonotary warbler (*Protonotaria citrea*) were associated with treefall canopy gaps; Acadian flycatcher (*Empidonax vireescens*) and prothonotary warbler were affiliated with standing water; and the American redstart (*Setophaga ruticilla*) showed a strong affinity for swamp chestnut oak (*Quercus michauxii*). Small forest openings (≤ 0.26 ha) comprising ≤ 22 percent of the total area of old growth bottomland forest do not appear to adversely affect and may enhance breeding bird diversity.

INTRODUCTION

Southern bottomland hardwood forests are critical as breeding, wintering, and en-route habitat during migration, contributing significantly to continental avifaunal diversity of Eastern North America (Smith and others 1993a). Alarming is the rate of loss of this unique resource, especially during the recent half-century, with a conversion of 80 percent of the Mississippi River Valley (Creasman and others 1992, Turner and others 1981) and 52 percent of all southern bottomland forests (Smith and others 1993a) to agriculture or cleared for development (MacDonald and others 1978, Rudis and Birdsey 1986). Moreover, remaining forests occur as fragments (Rudis and Birdsey 1986) and have undergone a variety of timber harvests. Indeed, all but an estimated 0.01 percent of presettlement old-growth bottomland forests has experienced significant anthropogenic disturbance (Smith and others 1993a). Furthermore, future management imposed on remaining bottomland forests will necessarily intensify to meet increasing demands on hardwood products (Barton 1986, Murphy 1975), especially with the recent surge in markets for hardwood pulp.

Arkansas was no exception to the pattern that occurred across Eastern North America, especially in southern forests (Sharitz and others 1992). Before European arrival, Arkansas landscapes were largely vast acreages of continuous, upland and bottomland deciduous forests; early settlement and agriculture, and more recently silviculture, dramatically modified forest habitats (James and Neal 1986).

Conversion and alteration of remaining bottomland hardwood forests have been so extensive that its continued existence as a functioning ecological system is uncertain (Creasman and others 1992, Ernst and Brown 1989). Because songbirds (Passeriformes) and other forest landbirds occupy a broad spectrum of habitats encompassing the full vertical forest profile, i.e., forest floor to canopy, and use a diverse array of resources as food

(e.g., plant material, soil and plant invertebrates) and as other necessary components of their life history, this vertebrate group represents an excellent barometer of forest ecosystem integrity and function.

Thus, a comparison of avifaunal species composition and abundance between undisturbed and second-growth forest should provide some insights regarding how well managed forests function as habitat for their indigenous biota; quantifying features associated with use of forest habitat by individual species would presumably identify essential stand-level components (or ecological correlates) necessary for successful reproduction. Moreover, the relationships between vegetative characteristics and avian distribution and abundance in southern bottomland hardwood forests are poorly documented. The purpose of this paper is to compare the bird community of a second-growth bottomland hardwood forest to a "paired" old-growth stand. Specific objectives were to: 1) determine whether breeding bird abundance and diversity were similar between old-growth and second-growth forests; 2) identify and quantify habitat features that were associated with distribution of bird species in old-growth and second-growth bottomland hardwood forests; and 3) determine whether these habitat attributes differed between old-growth and second-growth forests.

STUDY SITES

The study area was located approximately 8 km east of Fordyce, AR, along Moro Creek on the Moro Bottoms Natural Area (fig. 1). The Natural Area is a 70-ha tract of primarily old growth under the joint stewardship of the Arkansas Nature Conservancy and the Arkansas Natural Heritage Commission. The area is located in the upper West Gulf Coastal Plain (Hoiberg 1957 as cited in James and Neal 1986). The climate is hot and humid during the breeding season with a mean summer temperature of 27 °C. Mean annual rainfall is 123.4 cm, with much of the rain occurring in the spring.

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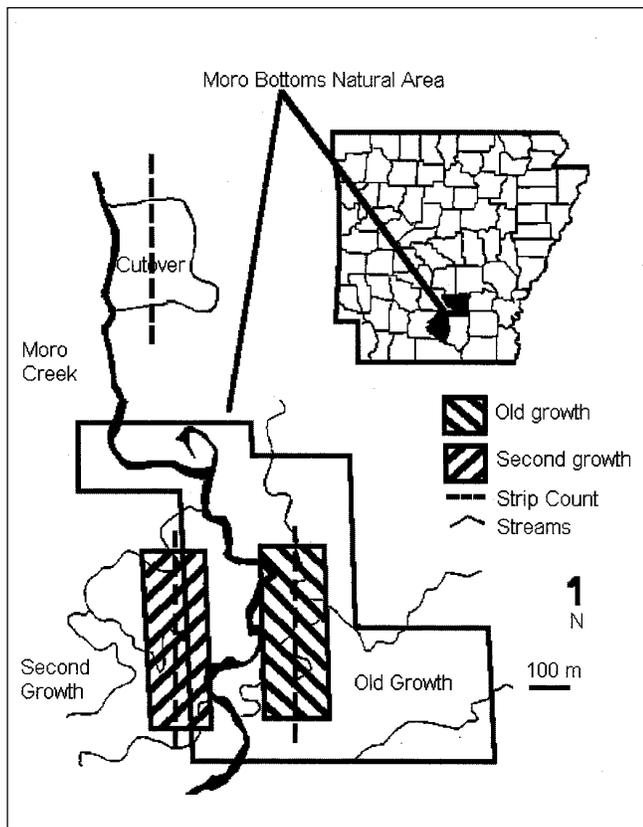


Figure 1—The study area, including Moro Bottoms Natural Area (large irregular shaped polygon) and adjacent private lands, Cleveland and Calhoun counties, AR, 1991 and 1992. (Hatched rectangles represent old-growth and second-growth spot-mapping grids.)

Portions of the study area adjacent to the creek are inundated periodically during the early part of the breeding season, but water usually does not persist for more than a week at a time. Several sloughs and creeks join the main channel of the stream such that water is abundant throughout the study area. The elevation of the site ranges 48 to 51 m above mean sea level.

The census areas consisted of two adjacent tracts of oak-gum-cypress (*Quercus* spp.-*Liquidambar styraciflua*-*Taxodium distichum*) bottomland hardwood forests located along Moro Creek. The first study site was a 12-ha tract of old growth east of Moro Creek in Cleveland County (fig. 1). Overstory on the old-growth site was dominated by sweetgum, black gum (*Nyssa sylvatica*), overcup oak (*Quercus lyrata*), and bald cypress. The understory was composed primarily of eastern hornbeam (*Carpinus caroliniana*) and American hop hornbeam (*Ostrya virginiana*). The herbaceous layer was poorly developed in areas of closed canopy. Dewberry (*Rubus* spp.) is common in areas of canopy gaps.

The second study site was a 12-ha second-growth stand of bottomland located to the west of Moro Creek in Calhoun County (fig. 1). This site experienced a high-grade harvest about 30 years before the study. Overstory dominants were similar to the old-growth site. The understory was composed

primarily of saplings of overstory trees and eastern hornbeam. The herbaceous layer was denser than in the old-growth study area and was comprised mostly of dewberry and grasses (Gramineae).

During August 1989, Moro Bottoms experienced a severe windstorm. Numerous windthrows occurred creating gaps in the overstory ranging in size from a single stem to about 0.3 ha). Because of these natural disturbances within the old growth and the proximity to managed second-growth forests, the Natural Area presented an excellent setting to examine the effects of recent natural and anthropogenic disturbances on habitat for forest landbirds.

PROCEDURES

Detailed maps of the old-growth and second-growth study sites were made that included major habitat features like Moro Creek and branching sloughs as well as all downed trees. All treefall canopy gaps were delineated by drawing lines connecting the trunks of mature trees at the gap edge. Maps of streams and canopy gaps were digitized into a Geographic Information System (GIS).

Habitat Sampling

A stratified, random-sampling procedure was used to locate an equal number of random points in the old-growth and second-growth study sites. The point-center quarter method (Cottam and Curtis 1956) was used to sample the overstory; tree height was included with tree species and d.b.h. measurements. Distance to the nearest snag, water, and gap also were measured. Together these data served as a null model of habitat features "available" within study sites for comparisons with measurements recorded where birds were seen and between study grids.

For singing male birds detected visually during spot-map censuses, several habitat variables were measured. Each bird's height from the ground was recorded using a clinometer; also its position in the vegetation (e.g., trunk, interior canopy, exterior canopy) was noted. In addition, tree species and height, diameter at breast height (d.b.h.), distance to the nearest snag, and distance to the nearest water were measured. A snag was defined as a dead tree >1.8 m tall with a d.b.h. of >10.2 cm (Thomas 1979). Diameter at breast height was measured only in 1992. On the old-growth site, distance from each singing male to the nearest gap was recorded. Canopy closure was quantified using a spherical densiometer (Lemmon 1956).

To quantify vegetation regrowth in canopy gaps, visual obstruction was measured using a density board (Nudds 1977). The board was 4 m high and marked off in 10-cm increments. The board was placed in the center of the longest axis of the gap. Readings were made at 5-m intervals from the board along the axis and along an axis perpendicular to it.

Avifaunal Sampling

The spot-map technique (International Bird Census Committee 1970) was employed to map the territories of breeding males in a 12-ha grid (600 m x 200 m) within both the old-growth and second-growth sites during the breeding season in 1991 and 1992. Grid boundaries were located at

least 50 m from any external edge. Numbered stakes were placed at 25-m intervals throughout the grid to facilitate locating each singing male's position on the grid. Weekly censuses were conducted on each grid. Locations of all male birds seen or heard were plotted on a map. Maps from each season were compiled by species and entered into the ARC/INFO GIS. Territories were derived as the minimum convex polygon that included all of the locations of a singing male (Mohr 1947). The area of each territory and the area covered by water and by gaps (old-growth site only) were calculated.

Strip count censuses were conducted weekly during the breeding season in 1991 and 1992. Strip count transects 50 m wide and 600 m long were established through the center of the old-growth and second-growth spot-map grids. All male birds seen or heard within the 50-m wide strip were recorded to provide an estimate of avian abundance for each study site. The time of each census was alternated weekly between morning and evening.

Statistical Analysis

All statistical analyses were performed using SAS 6.03 on an IBM personal computer. We used the Shapiro-Wilk test for normality (Shapiro and Wilk 1965) to examine the distribution of variables. When distributions departed from normality, or when variances were unstable or heterogeneous, we used nonparametric counterparts to test our ecological hypotheses. Statistical analyses almost invariably addressed common null hypotheses that were examined through multiple comparisons. Therefore, we followed the recommendations of Chandler (1995) and used sequential Bonferroni adjustments of *P*-values (Wright 1992). For a "family" (Chandler 1995:525) of multiple statistical tests, we selected an experiment-wise error rate of 10 percent; that is, the probability of a type I error for all individual comparisons collectively was < 0.1. We selected 10 percent, rather than the conventional 5 percent error rate, to mitigate a reduction in statistical power so that individual comparisons were not too conservative (Chandler 1995). Thus, corresponding individual, comparison-wise error rates varied according to the number of individual tests conducted and followed the general procedures for Bonferroni adjustments outlined by Wright (1992).

For example, multiple comparisons of habitat use were conducted in each habitat type to test the general hypothesis that distribution of birds was nonrandom. The general hypothesis was rejected with a 10 percent error rate if any of the underlying specific hypotheses was rejected. Individual comparisons were used to test underlying specific hypotheses, i.e., determine whether distribution in old growth or second growth was associated with any of a set of specific habitat features (e.g., snags). In this example, we made 13 comparisons of use against the same underlying availability distribution. In the most conservative scenario (i.e., where the adjusted comparison-wise *P*-value equals the experiment-wise error divided by the number of individual comparisons, Chandler 1995), the comparison-wise error rate of individual tests was 0.10/13, or 0.0077. That is, each comparison of use of a specific habitat feature in old growth or second growth to its corresponding availability occurred with an error rate of 0.77 percent. In

some circumstances, we reduced the total number of individual tests and increased statistical power by conducting comparisons sequentially according to *P*-values (Wright 1992:1009).

We used nonparametric test statistics for all univariate comparisons of habitat features between bird use (visual observations) and availability (random points). Distance to the nearest water, snag, and treefall canopy gap were tested for correlation using the Pearson correlation statistic (Kleinbaum and others 1988). No significant correlation occurred among any of the variables, so all variables were treated as independent variables in subsequent analyses. Because no significant difference existed in habitat distribution between years, 1991 and 1992 data from each habitat were combined to increase sample size and statistical power. Only birds with at least five visual records in each habitat type were included in analyses. Habitat use patterns of American redstart were analyzed although they were recorded only in second-growth habitat.

Tree species used by each bird species and corresponding height and d.b.h. values were compared to trees available (as estimated from a random sample of points) with a Kolmogorov-Smirnov Goodness-of-Fit (one-sample) test for continuous data (Zar 1984:55). Canopy closure and distance to nearest water, snag, and treefall canopy gap were compared to the same measures from random sites using a Wilcoxon signed rank test (Zar 1984).

Species composition and structure of avian communities were characterized with the Shannon-Weaver diversity index (Shannon and Weaver 1949). A Student's *t* test (Zar 1984) was used to test for significant differences between old-growth and second-growth habitats with spot-mapping and strip census results.

RESULTS

Bird Species Distribution, Density, and Diversity

Twelve spot-mapping censuses were conducted between May 26 and August 13, 1991, and 15 spot-mapping censuses were conducted between May 12 and August 15, 1992, on the old-growth and second-growth sites. In 1991 and 1992, there were 486 and 651 individuals and 543 and 591 individuals recorded in the old-growth and second-growth, respectively. Twelve and 15 strip-count censuses also were conducted in the old-growth and second-growth sites during the same time periods in 1991 and 1992, respectively.

A total of 38 species was detected in old growth, whereas 34 species were detected in second-growth habitat (table 1). The ten most common species recorded each in old-growth and second-growth habitats (according to weighted estimates of density from 1991 and 1992) are presented in table 2. For comparison, we include ranks of bird species recorded in four previous studies of bottomland hardwood forests. In our study, 12 warbler species (Parulinae) were detected in old growth, whereas nine warblers were detected in second-growth habitat. The white-eyed vireo (*Vireo griseus*) was the most common bird in both habitats in 1991 and in second-growth habitat in 1992 along with the Carolina wren (*Thryothorus ludovicianus*). The red-eyed

Table 1—Breeding bird density (pairs per 100 ha) derived from spot-mapping censuses by habitat and year on Moro Bottoms Natural Area, Arkansas, 1991 and 1992.

Species	Old growth		Second growth	
	1991	1992	1991	1992
Great blue heron (<i>Ardea herodias</i>)	*	*		
Yellow-crowned night-heron (<i>Nycticorax violaceus</i>)	*	*	*	*
Wood duck (<i>Aix sponsa</i>)	*	*	*	*
Red-shouldered hawk (<i>Buteo lineatus</i>)	*	*	*	*
Wild turkey (<i>Meleagris gallopavo</i>)	*	*	*	*
Yellow-billed cuckoo (<i>Coccyzus americanus</i>)			*	*
Barred owl (<i>Strix varia</i>)	*	*	*	*
Chimney swift (<i>Chaetura pelagica</i>)	*	*	*	*
Ruby-throated hummingbird (<i>Archilochus colubris</i>)	*	*	*	*
Red-bellied woodpecker (<i>Melanerpes carolinus</i>)	20	20	10	20
Downy woodpecker (<i>Picoides pubescens</i>)	20	20	10	10
Northern flicker (<i>Colaptes auratus</i>)	*			
Pileated woodpecker (<i>Dryocopus pileatus</i>)	*	10	*	
Eastern wood-peewee (<i>Contopus virens</i>)	10			
Acadian flycatcher (<i>Empidonax virens</i>)	30	40	30	30
Great crested flycatcher (<i>Myiarchus crinitus</i>)	20	20	10	10
American crow (<i>Corvus brachyrhynchos</i>)	*	*	*	*
Carolina chickadee (<i>Parus carolinensis</i>)	20	20	30	30
Tufted titmouse (<i>Parus bicolor</i>)	30	30	30	30
White-breasted nuthatch (<i>Sitta carolinensis</i>)	10	10	10	10
Carolina wren (<i>Thryothorus ludovicianus</i>)	30	40	40	61
Blue-gray gnatcatcher (<i>Poliophtila caerulea</i>)	*	*	10	10
White-eyed vireo (<i>Vireo griseus</i>)	51	51	71	61
Yellow-throated vireo (<i>Vireo flavifrons</i>)	10	10	*	*
Red-eyed vireo (<i>Vireo olivaceus</i>)	30	60	40	30

Table 1—Breeding bird density (pairs per 100 ha) derived from spot-mapping censuses by habitat and year on Moro Bottoms Natural Area, Arkansas, 1991 and 1992.

Species	Old growth		Second growth	
	1991	1992	1991	1992
Northern parula (<i>Parula americana</i>)	30	51	40	31
Black-and-white warbler (<i>Mniotilta varia</i>)	*	10	*	*
Yellow-throated warbler (<i>Dendroica dominica</i>)	10	10	10	10
Pine Warbler (<i>Dendroica pinus</i>)	10	10		
American redstart (<i>Setophaga ruticilla</i>)	*		40	40
Prothonotary warbler (<i>Protonotaria citrea</i>)	40	51	30	30
Swainson's warbler (<i>Limnothlypis swainsonii</i>)	*		10	10
Louisiana waterthrush (<i>Seiurus motacilla</i>)	*	10		
Kentucky warbler (<i>Oporornis formosus</i>)	20	40	20	40
Common yellowthroat (<i>Geothlypis trichas</i>)		10		20
Hooded warbler (<i>Wilsonia citrina</i>)	*	10	30	10
Worm-eating warbler (<i>Helmitheros vermivorus</i>)	*			
Summer tanager (<i>Piranga rubra</i>)	20	20	10	10
Northern cardinal (<i>Cardinalis cardinalis</i>)	40	30	51	40
Indigo bunting (<i>Passerina cyanea</i>)				10
Total density	451	584	522	542

* = species with too few sightings to delineate a breeding territory, or the species was too mobile to map accurately.

Table 2—Rank of 10 most abundant bird species in old-growth (OG) and second-growth (SG) habitats from Moro Bottoms Natural Area, Arkansas and from previous avifaunal studies in bottomland hardwood forest

Species	Moro Bottoms		Hoiberg ^a	Dickson ^b	Ford ^c	Hamel ^d
	OG	SG				
White-eyed vireo (<i>Vireo griseus</i>)	1	1	8	1	+	6
Red-eyed vireo (<i>Vireo olivaceus</i>)	2	3	1	7	+	5
Prothonotary warbler (<i>Protonotaria citrea</i>)	3	5	10	10	5	+
Northern parula (<i>Parula americana</i>)	4	4	–	+	+	1
Carolina wren (<i>Thryothorus ludovicianus</i>)	5	2	2	2	+	9
Acadian flycatcher (<i>Empidonax virescens</i>)	5	7	5	6	3	2
Northern cardinal (<i>Cardinalis cardinalis</i>)	7	6	4	5	2	4
Kentucky warbler (<i>Oporornis formosus</i>)	8	8	6	+	+	+
Tufted titmouse (<i>Parus bicolor</i>)	9	9	3	3	7	3
Red-bellied woodpecker (<i>Melanerpes carolinus</i>)	10	+	+	8	+	10
Downy woodpecker (<i>Picoides pubescens</i>)	10	+	+	+	8	+
Carolina chickadee (<i>Parus carolinensis</i>)	10	10	+	+	4	7
American redstart (<i>Setophaga ruticilla</i>)	+	+	9	–	–	+
Hooded warbler (<i>Wilsonia citrina</i>)	–	+	7	+	–	+
Yellow-billed cuckoo (<i>Coccyzus americanus</i>)	+	+	–	4	+	+
Swainson's warbler (<i>Limnothlypsis swainsonii</i>)	+	+	–	9	–	+
Blue-gray gnatcatcher (<i>Polioptila caerulea</i>)	+	+	+	–	1	8
Indigo bunting (<i>Passerina cyanea</i>)	+	+	–	–	6	+
Ruby-throated hummingbird (<i>Archilochus colubris</i>)	–	+	–	–	9	+
Common grackle (<i>Quiscalus quiscula</i>)	–	+	–	+	10	+

+ = species was recorded; – = species was not reported.

^aAdapted from Hoiberg 1957, cited in James and Neal (1986).

^bAdapted from Dickson (1978b).

^cAdapted from Ford (1990).

^dAdapted from birds recorded in old-growth bottomland hardwoods (Hamel 1989).

vireo (*Vireo olivaceus*) was the most common bird in old growth in 1992. The American redstart (*Setophaga ruticilla*) was a common bird in second-growth habitat, yet was only recorded once in old growth. The greatest density of breeding birds occurred in 1992 in old growth, whereas the lowest density was in old growth in 1991 (table 1).

Shannon-Weaver diversity indices derived from spot-mapping and strip-count censuses of old-growth forest were consistently greater, but not significantly different, than indices computed for second-growth habitat (table 3). Species richness also was not statistically different between habitats, but trends (table 3) were similar to diversity with a larger number of species recorded in old growth (29) as compared to second growth (27). Within a habitat type, no significant differences were detected either within years or between years for either sampling technique (e.g., spot-mapping in old growth between 1991 and 1992). We consistently recorded more species with the spot-mapping method, but spot-mapping and strip-count censuses produced similar species richness and diversity estimates.

The old-growth spot-mapping grid contained 24 gaps that ranged in size from 127.5 to 2685.5 m². Number of species and total number of birds recorded in gaps ranged 0 to 12 and 0 to 45, respectively. According to Spearman rank correlation analysis, species richness was positively correlated with area of treefall canopy gaps in 1991 ($r_s = 0.83, P < 0.001$) and 1992 ($r_s = 0.73, P < 0.001$). Total registrations also was positively correlated with gap area in 1991 ($r_s = 0.83, P < 0.001$) and 1992 ($r_s = 0.80, P < 0.001$). The highest values for species richness and total birds occurred in the largest gap.

Habitat Availability and Use

Habitat features—Comparison of distances measured from random points to various habitat features revealed significant differences between habitats. Average distance from random points to nearest snags and to surface water was significantly greater in old-growth than in second-growth habitat (table 4). Mean distance to the nearest tree was

Table 3—Shannon-Weaver diversity indices (H') and species richness (S) for spot-mapping and strip-count censuses among three forest habitats, Moro Bottoms Natural Area, Arkansas, 1991 and 1992

Habitat	Spot-mapping technique		Strip-count technique	
	H'	S	H'	S
Old growth				
1991	3.106	35	3.014	28
1992	3.099	33	3.095	30
Second growth				
1991	2.961	32	2.947	26
1992	3.021	32	3.037	28

Table 4—Means (x) and standard errors (SE) for all variables measured in random plots across old-growth and second-growth habitat, Moro Bottoms Natural Area, Arkansas, 1991 and 1992 (comparison-wise P-value: P < 0.0167)

Variable	Old growth		Second growth	
	x	SE	x	SE
Distance to water (m)	41.8	4.1	20.5	1.3 ^a
Distance to snag (m)	14.0	0.7	11.1	0.7 ^b
Distance to gap (m)	23.4	1.4	—	—
Canopy openness (percent)	24.1	1.1	27.3	1.3
Distance to tree (m)	3.5	.1	4.4	.2 ^c
D.b.h. (cm)	17.8	1.5	17.1	1.2
Tree height (m)	11.3	.7	11.0	.6
Basal area (m ² /ha)	20.4		11.9	
Stem density (trees/ha)	816.3		516.5	

^a Significant difference between old-growth and second-growth study sites, $P < 0.0001$.

^b Significant difference between old-growth and second-growth study areas, $P < 0.003$.

^c Significant difference between old-growth and second-growth study areas, $P < 0.001$.

significantly greater in second-growth habitat than in old growth. No significant difference in d.b.h. distribution or tree height distribution existed between habitats.

Tree species composition (fig. 2) was similar in old-growth and second growth forests. Eastern hornbeam was the most common tree in both habitats, comprising 49 percent of stem density in old-growth and 23 percent in second-growth habitat. Oaks had a relative density of 20 percent in second-growth study habitat compared to 8 percent in old growth.

Species habitat distribution—Perch heights varied among species and were significantly different between habitat types for the downy woodpecker (table 5). Acadian flycatchers occurred closer to water than expected, i.e., as compared to random points, in both old growth and second growth; this was true of prothonotary warblers in old growth (table 6). Acadian flycatchers were sighted directly over water in 68.0 percent of the observations. In second growth, Carolina wrens, tufted titmice, and white-eyed vireos all occurred farther from water than expected. Carolina wrens and Kentucky warblers also occurred farther from water than expected in old growth.

Snags were abundant across both study sites, occurring primarily in canopy openings. Carolina wrens in both habitats, and Kentucky warblers in old growth, were recorded closer to snags than were random sites (table 7). Carolina wrens and Kentucky warblers used snags as singing perches in 50 percent of our observations.

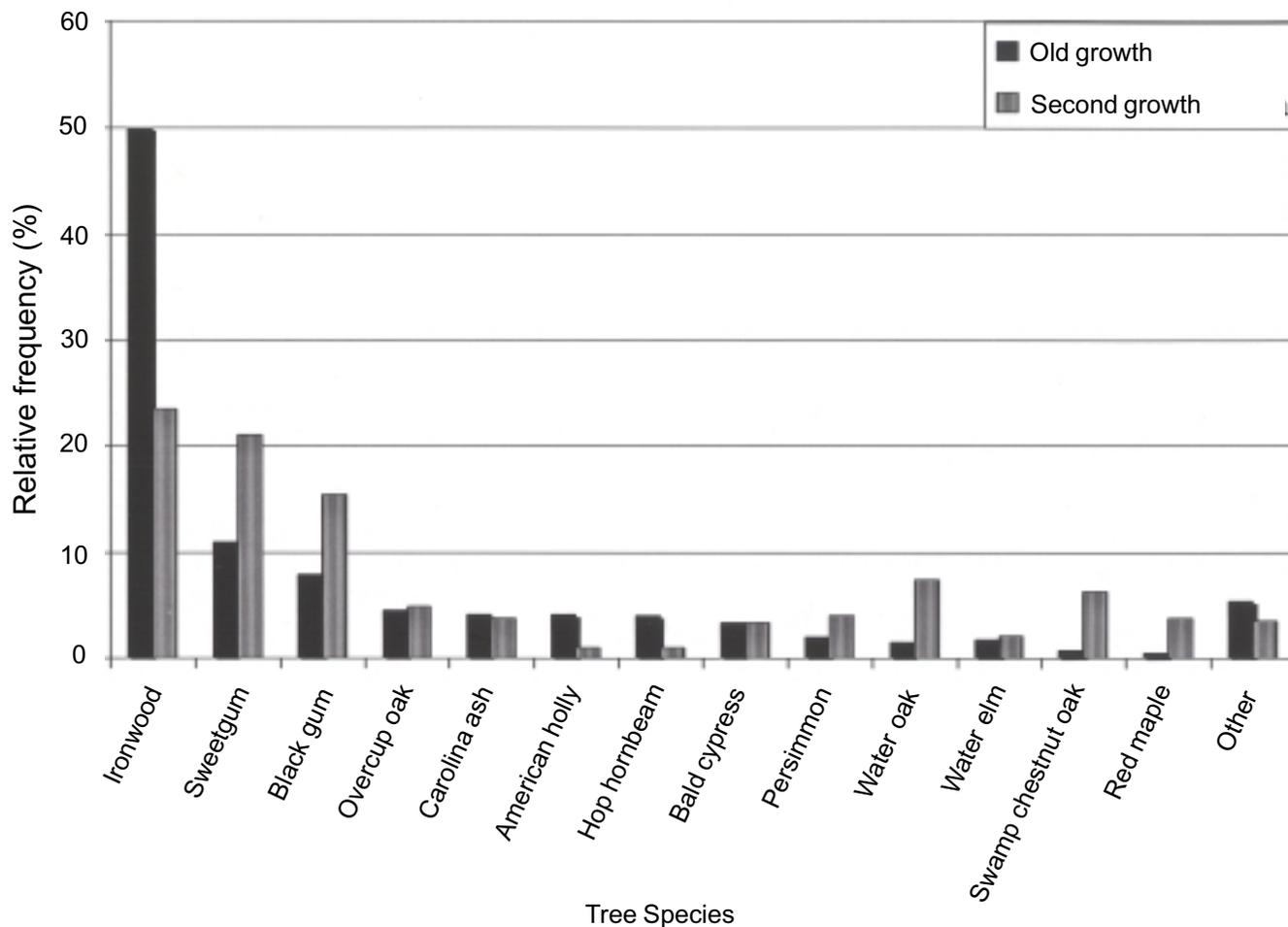


Figure 2—Relative frequency distribution (percent) of tree species in the old-growth and second growth study sites, Moro Bottoms Natural Area, Cleveland and Calhoun Counties, AR, 1991 and 1992.

Table 5—Sample size (N), mean perch height (x) and standard error (SE) of perch sites in meters for bird species in old-growth and second-growth habitat Moro Bottoms Natural Area, Arkansas, 1991 and 1992 (comparison-wise P -value: $P < 0.01$)

Species	Old growth			Second growth		
	N	x	SE	N	x	SE
Acadian flycatcher	25	5.5	0.5	15	4.1	0.3
American redstart	—	—	—	29	15.4	1.3
Carolina chickadee	6	9.3	1.9	9	8.4	.9
Carolina wren	14	2.6	.4	26	3.0	.4
Downy woodpecker	5	7.2	.9	5	14.8	2.4 ^a
Kentucky warbler	10	1.8	.4	12	1.5	.2
Northern cardinal	13	11.3	2.0	17	10.2	1.6
Prothonotary warbler	34	5.4	.5	19	5.2	.6
Red-bellied woodpecker	11	16.5	1.3	7	19.3	1.9
Tufted titmouse	11	10.8	1.3	9	9.9	1.8
White-eyed vireo	28	5.5	.3	30	5.9	.5

^a Significant difference ($P < 0.01$) in mean perch height between old-growth and second-growth study areas.

Table 6—Sample size (N), mean (x), standard error (SE), Wilcoxon test statistic (Z), and significance level (Prob > |Z|) for each species for distance to the nearest surface water (m) for each habitat, Moro Bottoms Natural Area, Arkansas, 1991 and 1992 (comparison-wise P-value: $P < 0.0077$)

Species/ random variable	N	x	SE	Z ^{a b}	Prob> Z
Old growth					
Acadian flycatcher	25	5.2	3.0	-6.485	0.0001
Carolina chickadee	6	45.2	13.1	1.331	.1833
Carolina wren	14	81.8	14.2	3.766	.0002
Downy woodpecker	5	33.0	15.1	-0.298	.7652
Kentucky warbler	10	88.1	24.1	2.708	.0068
Northern cardinal	13	28.5	5.0	.510	.6098
Prothonotary warbler	34	27.6	7.8	-3.240	.0012
Red-bellied woodpecker	11	60.0	14.3	1.799	.0716
Tufted titmouse	11	54.7	16.1	.662	.5079
White-eyed vireo	28	58.1	12.4	1.474	.1404
Distance to water (m)	93	41.8	4.1		
Second growth					
Acadian flycatcher	15	3.3	1.1	-4.871	.0001
American redstart	29	36.1	7.6	.511	.6013
Carolina chickadee	9	44.3	18.8	.792	.4282
Carolina wren	26	52.8	13.0	2.153	.0313
Downy woodpecker	52	3.0	3.3	.783	.4335
Kentucky warbler	12	40.0	17.9	.671	.5023
Northern cardinal	17	48.7	13.6	2.349	.0188
Prothonotary warbler	19	20.6	7.5	-1.496	.1345
Red-bellied woodpecker	7	27.3	10.4	.435	.6638
Tufted titmouse	9	87.3	27.9	3.039	.0024
White-eyed vireo	30	42.9	8.2	2.688	.0072
Distance to water (m)	96	20.5	1.3		

^a Calculated from use sites and 93 random sites in the old-growth study site using the Wilcoxon signed rank test.

^b Calculated from use sites and 96 random sites in the second-growth study site using the Wilcoxon signed rank test.

Carolina wrens, Kentucky warblers, prothonotary warblers, and white-eyed vireos were sighted closer to treefall canopy gaps than random points (table 8). Moreover, perch sites of the Carolina wren, Kentucky warbler, and white-eyed vireo had a greater mean percentage of canopy openness (table 9). The white-eyed vireo appeared to locate its territory around single canopy gaps >500 m². Although gaps composed only 22.0 percent of the old-growth study area, 38.0 percent and 35.4 percent of spot-mapping records occurred within treefall canopy gaps in 1991 and 1992, respectively. The reason for this positive association with canopy gaps is unclear, but occupied gaps had greater understory density (53.2 percent \pm 5.56) from forest floor to a height of four meters than gaps where birds had not been recorded (31.1 percent \pm 3.96). Only the Acadian flycatcher

appeared to avoid canopy gaps. In second-growth habitat they used areas with greater closed canopy (table 9), and in old-growth forest, Acadian flycatchers were sighted at greater distances than expected from canopy gaps (table 8).

Red-bellied woodpeckers in old-growth and American redstarts in second-growth habitat used trees that had greater d.b.h. than was generally available (table 10). These species and the Carolina chickadee preferred trees of greater height in both habitats than was generally available (table 11). Carolina wrens in old growth and Kentucky warblers in both habitats, used shorter trees than expected. Unfortunately, because d.b.h. was only measured in 1992, some species were omitted from the analysis due to insufficient sample size.

Table 7—Sample size (N), mean (x), standard error (SE), Wilcoxon test statistic (Z), and significance level (Prob >|Z|) of distance to the nearest snag (m) for each bird species in old-growth and second-growth habitat, Moro Bottoms Natural Area, Arkansas, 1991 and 1992 (comparison-wise P-value: $P < 0.0077$)

Species/ random variable	N	x	SE	Z ^{a b}	Prob> Z
Old growth					
Acadian flycatcher	25	15.6	2.2	0.681	0.4957
Carolina chickadee	6	22.3	6.2	1.817	.0708
Carolina wren	14	7.0	1.8	-3.591	.0003
Downy woodpecker	5	8.8	4.1	-1.171	.2414
Kentucky warbler	10	5.3	1.8	-3.210	.0013
Northern cardinal	13	13.8	2.0	.410	.6818
Prothonotary warbler	34	10.5	1.3	-1.923	.0544
Red-bellied woodpecker	11	15.5	3.5	.346	.7293
Tufted titmouse	11	13.4	2.8	-.410	.6815
White-eyed vireo	28	10.6	1.3	-1.826	.0680
Distance to snag (m)	93	14.0	0.7		
Second growth					
Acadian flycatcher	15	13.7	2.1	1.892	.0585
American redstart	29	13.4	1.8	1.186	.1871
Carolina chickadee	9	10.0	2.1	.285	.7757
Carolina wren	26	4.0	1.1	-4.771	.0001
Downy woodpecker	5	5.4	2.0	-1.401	.1612
Kentucky warbler	12	8.1	1.2	-.303	.7619
Northern cardinal	17	12.3	2.8	.046	.9632
Prothonotary warbler	19	10.8	1.5	.682	.4948
Red-bellied woodpecker	7	12.6	2.4	.937	.3487
Tufted titmouse	9	8.9	1.7	-.129	.8972
White-eyed vireo	30	11.2	1.6	.827	.3973
Distance to snag (m)	96	11.1	.7		

^a Calculated from use sites and 93 random sites in the old-growth study site using the Wilcoxon signed rank test.

^b Calculated from use sites and 96 random sites in the second-growth study site using the Wilcoxon signed rank test.

Finally, we compared use of tree species by birds to corresponding estimates of availability with a Kolmogorov-Smirnov (KS) goodness-of-fit test (Appendix 1). We discourage drawing inferences about tree species preferences, however, because of the small sample of observations obtained for each bird species, and because the KS goodness-of-fit test was not developed for use with nominal data. Still, the relative frequency distributions and computed statistics suggest nonrandom use of trees by most bird species. The American redstart showed the largest bias toward use of a single species with 65 percent of its use occurring in swamp chestnut oak (*Quercus michauxii*). Perch sites selected by other bird species were more evenly distributed across a variety of tree species (Appendix 1).

DISCUSSION

Assumptions and Implications

Moro Bottoms Natural Area was an excellent natural laboratory for examining birds of old-growth and second-growth habitats. Because this was not a replicated experiment, however, we caution generalizing results of our study to other southern bottomland hardwood forests. Moreover, there were several assumptions inherent in procedures used in this study, some of which bear significant implications on results and conclusions. For example, we assumed that our sample of species distributions across habitats reflected the variability that existed in each of the habitats. Most of the visual observations of birds were distributed among species that

Table 8—Sample size (N), mean (x), standard error (SE), Wilcoxon test statistic (Z), and significance level (Prob >|Z|) of recorded distances to the nearest canopy gap (m) for each bird species in old growth, Moro Bottoms Natural Area, Arkansas, 1991 and 1992 (comparison-wise P-value: P < 0.01)

Species/ random variable	N	x	SE	Z ^a	Prob> Z
Acadian flycatcher	25	37.7	5.4	2.734	0.0063
Carolina chickadee	6	21.5	4.4	.107	.9150
Carolina wren	14	6.4	2.9	-4.688	.0001
Downy woodpecker	5	15.2	5.6	-.865	.3873
Kentucky warbler	10	5.4	2.5	-3.555	.0004
Northern cardinal	13	17.5	3.0	-.864	.3874
Prothonotary warbler	34	10.9	1.6	-4.688	.0001
Red-bellied woodpecker	11	19.5	3.0	-.250	.8030
Tufted titmouse	11	39.9	12.1	.934	.3505
White-eyed vireo	28	5.2	1.1	-5.914	.0001
Distance to gap (m)	93	23.4	1.4		

^a Calculated from use sites and 93 random sites using the Wilcoxon signed rank test.

typically frequent the midstory or understory strata. Dense foliage and low light conditions in bottomland hardwood forests made it difficult to observe birds in the upper canopy. Canopy species commonly sighted tended to be those that were more active (e.g., American redstart) or more vocal (e.g., red-bellied woodpecker). Consequently, our results were probably biased toward species or individuals of a species that were more easily detected and observed. Also, spherical densimeters yield biased estimates of forest canopy cover (Cook and others 1995). Cover may be overestimated and spherical densimeters may be insensitive to variation in forest cover, especially in the mid-range of canopy closure.

In addition, microhabitat features important for successful reproduction among forest landbirds are numerous and include food, foraging substrate, water, singing perches, and nest sites. Because we only obtained direct observations of singing perches, limited conclusions can be drawn about bird habitat needs and microhabitat segregation among species.

Finally, there were numerous comparisons of habitat features between habitats and between used and available sites within each habitat. In one such comparison, we used the KS one-sample test to compare tree species distributions (i.e., use versus available) when our data did not strictly meet an important assumption of this analysis, namely that observations are continuous data from a ratio, interval, or ordinal scale of measurement (Zar 1984:55).

Also, because we did not apply a Bonferroni correction to each set of analyses (e.g., Neu and others 1974), there was an average of one chance in 20 (for $P < 0.05$) that a

statistical analysis could yield a spurious significant conclusion.

Forest Composition

Vegetation at Moro Bottoms appeared typical of bottomland hardwood forests of minor stream floodplains across the Southern United States. Clairain and Kleiss (1988) reported a similar assemblage of tree species for the Cache River Basin in eastern Arkansas. At Cache River and Moro Bottoms, forest types and corresponding overstory dominants were distributed according to a moisture gradient with cypress-tupelo inhabiting more hydric sites and overcup oak (*Quercus lyrata*) and swamp chestnut oak occurring on somewhat drier, mesic sites. Understory diversity was limited under closed canopy at both sites, a feature probably related to frequent and periodic prolonged inundation, as well as limited sunlight across the forest floor (Smith and others 1995).

Bird Species Distribution and Diversity

Moist bottomland hardwood forests of the Southern United States often support an abundant and diverse breeding bird community (Smith and others 1993a). James and Wamer (1982) reported that mature deciduous forests supported the highest avian diversity and density of all North American forest types. Similar results were reported for Arkansas where mature, moist forests had the highest breeding species diversities (Shannon-Weaver index = 2.91) of any habitat in the State (Shugart and James 1973). In our study, diversity indices computed from spot-mapping censuses of old growth averaged 3.10 (table 2).

It is generally recognized that there is a correlation between foliage height diversity and bird species diversity in several

Table 9—Sample size (N), mean (x), standard error (SE), Wilcoxon test statistic (Z), and significance level (Prob > |Z|) of canopy openness (percent) for each bird species in old growth and second-growth habitat, Moro Bottoms Natural Area, Arkansas, 1991 and 1992 (comparison-wise P-value: $P < 0.0077$)

Species/ random variable	N	x	SE	Z ^{ab}	Prob> Z
Old growth					
Acadian flycatcher	25	18.4	1.5	-1.554	0.1200
Carolina chickadee	6	15.7	3.4	-1.662	.0966
Carolina wren	14	57.5	2.8	6.077	.0001
Downy woodpecker	5	36.6	11.6	.751	.4527
Kentucky warbler	10	52.8	4.9	4.257	.0001
Northern cardinal	13	23.3	2.7	.687	.4920
Prothonotary warbler	34	31.6	3.0	2.554	.0107
Red-bellied woodpecker	11	22.3	1.6	1.518	.1291
Tufted titmouse	11	24.6	1.6	1.518	.1291
White-eyed vireo	28	36.1	2.1	5.231	.0001
Canopy openness (%)	93	24.1	1.1		
Second growth					
Acadian flycatcher	15	14.7	1.8	-2.823	.0048
American redstart	29	17.7	1.6	1.891	.0494
Carolina chickadee	9	30.8	3.4	1.440	.1499
Carolina wren	26	42.8	2.6	4.580	.0001
Downy woodpecker	5	25.2	4.4	.234	.8146
Kentucky warbler	12	53.5	4.9	4.137	.0001
Northern cardinal	17	26.6	3.1	.636	.5246
Prothonotary warbler	19	21.6	1.8	-.477	.6335
Red-bellied woodpecker	7	21.9	3.3	-.297	.7687
Tufted titmouse	9	30.8	3.4	.111	.9113
White-eyed vireo	30	31.0	1.5	2.663	.0077
Canopy openness (%)	96	27.3	1.3		

^a Calculated from use sites and 93 random sites in the old-growth study site using the Wilcoxon signed rank test.

^b Calculated from use sites and 96 random sites in the second-growth study site using the Wilcoxon signed rank test.

forests in the Eastern United States (MacArthur and MacArthur 1961). At Moro Bottoms, breeding bird diversity and richness increased with successional stage. In old growth, or mature forests in general, Dickson (1991) attributed high avian diversity to an increased number of canopy layers and tree age categories. As habitat complexity and heterogeneity increase, habitat requirements for a greater number of species can be met (Martin 1992). Similar results were reported for the Atchafalaya Basin by Kennedy (1977): bird species richness and diversity varied with foliage density, which increased from the earliest seral stage to the oldest seral stage.

In our study, old growth had a closed canopy interrupted by treefall canopy gaps, which provided several layers of herbaceous and woody vegetation. The understory was sparse except in canopy gaps where midstory and understory layers proliferated. This diverse canopy structure was not present in second-growth habitat where trees were generally spaced farther apart and where development of a dense low understory under a more open canopy was presumably facilitated.

Avian abundance also varies with forest habitat structure and complexity, which presumably facilitates partitioning of resources among conspecifics (Kennedy 1977), as well as

Table 10—Sample size (N), mean (x), standard error (SE), Kolmogrov-Smirnov test statistic (D), and significance level (Prob > KS) of perch site d.b.h. (cm) for each bird species in old-growth and second-growth habitat, Moro Bottoms Natural Area, Arkansas, 1991 and 1992 (comparison-wise P-value: $P < 0.0077$)

Species/ random variable	N	x	SE	D ^{a b}	Prob>KS
Old growth					
Acadian flycatcher	14	12.2	2.2	0.1935	0.7521
Carolina wren	12	7.8	2.0	.2769	.3891
Kentucky warbler	6	1.7	1.0	.5269	.0875
Northern cardinal	8	20.4	5.8	.2311	.8260
Prothonotary warbler	18	12.5	2.1	.1505	.8840
Red-bellied woodpecker	6	46.8	2.4	.8065	.0013
Tufted titmouse	6	41.6	12.1	.4731	.1603
White-eyed vireo	16	11.4	2.1	.1505	.9165
D.b.h. (cm)	93	17.8	1.5		
Second growth					
Acadian flycatcher	11	16.1	2.7	.2794	.4244
American redstart	18	46.1	3.5	.7601	.0001
Carolina wren	16	9.4	2.0	.2038	.5911
Kentucky warbler	7	1.3	0.6	.4479	.1459
Northern cardinal	10	24.0	5.3	.3604	.1900
Prothonotary warbler	12	12.0	2.2	.2083	.7435
Tufted titmouse	6	40.5	5.8	.6250	.0243
White-eyed vireo	19	13.6	2.3	.2889	.1415
D.b.h. (cm)	96	17.1	1.2		

^a Calculated from use sites and 93 random sites in the old-growth study site and using the Kolmogrov-Smirnov test.

^b Calculated from use sites and 96 random sites in the second-growth study site using the Kolmogrov-Smirnov test.

among species (Mannan and others 1984). That is, the number of conspecifics occupying a habitat is not necessarily reduced as habitat complexity and species diversity increases. In the Atchafalaya Basin, Kennedy (1977) reported that the greatest avian abundance occurred in bottomland hardwood forest, the latest seral stage among an array of successional seres examined, and the habitat with the greatest foliage complexity. In the Congaree Swamp and Santee Swamp, Hamel (1989:624) reported considerable overlap in bird communities (similarity index = 0.9) between old-growth and selectively cut stands and between selectively cut and clearcut stands. Similarity between old growth and second growth was intermediate (0.7); the lowest similarity in bird communities (0.6) existed between old-growth and clearcut stands (Hamel 1989:624).

In this study, breeding bird density varied inconsistently between years and habitats with total old-growth densities

exceeding those in second-growth habitat in 1992, but not in 1991 (table 3). Unfortunately, we did not estimate foliage complexity in either habitat (only understory density in gaps) and only measured five features related to forest structure. Of these only two differed between habitats (table 4). Second-growth habitat had greater snag density and showed greater spacing among stems >10 cm d.b.h., the latter of which may have reduced canopy cover in second growth habitat.

Avian density at Moro Bottoms was greater than that reported for a moist forest in the Ozark region of Arkansas (Shugart and James 1973). Average breeding bird density was 525 breeding pairs per 100 ha in Moro Bottoms, whereas 150 breeding pairs per 100 ha were observed in the Ozarks. However, total avian density at Moro Bottoms was appreciably lower than that reported for bottomland forests of western Tennessee (830 breeding pairs per 100

Table 11—Sample size (N), mean (x), standard error (SE), Kolmogrov-Smirnov test statistic (D), and significance level (Prob > KS) of perch site tree height (m) for each bird species in old-growth and second-growth habitat, Moro Bottoms Natural Area, Arkansas, 1991 and 1992 (comparison-wise P-value: $P < 0.0077$)

Species/ random variable	N	x	SE	D ^{a b}	Prob>KS
Old growth					
Acadian flycatcher	25	11.4	1.2	0.2433	0.1048
Carolina chickadee	6	16.8	2.7	.6984	.0069
Carolina wren	14	3.3	.4	.4770	.0008
Downy woodpecker	5	12.8	3.8	.2984	.7785
Kentucky warbler	10	2.1	.4	.6349	.0009
Northern cardinal	13	15.4	2.6	.2882	.2647
Prothonotary warbler	34	8.7	.8	.2011	.1945
Red-bellied woodpecker	11	26.5	2.2	.6984	.0001
Tufted titmouse	11	20.7	2.6	.6657	.0002
White-eyed vireo	28	8.8	.9	.1865	.3664
Tree height (m)	93	11.3	.7		
Second growth					
Acadian flycatcher	15	13.9	1.7	.3895	.0293
American redstart	29	24.4	1.2	.6563	.0001
Carolina chickadee	9	21.8	2.5	.6337	.0020
Carolina wren	26	5.7	1.0	.2247	.1976
Downy woodpecker	5	20.8	2.1	.6563	.0301
Kentucky warbler	12	2.3	.4	.6093	.0005
Northern cardinal	17	16.1	2.3	.3621	.0333
Prothonotary warbler	19	8.5	1.0	.1801	.6291
Red-bellied woodpecker	7	27.6	1.1	.8281	.0002
Tufted titmouse	9	23.7	2.2	.6562	.0012
White-eyed vireo	30	9.1	1.0	.1573	.5422
Tree height (m)	96	11.0	.6		

^a Calculated from use sites and 93 random sites in the old-growth study site using the Kolmogrov-Smirnov test.

^b Calculated from use sites and 96 random sites in the second-growth study site using the Kolmogrov-Smirnov test.

ha; Ford 1990) or breeding bird densities reported among all habitats of the Congaree Swamp (range 818 to 1572 pairs per 100 ha; Hamel 1989). In contrast, pine forests of the west Gulf Coastal Plain had 2 to 4 times lower densities than mature bottomland hardwood forests (Dickson 1978a).

Species common to Moro Bottoms were similar to communities reported for bottomland hardwood forests elsewhere (table 2). Regrettably, there are few remaining examples of bird communities of old-growth bottomland forests (Dickson 1978a, Hamel 1989). Except for Hamel (1989), previous studies of southern bottomland bird communities mostly come from sites where logging or other

land uses have influenced extent and composition of remaining forests (Dickson 1978b, Ford 1990). Fortunately, there was an earlier study from southern Arkansas (Hoiberg 1957, cited in James and Neal 1986) that could be included in our comparisons (table 2). The 10 most abundant species recorded in Moro Bottoms (pooled between habitats) almost completely overlapped (one exception from each study) the 10 most common species reported by Hoiberg (James and Neal 1986). Northern parula, the sixth most frequently observed species in our study, was the only species not ranked among Hoiberg's 10 most common species. In contrast, the hooded warbler (*Wilsonia citrina*) was the seventh most common species in the Hoiberg study, but was

not among the 10 most common species at Moro Bottoms. There also was substantial overlap between Moro Bottoms and the Atchafalaya Basin (Dickson 1978b) and between Moro Bottoms and the old-growth habitat of the Congaree Swamp (Hamel 1989) with eight and nine species, respectively, common to those communities (table 2). In west Tennessee bottomlands (Ford 1990), however, only six of the top ten species made the Moro Bottoms list.

At least some of the variation among studies can be explained as sampling error. For example, the 12-ha old-growth grid encompassed about 30 percent of the entire stand, but it did not include the complete range of elevation or microtopographic variation that existed throughout the stand (Zollner 1993). Alternatively, differences in species composition (or density) of ≥ 1 species across bottomland sites may reflect some habitat differences, albeit subtle, or even ephemeral. Hamel (1989) noted several species whose occurrence was limited to only one of the six forest habitats sampled in South Carolina. In our study, we noted variation across Moro Bottoms Natural Area in specific habitat features such as the presence of canebrakes. Canebrakes and other dense undergrowth are a favorite nesting habitat for Swainson's warblers.

Also, wood thrush may have been absent from our grids because those sites often were still flooded during spring when breeding males arrived. Indeed, it was not uncommon to have the Natural Area almost completely flooded for a few days in late June (Zollner 1993). Because of their dependence on soil invertebrates as a food base, wood thrush establishment of territories on our study grids may have been precluded by the extent and duration of flooding. Ford (1990:35) noted that the wood thrush had the lowest density (5 pairs per 100 ha) of widespread species in west Tennessee bottomlands where almost all of what remains is the lower elevation habitat, which was presumably too wet for clearing and conversion to agriculture.

Finally, some of the variation was almost certainly related to species-specific breeding ranges or because of the area-sensitive nature of some species (Robbins and others 1989). The American redstart, for example, was probably absent from south-central Louisiana (Dickson 1978b) because rarely (if ever) does this species breed that far south in Louisiana. Moro Bottoms Natural Area is part of a narrow, frequently interrupted, riparian system largely surrounded by pine plantations. The hairy woodpecker (*Picoides villosus*) may be precluded from occurring within small bottomland fragments; the cerulean warbler (*Dendroica cerulea*) was probably absent because of either of the aforementioned reasons.

Habitat Use

Water—Water is a dominant feature of bottomland hardwood forests (Smith 1977). Ford (1990) reported that the highest densities of birds in west Tennessee occurred in bottomland forests along an unchannelized river. Swift and others (1984) found the highest bird densities in Connecticut were associated with plots that included streams. They also reported a positive correlation between surface water coverage and species richness and density in both the foliage gleaning and ground foraging avian guilds.

Shugart and James (1973) classified the Acadian flycatcher, northern parula, Kentucky warbler, and American redstart as moist forest specialists in Arkansas. However, Shugart and James (1973) did not specifically examine the effects of surface water on singing perch site selection. All four of these moist forest specialists were abundant at Moro Bottoms; only the Acadian flycatcher, however, was closely associated with surface water. Somewhat surprising, the prothonotary warbler was not listed as a moist forest specialist (Shugart and James 1973), but also showed a strong affinity for water at Moro Bottoms. The importance of water to these two species also was reflected by the large proportion of Acadian flycatcher and prothonotary warbler territories that were comprised of water (Smith and others 1993b).

The Kentucky warbler, another moist forest specialist (Shugart and James 1973), surprisingly occurred farther from water than expected in Moro Bottoms (table 6). Thus, surface water alone may not be critical to some moist forest species; rather, it may be an ecological correlate of the moisture regime, such as invertebrate abundance. For Acadian flycatchers and prothonotary warblers, standing water may provide direct and indirect benefits as both species were often seen perching over or adjacent to streams. They seemed to use these areas as flyways along which they foraged. Conversely, the Kentucky warbler was not observed using these flyways and probably prefers the moist forest because of increased food associated with these habitats. Indeed, Smith (1977) noted the high abundance of insects and soil invertebrates in moist forests as compared to an upland post oak forest (*Quercus stellata*) in Arkansas.

The Carolina wren and the Kentucky warbler were the only species that occurred in drier sites of both old-growth and second-growth habitats. This may be related to the flood regimes in Moro Bottoms. These two species both feed on or near the ground and nest on the ground or in cavities (Carolina wren only) or low shrubs (Ehrlich and others 1988). In our study, foraging substrate within territories that were too close to streams would frequently have been unavailable because of flooding, which occurred several times throughout the 1991 and 1992 breeding seasons.

Snags—Snags were very abundant in both habitats. In second-growth habitat, this was to some extent a result of "habitat improvement" by a local hunting club; in old growth, stubs created by wind (i.e., snapped tops) and mortality from windthrow damage of adjacent trees probably contributed to snag abundance. Flooding and associated stress-induced mortality was probably common in both habitats. Thus, snags at Moro Bottoms were probably not a limiting resource as reported elsewhere (e.g., Dickson and others 1983). Most cavity nesters at Moro Bottoms showed no significant affinity for snags (table 7). Only the Carolina wren, which occasionally nests in cavities, and the Kentucky warbler showed an affinity for snags, especially snags created by treefalls. These snags were generally located in the center of canopy gaps where Carolina wrens and Kentucky warblers were frequently observed foraging and singing. In many circumstances, snags were the only elevated singing and display perches in the interior of gaps.

Gap Size—Internal patchiness in the form of treefall canopy gaps attracted a large number of bird species and individuals in Moro Bottoms. Openings created by treefalls lead to a high degree of habitat structural diversity (Urban and Smith 1989). This diversity is similar to that at the forest edge, but might be considered internal edge that operates at a finer scale (Noss 1988). Noss (1988) reported that the proportion of gaps in a forest was the best predictor of bird density in Florida. At Moro Bottoms, gaps represented 22 percent of the old-growth habitat, which was greater than the 3.4 percent reported by Noss (1988).

Birds concentrated in gaps presumably because of increased food resources (Noss 1988) and abundant favorable nest sites (Morse 1985). The dense shrub layer that develops in gaps offers concealment for nests, as well as an increased fruit and seed production over nongap areas of the forest. Blake and Hoppes (1986), in a mist net study of gaps in Illinois, reported more migratory frugivores, granivore-omnivores, and foliage gleaning insectivores in gap areas than in nongap areas.

Of the 10 species intensively studied in old growth at Moro Bottoms, four species showed a significant association with gaps (table 8): Carolina wren, Kentucky warbler, prothonotary warbler, and white-eyed vireo. As expected, these same species preferred areas with a more open canopy (table 9). Freemark and Collins (1992) included tufted titmouse and northern cardinal in a list of interior edge species, but excluded the Kentucky warbler. Noss (1991) also listed Carolina chickadee and red-bellied woodpecker as edge attracted species in Florida. Variation in affinities shown by species (Freemark and Collins 1992, Noss 1991) may be a result of differences in habitat across studies. Abundance and availability of gaps at Moro Bottoms may have made it difficult to discern the importance of internal patchiness by simply measuring distances to the nearest gap. Only those birds that spent most of the time in the gap interior showed statistically significant use. For the Kentucky warbler, included among forest interior species by Freemark and Collins (1992), the difference may be only in semantics. Kroodsmma (1984) reported that the Kentucky warbler avoided edge, but there was no apparent reference as to whether canopy gaps were considered edge.

The white-eyed vireo was the only species that clearly selected individual gaps based on the amount of vegetative cover in the understory and midstory. Emlen and others (1986) listed the absence of dense low shrubs as the main environmental constraint on white-eyed vireos. Ford (1990) reported that white-eyed vireo density in Tennessee increased with increasing height of the herbaceous layer and increasing stem density. Outline drawings of the “niche-gestalt” for this species (James 1971) seemed to show that they preferred areas of open canopy with a dense low shrub cover. The white-eyed vireo was the only species whose territory contained a significantly greater proportion of canopy gaps (65 percent) than expected in Moro Bottoms (22 percent) (Smith and others 1993b). In contrast, the Acadian flycatcher appeared to avoid gaps by using areas with a closed canopy. Ford (1990) found Acadian flycatchers to be negatively correlated with shrub cover. Noss (1988)

and Kroodsmma (1984) also listed this species as avoiding edge.

Tree species, d.b.h., and height—The frequency distribution of tree species used by birds was significantly different from the available distribution for all avian species (table 12). This difference may be related to height of various tree species; for example, the white-eyed vireo perched most often in eastern hornbeam which rarely (if ever) reaches a height of 15 m. Acadian flycatchers seemed to prefer Carolina ash (*Fraxinus caroliniana*) and water elm (*Planera aquatica*). This preference may be site specific, associated with perching over water, which is where these tree species grow, rather than because of the attributes of the trees. One probable example of a strict preference for tree species in our study was the frequent use of swamp chestnut oak by the American redstart. Sweetgum and black gum were much more abundant in second-growth habitat (fig. 2), yet the American redstart was nearly always seen in swamp chestnut oak. Large leaves and dense foliage, which are typical of the swamp chestnut oak, presumably provide abundant foraging substrate, an attractive feature for insectivorous leaf-gleaning specialists such as the American redstart.

Ecological and Management Implications

The high avian diversity associated with undisturbed mature deciduous hardwood forests may be related to small, naturally occurring canopy openings, <2 ha, created by windstorms and fire. These canopy gaps are responsible for much of the foliage and structural variation within these forests (Urban and Smith 1989). Large logs and snags remaining after disturbance provide foraging and nesting substrate for numerous bird species of old-growth forests (Juday 1988, Thomas and others 1988). Approximately 14 species of Arkansas' birds are associated with edge habitat created by canopy gaps (Shugart and James 1973).

In contrast, anthropogenic disturbances, such as timber management, typically occur more frequently, create larger forest canopy openings, and result in more extensive cumulative disturbance across landscapes than natural disturbance regimes (Runkle 1982, 1991). Larger gaps (i.e., >2 ha) created by most regeneration and some thinning operations may reduce species diversity by displacing canopy or area-sensitive species and allowing invasion of common early succession and edge species (Urban and Smith 1989). Clearcutting, the harvest method generally practiced in Arkansas, creates larger canopy openings with harder, external edges (Noss 1988) than natural disturbance processes. Consequently, breeding forest interior species that depend on larger expanses of continuous mature forests have declined in many portions of their historical range (Freemark and Collins 1992, Hamel and others 1998).

The potential exists to modify timber harvest practices to promote avian diversity (Thompson and others 1992). Uneven-aged stands resembling presettlement forests could perhaps be achieved with silviculture prescriptions such as single tree or small group selection, which produce relatively small canopy gaps. However, additional research is needed on the effects of gap size and interspersal across landscapes on bird habitat use, especially as it relates to

Table 12—Sample size (N), Kolmogrov-Smirnov test statistic (D), significance level (Prob > KS) and relative frequency (percent) of tree species^a used by birds perching in old-growth and second-growth bottomland hardwoods, Moro Bottoms Natural Area, Arkansas, 1991 and 1992

Species	N	D ^{b c}	Prob >KS	CC	FC	LS	NS	QL	QM	TD	Other
Old growth											
Acadian flycatcher	25	0.9000	0.0031	21	24	—	6	—	—	12	12
Carolina chickadee	6	.9500	.0015	34	—	17	—	—	17	—	34
Downy woodpecker	5	.9500	.0180	20	—	40	—	—	—	—	40
Northern cardinal	13	.9000	.0004	45	—	15	8	8	—	8	16
Prothonotary warbler	34	.6272	.0075	42	15	3	—	6	—	3	30
Red-bellied woodpecker	11	.9000	.0011	9	—	36	9	9	27	—	9
Tufted titmouse	11	.9000	.0002	—	9	27	9	18	—	9	27
White-eyed vireo	28	.7000	.0124	34	5	5	—	—	—	—	57
Second growth											
Acadian flycatcher	15	.6875	.0200	19	13	13	—	—	—	25	31
American redstart	29	.6625	.0118	—	—	—	4	18	65	—	18
Carolina chickadee	9	.8125	.0032	—	—	22	22	—	—	11	44
Downy woodpecker	5	.9375	.0236	—	—	40	40	—	—	—	20
Northern cardinal	17	.6875	.0200	8	—	8	32	40	—	—	48
Prothonotary warbler	19	.6250	.0222	21	11	—	11	—	—	—	57
Red-bellied woodpecker	7	.9999	.0128	—	—	43	29	—	—	29	—
Tufted titmouse	9	.8125	.0131	22	—	11	33	22	11	—	—
White-eyed vireo	30	.5625	.0918	40	—	23	—	—	—	—	36

^a CC = *Carpinus caroliniana*; FC = *Fraxinus caroliniana*; LS = *Liquidambar styraciflua*; NS = *Nyssa sylvatica*; QL = *Quercus lyrata*; QM = *Quercus michauxii*; TD = *Taxodium distichum*; O = other.

^b Calculated from use sites and 93 random sites in the old-growth study site using the Kolmogrov-Smirnov test.

^c Calculated from use sites and 96 random sites in the second-growth study area using the Kolmogrov-Smirnov test.

reproductive success. Only then can prescriptions be developed to minimize negative impacts of forest management on indigenous avifauna.

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REFERENCES

- Affi, A. A.; Clark, V.** 1990. Computer aided multivariate analysis. New York, NY: Van Nostrand Reinhold Co. 503 p.
- Anonymous.** 1991. North American bird banding. Ontario: Minister of Supply Services. Vol. 1.
- Barton, K.** 1986. Federal wetlands protection programs. In: DiSilvestro, D.L., ed. Audubon Wildlife Report - 1986. New York, NY: Audubon Society: 373-411.
- Beer, J.R.; Fenzel, L.D.; Hanson, N.** 1956. Minimum space requirements of some nesting passerine birds. Wilson Bulletin. 68: 200-209.
- Blake, J.G.; Hoppes, W.G.** 1986. Influence of resource abundance on use of treefall gaps by birds in an isolated woodlot. Auk. 103: 328-340.
- Brewer, R.** 1955. Sizes of home ranges in eight bird species in a southern Illinois swamp thicket. Wilson Bulletin. 67: 140-142.
- Brewer, R.** 1961. Comparative notes on the life history of the Carolina chickadee. Wilson Bulletin. 73: 348-373.

- Chandler, C.R.** 1995. Practical considerations in the use of simultaneous inference for multiple tests. *Animal Behaviour*. 49: 524–527.
- Clairain, E.J.; Kleiss, B.A.** 1988. Functions and values of bottomland hardwood forests along the Cache River, Arkansas: implications for management. In: Hook, D.D.; Lea, R., eds. Proceedings of the symposium the forested wetlands of the Southern United States. Gen. Tech. Rep. SE-50. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: 67–91.
- Cook, J.G.; Stutzman, T.W.; Bowers, C.W. [and others].** 1995. Spherical densimeters produced biased estimates of forest canopy cover. *Wildlife Society Bulletin*. 23(4): 711–717.
- Cottam, G.; Curtis, J.T.** 1956. The use of distance measures in phytosociological sampling. *Ecology*. 37: 451–460.
- Creasman, L.; Craig, N.J.; Swan, M.** 1992. The forested wetlands of the Mississippi River: an ecosystem in crisis. Baton Rouge, LA: The Louisiana Nature Conservancy. 23 p.
- Dickson, J.G.** 1978a. Forest bird communities of the bottomland hardwood forest. In: DeGraaf, R.M., ed. Proceedings of the workshop management of southern forests for nongame birds. Gen. Tech. Rep. SE-14. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: 63–93.
- Dickson, J.G.** 1978b. Seasonal bird populations in a south central Louisiana bottomland hardwood forest. *Journal of Wildlife Management*. 42: 875–883.
- Dickson, J.G.** 1991. Birds and mammals of pre-colonial southern old growth forests. *Natural Areas Journal*. 11: 26–33.
- Dickson, J.G.; Connor, R.N.; Williamson, J.H.** 1983. Snag retention increases bird use in a clearcut. *Journal of Wildlife Management*. 47: 799–804.
- Ehrlich, P.R.; Dobkin, D.S.; Wheye, D.** 1988. The birders handbook: a field guide to the natural history of North American birds. New York: Simon and Schuster. 784 p.
- Emlen, J.T.; Dejong, M.J.; Jaeger, M.J. [and others].** 1986. Density trends and range boundary constraints along a latitudinal gradient. *Auk*. 103: 791–803.
- Ernst, J.P.; Brown, V.** 1989. Conserving endangered species on southern forested wetlands. In: Hook, D.D.; Lea, R. eds. Proceedings of the symposium the forested wetlands of the Southern United States. Gen. Tech. Rep. SE-50. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: 135–145.
- Ford, R. P.** 1990. Habitat relationships of breeding birds and wintering birds in forested wetlands of west Tennessee. Knoxville, TN: University of Tennessee. 129 p. M.S. thesis.
- Freemark, K.; Collins, B.** 1992. Landscape ecology of breeding birds in temperate forest fragments. In: Hagan, J.M.; Johnston, D.W., eds. Ecology and conservation of neotropical migrant landbirds. Washington, D.C: Smithsonian Institution Press: 443–454.
- Hamel, P.B.** 1989. Breeding bird populations on the Congaree Swamp National Monument, South Carolina. In: Sharitz, R.R.; Gibbons, J.W., eds. Freshwater wetlands and wildlife; 1989; Oak Ridge, TN. Conference 8603101, DOE Symposium Series No. 61. Oak Ridge, TN: U.S. Department of Energy, Office of Scientific and Technical Information: 617–628.
- Hamel, P.B.; Cooper, R.J.; Smith, W.P.** 1998. The uncertain future for cerulean warblers in the Mississippi Alluvial Valley. In: Proceedings of conference The Delta: Connecting points of view for sustainable natural resources; 1996 August 13-16; Memphis, TN. Madison, MS: U.S. Department of Agriculture, Natural Resources Conservation Service: 95–109.
- Holder, T.H.** 1970. Disappearing wetlands in eastern Arkansas. Little Rock, AR: Arkansas Planning Commission. 72 p.
- Holmes, R.T.; Sherry, T.W.** 1992. Site fidelity of migratory warblers in temperate breeding and neotropical wintering areas: implications for population dynamics, habitat selection, and conservation. In: Hagan, J.M.; Johnston, D.W., eds. Ecology and conservation of neotropical migrant landbirds. Washington, D.C: Smithsonian Institution Press: 408–418.
- International Bird Census Committee.** 1970. An international standard for a mapping method in bird census work recommended by the International Bird Census Committee. *Audubon Field Notes*. 24: 722–726.
- James, D.A.; Neal, J.C.** 1986. Arkansas birds. Fayetteville, AR: University of Arkansas Press. 402 p.
- James, F.C.** 1971. Ordinations of habitat relationships among breeding birds. *Wilson Bulletin*. 83: 215–236.
- James, F.C.; Wamer, N.O.** 1982. Relationships between temperate forest bird communities and vegetation structure. *Ecology*. 63: 159–171.
- Juday, G.P.** 1988. Old growth forests and natural areas: an introduction. *Natural Areas Journal*. 8: 3–6.
- Kennedy, R.S.** 1977. Ecological analysis and population estimates of the birds of the Atchafalaya River Basin in Louisiana. Baton Rouge, LA: Louisiana State University. 201 p. Ph.D. dissertation.
- Kleinbaum, D.G.; Kupper, L.L.; Muller, K.E.** 1988. Applied regression and other multivariable methods. Boston, MA: PWS-Kent Publishing Company. 718 p.
- Kroodsma, R.L.** 1984. Effect of edge on breeding forest bird species. *Wilson Bulletin*. 96: 426–436.
- Lemmon, P.E.** 1956. A spherical densimeter for estimating forest overstory density. *Forest Science*. 2: 314–320.
- MacArthur, R.H.; MacArthur, J.W.** 1961. On bird species diversity. *Ecology*. 42: 594–598.
- MacDonald, P.O.; Frayer, W.E.; Clauser, J.K.** 1979. Documentation, chronology, and future projections of bottomland hardwood habitat loss in the lower Mississippi Alluvial Plain. State College, PA: HRB Singer, Inc. Vol.1.
- Mannan, R.W.; Morrison, M.L.; Meslow, E.C.** 1984. The use of guilds in forest bird management. *Wildlife Society Bulletin*. 12: 426–430.
- Martin, T.E.** 1992. Breeding productivity considerations: what are the appropriate habitat features for management. In: Hagan, J.M.; Johnston, D.W., eds. Ecology and conservation of neotropical migrant landbirds. Washington, D.C.: Smithsonian Institution Press: 443–454.
- Mohr, C.O.** 1947. Table of equivalent populations of North American small mammals. *American Midland Naturalist*. 37: 223–249.

- Morse, D.H.** 1985. Habitat selection in North American Parulid warblers. In: Cody, M.L. ed. *Habitat selection in birds*. Orlando, FL: Academic Press: 131–157.
- Murphy, P.A.** 1975. Louisiana forests: status and outlook. *Resour. Bull. SO-53*. New Orleans, LA: U.S. Department of Agriculture, Forest Service. Southern Forest Experiment Station. 12 p.
- Neu, C.W.; Byers, C.R.; Peck, J.M.** 1974. A technique for analysis of utilization-availability data. *Journal of Wildlife Management*. 38: 541–545.
- Noss, R.F.** 1988. Effects of edge and internal patchiness on habitat use by birds in a Florida hardwood forest. Gainesville, FL: University of Florida. 109 p. Ph.D. dissertation.
- Noss, R.F.** 1991. Effects of edge and internal patchiness on avian habitat use in an old growth Florida hammock. *Natural Areas Journal*. 11: 34–47.
- Nudds, T.D.** 1977. Quantifying the vegetation cover of wildlife structure. *Wildlife Society Bulletin*. 5: 113–117.
- Robbins, C.S.; Sauer, J.R.; Greenberg, R.S.; Droege, S.** 1989. Population declines in birds that migrate to the Neotropics. *Proceedings of the National Academy of Science*. 86: 7658–7662.
- Rudis, V.A.; Birdsey, R.A.** 1986. Forest resource trends and current conditions in the Lower Mississippi Valley. *Resour. Bull. SO-116*. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station. 7 p.
- Runkle, J.R.** 1982. Patterns of disturbance in some old-growth mesic forests of Eastern North America. *Ecology*. 63(5): 1533–1546.
- Runkle, J.R.** 1991. Gap dynamics of old-growth eastern forests: management implications. *North America. Natural Areas Journal*. 11(1): 19–25.
- Shannon, C.E.; Weaver, W.** 1949. *The mathematical theory of communication*. Urbana, IL: University of Illinois Press. 177 p.
- Shapiro, S.S.; Wilk, M.B.** 1965. An analysis of variance test for normality. *Biometrika*. 52: 591–611.
- Sharitz, R.R.; Boring, L.R.; Van Lear, D.H.; Pinder, J.E.** 1992. Integrating ecological concepts with natural resource management of southern forests. *Ecological Applications*. 2: 226–237.
- Sharpe, G.W.; Hendee, C.W.; Sharpe, W.F.** 1986. *Introduction to forestry*. New York, NY: McGraw-Hill Book Co. 629 p.
- Shugart, H.H.; James, D.** 1973. Ecological succession in breeding bird populations in northeast Arkansas. *Auk*. 90: 62–77.
- Smith, K.G.** 1977. Distribution of summer birds along a forest moisture gradient in an Ozark watershed. *Ecology*. 58: 810–819.
- Smith, W.P.; Devall, R.M.; Parresol, B.R.** 1995. Windthrow gaps, herbivory, and diversity of old-growth bottomland hardwood forests. Completion Report, Challenge Cost-Share Agreement 19-90-045. Stoneville, MS: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station. 123 p.
- Smith, W.P.; Hamel, P.B.; Ford, R.P.** 1993a. Mississippi Alluvial Valley forest conversion: implications for Eastern North America. *Proceedings of the Southeastern Association of Fish and Wildlife Agencies*. 47: 460–469.
- Smith, W.P.; Townley, W.K.; Hunt, H.E.** 1993b. Neotropical migrant songbird breeding behavior and ecology relative to disturbance in bottomland hardwood forests. Completion Report Challenge Cost-Share Agreement No. 19-90-045. Stoneville, MS: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station. 102 p.
- Swift, B.L.; Larson, J.S.; DeGraff, R.M.** 1984. Relationship of breeding bird density and diversity to habitat variables in forested wetlands. *Wilson Bulletin*. 96: 48–59.
- Thomas, J.W.** 1979. Wildlife habitat in managed forests: the Blue Mountains of Oregon and Washington. *Agric. Handb. No. 553*. Washington, D.C.: U.S. Department of Agriculture, Forest Service. 512 p.
- Thomas, J.W.; Ruggiero, L.F.; Mannan, R.W. [and others].** 1988. Management and conservation of old growth forests in the United States. *Wildlife Society Bulletin*. 16: 252–262.
- Thompson, F.R.; Dijak, W.D.; Kulowiec, T.G.; Hamilton, D.A.** 1992. Breeding bird populations in Missouri Ozark forests with and without clearcutting. *Journal of Wildlife Management*. 56: 23–29.
- Turner, R.E.; Forsythe, S.W.; Craig, N.J.** 1981. Bottomland hardwood forest land resources of the Southeastern United States. In: Clark, J.R.; Benforado, J., eds. *Wetlands of bottomland hardwood forests*. Proceedings of a workshop on bottomland hardwood forest wetlands of the Southeastern United States; 1980 June 1-5; Lake Lanier, GA. *Developments in Agricultural and Managed-forest*. *Ecology* 11:13–28.
- Urban, D.L.; Smith, T.M.** 1989. Microhabitat patterns and the structure of forest bird communities. *American Naturalist*. 133: 811–829.
- Wilcove, D.S.** 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology*. 66: 1211–1214.
- Wright, S.P.** 1992. Adjusted *P*-values for simultaneous inference. *Biometrics*. 48: 1005–1013.
- Zar, J. H.** 1984. *Biostatistical analysis*. Prentice Hall Inc., Englewood Cliffs, NJ: Prentice-Hall, Inc. 718 p.
- Zollner, P. A.** 1993. Ecology of the swamp rabbit in south-central Arkansas. Mississippi State, MS: Mississippi State University. 163 p. M.S. thesis.