Avian Response to Bottomland Hardwood Reforestation: The First 10 Years

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Abstract

Bottomland hardwood forests were planted on agricultural fields in Mississippi and Louisiana predominantly using either *Quercus* species (oaks) or *Populus deltoides* (eastern cottonwood). We assessed avian colonization of these reforested sites between 2 and 10 years after planting. Rapid vertical growth of cottonwoods (circa 2–3 m/year) resulted in sites with forest structure that supported greater species richness of breeding birds, increased Shannon diversity indices, and supported greater territory densities than on sites planted with slower-growing oak species. Grassland birds (*Spiza americana* [Dickcissel] and *Sturnella magna* [Eastern Meadowlark]) were indicative of species breeding on oak-dominated reforestation no more than 10 years old. *Agelaius phoeniceus* (Red-winged Blackbird) and *Colinus virginianus* (Northern Bobwhite) characterized cottonwood reforestation no more than 4 years old, whereas 14 species of shrub-scrub birds (e.g., *Passerina cyanea* [Indigo Bunting]) and early-successional forest birds (e.g., *Vireo gilvus* [Warbling vireo]) typified cottonwood reforestation 5 to 9 years after planting. Rates of daily nest survival did not differ between reforestation strategies. Nest parasitism increased markedly in older cottonwood stands but was overwhelmed by predation as a cause of nest failure. Based on Partners in Flight prioritization scores and territory densities, the value of cottonwood reforestation for avian conservation was significantly greater than that of oak reforestation during their first 10 years. Because of benefits conferred on breeding birds, we recommend reforestation of bottomland hardwoods should include a high proportion of fast-growing early successional species such as cottonwood.

Key words: birds, bottomland, colonization, density, forest, hardwood, Neotropical migrants, reforestation, restoration.

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Introduction

The vast expanse of bottomland hardwood forest historically found within the Mississippi Alluvial Valley has been reduced to less than 25% of its original area (Twedt & Loesch 1999). Most of this forest loss resulted from flood control projects that made possible the conversion of forested wetlands to agricultural production. However, hardwood forest destruction in this floodplain is not uniquely anthropogenic. Indeed, forests have been continually destroyed concomitant with erosion and deposition cycles of the Mississippi River and its tributaries (Saucier 1994). Primary succession on consolidated river deposits concurrently renewed these bottomland hardwood forests beginning with colonization by *Populus deltoides* (eastern cottonwood) or *Salix nigra* (black willow, Hodges 1997). These temporary pioneer forest types are short-lived and are replaced by riverfront forests dominated by *Platanus occidentalis* (American sycamore), *Carya illinoensis* (sweet pecan), *Fraxinus pennsylvanica* (green ash), *Ulmus americana* (American elm), and *Celtis laevigata* (sugarberry). Seasonally wet oak-hardwood forests, dominated by *Liquidambar styraciflua* (sweetgum) and *Quercus* species (oaks), typically succeed riverfront forests (Kennedy & Nowacki 1997).

Landscape level conservation plans (Loesch et al. 1994; Mueller et al. 2000) proposed habitat objectives for migratory bird conservation that substantially increase forest area in the Mississippi Alluvial Valley. However, because of altered riverine hydrology (e.g., levees, revetments, etc.) currently only very limited areas are subject to primary succession on newly formed land. Thus, most of the proposed increase in forest area must result from reforestation of former forests that are currently in agricultural production. On public lands reforestation in support of forest habitat objectives has been spearheaded by the U.S. Fish and Wildlife Service (Haynes et al. 1995) and state wildlife conservation agencies (Savage et al. 1989). However, because nearly 90% of this vast floodplain is privately owned, reforestation on private lands is essential to achieve conservation goals.

To enlist the cooperation of private landowners, reforestation must be economically attractive. One economic incentive is public–private partnerships such as the conservation programs developed by the U.S. Department of Agriculture (e.g., Conservation Reserve Program and Wetland Reserve Program). Using reforestation strategies developed by public conservation agencies, these programs have made remarkable progress toward restoring marginal agricultural lands to forested wetlands, with more than 100,000 ha expected to be restored within the Mississippi Alluvial Valley (Stanturf et al. 1998).

Nearly 80% of the area reforested on public lands and under conservation partnerships within the Mississippi Alluvial Valley were planted using heavy-seeded oak and pecan species (King & Keeland 1999). These heavy-seeded species were planted because of their presumed restricted seed dispersal, their mast production for wildlife (Haynes & Moore 1988), and high timber value (Meadows & Stanturf 1997).

An alternative reason for converting cropland to hardwood forest, albeit less widely practiced, is for production of pulpwood and biofuels (Land et al. 1996). These intensively managed plantations emphasize fast-growing early successional tree species such as cottonwood, willow, sycamore, and sweetgum. Financial return from short-rotation harvests of these forests can be sufficient to warrant conversion of marginal agricultural lands to agroforest production (Strauss & Wright 1991; Amacher et al. 1998). As such, current projections estimate that production of short-rotation woody crops in the southeastern United States would increase from 12,000 ha in 1995 to more than 27,000 ha by the year 2000 (Land et al. 1996). Because lack of short-term financial return can inhibit restoration of former bottomland forests, partial harvest of trees planted for pulpwood can provide the short-term financial incentive required for long-term conversion from agriculture to managed hardwood forest (Twedt & Portwood 1997).

A landowner's reasons for reforestation often dictate which silvicultural practices are used, especially with regard to tree species planted within the restrictions that are imposed by soil type and site hydrology (Baker & Broadfoot 1979). Thus, reforestation to provide forest habitat for specific wildlife species (e.g., deer) may result in a markedly different developing forest than reforestation to produce merchantable forest products from short-rotation harvests. These differences in forest structure and the temporal development of different tree species are likely to impact avian communities colonizing reforested sites. Differential use of reforested sites may conceivably influence attainment of avian population goals, which are currently based solely on area-dependent habitat objectives.

To assess avian response to different strategies of reforestation in the Mississippi Alluvial Valley, we determined avian species richness, Shannon diversity indices, and territory densities of breeding birds on reforested sites within 10 years of planting. We chose to examine richness, diversity, and abundance under the assumption that supporting more bird numbers and species is one measure of the reforested habitat's suitability. However, because more diverse and abundant avifauna might not reflect the habitat's suitability for avian reproduction, we also located and monitored nests of breeding birds to determine nest survival rates. Of particular interest were potential differences in avian colonization between reforestation that emphasized heavy-seeded mast-producing trees, as is typical for wildlife management objectives, and reforestation focused on fast-growing trees for production of pulpwood.

Study Areas

Twenty reforested stands (aged 2–10 years) were selected for study within Issaquena County, Mississippi and Madison Parish, Louisiana; all study sites were within a 28-km radius of a point (32° 30′ N, 91° 09′ W) northeast of Tallulah, Louisiana. This landscape was a matrix of forest and agriculture that contained 36% forest cover. Mean area of study stands was 48.9 ± 6.2 (± SE; range = 28–140) ha. All stands were adjacent to or within a contiguous forested matrix containing mature bottomland hardwood forests. Reforestation was undertaken following recommended silvicultural methodologies (Stanturf et al. 1998).

Five stands, planted predominantly with *Quercus nigra* (water oak), *Q. phellos* (willow oak), and *Q. nuttallii* (Nuttall oak), were direct seeded at 8–17 kg acorns/ha. Two stands, planted predominantly with oaks and green ash, were planted using 1-year-old bareroot seedlings. Pecan was a minor component of some direct-seeded stands but constituted nearly 30% of planted seedlings in one stand.

Eleven cottonwood stands were planted using 38-cm stem cuttings, whereas 2 cottonwood stands were regenerated from root sprouts (coppice) after complete harvest for pulpwood. One of the planted cottonwood stands was "underplanted" with oak and green ash seedlings when cottonwood stem cuttings were 2 years old (Twedt & Portwood 1997).

Stem cuttings, seedlings, and coppice regrowth were spaced every 3.7 m (circa 730 stems/ha). All sites were subject to minor seasonal flooding, but four cottonwood stands were not protected by levees and experienced deep-water (>2 m) flooding during winter.

Methods

Within each reforested stand we established a 13.5-ha study plot that was flagged at strategic coordinate locations (50- or 100-m intervals) to facilitate accurate recording of bird locations. Between late April and early July 1996 and 1997 we conducted 28 avian surveys (consisting of 218 stand visits) on study plots using Breeding Bird Census methodology (Svensson et al. 1970). Twelve study plots were surveyed during only 1 year, whereas 8 study plots were surveyed both years. From each survey we determined species richness and a Shannon diversity index. Additionally, we estimated territory density of breeding birds from spot mapping associated with Breeding Bird Censuses. We excluded species assigned "visitor" or nonbreeding status on Breeding Bird Censuses. Territory densities were expressed as number of territories per 100 ha. Nest survival, nest predation, and parasitism rates were determined by locating and revisiting nests at 3- or 4-day intervals following recommended protocols to assess nest fates (Martin & Geupel 1993; Ralph et al. 1993).

Mean number of tree species, maximum tree height, and woody stem density were assessed on reforested stands using an average of 7.0 ± 0.8, systematically located, 0.04-ha circular plots (James & Shugart 1970). Mean vegetation density was estimated at ground level, 2.5 m, and 5 m from four readings of a 0.25-m^2 lateral cover density board (Thomson 1975); readings were taken in cardinal directions at a distance of 11.3 m from plot centers. Vegetative cover was the proportion of 10 × 10–cm squares that were more than 50% obscured, for a maximum value of 1.0 (25 squares × 4 readings). Similarly, angular canopy cover (Nuttle 1997a) was obtained as the mean of four measurements at 11.3 m from plot centers using a concave spherical densiometer (Model C, Forest Densiometers, Bartlesville, OK, U.S.A.).

Statistical Analysis

We compared species richness, Shannon diversity, and total territory density of breeding birds between cottonwood ($n = 13$) and oak-dominated ($n = 7$) reforestation using Mann-Whitney U tests. For stands surveyed both years, mean stand values for these statistics were computed for use in Mann-Whitney tests. To relate measured habitat variables to the bird community within surveyed stands, we used canonical correspondence analysis (CCA) (Ter Braak 1986). We used a clustering algorithm (unweighted pair-group method using arithmetic means) on bird territory densities to confirm apparent stand groupings identified in CCA.

We compared bird territory densities from this study with similar data from other studies within the Mississippi Alluvial Valley. Breeding Bird Census data were obtained from six stands planted with cottonwood (Tomlinson 1977), and comparable avian densities were extrapolated from point count data presented by Nuttle (1997b) for reforested oak stands that were less than 4 years old, 7 to 15 years old, and 21 to 27 years old. Because comparable habitat data were not available for these other sites, we subjected these data to detrended correspondence analysis (DCA) (Hill & Gauch 1980).

Indicator species analysis (Dufréne & Legendre 1997) that combined relative abundance and frequency of occurrence was used to assess species affinities for stand groupings identified from CCA and cluster analysis. Finally, we calculated a relative bird conservation value for each stand and compared these values among stand groupings. Conservation values were derived by combining mean territory density for each species (territories/100 ha) and its respective Partners in Flight (PIF) prioritization score (Colorado Bird Observatory 1998; Carter et al. 2000) within the Mississippi Alluvial Valley as

$$\text{Conservation value} = \sum \frac{\text{territory density} \cdot \text{prioritization score}}{100}$$

Estimates of daily nest survival were calculated (Mayfield 1961, 1975) and their associated variances derived (Hensler & Nichols 1981). We compared daily nest survival of all nests combined and for *Agelaius phoeniceus* (Red-winged blackbird) nests among stand groupings using program CONTRAST (Hines & Sauer 1989; Sauer & Williams 1989).

Results

We detected a total of 48 bird species holding territories or parts of territories in reforested stands (Table 1). Species richness (S) was greater in cottonwood stands ($S = 16.7 \pm 1.2$; $p < 0.01$) than in oak-dominated stands ($S = 8.1 \pm 1.1$). Similarly, territory density, summed over all bird species, was greater in cottonwood stands (412 ± 28) than in oak stands (257 ± 31; $p < 0.01$), and cottonwoods yielded greater Shannon diversity indices (H) ($H = 2.25 \pm 0.09$; $p < 0.01$) than did oaks ($H = 1.52 \pm 0.16$).

The relationship between vegetation and bird territory densities was effectively identified using CCA. In relating habitat characteristics (Table 2) to avian communities, both the first and second canonical axes were correlated ($r > 0.87$; $p \leqslant 0.01$) with measured habitat variables and accounted for 43% of the variation in species territorial abundance. Reforested sites were separated along the first canonical axis (Fig. 1) primarily by maximum tree height ($r = 0.96$) and canopy cover ($r = 0.80$). Separation along the second axis (Fig. 1) was primarily attributed to the contrast between density of

Table 1. Territory density, species richness, Shannon diversity index, conservation value, Partners in Flight prioritization score (PIF-PS; range, 0–35), and number of territories per 100 ha for birds breeding on reforested sites within Issaquena County, Mississippi and Madison Parish, Louisiana during 1996 and 1997.

			4- to 10-Year-Old Oak Dominated[a] (n = 7)	*2- to 4-Year-Old Cottonwood*[a] (n = 6)	*5- to 9-Year-Old Cottonwood*[a] (n = 7)
Total territory density			257.3 ± 30.8	380 ± 29.4	449.1 ± 47.7
Species richness			8.1 ± 1.1	14.1 ± 1.3	19.7 ± 1.5
Shannon diversity			1.5 ± 0.1	2.0 ± 0.1	2.5 ± 0.1
Conservation value[b]			43.0 ± 5.5	60.2 ± 6.6	75.8 ± 7.9
Conservation value[b] (considering only species with PIF-PS ≥ 20)			22.0 ± 3.1	18.9 ± 5.1	30.6 ± 3.5
Species	*Scientific Name*	*PIF-PS*			
Green Heron	*Butorides striatus*	14	0.0 ± 0.0	0.6 ± 0.6	0.0 ± 0.0
Wild Turkey	*Meleagris gallopavo*	18	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0
Northern Bobwhite[c]	*Colinus virginianus*	20	0.0 ± 0.0	5.8 ± 2.4	2.1 ± 1.2
Mourning Dove	*Zenaida macroura*	14	13.0 ± 4.4	19.4 ± 8.5	1.7 ± 1.1
Yellow-billed Cuckoo	*Coccyzus americanus*	22	1.6 ± 1.6	8.3 ± 3.5	7.3 ± 1.3
Eastern screech Owl	*Otus asio*	17	0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0
Barred Owl	*Strix varia*	16	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.3
Ruby-throated Hummingbird	*Archilochus colubris*	19	2.3 ± 1.1	2.2 ± 1.0	8.5 ± 1.3
Red-bellied Woodpecker	*Melanerpes carolinus*	17	0.0 ± 0.0	0.2 ± 0.2	4.1 ± 1.2
Downy Woodpecker[d]	*Picoides pubescens*	14	0.0 ± 0.0	0.1 ± 0.1	6.6 ± 1.7
Hairy Woodpecker	*Picoides villosus*	14	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.3
Eastern Wood-pewee[d]	*Contopus virens*	20	0.0 ± 0.0	0.1 ± 0.1	8.2 ± 2.2
Acadian Flycatcher[d]	*Empidonax virescens*	20	0.0 ± 0.0	0.6 ± 0.6	11.3 ± 4.2
Great-crested Flycatcher	*Myiarchus crinitus*	16	0.0 ± 0.0	0.1 ± 0.1	0.2 ± 0.2
Eastern Kingbird	*Tyrannus tyrannus*	18	0.0 ± 0.0	0.1 ± 0.0	0.0 ± 0.0
Loggerhead Shrike	*Lanius ludovicianus*	19	0.0 ± 0.0	1.2 ± 1.2	0.0 ± 0.0
White-eyed Vireo[d]	*Vireo griseus*	22	0.0 ± 0.0	0.0 ± 0.0	9.0 ± 3.9
Bell's Vireo	*Vireo bellii*	23	0.0 ± 0.0	1.2 ± 1.2	0.0 ± 0.0
Yellow-throated Vireo	*Vireo flavifrons*	19	0.0 ± 0.0	0.1 ± 0.1	1.6 ± 1.1
Warbling Vireo[d]	*Vireo gilvus*	16	0.0 ± 0.0	16.3 ± 8.0	22.2 ± 6.3
Red-eyed Vireo	*Vireo olivaceus*	15	0.0 ± 0.0	0.0 ± 0.1	0.6 ± 0.5
Blue Jay	*Cyanocitta cristata*	13	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0
Carolina Chickadee[d]	*Poecile carolinensis*	20	0.0 ± 0.0	0.0 ± 0.0	10.4 ± 3.3
Tufted Titmouse[d]	*Baeolophus bicolor*	14	0.0 ± 0.0	0.1 ± 0.1	3.3 ± 1.3
Carolina Wren[d]	*Thryothorus ludovicianus*	17	0.2 ± 0.2	1.8 ± 1.3	15.8 ± 4.0
Blue-gray Gnatcatcher[d]	*Polioptila caerulea*	19	0.0 ± 0.0	0.3 ± 0.3	14.2 ± 5.7
Eastern Bluebird	*Sialia sialis*	14	0.0 ± 0.0	3.8 ± 2.5	0.2 ± 0.2
Wood Thrush	*Hylocichla mustelina*	22	0.0 ± 0.0	0.0 ± 0.0	0.6 ± 0.3
Northern Mockingbird	*Mimus polyglottos*	14	0.4 ± 0.3	4.3 ± 4.3	0.0 ± 0.0
Brown Thrasher	*Toxostoma rufum*	17	0.0 ± 0.0	0.6 ± 0.6	0.0 ± 0.0
Prothonotary Warbler	*Protonotaria citrea*	24	0.0 ± 0.0	1.2 ± 1.2	5.6 ± 4.6
Swainson's Warbler	*Limnothlypis swainsonii*	29	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.5
Kentucky Warbler	*Oporornis formosus*	22	0.0 ± 0.0	0.0 ± 0.0	1.1 ± 0.7
Common Yellowthroat	*Geothlypis trichas*	16	17.7 ± 6.6	12.8 ± 7.1	9.3 ± 6.6
Yellow-breasted Chat	*Icteria virens*	21	16.9 ± 8.7	11.6 ± 9.0	48.5 ± 17.5
Summer Tanager[d]	*Piranga rubra*	18	0.0 ± 0.0	0.0 ± 0.0	0.6 ± 0.2
Eastern Towhee	*Pipilo erythrophthalmus*	15	1.2 ± 1.0	8.1 ± 4.1	24.2 ± 9.6
Northern Cardinal[d]	*Cardinalis cardinalis*	12	4.2 ± 2.6	28.5 ± 4.3	59.5 ± 6.6
Blue Grosbeak	*Guiraca caerulea*	16	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0
Indigo Bunting[d]	*Passerina cyanea*	18	14.8 ± 8.8	54.0 ± 9.6	75.3 ± 6.2
Painted Bunting	*Passerina ciris*	24	0.7 ± 0.5	0.0 ± 0.0	0.1 ± 0.1
Dickcissel[e]	*Spiza americana*	21	47.9 ± 9.2	11.6 ± 7.9	0.0 ± 0.0
Red-winged Blackbird[c]	*Agelaius phoeniceus*	12	87.6 ± 8.5	125.0 ± 13.6	3.5 ± 1.2
Eastern Meadowlark[e]	*Sturnella magna*	17	8.1 ± 3.9	0.0 ± 0.0	0.0 ± 0.0
Common Grackle	*Quiscalus quiscula*	16	1.0 ± 1.0	1.8 ± 0.8	1.8 ± 1.1
Brown-headed Cowbird[d]	*Molothrus ater*	13	2.1 ± 1.4	11.1 ± 3.0	35.1 ± 4.7
Orchard Oriole	*Icterus spurius*	22	10.2 ± 4.5	17.0 ± 4.8	16.4 ± 5.5
Baltimore Oriole	*Icterus gallbula*	20	0.0 ± 0.0	33.0 ± 13.4	24.8 ± 6.6

Species are listed in taxonomic order (American Ornithological Union, *http://www.aou.org/aou/birdlist.html*).
[a]Values are means ± SE.

[b] Conservation value $= \sum \frac{\text{Territory density} \bullet \text{Prioritization score}}{100}$.

[c]Species indicative ($p \leq 0.01$) of 2- to 4-year-old cottonwood sites.
[d]Species indicative ($p \leq 0.01$) of 5- to 9-year-old cottonwood sites.
[e]Species indicative ($p \leq 0.01$) of 4- to 10-year-old oak-dominated sites.

Table 2. Vegetative characteristics on reforested stands planted predominantly with oaks or cottonwood within the Mississippi Alluvial Valley in Mississippi and Louisiana.

	Oak (ages 4–10) n = 7	*Cottonwood (ages 2–4)* n = 6	*Cottonwood (ages 5–9)* n = 7
Maximum tree height (m)	3.69 ± 0.94	8.11 ± 1.18	15.33 ± 0.92
Number of tree species/0.04 ha	4.82 ± 0.63	4.82 ± 0.13	2.24 ± 0.55
Number of stems/ha	1941 ± 819	714 ± 78	984 ± 103
Vegetation density at ground	0.98 ± 0.01	0.85 ± 0.04	0.89 ± 0.05
Vegetation density at 2.5 m	0.19 ± 0.03	0.60 ± 0.08	0.40 ± 0.12
Vegetation density at 5 m	0.05 ± 0.04	0.53 ± 0.07	0.17 ± 0.05
Angular canopy cover	0.05 ± 0.02	0.62 ± 0.07	0.72 ± 0.04

Values are means ± SE. Vegetation density is the proportion (range, 0–1) of 10 × 10–cm squares that were more than 50% obscured from four readings of a 0.25-m^2 lateral cover density board (Thomson 1975) at a distance of 11.3 m. Canopy cover is the proportion (range, 0–1) of sky obscured by vegetation using a spherical densiometer (Nuttle 1997a).

vegetation at ground level ($r = -0.61$) and vegetation density at heights of 2.5 and 5 m ($r \geq 0.68$).

Thus, oak-dominated stands were located in the lower left quadrant of the CCA axes (Fig. 1), indicative of their relatively short tree heights and dense herbaceous vegetation at ground level. This vegetative structure was supportive of grassland bird species such as *Spiza americana* (Dickcissel) (Fig. 2). Conversely, all cottonwood stands at least 5 years old were clustered on the right edge of the CCA axes (Fig. 1) due to their tall tree heights and more dense canopy cover (Table 2). These habitat characteristics were conducive to colonization by forest birds.

Older cottonwood stands spanned the origin along the second canonical axis, indicating variation in the density of vegetation at ground level and in the midstory, which also impacted avian territory densities. Closer inspection revealed that all reforested sites subject to deep-water flooding were in the upper right quadrant of the canonical axes. Stands subjected to deep-water flooding generally had herbaceous vegetation that was limited to species that initiated growth after floodwater receded; these stands were depauperate of bird species compared with stands with robust understory vegetation.

Younger cottonwood stands, because of their rapid vertical growth (circa 2–3 m/yr), were widely spread along the first canonical axis. Although similarly widespread along the second canonical axis, with one exception, all younger cottonwood stands were above the origin, suggesting low densities of ground vegetation. Lack of vegetation at ground level within these younger cottonwood stands probably resulted from mechanical cultivation to control weeds during the first 2 years after planting and from dense horizontal branching that shaded ground vegetation during their third and fourth growing seasons.

Percent forest cover within 1 km of the study plots varied widely among oak plantings (range, 12–74%) and among cottonwood plantings (range, 14–87%). Because of this high variability forest cover within 1 km of study sites did not differ ($t = 1.52$, $df = 18$, $p = 0.15$) between oak plantings (44 ± 8%) and cottonwood plantings (61 ± 7%).

The three generalized groupings of reforested stands (oak-dominated, ≤4-year-old cottonwood, and ≥5-year-old cottonwood) observed on CCA axes (Fig. 1) were reiterated in the results of cluster analysis based on bird territory densities. Three clusters accounted for 75% of the information on territory density. All oak-dominated stands clustered together and all older (≥5 years old) cottonwood stands were in another cluster. Younger (≤4 years old) cottonwood stands formed the third cluster, with two exceptions: One 2-year-old cottonwood stand clustered with the oak-dominated stands, whereas one 4-year-old cottonwood stand clustered with the older cottonwood stands.

Bird species segregated along the vegetation gradients depicted in the ordination space resulting from CCA (Fig. 2). The first canonical axis depicted grassland species (e.g., Dickcissel) on the left, shrub-scrub species (e.g., *Icterus spurius* [Orchard oriole]) centrally, and forest birds (e.g., *Empidonax virescens* [Acadian Flycatcher]) on the right. Although less distinctly separated, birds were generally distributed along the second canonical axis based on their preference for dense or sparse understory vegetation. Species with lower scores on the second axis generally were associated with dense shrubby understories (e.g., *Vireo griseus* [White-eyed Vireo], *Icteria virens* [Yellow-breasted Chat]). Conversely, species above the axis origin tended to be those that forage in the open (e.g., *Sialia sialis* [Eastern Bluebird], *Lanius ludovicianus* [Loggerhead Shrike]) or in open understories (e.g., *Icterus galbula* [Baltimore Oriole], *Myiarchus crinitus* [Great-crested Flycatcher]).

Within the DCA ordination space that compared data from this study with data from other studies in the Mississippi Alluvial Valley (Fig. 3), oak-dominated stands segregated from cottonwood stands with the exception

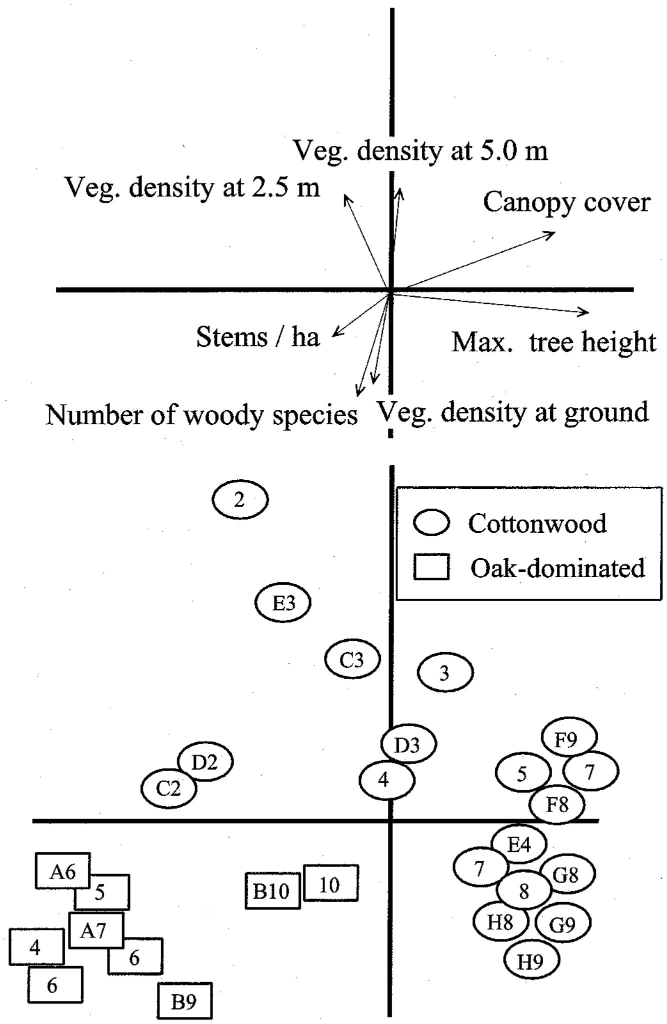

Figure 1. Ordination space generated from the first two axes of canonical correlation analysis relating avian territory density to measured habitat characteristics on reforested sites. Avian densities were from 28 Breeding Bird Censuses conducted during 1996 and 1997. Length and direction of arrows indicate that tree height and canopy cover impact the avian community along the horizontal axis, whereas number of woody species and vegetation density affect community composition along the vertical axis. Thus, stands with tall trees and increased canopy cover (e.g., older cottonwood stands) have high scores on the horizontal axis. Conversely, oak stands with shorter stature and increased vegetation density at ground level are in the lower left quadrant. Ovals represent sites planted predominantly with *Populus deltoides* (eastern cottonwood), whereas rectangles represent sites planted predominantly with *Quercus* species (oaks). The number within figures is the age of the stand, whereas letters uniquely identify stands surveyed both years.

of older (21- to 27-year-old) oak stands. Bird assemblages in these older oak stands were similar to bird communities in 5- to 9-year-old cottonwood stands.

Indicator species analysis identified 18 species as indicative ($p \leq 0.01$) of one of three reforestation stand groupings. Two grassland species, Dickcissel and Eastern Meadowlark, were indicative of oak-dominated stands, whereas Red-winged Blackbird and Northern Bobwhite were indicative of younger cottonwood stands. The remaining 14 species, generally characterized as shrub-scrub species or early-successional forest species, were indicative of older cottonwood stands (Fig. 2).

The relative conservation value for birds differed significantly ($F = 6.21$; $df = 2,17$; $p < 0.01$) among the three stand groupings (Table 1). The conservation values of no more than 10-year-old oak stands (range, 29–66) were less than ($p < 0.01$) those of 5- to 9-year-old cottonwood stands (range, 46–107) but did not differ ($p = 0.09$) from those of younger ($\leq$4 years old) cottonwood stands (range, 42–87). Even though the conservation value of oak plantings was less than that of cottonwoods, a higher proportion of their conservation value was contributed by birds with high PIF priority scores (Table 1). Indeed, over half of the conservation value of oak plantings was contributed by birds with PIF priority scores of at least 20, whereas high priority birds contributed only 41 and 32% of the conservation value of older and younger cottonwood stands, respectively.

We located and monitored 832 nests of 26 species on reforested stands (Table 3). Only Red-winged Blackbird nests were sufficiently abundant within all reforestation strategies to warrant species-specific comparison among stand groupings. Neither daily survival of all nests ($\chi^2 = 1.05$; $df = 2$; $p = 0.59$) nor daily survival of Red-winged Blackbird nests ($\chi^2 = 1.10$; $df = 2$; $p = 0.58$) differed among oak, young cottonwood, and older cottonwood stands (Table 3). Nest parasitism by *Molothrus ater* (Brown-headed Cowbird) was rare in oak stands, where 1% of nests ($n = 152$) were parasitized, and in no more than 4-year-old cottonwood stands, where 3% of nests ($n = 93$) were parasitized. However, in at least 5-year-old cottonwood stands, cowbirds were abundant enough to be considered an indicator species (Table 1), and the percentage of nests parasitized (23%; $n = 580$) markedly increased.

The predation rate for all nests (63%) was virtually identical among oak-dominated stands, no more than 4-year-old cottonwoods, and at least 5-year-old cottonwoods. Frequently, we were unable to discern the identity of depredating species, but one predator, *Solenopsis invicta* (imported fire ant), was implicated in at least 9% of all predation events.

Discussion

Brown-headed Cowbirds were indicative of older cottonwood stands, and 23% of nests within these reforested

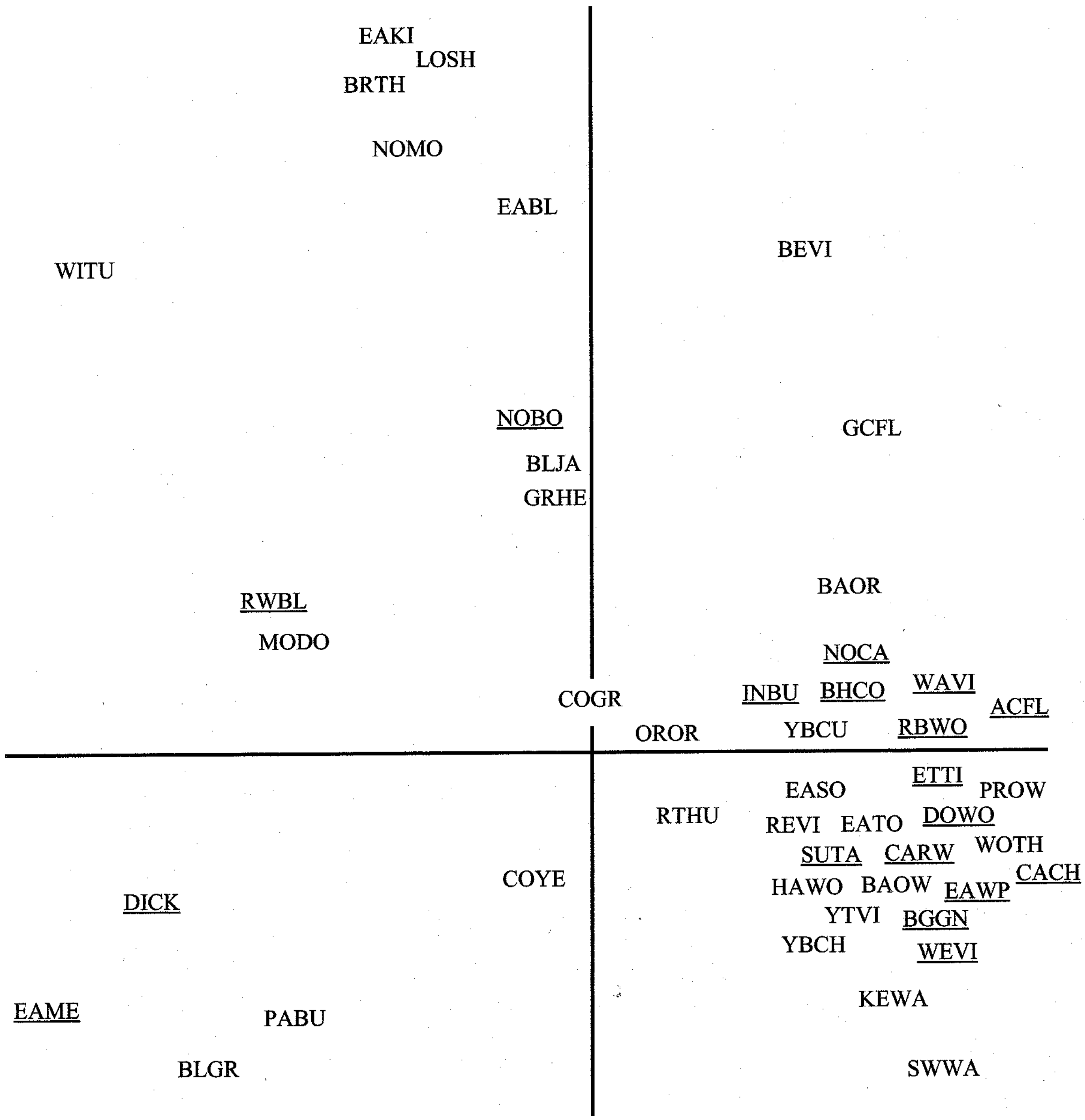

Figure 2. Distribution of avian species (species codes from USGS North American Bird Banding Manual: *www.pwrc.usgs.gov/bbl/manual/aspeclst.htm*) in ordination space generated from the first two axes of canonical correlation analysis relating avian territory density on reforested sites to measured habitat characteristics. Birds at right are characteristic of older (5- to 10-year-old) cottonwood stands, birds at upper left typify younger (≤4-year-old) cottonwood stands, and birds at lower left are found primarily on less than 10-year-old oak stands. Underlined species are indicative (Indicator Species Analysis, $p < 0.01$) of one of three stand groupings (oaks, young cottonwood, or older cottonwood) as identified in Table 1.

stands were parasitized compared with less than 3% of nests parasitized within oak and young (no more than 4-year-old) cottonwood stands. However, even in older cottonwood stands cowbird parasitism was relatively unimportant to overall nest survival because of high (63%) predation rates. High predation rates were the primary factor contributing to overall low nesting success. Low nesting success on both oak and cottonwood sites may indicate these areas function as populations sinks, where reproductive output fails to compensate for mortality. For example, in the oak reforestation stands nesting successes of Red-winged Blackbird (18%) and Dickcissel (25%) were less than nesting successes for these species on sink habitats in Missouri (McCoy et al. 1999).

Although our study stands were all within a 28-km radius circle, reforestation strategies were not randomly assigned to reforested sites. Thus, because all cottonwood stands were in Mississippi differences detected in avian

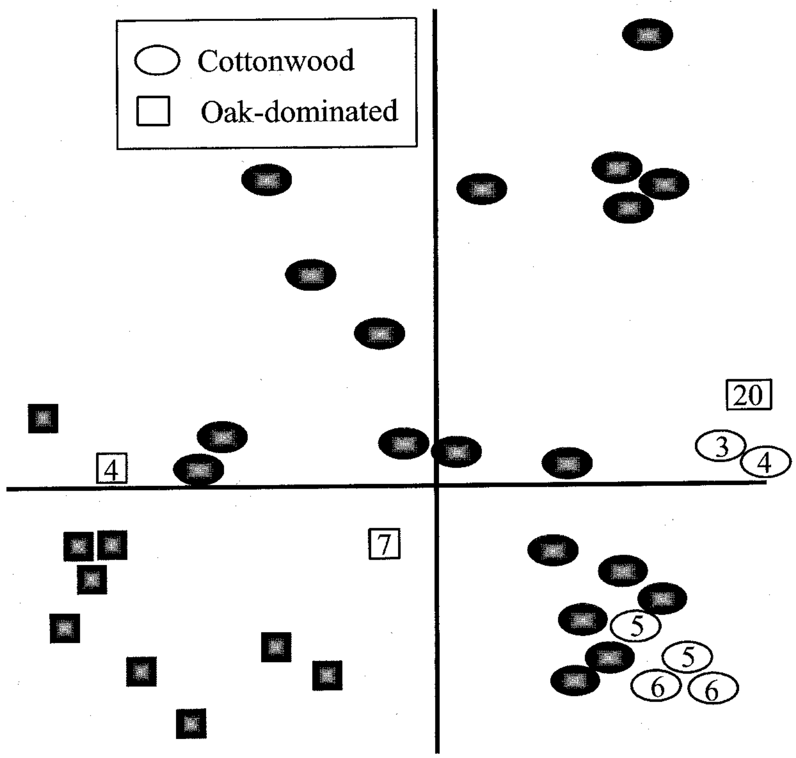

Figure 3. Detrended correspondence analysis ordination space based on territory densities obtained from Breeding Bird Censuses on reforested sites from this study and from data reported by Tomlinson (1977) for *Populus deltoides* (eastern cottonwood) and Nuttle (1997b) for *Quercus* species (oaks). Shaded symbols represent data from this study. Number within open symbols is number of years since planting. The bird communities reported in the literature correspond well with the bird communities we observed on reforested sites, except for the birds on 20-year-old oak plantings, which more closely resemble the avian community on 5- to 10-year-old cottonwood stands.

communities could conceivably be confounded with geographic location. However, the results of CCA and cluster analysis indicted that the oak stands located in Mississippi were similar to those in Louisiana, suggesting that the avian communities on these study plots were not related to their geographic location. Furthermore, when we compared our results with published data on avian densities from other locations in the Mississippi Alluvial Valley, all oak-dominated stands were segregated from cottonwood stands with the exception of more than 20-year-old oak stands. Thus, based on the juxtaposition of our data and data from other published sources within DCA ordination space, we appear justified in our conclusion that reforestation strategy, and not geographic location, accounted for observed differences in avian communities.

During the past two decades reforestation in support of conservation objectives has often been limited to planting oaks and pecan. However, the benefit of planting oaks, instead of other tree species, for conservation of forest songbirds is questionable. As shown by this study, forest bird colonization of reforested sites is closely linked to the development of vertical forest structure (i.e., maximum tree height and canopy cover). Planting entire stands to fast-growing tree species clearly promotes colonization of these sites by forest birds. However, we hypothesize that providing even limited vertical structure on reforested stands, in the form of small patches or rows of fast-growing trees, may enhance colonization by forest birds (Twedt & Wilson 2001).

Avian species richness, Shannon diversity, and total territory density were greater in cottonwood stands than in oak-dominated stands, suggesting that reforestation using cottonwoods is "superior" for conservation of breeding birds during the first 10 years after planting. However, bird species assemblages varied markedly between reforestation strategies and between age classes of cottonwoods, thereby obscuring their value to the conservation of priority bird species. Indeed, although oak-dominated stands had less total conservation value for birds, most of this value was comprised of high priority bird species. Further, they provided the greatest conservation value for any single species (Dickcissel, conservation value = 15.5). However, because most of these higher priority species are typical of grasslands (Hamel 1992), we suspect that similar conservation values would be attained without reforestation, through the process of old-field succession.

Allen (1997) reviewed existing literature on old-field succession within the Mississippi Alluvial Valley and concluded that, in the absence of active reforestation, "tree seedlings begin to establish themselves as early as the first year and gradually increase in number and size such that they become dominant at around the tenth year; after about 25 years, the stand looks like a young forest." Our data indicate that forest birds are not colonizing stands planted with oaks before the tenth year after planting, a time interval similar to when trees begin to dominate stands without reforestation. Nuttle (1997b)

Table 3. Number of nests located (*n*) and mean and SE of daily nest survival (Mayfield 1961, 1975) for birds (scientific names in Table 1) breeding in reforested stands planted with predominantly oak or cottonwood within the Mississippi Alluvial Valley in Mississippi and Louisiana, 1996 and 1997.

	Oak-dominated (ages 4–10)			*Cottonwood (ages 2–4)*			*Cottonwood (ages 5–9)*		
Species	n	*Mean*	*SE*	n	*Mean*	*SE*	n	*Mean*	*SE*
Mourning Dove	16	0.921	0.022	6	0.919	0.045	20	0.914	0.022
Yellow-billed Cuckoo	—	—	—	3	0.714	0.171	15	0.933	0.022
Ruby-throated Hummingbird	—	—	—	—	—	—	7	0.944	0.024
Red-bellied Woodpecker	—	—	—	—	—	—	1	0.941	0.057
Eastern Wood-pewee	—	—	—	—	—	—	3	0.964	0.035
Acadian Flycatcher	—	—	—	—	—	—	5	0.942	0.028
Loggerhead Shrike	—	—	—	1	1.000	0.000	—	—	—
White-eyed Vireo	—	—	—	—	—	—	7	0.968	0.018
Yellow-throated Vireo	—	—	—	—	—	—	1	1.000	0.000
Warbling Vireo	—	—	—	—	—	—	13	0.972	0.011
Carolina Chickadee	—	—	—	—	—	—	1	1.000	0.000
Carolina Wren	—	—	—	—	—	—	6	0.926	0.032
Blue-gray Gnatcatcher	—	—	—	—	—	—	32	0.944	0.013
Brown Thrasher	—	—	—	1	1.000	0.000	—	—	—
Prothonotary Warbler	—	—	—	—	—	—	4	0.950	0.034
Common Yellowthroat	—	—	—	—	—	—	2	0.818	0.116
Yellow-breasted Chat	1	0.800	0.179	—	—	—	142	0.922	0.008
Eastern Towhee	1	1.000	0.000	—	—	—	71	0.926	0.010
Northern Cardinal	—	—	—	6	0.953	0.023	107	0.934	0.007
Indigo Bunting	—	—	—	—	—	—	84	0.919	0.010
Dickcissel	43	0.948	0.011	3	0.850	0.080	—	—	—
Red-winged Blackbird	86	0.934	0.009	68	0.921	0.011	31	0.937	0.013
Eastern Meadowlark	1	0.875	0.117	—	—	—	—	—	—
Common Grackle	—	—	—	—	—	—	1	0.941	0.057
Orchard Oriole	4	0.945	0.031	1	—	—	18	0.944	0.016
Baltimore Oriole	—	—		4	0.939	0.034	16	0.967	0.015
Total Nests	152	0.936	0.006	93	0.925	0.009	587	0.933	0.003

Species are listed in taxonomic order *http://www.aou.org/aou/birdlist.html*

found that the bird community in 21- and 27-year-old stands planted with oaks was similar to the bird community within mature bottomland hardwood forests (Morisita similarity index = 0.88). Not surprisingly, this is the same amount of time (ca. 25 years) at which abandoned fields begin to look like young forests. Although additional research on bird communities colonizing stands without active reforestation (i.e., abandoned fields) is needed, currently there is scant evidence that reforestation using slow-growing tree species benefits songbird conservation more than passive restoration via natural succession of vegetation.

Because of greater abundance of high priority forest bird species, the overall conservation value of cottonwood reforestation significantly exceeded the conservation value of oak-dominated reforestation. Thus, at least for the first 10 years after planting, reforestation using short-rotation early successional tree species clearly provides greater conservation value for breeding bird populations within the Mississippi Alluvial Valley than does reforestation using oaks or similar slow-growing species. The importance of using fast-growing tree species may be especially crucial when private land agreements are not under perpetual easements but are only protected by limited-duration (e.g., 30 years) easements.

Management Recommendations

If reforestation is warranted, we recommend planting a mixture of species that contains predominantly fast-growing early-successional tree species. Thereafter, managers may use silvicultural manipulations to achieve desired tree species composition. Only when the primary objective is to obtain a majority of oaks for timber harvest do we recommend reforestation using predominantly oaks. Planting solely heavy-seeded slow-growing tree species appears to have only limited justification for avian conservation.

Even though stands planted with cottonwood achieve bird assemblages characteristic of young forests in as few as 5 years after planting, many wildlife managers view early-successional species, such as cottonwood, as having limited benefit to wildlife and are reluctant to incorporate these species into planting schemes. Indeed, if cottonwoods are planted for production of pulpwood or biofuels, their value as avian habitats is limited to the time between harvests. Thus, the conservation value of forests managed for long-rotation timber harvest or managed to attain large mature trees (including reforested sites planted predominantly with oaks) will eventually attain and surpass the avian conservation values found in stands managed for short-rotation harvests. However, when fast-growing trees are planted as an integral part of long-rotation management, we believe that avian conservation values are achieved more rapidly and that ecological interactions and complex species-site relationships of forest succession (Hodges 1997) will provide even greater benefits for birds.

Ecologically, cottonwood is relatively short-lived, and because of its intolerance to shade it does not succeed itself (Meadow & Stanturf 1997). Thus, other species, such as sweet pecan, green ash, and sugarberry, will replace cottonwood over time (Johnson 1981). However, markedly increasing the proportion of oaks within these stands may require modified reforestation strategies (Twedt & Portwood 1997), silvicultural techniques such as shelterwood or group selection harvest (Meadows & Stanturf 1997), or possibly controlled burning (Barnes & Van Lear 1998). Ultimately, "the important point is that bottomland red oaks, though greatly outnumbered and quite inconspicuous in many young, even-aged stands, can gradually out-compete the initially dominant pioneer species and eventually dominate the mature stand" (Meadows & Hodges 1997). Thus, we encourage managers, whose reforestation objectives are to attain a high proportion of oaks in the mature forest, to exploit the interrelationships of bottomland hardwood species by planting early-successional species that promote rapid stand development for use by forest songbirds and subsequently to use silvicultural management to achieve their desired stand composition.

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