

# Effects of Selective Logging on Breeding Bird Communities in Bottomland Hardwood Forests in Louisiana

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## Abstract

Bottomland hardwood forests of the southeastern United States support a rich avifauna, including >20 species of conservation concern; understanding the impact of land use practices on these communities is critical to their conservation. Selective timber harvesting is a common management practice in southern bottomland hardwood forests, but little research has examined impacts >5 years after harvesting. We studied breeding bird communities in selectively harvested bottomland forests in northeastern Louisiana during 2003–2004. We conducted point counts in recently harvested stands (1–5 yr postharvest) and older harvests (12–18 yr postharvest); we paired each with a reference stand that had not been harvested for >30 years. Of 35 species with sufficient detections for analysis, we found evidence that abundances of 17 species differed among treatments. Three species were sensitive to creation of canopy openings by timber harvests, including 2 species of concern in the Mississippi Alluvial Valley, USA, prothonotary warbler (*Protonotaria citrea*) and Acadian flycatcher (*Empidonax vireescens*). However, 4 species of concern often associated with densely vegetated canopy gaps were more abundant in older harvests than in reference stands: Swainson's warbler (*Limnothlypis swainsonii*), hooded warbler (*Wilsonia citrina*), white-eyed vireo (*Vireo griseus*), and Kentucky warbler (*Oporornis formosus*). As expected, a suite of species typically associated with shrub and forest-edge habitats was more abundant in recent harvests than in reference stands. We conclude that selective logging has a strong influence on bird abundances in both recent and older harvests in bottomland forests. With the exception of Acadian flycatcher, older harvests and reference stands supported similar abundances of the species typically found in closed-canopy bottomland forests. In addition, older harvests supported substantially higher abundances of gap-dependent species than other treatments. Our results should be useful to land managers and conservation planners evaluating short- and long-term effects of timber management practices on breeding birds in the Mississippi Alluvial Valley. However, measures of breeding productivity are necessary to evaluate more fully the habitat quality of harvested forests. (JOURNAL OF WILDLIFE MANAGEMENT 70(5):1416–1424; 2006)

## Key words

bottomland hardwood forests, canopy gaps, forestry, point counts, silviculture, songbirds, success, timber harvest.

Bottomland hardwood forests were historically the dominant cover type in the Mississippi Alluvial Valley (MAV), USA. However, >80% of bottomland hardwood forests in the MAV have been converted to agricultural and other nonforest uses; remaining forests are highly fragmented (Twedt and Loesch 1999). Logging has occurred in nearly all bottomland forests at least once and virtually no old-growth stands remain (Smith et al. 1993). Old-growth bottomland forests were comprised of a mosaic of stands of different ages due to natural disturbances such as hurricanes, tornadoes, and fire (Hamilton et al., in press). Tree-fall gaps and small group blowdowns created a heterogeneous canopy structure. In contrast, older second-growth stands are comprised of trees of similar size-classes and have a closed-canopy structure with sparse understory vegetation. Selective timber harvesting is a common management practice in southern bottomland forests and provides a sustainable supply of timber, restores bottomland forests to the uneven-aged structure found in old-growth forests, and provides habitat diversity (Meadows and Stanturf 1997). Selective harvesting strategies form a continuum from single-tree selection to group-selection harvests and create

canopy gaps  $\leq 0.50$  ha (Meadows and Stanturf 1997). Over time, canopy gaps created by selective harvests become densely vegetated with saplings, shrubs, vines, and herbaceous vegetation.

More than 70 species of birds breed in bottomland hardwood forests in the southeastern United States (Pashley and Barrow 1993), including >20 species of management concern (Partners in Flight [PIF] 2001). Several priority species, including Swainson's warbler (*Limnothlypis swainsonii*), Kentucky warbler (*Oporornis formosus*), and hooded warbler (*Wilsonia citrina*), are often associated with small gaps in the forest canopy created by tree-fall, particularly 10–25-year-old tree-fall gaps (Pashley and Barrow 1993). Selective timber harvesting increases the availability of densely vegetated canopy gaps and may result in an increased abundance of gap-dependent species (Annand and Thompson 1997, Robinson and Robinson 1999). However, habitat fragmentation caused by timber harvesting may have a negative impact on forest-interior and canopy-nesting species of management concern in southeastern bottomland forests (Pashley and Barrow 1993). Rates of nest predation and brood parasitism by brown-headed cowbirds (*Molothrus ater*) may increase in fragmented forests (Brittingham and Temple 1983, Faaborg et al. 1995), although effects may depend on landscape context (Lahti 2001).

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Researchers have investigated the short-term impacts of selective harvesting on bird communities in bottomland forests (Twedt et al. 1999, Moorman and Gynnn 2001). However, despite the widespread use of selective timber harvesting as a management practice, little research has addressed impacts on bird communities >5 years after timber harvesting since the structure of canopy gaps created by selective harvests changes dramatically over time. As a result, researchers have a poor understanding of the long-term influences of selective timber-harvesting practices on the avian community. These data are critical to conservation planning efforts for avian communities in southern bottomland forests. Our objectives were to assess the relative abundance of breeding birds in recent selective harvests (1–5 yr postharvest), older harvests (12–18 yr postharvest), and reference stands (>30 yr postharvest) in bottomland forests in Louisiana and examine the relationship between avian abundance and habitat structure. Specifically, we evaluated evidence for the influence of selective harvesting on the abundance of forest-interior species, gap-dependent species, brown-headed cowbirds, and avian nest predators.

## Study Area

We conducted this study in 2003 and 2004 on 3 state wildlife management areas (WMAs) located in northeastern Louisiana within the Mississippi Alluvial Valley physiographic region. All 3 WMAs consisted of relatively large blocks of bottomland forest. Big Lake WMA consisted of 7,500 ha in Franklin, Madison, and Tensas parishes (32°10'N, 91°30'W) and formed a contiguous block of forest with the 26,000-ha Tensas River National Wildlife Refuge. Dewey Wills WMA was comprised of 24,000 ha in Catahoula and LaSalle parishes (31°25'N, 91°83'W). Red River and Three Rivers WMAs formed a contiguous 25,000-ha block in Concordia parish (31°15'N, 91°42'W) and we considered them as a single area. The WMAs were islands of bottomland hardwood forest habitat in a predominantly agricultural landscape. All 3 areas were flat, poorly drained, and seasonally flooded by overflow from various rivers, bayous, and lakes.

We selected 24 stands for study distributed evenly across the 3 WMAs, including 12 selectively harvested stands and 12 reference stands not harvested for >30 years. We classified land cover within a 5-km-radius circle of each stand using digital orthophoto quarter-quadrangles with 1-m resolution in ArcGIS 8.2 (Environmental Systems Research Institute, Redlands, California). The Louisiana Department of Wildlife and Fisheries digitized timber-harvest boundaries. Land cover surrounding study plots consisted mainly (64.7 ± 1.9%) of closed-canopy forests that had not been harvested for >30 years. Stands selectively harvested 1–18 years prior to this study comprised 10.9 ± 0.9% of land cover, and agricultural fields and other nonforested areas comprised 24.4 ± 2.5% of land cover. Each WMA contained a similar percentage (7–13%) of forest harvested <19 years prior to this study. We surveyed birds in management units of 53–476 ha, where a combination of individual and group-selection

timber harvests prescribed to enhance wildlife habitat removed approximately 30% of the basal area.

In areas with prolonged flooding (>3 months per yr), forest cover predominantly consisted of overcup oak (*Quercus lyrata*) and water hickory (*Carya aquatica*; Society of American Foresters [SAF] cover type 96; Eyre 1980). On areas with less prolonged flooding (1–3 months/yr), forests were composed of sugarberry (*Celtis laevigata*), American elm (*Ulmus americana*), and green ash (*Fraxinus pennsylvanica*; SAF cover type 93; Eyre 1980). On ridges, forests were comprised mostly of sweetgum (*Liquidambar styraciflua*) and willow oak (*Q. p.*; SAF cover type 92; Eyre 1980). On drier sites, the understory and midstory layers were highly developed and contained seedlings and saplings of canopy trees, shrubs, vines, deciduous holly (*Ilex decidua*), hawthorn (*Crataegus* spp.), and palmetto (*Sabal minor*). In areas with prolonged flooding, the understory was poorly developed.

## Methods

### Bird Surveys

We used point counts to assess the relative abundance of songbirds in 24 stands (Ralph et al. 1993). We compared abundances of birds in stands 1–5 years postharvest ( $n = 6$ ), 12–18 years postharvest ( $n = 6$ ), and >30 years postharvest (hereafter, “reference stands”;  $n = 12$ ). We paired each harvested stand with an adjacent reference stand with similar forest cover type (Eyre 1980) and hydrology. We used a paired design to minimize variation due to landscape-level effects, such as proximity to agricultural fields or other nonforested areas. We had a balanced study design across the 3 study areas with equal numbers of harvested and reference stands at each area.

Within each of 24 stands we established 3 point-count stations along transects (72 points total). We selected starting points for transects randomly along roads or trails bordering stands. We located points 250 m apart along transects that were >150 m from roads or habitat edges. We conducted unlimited-radius point counts at each station for 10 minutes during the first 3 hours after sunrise. We used unlimited-radius counts because substantial differences in vegetation structure among treatments made it difficult to judge distance consistently (Ralph et al. 1993). We surveyed points 3 times per year in both 2003 and 2004, with the exception of one pair of stands (containing 6 points) at Big Lake that we surveyed only in 2004. We conducted counts between 22 April and 28 June at 3–4-week intervals by 2 observers. We surveyed paired stands (reference-harvested) during the same morning by a single observer to minimize observer bias and bias due to daily variation in bird activity. Over the field season, observers rotated among stands and alternated the daily order in which we surveyed paired stands. We did not conduct counts during periods of rain or high wind (Beaufort >3).

We recorded the species and sex (if known) of all birds heard or seen during counts. We subdivided counts into 3 intervals (0–3 min, 3–5 min, and 5–10 min) and recorded the interval during which we first detected each bird. We estimated horizontal detection distances to each bird in 3 classes (0–25 m, 0–50 m, and >50 m). Because we conducted counts in

densely forested habitats, we were not able to use laser rangefinders to obtain more precise distance estimates.

### Vegetation Sampling

We sampled vegetation at each point-count location along a 100-m transect centered on the point. We established each transect a random compass direction. At 10-m intervals along each transect we estimated percent canopy cover using a spherical densiometer and measured ground cover with a 1-m<sup>2</sup> Daubenmire frame (Daubenmire 1959), recording the percent cover of herbaceous vegetation, woody debris, and leaf litter. We recorded species and diameter at breast height (dbh) of all trees  $\geq 8$ -cm dbh occurring within a 4  $\times$  100-m strip centered on each transect. We assigned trees  $< 8$ -cm dbh occurring within a 2  $\times$  100-m strip centered on each transect to 2 dbh classes: 3–8 cm and  $< 3$  cm. We measured heights of the 5 tallest trees along each transect with a clinometer to estimate canopy height.

We made categorical estimates (1–5) of 3 additional variables within a 50-m radius of each point: shrub cover (0.5–2 m), midstory density (2–10 m), and the proportion of each plot that was periodically flooded. Periodically flooded areas contained standing water, bare ground, or leaf litter with no vegetation. We made and averaged estimates twice, in May and June 2004.

### Data Analysis

**Bird surveys.**—Count data fit a Poisson distribution (Stokes et al. 2000), and we modeled the relationship between relative abundance (sum of 3 counts at each point per year) and harvest treatment in PROC GENMOD (SAS Institute 1999) using Poisson regression with a logit link function. We treated points as a repeated measure within stands. We used generalized estimating equations in PROC GENMOD to estimate coefficients and standard errors for model parameters (SAS Institute 1999).

We used an information-theoretic approach to evaluate evidence for alternative models explaining variation in bird abundances among harvested and reference stands (Burnham and Anderson 2002). We formulated a set of a priori candidate models that were biologically plausible using an approach similar to that of Hayes et al. (2003). The models we evaluated were: 1) Different abundances among reference stands (C), older harvests (O), and recent harvests (R):  $C \neq O \neq R$ ; 2) identical abundances in older and recent harvests, but different from those in reference stands:  $C \neq (O = R)$ ; 3) identical abundances in reference and recent harvests, but different from those in older harvests:  $O \neq (C = R)$ ; 4) identical abundances in reference stands and older harvests, but different from those in recent harvests:  $R \neq (C = O)$ ; and 5) identical abundances in all treatments:  $C = O = R$ . Because habitat variables were highly collinear with treatments, we did not include these variables in our initial set of models. We included year and area effects in all models to account for variation not explained by treatment.

We evaluated goodness-of-fit of the global model for each species using the deviance statistic, which indicates whether count data fit a Poisson distribution or are overdispersed

(Burnham and Anderson 2002). When we found evidence of overdispersion (deviance  $> 1$ ), we calculated quasi-Akaike's Information Criterion adjusted for small sample sizes (QAIC<sub>c</sub>) values for the entire set of candidate models using methods in Burnham and Anderson (2002). Otherwise, we calculated AIC<sub>c</sub> values to correct for small sample sizes. We ranked models by AIC<sub>c</sub> or QAIC<sub>c</sub> values and calculated  $\Delta_i$ , the difference between AIC<sub>c</sub> or QAIC<sub>c</sub> values of each model and the model with lowest value; we considered models with  $\Delta_i < 2$  of the best model to have strong support. We calculated Akaike weights,  $w_i$ , to quantify the degree of support for each model. When  $w_i < 0.9$  for the best model, we used the entire set of candidate models to calculate model-averaged parameter coefficients and unconditional standard errors for each variable of interest (Burnham and Anderson 2002). We reported abundances in recent and older harvests as a percentage of abundances in reference stands by exponentiating parameter coefficients and multiplying them by 100%. Thus, the focus of our analysis was to investigate the size of treatment effects, not to test hypotheses about whether treatment effects existed (Anderson et al. 2000). When model-averaged confidence intervals included 100%, we inferred a lack of evidence for a treatment effect.

Following model selection, we determined whether relationships between avian abundance and treatment were consistent during the 2 years of the study and across the 3 study areas by adding year by treatment and area by treatment interaction terms to competing models ( $\Delta_i < 2$ ). We did not find evidence that year by treatment interaction terms improved model fit based on AIC<sub>c</sub> or QAIC<sub>c</sub> values for any species analyzed. We found evidence of area by treatment interactions for 2 of 35 species included in analyses, Acadian flycatcher and red-eyed vireo (*Vireo olivaceus*). For these species, we analyzed data separately by area, and for all other species, we pooled data from the 3 areas.

We evaluated whether occurrence of treatment effects differed for species with different Partners in Flight concern status (regional score  $\geq 20$  or not) and breeding bird survey (BBS) population trend (significantly increasing or decreasing) from 1966–2002 for the Mississippi Alluvial Valley (Sauer et al. 2004). To report results, we classified species as forest-interior, forest-edge, or edge species based on Freemark and Collins (1992). Several species found on our sites were not included in Freemark and Collins (1992) and we based classifications of these species on accounts in Hamel (1992). Although these classifications provided a framework for presenting results, we recognize their limitations (Villard 1998).

**Detection probabilities.**—We used a removal model (Farnsworth et al. 2002) to evaluate whether detection probabilities differed among treatments. With count data from 3 time intervals, we used SURVIV (White 1983) to calculate a maximum-likelihood estimator of the detection probability of each species during 10-minute counts. Because we based our analysis of bird abundances on count data (i.e., integers) using Poisson regression, we could not adjust counts by detection probabilities within the regression

**Table 1.** Habitat characteristics in reference stands (>30 yr postharvest,  $n = 12$ ), older selective harvests (12–18 yr postharvest,  $n = 6$ ), and recent selective harvests (1–5 yr postharvest,  $n = 6$ ) in bottomland hardwood forests in Louisiana, USA, 2003–2004.

Variable <sup>a</sup>	Reference stands		Older harvests		Recent harvests	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Basal area (m <sup>2</sup> /ha)	27.6	1.7	21.8	2.4	18.4	1.2
Trees >24 cm/ha	163.8	12.5	125.0	26.9	93.1	15.1
Trees 8–24 cm/ha	301.3	30.6	355.6	61.5	145.8	24.2
Trees 3–8 cm/ha	994.6	161.7	1,550.3	230.7	1,080.8	351.2
Trees <3 cm/ha	1,485.0	288.9	2,367.1	674.4	2,036.5	379.4
Canopy closure (%)	96.5	0.7	94.9	1.2	74.1	1.9
Canopy height (m)	24.3	1.5	23.3	1.4	23.5	1.2
Ground cover (%)	38.0	7.7	36.8	5.8	63.1	7.4
Woody debris (%)	5.9	2.6	4.6	0.8	7.7	1.5
Flooding <sup>b</sup>	2.8	0.4	2.8	0.5	3.0	0.4
Midstory density <sup>b</sup>	2.7	0.1	4.3	0.3	2.0	0.0
Shrub cover <sup>b</sup>	1.8	0.1	3.2	0.4	4.8	0.2

<sup>a</sup> We measured each variable at 3 points within each stand and averaged across stands.

<sup>b</sup> We estimated midstory density, shrub cover, and percent flooding visually and placed estimates into 1 of 5 classes (1 = 0–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80%, and 5 = 81–100%).

analysis. Instead, we used CONTRAST (Hines and Sauer 1989) to test the null hypothesis of no difference in detection probabilities among treatments. We were unable to calculate detection probabilities when we recorded more individuals in the final interval than in the first 2 intervals combined; in these cases, we did not meet the assumptions of the removal model.

Although we collected distance data, we did not calculate density estimates because our data did not meet assumptions of distance sampling (Buckland et al. 2001). First, we could not assume that distance measurements were accurate in our densely forested habitats (Hutto and Young 2003). Because of dense vegetation, we could not use laser rangefinders, and our markers indicating distance bands were often obscured at distances >25 m. Second, we estimated horizontal (ground) distances to each bird, but radial distance is the preferred metric for using DISTANCE (Buckland et al. 2001). At our sites, canopy heights typically exceeded 25 m, and a bird 0 m horizontally from the observer could be >20 m away.

**Bird-habitat relationships.**—We also evaluated relationships between patch-scale habitat characteristics and relative abundances of Acadian flycatcher, prothonotary warbler, and Swainson's warbler. We selected these species because they exhibited negative (Acadian flycatcher and prothonotary warbler) and positive (Swainson's warbler) responses to selective harvesting and are species of concern. We used Poisson regression in PROC GENMOD to fit models and treated points within stands as a repeated measure. First, we evaluated collinearity among 12 habitat variables (Table 1). When 2 variables were highly correlated ( $r > 0.50$ ), we removed one variable from the analysis. From remaining variables, we chose 5 variables we considered to be biologically relevant to the selected species: canopy cover, basal area, midstory density, herbaceous ground cover, and flooding. Starting with the global model (5 variables), we used backward elimination to remove variables with the largest  $P$  values (TYPE3 option). We used  $AIC_c$  or  $QAIC_c$  values to select the most parsimonious model for each species and calculated Akaike weights,  $w_i$ , using the set of

all models evaluated (Burnham and Anderson 2002). Because this analysis was exploratory, we only reported the direction (positive or negative) of correlations between covariates and relative abundance using the best model.

## Results

### Bird Surveys

We detected 8,279 individuals of 59 species during 414 point counts. We included 35 species detected during >15 point counts in statistical analyses; we detected 8,172 individuals of these species. Of 35 species included in our analysis, we found evidence that 17 species differed significantly in abundance among treatments based on model-averaged results (Table 2). We also reported results of model selection for each species that exhibited evidence of treatment effects (Appendix A) and actual counts for each species by treatment (Appendix B).

We found that 3 species were more abundant in reference stands than in harvested stands (Table 2). Acadian flycatcher was only 49–74% as abundant in recent harvests as in reference stands. In addition, at 2 of our 3 study sites, Acadian flycatcher was only 55% as abundant in older harvests as in reference stands. Across all study areas, prothonotary warbler was only 66% as abundant in recent harvests as in reference stands. Red-eyed vireo was only 17% and 21% as abundant in recent harvests as in reference stands at Dewey Wills and Red River, respectively, but did not differ in abundance among treatments at Big Lake. At all study areas, pileated woodpecker (*Dryocopus pileatus*) and hairy woodpecker (*Picoides villosus*), both considered forest-interior species, did not differ in abundance among treatments. In addition, 5 species of concern typically classified as forest-edge species did not differ in abundance among treatments: ruby-throated hummingbird (*Archilochus colubris*), Carolina chickadee (*Poecile carolinensis*), wood thrush (*Hylocichla mustelina*), yellow-throated vireo (*Vireo flavifrons*), and northern parula (*Parula americana*).

Four species often associated with densely vegetated canopy gaps were more abundant in older harvests than in reference

**Table 2.** Model-averaged estimates of the number of detections of breeding birds in older selective harvests (12–18 y postharvest) and recent selective harvests (1–5 yr postharvest) expressed as a percentage of the number of detections in reference stands (>30 yr postharvest) in bottomland forests in Louisiana, USA, 2003–2004.

Species	Older harvests		Recent harvests	
	$\bar{x}$	CI <sup>a</sup>	$\bar{x}$	CI
More abundant in reference stands than in older or recent harvests				
Acadian flycatcher ( <i>Empidonax virescens</i> ) <sup>b</sup>	55.1	35.7–85.5	49.0	28.4–84.5
Red-eyed vireo ( <i>Vireo olivaceus</i> ) <sup>c</sup>	39.8	13.3–66.4	17.4	6.4–47.9
More abundant in reference stands than in recent harvests				
Acadian flycatcher <sup>d</sup>	101.4	93.4–110.1	74.1	58.2–94.2
Prothonotary warbler ( <i>Protonotaria citrea</i> )	101.1	75.6–135.3	66.0	52.6–82.9
Red-eyed vireo <sup>d</sup>	109.0	81.9–145.9	20.7	9.6–44.5
More abundant in older harvests than in reference stands				
Swainson's warbler ( <i>Limnothlypis swainsonii</i> )	1,723.6	245.5–12,030.1	319.0	25.2–4,044.7
Hooded warbler ( <i>Wilsonia citrina</i> )	330.4	169.6–642.4	48.7	17.0–139.4
White-eyed vireo ( <i>Vireo griseus</i> )	133.1	109.7–161.7	103.8	89.0–121.2
More abundant in older and recent harvests than in reference stands				
Kentucky warbler ( <i>Oporornis formosus</i> )	207.2	126.2–339.7	196.8	115.6–334.9
More abundant in recent harvests than in reference stands				
Eastern towhee ( <i>Pipilo erythrophthalmus</i> )	701.5	61.4–7,983.8	1,473.2	217.5–9,948.4
Orchard oriole ( <i>Icterus spurius</i> )	50.7	9.1–282.9	593.0	231.6–1,518.0
More abundant in recent harvests than in reference stands				
Painted bunting ( <i>Passerina ciris</i> )	98.0	50.0–192.7	405.5	234.0–709.9
Mourning dove ( <i>Zenaidura macroura</i> )	96.3	71.9–129.0	350.0	198.0–617.2
Indigo bunting ( <i>Passerina cyanea</i> )	113.2	85.6–150.0	250.9	199.4–315.8
Eastern wood-pewee ( <i>Contopus virens</i> )	103.0	76.2–139.5	192.7	109.6–338.7
Brown-headed cowbird ( <i>Molothrus ater</i> )	99.4	88.8–111.1	177.3	100.4–313.3
Yellow-breasted chat ( <i>Icteria virens</i> )	105.3	71.2–156.0	133.0	636.0–2,785.5
Red-bellied woodpecker ( <i>Melanerpes carolinus</i> )	98.1	83.3–115.5	128.7	110.3–150.0
Yellow-billed cuckoo ( <i>Coccyzus americanus</i> )	111.2	69.8–177.5	121.8	100.8–147.1

<sup>a</sup> Confidence intervals including 100% are interpreted as evidence of no treatment effect. Estimates were derived from Poisson regression analyses. Species for which there was no evidence of a treatment effect in either older or recent harvests: American crow, barred owl (*Strix varia*), blue-gray gnatcatcher (*Poliophtila caerulea*), blue jay, Carolina chickadee, Carolina wren (*Thryothorus ludovicianus*), downy woodpecker (*Picoides pubescens*), great crested flycatcher (*Myiarchus crinitus*), hairy woodpecker, northern cardinal (*Cardinalis cardinalis*), northern parula, pileated woodpecker, red-eyed vireo (Big Lake Wildlife Management Area [WMA]), red-shouldered hawk (*Buteo lineatus*), ruby-throated hummingbird, summer tanager, tufted titmouse (*Baeolophus bicolor*), wood thrush, yellow-throated vireo.

<sup>b</sup> Treatment effects at Dewey Wills and Big Lake. Results for Red River presented separately because there was evidence of a treatment by WMA interaction.

<sup>c</sup> Treatment effects at Dewey Wills. Results are presented separately by WMA because there was evidence of a treatment by WMA interaction.

<sup>d</sup> Treatment effects at Red River. Results are presented separately by WMA because there was evidence of a treatment by WMA interaction.

stands. These included 3 forest-interior species, Swainson's warbler, hooded warbler, and Kentucky warbler; and 1 forest-edge species, white-eyed vireo. Swainson's warbler was very uncommon on our study sites, particularly in reference stands (Appendix B), but was 1,724% as abundant in older harvest as in reference stands; hooded warbler (330%) and Kentucky Warbler (207%) also exhibited dramatic increases in older harvests relative to reference stands.

Nearly all edge and shrub-nesting species included in our analysis exhibited increased abundances in recently harvested stands, including eastern towhee (*Pipilo erythrophthalmus*; 1,473%), orchard oriole (*Icterus spurius*; 593%), painted bunting (*Passerina ciris*; 406%), mourning dove (*Zenaidura macroura*; 350%), indigo bunting (*Passerina cyanea*; 251%), and yellow-breasted chat (*Icteria virens*; 133%). Two forest-edge species were also more abundant in recent harvests than reference stands, red-bellied woodpecker (*Melanerpes carolinus*; 129%) and yellow-billed cuckoo (*Coccyzus americanus*; 122%). Kentucky warbler is a forest-interior species, but was 197% as abundant in recent harvests as in reference stands. Eastern wood-pewee

(*Contopus virens*), a canopy-nesting species, was 193% as abundant in recent harvests as in other treatments. Finally, we found Brown-headed cowbirds in relatively low numbers in all treatments, but they were 177% as abundant in recent harvests as in reference stands.

Of 35 species included in our analysis, 16 are priority species (breeding score  $\geq 20$ ) in the MAV (PIF 2001). Of these 16 species, 2 were more abundant in reference stands than in one or both harvested treatments, 9 were more abundant in one or both harvested treatments than in reference stands, and 5 did not exhibit differences in abundance among treatments. Populations of 7 of 35 species in our analysis have experienced significant long-term declines based on BBS data and 4 species have increased significantly (Sauer et al. 2004). Of declining species, prothonotary warbler was more common in reference stands than in recently harvested stands; white-eyed vireo was more abundant in older harvests than in reference stands; and eastern wood-pewee, painted bunting, and orchard oriole were more abundant in recent harvests than in reference stands. Northern parula and Carolina chickadee are also declining, but they did not differ in abundance among

**Table 3.** Competing models ( $\Delta_i < 2$  of the best model) explaining relationships between songbird abundance and habitat variables in bottomland hardwood forests in Louisiana, USA, 2003–2004.<sup>a</sup>

Species	Competing models <sup>b</sup>	K <sup>c</sup>	$\Delta_i^d$	$w_i^e$
Acadian flycatcher	Canopy cover +, flooding +, basal area +, midstory density –, ground cover +	6	0.00	0.93
Prothonotary warbler	Flooding +, basal area +, canopy cover +, ground cover +	5	0.00	0.62
	Flooding +, basal area +, canopy cover +, ground cover +, midstory density –	6	1.94	0.23
Swainson's warbler	Midstory density +, canopy cover –, ground cover –	4	0.00	0.46
	Midstory density +, canopy cover –	3	1.28	0.24
	Midstory density +, canopy cover –, ground cover –, flooding –	5	1.85	0.18

<sup>a</sup> Results were derived from Poisson regression analyses.

<sup>b</sup> Negative and positive signs indicate the sign of the variable coefficient. Explanatory variables in the global model included percent canopy cover, basal area, midstory density, percent ground cover, and percent flooding.

<sup>c</sup> Number of parameters in each model, including the intercept.

<sup>d</sup> Difference in Akaike's Information Criterion adjusted for small sample sizes (AIC<sub>c</sub>) or quasi-AIC<sub>c</sub> values between the best-fitting model and model *i*.

<sup>e</sup> Akaike weights, scaled 0–1, indicate the degree of relative support for each model.

treatments. Of species with increasing populations, red-bellied woodpecker and eastern towhee were more common in recent harvests than in reference stands, and American crow (*Corvus brachyrhynchos*) and summer tanager (*Piranga rubra*) did not differ in abundance among treatments.

### Detection Probabilities

We found no differences in detection probabilities among treatments for any species (all *P* values > 0.05, using CONTRAST [Hines and Sauer 1989]). Thus, we did not adjust counts to account for different detection probabilities among treatments prior to our analysis.

### Bird–Habitat Relationships

Reference stands and older harvests had greater percent canopy cover (97% and 95%, respectively) than recent harvests (74%; Table 1). Reference stands also had substantially more basal area (28 m<sup>2</sup>/ha) and trees >24-cm dbh (164/ha) than recent harvests, which had a basal area of 18 m<sup>2</sup>/ha and only 93 trees >24 cm/ha. Older harvests had greater midstory density than other treatments; recent harvests had greater percent herbaceous ground cover (63%) and more shrub cover than other treatments (Table 1).

Prothonotary warbler abundances were positively associated with 4 habitat features. In order of importance, these were flooding, basal area, canopy cover, and herbaceous ground cover (Table 3). Acadian flycatcher abundances had a positive correlation with the same habitat features as prothonotary warbler, but the most important variable was canopy cover rather than flooding. In addition, Acadian flycatcher numbers had a negative correlation with midstory density. In contrast, Swainson's warbler abundances had a positive association with midstory density and a negative association with percent canopy cover and herbaceous ground cover. We analyzed data separately by year and WMA. The results of model selection were identical to results with years and WMAs combined.

### Discussion

We found that effects of selective harvesting on breeding bird abundances varied by species and by habitat affiliation. We found similar abundances of most forest-interior and forest-edge species in reference stands and older selective harvests. However, we found reductions of >25% in abundances of 3

forest-interior species, prothonotary warbler, Acadian flycatcher, and red-eyed vireo, in recent harvests compared to reference stands. Prothonotary warbler abundances recovered to levels found in reference stands within 12–18 years of selective harvesting, but Acadian flycatcher abundances did not recover at 2 of our 3 study sites. Researchers have found prothonotary warbler to be less abundant in recently harvested bottomland forests (Twedt et al. 1999) and in hurricane-created canopy gaps (Torres and Leberg 1996) than in undisturbed stands. In upland deciduous forests, Acadian flycatcher and red-eyed vireo have exhibited varying responses to selective harvesting; researchers have found these species to decrease in abundance at some harvested sites and show no response at other sites (Annand and Thompson 1997, Rodewald and Smith 1998, Robinson and Robinson 1999, Jobs et al. 2004).

Gap species, including Swainson's warbler, hooded warbler, and Kentucky warbler, were uncommon in reference stands and abundances increased by >200% in older harvests. Swainson's warblers have previously been associated with dense mid-story vegetation in bottomland forests (Somershoe et al. 2003), and hooded warblers were associated with logged canopy gaps in upland forest (Whittam et al. 2002). Only 2 previous studies of breeding birds in selective logged deciduous forests examined older harvests (>10 yr old; Robinson and Robinson 1999, Jobs et al. 2004), and neither study was conducted in a bottomland forest. Robinson and Robinson (1999) found that abundances of gap species peaked in recent selective harvests (1–5 yr old) and declined in older harvests (10–15 yr old). In contrast, we found greater abundances of gap species in 12–18-year-old harvests than in 1–5-year-old harvests. In bottomland forests, regenerating vegetation on harvested sites grows more slowly on wetter sites than on ridges (Meadows and Stanturf 1997), and probably grows substantially slower than at upland sites studied by Robinson and Robinson (1999). As a result, habitat conditions for gap-dependent species appear to peak later in harvested bottomland forests than in upland forests.

As expected, many shrub and forest-edge species were more abundant in recent harvests than in reference stands. Previous studies conducted in selectively harvested upland deciduous forests (Annand and Thompson 1997, Robinson and

Robinson 1999) and bottomland forests (Twedt et al. 1999) reported similar results. Most of the species found in high numbers in recent harvests nest in shrubs or on the ground, and these stands provided abundant nesting cover.

Brown-headed cowbird numbers were also highest in recent harvests. Recent harvests had a relatively open canopy structure, and the abundance of cowbirds in bottomland forests increases with the size of canopy gaps (Moorman and Guynn 2001). Recent harvests also supported relatively high numbers of 2 frequent host species, indigo bunting and white-eyed vireo, which may have attracted cowbirds to these stands (Thompson et al. 2000). Cowbirds were substantially less abundant in all treatments on our study sites than in selectively harvested forests in Illinois (Robinson and Robinson 1999). The majority of our study sites were located <10 km from an agricultural edge, well within the commuting distance of cowbirds (Rothstein et al. 1984, Curson et al. 2002). However, most nearby agricultural lands were devoted to row-crops rather than to livestock production and lack of prime feeding sites near our study areas may have limited cowbird numbers (Robinson et al. 1995).

Abundances of avian nest predators showed a mixed response to timber harvesting. We found no differences in abundances of blue jay (*Cyanocitta cristata*) or American crow among treatments, but numbers of both species were relatively low in all treatments. Red-bellied woodpeckers depredate nests of several songbird species in bottomland forests (Hazler et al. 2004). We found the greatest abundances of red-bellied woodpeckers in recent harvests; however, this species was common in all treatments.

## Management Implications

Our study sites contained a relatively small proportion of harvested forest; only 7–13% of each WMA consisted of older or recent harvests. If the proportion of harvested forest

increases, effects on forest-interior species, such as prothonotary warbler (one of the most highly ranked species of concern in the MAV; PIF 2001), may be more severe than our results suggest (Donovan et al. 1997). Managers need to evaluate effects of forestry practices on bird populations within the context of the amount of local and regional forest cover (Thompson et al. 1995). In addition, abundance may not be an accurate indicator of habitat quality (Van Horne 1983), and information on breeding productivity and adult and juvenile survival in harvested stands is necessary to evaluate more fully effects of forestry practices on avian populations. Recent harvests provided habitat for several early successional species that have experienced long-term population declines (Sauer et al. 2004) and are species of concern, including orchard oriole, painted bunting, and yellow-breasted chat. However, other habitats in the Mississippi Alluvial Valley, such as bottomland hardwood reforestation sites, provide habitat for these shrub-nesting species, as well as some forest-edge species such as white-eyed vireo and yellow-billed cuckoo (Twedt et al. 2002). Obtaining an appropriate balance of closed-canopy forest for species sensitive to harvest disturbance and gaps of different ages to support species needing intermediate and early successional habitats involves trade-offs and will continue to be a management challenge.

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**Appendix A.** Competing models ( $\Delta_i < 2$ ) explaining variation in abundance of birds in reference stands (C; >30 yr postharvest), older selective harvests (O; 12–18 yr postharvest), and recent selective harvests (R; 1–5 yr postharvest) in bottomland forests in Louisiana, USA, 2003–2004. Results are presented only for species for which there was evidence of a treatment effect based on model-averaged results.

Species	Competing models	$\Delta_i^a$	$w_i^b$
Acadian flycatcher <sup>c</sup>	C ≠ (O = R)	0.00	0.62
	C ≠ O ≠ R	1.13	0.35
Red-eyed vireo <sup>d</sup>	C ≠ (O = R)	0.00	0.51
	C ≠ O ≠ R	0.23	0.46
Acadian flycatcher <sup>e</sup>	C ≠ (O = R)	0.00	0.66
	C ≠ O ≠ R	1.84	0.27
Red-eyed vireo <sup>e</sup>	R ≠ (C = O)	0.00	0.74
	R ≠ (C = O)	0.00	0.42
Prothonotary warbler	C ≠ O ≠ R	0.28	0.37
	C ≠ (O = R)	1.54	0.20
Hooded warbler	C ≠ O ≠ R	0.00	0.80
	C ≠ O ≠ R	0.00	0.56
Swainson’s warbler	O ≠ (C = R)	0.73	0.39
	O ≠ (C = R)	0.00	0.63
White-eyed vireo	C ≠ O ≠ R	1.58	0.29
	C ≠ (O = R)	0.00	0.69
Kentucky warbler	C ≠ O ≠ R	1.87	0.27
	C ≠ O ≠ R	0.00	0.49
Eastern towhee	R ≠ (C = O)	0.66	0.35
	C ≠ O ≠ R	0.00	0.50
Orchard oriole	R ≠ (C = O)	0.01	0.50
	R ≠ (C = O)	0.00	0.74
Painted bunting	R ≠ (C = O)	0.00	0.73
	C ≠ O ≠ R	1.99	0.27
Mourning dove	C ≠ O ≠ R	0.00	0.55
	R ≠ (C = O)	0.43	0.45
Indigo bunting	R ≠ (C = O)	0.00	0.64
	R ≠ (C = O)	0.00	0.73
Eastern wood-pewee	R ≠ (C = O)	0.00	0.73
	R ≠ (C = O)	0.00	0.73
Brown-headed cowbird	R ≠ (C = O)	0.00	0.73
	R ≠ (C = O)	0.00	0.73
Yellow-breasted chat	R ≠ (C = O)	0.00	0.74
	C ≠ (O = R)	0.00	0.37
Red-bellied woodpecker	R ≠ (C = O)	0.45	0.29
	C ≠ O ≠ R	1.06	0.22

<sup>a</sup> Difference in Akaike’s Information Criterion adjusted for small sample sizes (AIC<sub>c</sub>) or quasi-AIC<sub>c</sub> values between the best-fitting model and model *i*.

<sup>b</sup> Akaike weights, scaled 0–1, indicate the degree of relative support for each model.

<sup>c</sup> Treatment effects at Big Lake and Dewey Wills. Results for Red River are presented separately because there was evidence of a treatment by Wildlife Management Area (WMA) interaction.

<sup>d</sup> Treatment effects at Dewey Wills. Results are presented separately by WMA because there was evidence of a treatment by WMA interaction.

<sup>e</sup> Treatment effects at Red River. Results are presented separately by WMA because there was evidence of a treatment by WMA interaction.

**Appendix B.** Mean number of detections of breeding birds in reference stands (>30 yr postharvest,  $n = 12$ ), older selective harvests (12–18 yr postharvest,  $n = 6$ ), and recent selective harvests (1–5 yr postharvest,  $n = 6$ ) in bottomland hardwood forests in Louisiana, USA, 2003–2004.

Species	Reference stands		Older harvests		Recent harvests	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Acadian flycatcher	1.71	0.07	1.29	0.09	1.05	0.09
American crow	0.89	0.06	0.79	0.08	0.94	0.10
Barred owl	0.17	0.03	0.09	0.03	0.19	0.04
Blue-gray gnatcatcher	0.59	0.04	0.46	0.05	0.61	0.06
Blue jay	0.09	0.02	0.14	0.04	0.07	0.03
Brown-headed cowbird	0.35	0.04	0.34	0.06	0.61	0.08
Carolina chickadee	0.69	0.05	0.47	0.06	0.64	0.08
Carolina wren	2.19	0.07	1.99	0.09	2.49	0.11
Downy woodpecker	0.30	0.03	0.26	0.04	0.36	0.06
Eastern towhee	0.00	0.00	0.04	0.02	0.10	0.03
Eastern wood-pewee	0.12	0.02	0.12	0.03	0.24	0.05
Great crested flycatcher	0.20	0.03	0.19	0.04	0.23	0.05
Hairy woodpecker	0.11	0.02	0.07	0.03	0.07	0.03
Hooded warbler	0.14	0.03	0.44	0.06	0.06	0.03
Indigo bunting	0.64	0.05	0.81	0.07	1.65	0.11
Kentucky warbler	0.16	0.03	0.36	0.05	0.31	0.05
Mourning dove	0.15	0.03	0.14	0.04	0.51	0.07
Northern cardinal	1.98	0.07	2.02	0.11	2.00	0.11
Northern parula	0.42	0.05	0.50	0.07	0.40	0.06
Orchard oriole	0.03	0.01	0.01	0.01	0.16	0.04
Painted bunting	0.08	0.02	0.07	0.03	0.31	0.06
Pileated woodpecker	0.31	0.03	0.35	0.05	0.26	0.05
Prothonotary warbler	0.99	0.07	0.84	0.08	0.61	0.07
Red-bellied woodpecker	1.07	0.06	1.06	0.09	1.36	0.09
Red-eyed vireo	0.65	0.05	0.63	0.07	0.22	0.05
Red-shouldered hawk	0.25	0.04	0.12	0.03	0.18	0.04
Ruby-throated hummingbird	0.11	0.02	0.11	0.03	0.14	0.04
Summer tanager	0.31	0.04	0.29	0.05	0.26	0.05
Swainson's warbler	<0.01	<0.01	0.12	0.03	0.03	0.02
Tufted titmouse	1.40	0.07	1.16	0.08	1.36	0.10
Warbling vireo	1.41	0.07	1.91	0.09	1.55	0.11
Wood thrush	0.04	0.02	0.10	0.03	0.04	0.02
Yellow-breasted chat	0.06	0.02	0.07	0.03	0.91	0.11
Yellow-billed cuckoo	1.05	0.06	1.23	0.09	1.35	0.12
Yellow-throated vireo	0.23	0.03	0.14	0.04	0.33	0.06