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## Breeding birds in managed forests on public conservation lands in the Mississippi Alluvial Valley

Daniel J. Twedt<sup>a,\*</sup>, R. Randy Wilson<sup>b</sup><sup>a</sup>USGS Patuxent Wildlife Research Center, University of Memphis, Memphis, TN 38152, United States<sup>b</sup>U.S. Fish and Wildlife Service, 6578 Dogwood View Parkway, Suite B, Jackson, MS 39213, United States

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## ABSTRACT

Managers of public conservation lands in the Mississippi Alluvial Valley have implemented forest management strategies to improve bottomland hardwood habitat for target wildlife species. Through implementation of various silvicultural practices, forest managers have sought to attain forest structural conditions (e.g., canopy cover, basal area, etc.) within values postulated to benefit wildlife. We evaluated data from point count surveys of breeding birds on 180 silviculturally treated stands (1049 counts) that ranged from 1 to 20 years post-treatment and 134 control stands (676 counts) that had not been harvested for >20 years. Birds detected during 10-min counts were recorded within four distance classes and three time intervals. Avian diversity was greater on treated stands than on unharvested stands. Of 42 commonly detected species, six species including Prothonotary Warbler (*Prothonotaria citrea*) and Acadian Flycatcher (*Empidonax virens*) were indicative of control stands. Similarly, six species including Indigo Bunting (*Passerina cyanea*) and Yellow-breasted Chat (*Icteria virens*) were indicative of treated stands. Using a removal model to assess probability of detection, we evaluated occupancy of bottomland forests at two spatial scales (stands and points within occupied stands). Wildlife-forestry treatment improved predictive models of species occupancy for 18 species. We found years post treatment (range = 1–20), total basal area, and overstory canopy were important species-specific predictors of occupancy, whereas variability in basal area was not. In addition, we used a removal model to estimate species-specific probability of availability for detection, and a distance model to estimate effective detection radius. We used these two estimated parameters to derive species densities and 95% confidence intervals for treated and unharvested stands. Avian densities differed between treated and control stands for 16 species, but only Common Yellowthroat (*Geothlypis trichas*) and Yellow-breasted Chat had greater densities on treated stands.

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## 1. Introduction

Prior to extensive forest modification and management by humans, we surmise birds evolved to utilize the complex vegetative structure of bottomland forests that developed in response to natural disturbances of the forest canopy. These perturbations of the canopy resulted from extreme weather events or natural tree mortality with a resultant heterogeneous forest structure that tended to have varying numbers and area of canopy gaps as well as large retained legacy trees that ranged in senescence from vigorous to decadent. Sunlight penetration through canopy fenestrations encourages growth of herbaceous understory vegetation (Canham et al., 1990) that birds may use for foraging and shelter,

but these gaps also provide sites for regeneration of shade-intolerant trees (Bugmann, 2001). Likewise, the diversity of silvicolous wildlife appears to benefit from biological legacy structures (Franklin, 1990) as well as increased coarse woody debris (Wu et al., 2005) provided by decadent trees. However, because natural disturbances occur stochastically, heterogeneous stand structure may develop on only a portion of the landscape. Thus within landscapes where forest has largely been converted to other use, such as in the Mississippi Alluvial Valley (Twedt and Loesch, 1999), stands with these conditions are increasingly rare.

Despite the presumed benefits of heterogeneous forest structure, managers of bottomland forests have most often employed even-aged harvests (e.g., clear felling, seed tree, or shelterwood; Meadows and Stanturf, 1997) in an effort to regenerate and maintain the presence of commercially valuable, shade-intolerant tree species, especially red oaks (*Quercus* spp.; Section Lobatae).

\* Corresponding author.

E-mail address: [dtwedt@usgs.gov](mailto:dtwedt@usgs.gov) (D.J. Twedt).

Although these even-aged harvests, which remove all or most of the forest canopy, are often successful at regenerating shade-intolerant tree species (Clatterbuck and Meadows, 1993), they have been less successful at maintaining the wildlife diversity often associated with older forests subjected to natural perturbations. Characteristically after even-aged harvest, early seral stages of forest regeneration are followed by periods of canopy closure and competitive exclusion (Franklin et al., 2002), before returning to commercially merchantable stands. Thus after complete canopy removal, we believe the resultant stands of 'next-generation' forest tend to be even-aged and relatively homogeneous, with closed canopies and little vertical or horizontal diversity. Regenerated stands are typically reentered for repeat harvest before natural disturbances influence forest structure.

Because red oaks confer benefits upon wildlife species, especially their production of hard mast, retention of these keystone species is desirable within bottomland forests (McShea et al., 2007). However, the extensive removal of forest canopy typically used to regenerate shade-intolerant tree species, such as red oaks, generally results in wholesale change in the wildlife communities that inhabit these managed forests. That is, species that are dependent upon forest canopy are displaced by those species using early seral or shrub-scrub habitats (Hunter et al., 2001). Over time, forest succession tends to revivify those wildlife species that were present before harvest. Even so, homogenous closed canopies, as often found in maturing stands that were previously subjected to even-aged harvest, typically lack the structural legacy and decadence that attract some wildlife species. As such, extensive canopy removal practiced over long durations or on expansive landscapes, even when stands of different ages are present within these landscapes, may modify their wildlife communities by increasing abundance of common generalist species and extirpating habitat-specialist species. Therefore, extensive canopy removal associated with even-aged silviculture appears at odds with development of a complex vegetative structure in bottomland forests as occurs in response to long-term, natural disturbance of the forest canopy.

Wildlife-forestry (i.e., the art and science of managing forests for wildlife) advocates partial canopy removal to emulate the patchy perturbations of natural disturbance, actively promotes regeneration and retention of shade-intolerant tree species (Twedt and Somershoe, 2013), while mitigating the detrimental effects associated with extensive canopy removal (Twedt, 2012). Wildlife-forestry focuses on providing a sustainable, prescribed forest structure conducive for wildlife habitat using silvicultural methods that are commercially viable. Often the goals are to preserve existing biodiversity, maintain occupancy by canopy dependent species, retain uncommon species, and encourage colonization or increased abundance of species favoring early seral habitats, while concurrently regenerating shade-intolerant tree species.

In the Mississippi Alluvial Valley, biologists and foresters have quantified a set of landscape conditions and stand-level structural characteristics deemed desirable for wildlife habitat (Lower Mississippi Valley Joint Venture [LMJV] Forest Resource Conservation Working Group, 2007). Habitat conditions that result from wildlife-forestry prescriptions vary among sites and forest types. Moreover, managers have leeway to prescribe treatments of different intensity, including clear-cutting stands when deemed most appropriate, to achieve desired stand conditions for wildlife that include an average of 60%–70% overstory canopy cover (or alternatively basal area of 13.7–16 m<sup>2</sup>/ha) distributed heterogeneously within the stand. Also desired, are a midstory and understory between 25% and 40% cover, at least five dominant trees per ha, small and large cavity trees, as well as dead or stressed trees to contribute to coarse woody debris. Yet to ensure future merchantability of stands, shade-intolerant tree regeneration should

be present on 30–40% of the stand (LMJV Forest Resource Conservation Working Group, 2007).

We sought to evaluate the association of breeding birds with bottomland forest habitat conditions created via wildlife-forestry silviculture on public conservation lands within the Mississippi Alluvial Valley. Our general objective was to evaluate avian use of bottomland hardwood stands after implementation of silvicultural treatments prescribed to promote desired forest conditions for wildlife. Our specific objectives were to: (1) compare avian diversity in forest stands subjected to silvicultural treatment and in forest stands not subjected to silvicultural treatment (i.e., control stands); (2) determine bird species indicative of treated or control stands; (3) estimate densities of avian species in treated or control stands of bottomland hardwood forests; (4) estimate the probability that a bird species occupies a forest stand; and (5) estimate the probability of occupancy at surveyed locations within occupied stands.

## 2. Study area

Our study area was the Mississippi Alluvial Valley floodplain, which encompasses parts of seven U.S. states, from southern Illinois through southern Louisiana along the Mississippi River. Because our objective was to evaluate the relationship of birds to wildlife-forestry being prescribed to improve habitat conditions for wildlife on public conservation lands, our study sites were limited to lands being managed by state or federal agencies, ostensibly to attain habitat conditions defined by the Lower Mississippi Valley Joint Venture, Forest Resource Conservation Working Group (2007). Therefore, our study sites were limited to public conservation lands (i.e., State Wildlife Management Areas [WMA], National Wildlife Refuges [NWR], and National Forests [NF]) within Tennessee, Arkansas, Mississippi and Louisiana.

## 3. Methods

### 3.1. Site selections

We randomly selected up to five public conservation land units (e.g., WMA, NWR, NF) within each of the four states based on the number of available conservation units (Fig. 1). Random selections were made for each year of study (2006–2012), with all conservation units available for selection during each year (i.e., with replacement).

Within each selected conservation unit, we used previously demarcated forest management compartments, hereafter referred to as stands, as our study units. We used a geographic information system (GIS) database of historical silvicultural actions maintained by the Lower Mississippi Valley Joint Venture to identify forest stands subjected to silvicultural treatment. We consulted local foresters or area managers to verify and update silvicultural treatments within the GIS database. We defined treated stands as the entirety of contiguous forest cover within a stand that managers prescribed for treatment, regardless of uniformity of treatment within the stand. Year of treatment was the year of initiation within the stand even if prescribed treatment was completed in a subsequent year. For conservation land units with fewer than four treated stands, we selected all treated stands on the unit for study. During the first year of study, if more than four treated stands were present on a selected unit, we randomly selected up to four treated stands for study. However, we annually appraised the age (i.e., years post-treatment) distribution of treated stands and, after the first year, on units with more than four treated stands available for study, we preferentially selected stands of under-represented ages to ensure our sample spanned the

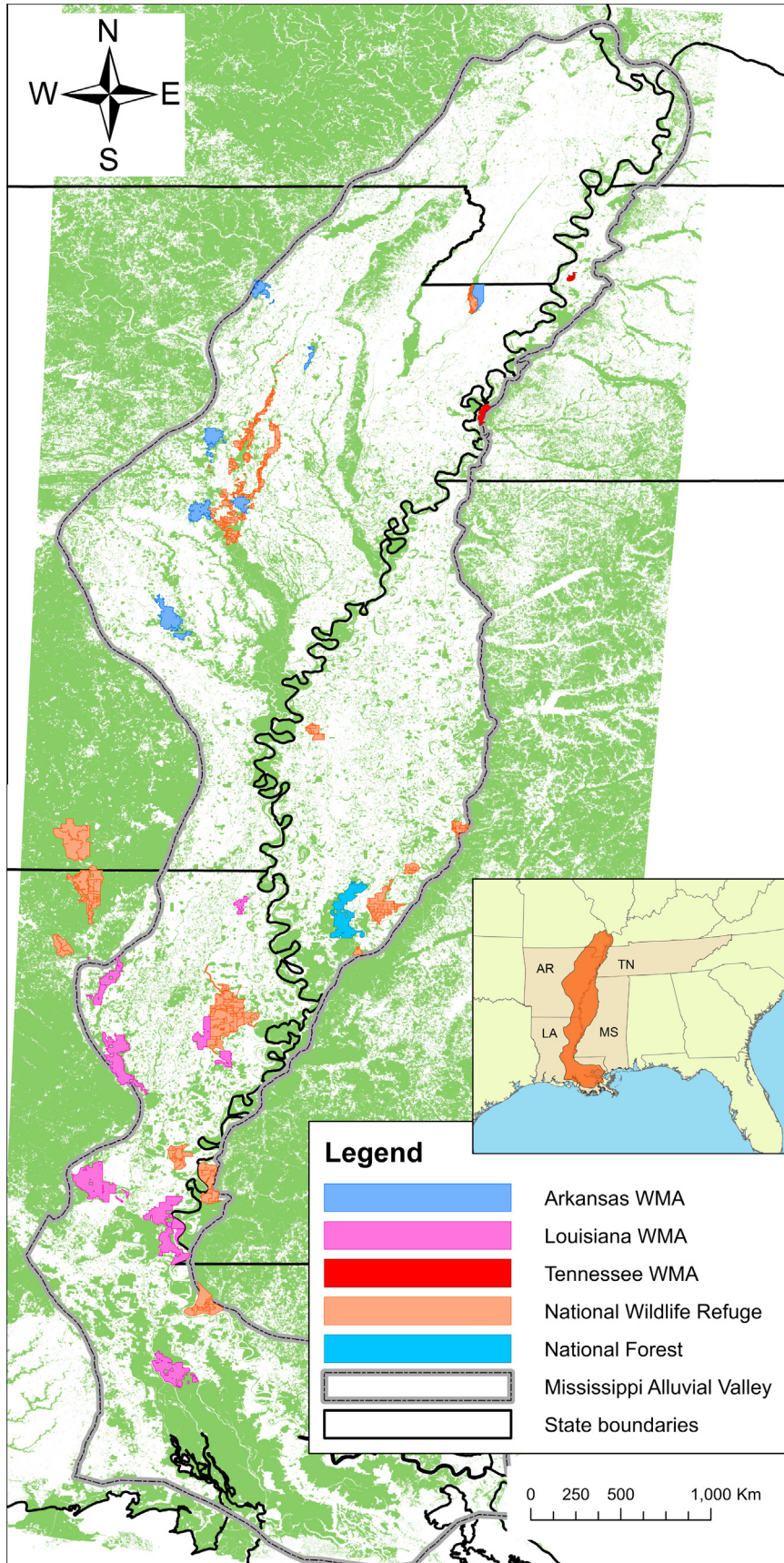


Fig. 1. Public conservation lands in and adjacent to the Mississippi Alluvial Valley surveyed for birds within forest stands during May–June, 2006–2012.

1–20 years post-treatment chronosequence of treatments depicted in Fig. 1 of Twedt and Wilson (2016).

In addition, we selected one untreated control stand for study on each selected conservation unit. Typically, control stands had not been subject to treatment since coming under public management, but any stand not subjected to silvicultural treatment within the past 20 years was considered a suitable control stand. If a selected unit had no treated stands available, we selected two control stands for surveys. Local area managers or foresters subjectively chose control stands from among all available untreated stands with preference for stands that were of the same Society of American Foresters forest type (Eyre, 1980) as were the majority of treated stands. We asked managers to include stands designated as natural areas or 'old-growth areas' among control stands if such designated areas were present.

### 3.2. Bird surveys

Surveyed stands were typically >40 ha and were surveyed at six sampling locations that were systematically located 250-m apart from a random start location and were >100-m from a primary road or an agricultural edge (Appendix A). However, a few stands that had insufficient area (<40 ha) to encompass six survey locations were surveyed using four similarly distributed point locations. In addition, managers of one conservation unit chose to survey stands >40 ha using only four sampling locations per stand.

An experienced bird surveyor visited each sample location once between 15 May and 30 June, during clement weather (i.e., no rain or excessive wind). During each visit, an avian point count was conducted (Hamel et al., 1996; Buckland, 2006) during which observers recorded the first detection of each bird within radial distance bands of 0–25 m, >25–50 m, >50–100 m, and >100–150 m, and within time intervals of 0–3 min, >3–5 min, and >5–10 min. Birds detected beyond 150 m or deemed to be flying over but not using the forest were omitted from analysis.

### 3.3. Vegetation surveys

We assessed forest structure from variable radius plots, sampled using a 10 basal area factor (BAF) prism (Avery and Burkhart, 2002). Two vegetation plots were associated with each bird survey location, one at point center and one near the edge of the bird-count radius at ~100 m from point center; except for surveys conducted during 2006 when only a single centrally located vegetation survey was obtained. At each vegetation assessment plot, for each bole of sufficient girth to be included in the 10 BAF prism survey, we recorded the species and diameter at breast height within four size classes: 10–<25 cm, 25–<50 cm, 50–76 cm, and >76 cm. In addition, we assessed the presence of other vegetation as was visually discernable at the sampling location on an ordinal scale: 1 = none, 2 = sparse, 3 = moderate, or 4 = heavy. However, the category percentages of this ordination scale varied among vegetation types: Vines and cane being 0, >0–<25, 25–50, >50%; understory (<3 m in height) and midstory (3–9 m) set at 0, >0–<25, 25–60, >60%; and overstory canopy (>9 m) slightly higher at 0, >0–<50, 50–80, >80% (Wilson et al., 2007).

### 3.4. Statistical analysis

We compared forest structure characteristics between treated and control stands using analysis of variance. Forest stands were our experimental units, whereas point count locations were sampling units.

To evaluate the influence of silvicultural treatment on forest bird communities we compared species richness and Simpson's species diversity within treated and control stands based on rarefaction estimates (Colwell et al., 2012) using the R-based, iNEXT-package for interpolation and extrapolation of species diversity (Hsieh et al., 2015). We identified those bird species which were most associated with treated or control stands using Indicator Species Analysis (Dufrêne and Legendre, 1997) implemented in PC-Ord 6.0 (McCune and Mefford, 2011).

3.5. Density estimates

To estimate densities of avian species within treated and control stands, we estimated two parameters using the conditional multinomial maximum likelihood estimation (cmulti) function of the R-based, detect-package for analyzing wildlife data with detection error (Sólymos et al., 2014). Phi ( $\phi$ ), the probability that a bird species was available for detection (i.e., singing or presentation rate) was estimated from temporal data in three detection periods (1–3, >3–5, and >5–10 min) using a removal model (Sólymos et al., 2013). We estimated the proportion of the surveyed radius ( $\tau$ ) that was the effective detection radius (EDR) for each species from observed distances in four distance intervals (0–25, >25–50, >50–100, and >100–150 m) using distance models (Sólymos et al., 2013). The EDR is the distance beyond which as many birds were counted as were missed within, thereby being functionally equivalent to the area wherein all detectable birds of the species were censused (Meadows et al., 2012). From these estimated parameters, we derived species-specific densities and associated 95% confidence intervals for treated and control stands following Sólymos et al. (2013) as:

$$\hat{D} = Y_{..} / A \hat{p}(t_j) \hat{q}(r_K),$$

where  $\hat{D}$  is the density per unit area ( $m^2$ ),

$A = (\pi r_K^2)$  is the area sampled, and  $r_K$  is the maximum count radius, beyond which observations were not recorded,

$\hat{p}(t_j) = [1 - e^{-(t_j \phi)}]$  is the probability an individual bird was available for detection during the total cumulative time interval ( $t_j$ ), and

$\hat{q}(r_K) = \left[ \frac{\tau^2}{r_K^2} \left( 1 - e^{-(r_K^2 / \tau^2)} \right) \right]$  is the probability that an individual bird is detected within count radius  $r_K$  and  $\tau$  is the effective detection radius (EDR) at which as many of the available birds are detected beyond as are undetected within (Buckland et al., 2001).

Density estimates were expressed per to  $km^2$  as  $\hat{D} * 1000,000$ .

We assumed the population was closed during the sampling interval  $t_j$  within  $r_K$  and that individuals were counted only once. We used three time intervals within  $t_j$ , with start time  $t_0 = 0$  and end times  $t_j, j = 3, 5, 10$ . We used four consecutive distance bands with  $r_0 = 0$  and radii  $r_k, k = 25, 50, 100, 150$ ; with  $K$  being the maximum distance of 150 m. For species with estimated densities on both treated and control stands, we assumed a treatment effect if confidence intervals ( $CI_{95\%}$ ) did not overlap. When separate density estimates were not estimable for treated and control stands, we estimated species density for all bottomland forest on public conservation lands in the Mississippi Alluvial Valley.

### 3.6. Occupancy analysis

For each species evaluated, we estimated three parameters using occupancy analysis: psi ( $\psi$ ), the probability that a stand was occupied by the species; theta ( $\theta$ ), the probability that the species occurred at a surveyed location within an occupied stand (i.e., a measure of how ubiquitous the species was within occupied stands); and p, the probability of detection (MacKenzie et al., 2003, 2006; Nichols et al., 2008; Pavlacky et al., 2012). Thus, we evaluated occupancy by bird species at two spatial scales, a forest stand and points within occupied forest stands.

To accomplish this, we grouped point count detection data into two equal 5-min observation periods by combining 0–3 min and >3–5 min detection intervals. These data were then reduced to presence/absence (1, 0) based on whether or not the species being evaluated was detected at the point. Because this was a removal model, if the species of interest was detected during the first 5-min observation interval, the second 5-min observation interval was truncated (i.e., treated as if no observation was conducted).

We initially looked at four models to evaluate the effects of silvicultural treatment: (1) no treatment effect, (2) treatment effected  $\psi$  only, (3) treatment effected  $\Theta$  only, and (4) treatment effected both  $\psi$  and  $\Theta$ . We examined Akaike Information Criteria (AIC) and if any model with a treatment effect was supported (i.e., model weight > 0.20), we subsequently included the number of years post-treatment as a covariate measure of temporal influence on treatment. The number of years post treatment effected only treated stands. In addition, we evaluated the influence of three forest structure covariates within each respective treatment: (1) total basal area, (2) relative percent overstory (ordinal rank), and (3) variance of basal area. We chose these covariates because we deemed them representative of overall stand conditions, and we believed managers would be able to use these measures to help guide future silvicultural prescriptions. Covariate values used were each associated with a point count sample (i.e., the mean from two vegetation plots associated with a point count location). We applied covariates within separate predictive models and compared results using AIC. If multiple models were competing as evidenced by AIC < 2 or predictive model weight > 0.2, we used model averaging to produce a final model (Burnham and Anderson, 2002; Symonds and Moussalli, 2011; Doherty et al., 2012).

If any covariates were included among supported models, we report their positive or negative effect on occupancy ( $\psi$  or  $\Theta$ ). However, we assessed the strength of support for a covariate by examining its confidence interval and odds ratio (McHugh, 2009). Covariates were deemed as strongly influencing models only if the estimated confidence interval on their odds ratio did not include 1 (i.e., equal odds).

Finally, we assessed the effect of time of survey (i.e., hours since dawn) as a covariate influencing probability of detection ( $p$ ). We only present models for species where  $p \geq 0.25$  to reduce the likelihood of biased estimates of occupancy (MacKenzie et al., 2002).

#### 4. Results

From 2006 through 2012, avian surveys were conducted in 314 forest stands located on 31 State or Federal conservation lands.

**Table 1**  
Mean ( $\pm$  SE) number of years since treatment, basal area, and overstory rank (1–4 scale) of 314 bottomland hardwood forest stands in the Mississippi Alluvial Valley at time of bird survey during May–June, 2006–2012.

Treatment description	Stands (n)	Years post-treatment	Basal area (ft <sup>2</sup> /acre)	Overstory rank
Individual selection <sup>a</sup>	50	11.3 $\pm$ 0.8	86.8 $\pm$ 3.4	3.04 $\pm$ 0.05
Thinning	83	9.4 $\pm$ 0.6	85.4 $\pm$ 3.9	2.95 $\pm$ 0.04
Group selection <sup>b</sup>	11	10.4 $\pm$ 1.4	78.3 $\pm$ 10.1	2.76 $\pm$ 0.13
Thinning & group selection <sup>c</sup>	25	7.4 $\pm$ 1.1	76.5 $\pm$ 4.4	2.82 $\pm$ 0.09
Shelterwood <sup>d</sup>	11	6.6 $\pm$ 1.6	48.6 $\pm$ 8.3	2.12 $\pm$ 0.16
Treated stands	180	9.5 $\pm$ 0.4	81.9 $\pm$ 2.3	2.89 $\pm$ 0.03
Untreated <sup>e</sup>	117	0	105.1 $\pm$ 3.5	3.23 $\pm$ 0.06
Unmanaged <sup>f</sup>	17	0	101.9 $\pm$ 4.2	3.36 $\pm$ 0.07
Control stands	134	0	104.7 $\pm$ 3.1	3.25 $\pm$ 0.05

<sup>a</sup> Treated as individual tree selection, selection harvest, or firewood cut.

<sup>b</sup> Subjected to group selection harvest with or without associated individual tree selection.

<sup>c</sup> Combination of group selection and thinning within the same stand.

<sup>d</sup> Treated as shelterwood cut, seed-tree cut, or functional clearcut with residual trees retained.

<sup>e</sup> Managed stands that had not been treated for >20 years.

<sup>f</sup> Unmanaged stands designated as natural areas, research areas, old-growth, or set-aside areas.

Silvicultural treatments prescribed to enhance habitat suitability for wildlife (LMJV Forest Resource Conservation Working Group, 2007) applied to 180 of these surveyed stands from 1 to 20 year before surveys, averaged 9.5 years (SE = 0.4). Although treatments were ostensibly prescribed to attain a targeted forest structure, applied treatments varied greatly in intensity. Descriptive monikers for these silvicultural treatments, as reported by operational foresters, ranged from those described as individual selection cuts to functional clearcuts. For characterization of treatments, we grouped them into five broadly descriptive classes (Table 1). However, terminology used to describe treatments was not standardized for this study and therefore, we caution that resultant forest structure likely varied among and within these reported designations.

Mean reduction of 22% of total basal area on treated stands was significant ( $F_{1,312} = 36.22$ ,  $P < 0.01$ ), but notably the proportion of total basal area that was comprised of dead trees (snags) and large ( $\geq 50$  cm) diameter trees, at circa 3% and 33% respectively, was similar on treated and control stands. The ordinal rank of neither vine nor cane abundance differed ( $F_{1,312} < 0.57$ ,  $P > 0.45$ ) between treated and control stands, but we detected more understory and less overstory and midstory cover on treated stands ( $F_{1,312} > 6.55$ ,  $P \leq 0.01$ ). The variance in basal area was reduced on treated stands ( $F_{1,312} = 10.02$ ,  $P < 0.01$ ).

During 1275 point counts (1049 on treated stand; 676 on control stands) within 314 bottomland forest stands, we detected 33,823 individual birds (19,951 in treated stands; 13,872 in controls). We detected 74 species on treated stands and 72 species on control stands, but estimated species richness via rarefaction did not differ between control stands (76.5  $\pm$  4.8;  $CI_{95\%} = 72.8$ –96.8) and treated stands (82.1  $\pm$  7.1;  $CI_{95\%} = 75.8$ –109.6). Even so, avian diversity was greater on wildlife-forestry managed stands with Simpson Index of 20.1  $\pm$  0.2 on control stands and 21.7  $\pm$  0.2 on treated stands.

Of all detected species, 42 species were common such that we observed them on  $\geq 10$  stands. Observed indicator values (IV) for six of these species (American Crow [*Corvus brachyrhynchos*], Common Yellowthroat [*Geothlypis trichas*], Gray Catbird [*Dumetella carolinensis*], Indigo Bunting [*Passerina cyanea*], Kentucky Warbler [*Geothlypis formosa*], and Yellow-breasted Chat [*Icteria virens*]) suggested they were indicative of the bird communities on treated sites (IV  $\geq 10.5$ ,  $P \leq 0.026$ ). An equal number of these common species (Acadian Flycatcher [*Empidonax vireescens*], Carolina Chickadee [*Poecile carolinensis*], Northern Cardinal [*Cardinalis cardinalis*], Northern Parula [*Setophaga americana*], Prothonotary Warbler [*Protonotaria citrea*], and Red-eyed Vireo [*Vireo olivaceus*]) were

indicative of the bird communities on control sites ( $IV \geq 46.0$ ,  $P \leq 0.003$ ). In addition, there was some evidence ( $IV = 41.5$ ,  $P = 0.078$ ) of increased association of Brown-headed Cowbirds with treated sites.

We estimated densities of breeding birds in bottomland forests for 43 species (Table 2). For 23 species, estimated densities did not differ between treated and control stands, as evidenced by overlapping  $CI_{95\%}$ . Estimated densities for 16 species differed on treated and control stands but only two of these species, Common Yellowthroat and Yellow-breasted Chat, had greater densities on treated sites. Insufficient detections undermined separate density estimates within treated and control stands for four species: American Redstart (*Setophaga ruticilla*), Common Grackle (*Quiscalus quiscula*), Gray Catbird (*Dumetella carolinensis*), and Red-winged Blackbird (*Agelaius phoeniceus*). Therefore, we estimated detection probabilities, effective detection distances, and densities of these species within bottomland forest on public conservation lands irrespective of silvicultural treatment (Table 2).

Within occupancy analysis, estimated probability of detection exceeded 25% ( $p \geq 0.25$ ) for 27 species (Table 3). Time of survey (i.e., hours since dawn) influenced detection probability for all species except Yellow-billed Cuckoo (*Coccyzus americanus*). Detection of the majority of species (15) decreased later in the morning but detections of 11 species increased later in the morning (Table 3).

Treatment influenced the probability that a stand was occupied ( $\psi$ ) for 18 species: 10 species were more likely to occupy treated stands whereas eight species were more likely to occupy control stands. Only occupancies of Downy Woodpecker (*Picoides pubescens*) and Yellow-breasted Chat were strongly influenced by treatment, both species being more likely to occupy treated stands (Table 3). For 11 species, occupancy models with the most support included an effect for number of years post-treatment: for eight of these species their probability of occupancy was reduced over time, presumably as habitat returned to conditions more similar to those before treatment (Table 3). Number of years post-treatment had a strong negative influence on occupancy of Eastern Wood-pewee (*Contopus virens*) and Swainson's Warbler (*Limnithlypis swainsonii*), whereas Great-crested Flycatcher (*Myiarchus crinitus*) exhibited a strong positive response (Fig. 2). Occupancy of several other species, such as Yellow-breasted Chat (Fig. 2), were also influenced by time since treatment (Table 3). Basal area influenced occupancy of nine species: six of these species were positively influenced by basal area, thus indicating increased occupancy in stands with greater density or with larger trees (Table 3). Finally, overstory density influenced stand occupancy of nine species but its influence was equivocal, as four species exhibited a positive response whereas five species had a negative association (Table 3).

Within occupied stands, wildlife-forestry treatments influenced occupancy at survey points ( $\theta$ ) for 24 species (Table 4), which included seven species for which wildlife-forestry treatment did not influence the probability that the stand was occupied (Table 3). The influence of wildlife-forestry treatment varied among species. For 13 species, occupancy at survey points was positively influenced by wildlife-forestry treatment, including a strong influence on Indigo Bunting. Conversely, for 11 species point occupancy was negatively influenced by wildlife-forestry treatment, including strongly negative influences on Northern Cardinal, Northern Parula, and Prothonotary Warbler. Of the species that responded to treatment, point occupancies of 16 of these species were influenced by number of years post-treatment: four species responding strongly negatively and three species strongly positively (Table 4). Point occupancies of 10 species were negatively related with number of years post-treatment, but point occupancies of six species were positively related to this time since treatment covariate. Basal area influenced point occupancies of 12 species, seven positively

and five negatively (Table 4). Northern Parula and Prothonotary Warbler were more likely to occupy points with greater density of or larger trees (i.e., greater basal area), whereas American Redstart was less likely to occupy points with high basal area. Similarly, overstory canopy influenced point occupancies of 13 species. Again, responses to overstory canopy were ambiguous; with eight species responding negatively, including strong responses by Carolina Wren (*Thryothorus ludovicianus*) and White-eyed Vireo (*Vireo griseus*), and five species responding positively, including strong responses by Northern Cardinal and Yellow-breasted Chat (Table 4). Variance in basal area was not included as a covariate for any of the best models for stand occupancy or for within stand point occupancy.

## 5. Discussion

Our study included wildlife-forestry treatments that spanned all ages from 1 to 20 years post-treatment (Twedt and Wilson, 2016). The mean age of stands between treatment and survey was  $9.5 \pm 0.4$  years. The number of years post-treatment influenced stand occupancy of 10 species (3 positively) and within stand, point occupancy of 16 species (6 positively). However, habitat conditions markedly changed within treated stands over time, often tending to revert to their pretreatment state. These changes in habitat conditions are likely reflected in the changes in occupancy relative to number of years post-treatment (Fig. 2). Notably, others (Twedt and Somershoe, 2009; Porneluzi et al., 2014) found that the effects of silvicultural treatment on most bird species waned within 12–15 years, with densities thereafter returning to pretreatment levels. This reflects the need for continued management to maintain benefits of silviculture for some bird species. Because for some bird species in our study the effects of silvicultural treatment may have dissipated for surveys conducted within older treated stands, our results may appear to be less manifest than those of previous studies that examined forest management effects on birds within a relatively few years after treatments were implemented (Moorman and Guynn, 2001; Gram et al., 2003; Tozer et al., 2010). Moreover, many of our treated stands had relatively little change in vegetation structure compared to control stands. Indeed, compared to control stands, 74% of treated stands had <20% reduction in basal area at time of our surveys. This suggests differences in vegetation structure between treated and control stands were modest.

Despite the ranges in age post-treatment and habitat conditions on our study stands, we did find an increase in species diversity associated with wildlife-forestry treatments. Increased diversity was likely attributed to increased occupancy, and more regular occurrence, of birds using early seral habitats. Indeed, most of the species indicative of treated stands were species typically associated with forest edges, gaps in forest canopy, or early seral vegetation conditions, including Common Yellowthroat, Gray Catbird, Indigo Bunting, Kentucky Warbler, and Yellow-breasted Chat.

Densities of 16 bird species differed between treated and control stands but only two of these species (Common Yellowthroat and Yellow-breasted Chat) had greater densities on treated stands. The wide range of treatment age, denoted as the number of years post-treatment, and the modest differences in vegetation condition between treated and control stands at the time of our surveys may have contributed to the dearth of species exhibiting different densities on treated on control stands. This differed markedly from previous studies in bottomland forests wherein higher densities on treated stands were prevalent. Indeed, Twedt and Somershoe (2009) found nine of 14 species that differed in density had greater density on stands managed by wildlife-forestry silviculture. Similarly, Heltzel and Leberg (2006) reported an increased number of

**Table 2**  
Estimated avian density (D: birds/km<sup>2</sup>) and 95% confidence interval (CI) for species that differed in density between stands subjected to wildlife forestry silvicultural treatment (t) and control stands (c) within bottomland forest on public conservation lands in the Mississippi Alluvial Valley that were surveyed for species from 2006 to 2012. The numbers of detections (n) during 10-min point counts (1049 on treated stand; 676 on control stands) were used to estimate species-specific probability of detection (P<sub>a</sub>) and effective detection radius (EDR; m).

Species		Detection probability		EDR		Density (birds/km <sup>2</sup> )		
Common and scientific name	n	P <sub>a</sub>	95% CI	m	95% CI	D	95% CI	
Acadian Flycatcher,	c	1158	0.96	0.95–0.97	42	40–43	327.9	304–354
<i>Empidonax virescens</i>	t	1162	0.93	0.91–0.95	51	49–52	147.4	136–161
American Crow,	c	321	0.94	0.90–0.96	224 <sup>a</sup>	139–359 <sup>a</sup>	11.4	11–13
<i>Corvus brachyrhynchos</i>	t	668	0.92	0.89–0.95	— <sup>b</sup>	— <sup>b</sup>	15.5	15–17
American Redstart,	c	21	0.96	0.83–1.00	45	36–55	2.7 <sup>c</sup>	2–5
<i>Setophaga ruticilla</i>	t	7						
Barred Owl,	c	47	0.68	0.35–0.95	267 <sup>a</sup>	46–1554 <sup>a</sup>	2.3	2–30
<i>Strix varia</i>	t	101	0.54	0.26–0.87	— <sup>b</sup>	— <sup>b</sup>	4.0	2–55
Blue-gray Gnatcatcher,	c	553	0.96	0.94–0.97	27	26–28	369.5	331–414
<i>Poliophtila caerulea</i>	t	913	0.96	0.94–0.97	36	35–37	225.1	207–246
Blue Jay,	c	137	0.83	0.70–0.93	66	59–73	18.1	13–26
<i>Cyanocitta cristata</i>	t	180	0.82	0.70–0.91	85	76–95	9.7	7–14
Brown-headed Cowbird,	c	241	0.66	0.49–0.81	43	40–46	92.2	64–142
<i>Molothrus ater</i>	t	485	0.76	0.67–0.84	50	48–53	76.6	63–95
Carolina Chickadee,	c	566	0.87	0.83–0.91	42	40–44	172.2	150–199
<i>Poecile carolinensis</i>	t	649	0.85	0.80–0.89	48	46–50	102.4	89–119
Carolina Wren,	c	1012	0.92	0.89–0.94	57	55–59	159.6	146–176
<i>Thryothorus ludovicianus</i>	t	1501	0.93	0.92–0.95	58	56–59	147.2	137–159
Common Grackle,	c	13	0.35	0.03–1.00	99	74–133	2.3 <sup>c</sup>	1–47
<i>Quiscalus quiscula</i>	t	26						
Common Yellowthroat,	c	19	0.98	0.87–1.00	38	29–49	6.3	4–12
<i>Geothlypis trichas</i>	t	66	0.94	0.86–0.99	50	44–57	8.4	6–12
Downy Woodpecker,	c	246	0.51	0.31–0.75	49	45–52	95.2	56–182
<i>Picoides pubescens</i>	t	419	0.67	0.55–0.79	57	54–60	58.8	45–80
Eastern Towhee,	c	70	0.97	0.93–0.99	38	33–43	23.8	18–33
<i>Pipilo erythrophthalmus</i>	t	147	0.84	0.73–0.93	56	51–61	16.9	13–24
Eastern Wood-pewee,	c	297	0.84	0.75–0.90	72	67–77	32.8	27–42
<i>Contopus virens</i>	t	508	0.93	0.90–0.95	78	73–83	28.0	25–32
Gray Catbird,	c	3	0.96	0.88–0.99	51	43–60	2.9 <sup>c</sup>	2–5
<i>Dumetella carolinensis</i>	t	36						
Great-crested Flycatcher,	c	348	0.84	0.77–0.90	63	60–67	48.5	40–60
<i>Myiarchus crinitus</i>	t	458	0.87	0.81–0.91	71	67–75	32.0	27–38
Hairy Woodpecker,	c	44	0.59	0.23–0.96	53	45–62	12.6	6–46
<i>Picoides villosus</i>	t	46	0.35	0.03–1.00	59	50–70	11.2	3–159
Hooded Warbler,	c	114	0.94	0.88–0.98	47	42–52	25.7	20–34
<i>Setophaga citrina</i>	t	153	0.84	0.73–0.93	52	47–56	20.8	16–29
Indigo Bunting,	c	570	0.93	0.90–0.95	58	55–60	86.9	77–98
<i>Passerina cyanea</i>	t	997	0.91	0.88–0.93	66	63–68	77.9	71–86
Kentucky Warbler,	c	145	0.69	0.49–0.86	63	57–69	25.1	17–42
<i>Geothlypis formosa</i>	t	274	0.85	0.77–0.91	57	53–61	30.6	25–39
Northern Cardinal,	c	1275	0.95	0.93–0.96	60	58–62	178.1	165–192
<i>Cardinalis cardinalis</i>	t	1641	0.91	0.89–0.93	64	62–66	133.4	124–144
Northern Flicker,	c	23	0.82	0.49–0.99	179 <sup>a</sup>	58–557 <sup>a</sup>	0.9	0.8–7
<i>Colaptes auratus</i>	t	40	0.68	0.32–0.96	112	78–160 <sup>a</sup>	1.7	0.9–6
Northern Parula,	c	456	0.86	0.81–0.91	48	45–50	109.2	93–130
<i>Setophaga americana</i>	t	466	0.87	0.82–0.92	56	53–59	52.1	45–61
Orchard Oriole,	c	23	0.71	0.29–0.99	50	40–64	6.0	3–23
<i>Icterus spurius</i>	t	46	0.34	0.03–1.00	57	48–67	12.8	3–206
Painted Bunting,	c	21	0.56	0.10–1.00	46	36–59	8.2	3–71
<i>Passerina ciris</i>	t	49	0.65	0.31–0.95	55	47–65	7.5	4–22
Pileated Woodpecker,	c	329	0.82	0.74–0.89	97	88–107	22.0	18–29
<i>Dryocopus pileatus</i>	t	455	0.81	0.74–0.88	117	107–128	15.3	13–19
Prothonotary Warbler,	c	797	0.96	0.94–0.97	49	47–51	161.1	147–177
<i>Protonotaria citrea</i>	t	765	0.91	0.88–0.93	63	60–65	65.5	59–74
Red-bellied Woodpecker,	c	774	0.84	0.79–0.88	68	65–71	95.4	84–110
<i>Melanerpes carolinus</i>	t	1164	0.87	0.84–0.90	75	72–78	73.4	66–82
Red-eyed Vireo,	c	423	0.95	0.92–0.97	48	46–51	90.3	79–103
<i>Vireo olivaceus</i>	t	474	0.94	0.91–0.96	54	51–57	52.1	46–59
Red-headed Woodpecker,	c	32	0.86	0.61–0.98	45	37–55	8.7	5–18
<i>Melanerpes erythrocephalus</i>	t	55	0.68	0.37–0.94	73	62–87	4.7	2–12
Red-shouldered Hawk,	c	84	0.85	0.69–0.95	160 <sup>a</sup>	99–258 <sup>a</sup>	3.3	3–6
<i>Buteo lineatus</i>	t	126	0.84	0.71–0.93	192 <sup>a</sup>	110–337 <sup>a</sup>	3.2	3–5
Ruby-throated Hummingbird,	c	134	0.44	0.18–0.83	19	18–22	379	162–1166
<i>Archilochus colubris</i>	t	221	0.40	0.17–0.74	19	18–20	473.5	217–1277
Red-winged Blackbird,	c	48	1.00	1.00–1.00	37	31–43	6.6 <sup>c</sup>	5–9
<i>Agelaius phoeniceus</i>	t	0						
Summer Tanager	c	325	0.72	0.60–0.83	55	51–58	71.2	55–97
<i>Piranga rubra</i>	t	458	0.81	0.74–0.88	62	59–65	44.9	38–55
Swainson's Warbler,	c	44	0.86	0.66–0.97	47	40–55	10.9	7–20
<i>Limnithlypis swainsonii</i>	t	65	0.92	0.80–0.98	52	46–60	7.8	6–12

Table 2 (continued)

Species			Detection probability		EDR		Density (birds/km <sup>2</sup> )	
Common and scientific name	n		P <sub>a</sub>	95% CI	m	95% CI	D	95% CI
Tufted Titmouse,	c	1072	0.92	0.90–0.94	59	57–61	159.7	146–175
<i>Baeolophus bicolor</i>	t	1541	0.92	0.90–0.93	61	59–63	137.7	128–149
White-breasted Nuthatch,	c	99	0.85	0.72–0.95	43	39–48	29.0	21–43
<i>Sitta carolinensis</i>	t	124	1.00	0.63–0.91	64	58–72	9.1	8–18
White-eyed Vireo,	c	545	0.94	0.91–1.00	44	42–46	141.5	121–160
<i>Vireo griseus</i>	t	891	0.91	0.88–0.93	50	49–52	117.4	106–130
Wood Thrush,	c	60	0.93	0.82–0.98	64	58–72	7.4	6–10
<i>Hylocichla mustelina</i>	t	86	0.91	0.80–0.97	64	58–72	7.0	5–10
Yellow-breasted Chat,	c	47	0.97	0.91–1.00	53	45–62	8.1	6–12
<i>Icteria virens</i>	t	521	0.93	0.90–0.95	69	65–72	36.3	32–42
Yellow-billed Cuckoo,	c	894	0.82	0.77–0.86	81	78–85	80.2	70–93
<i>Coccyzus americanus</i>	t	1374	0.83	0.79–0.86	98	93–103	58.2	52–66
Yellow-throated Vireo,	c	73	0.84	0.67–0.95	46	41–53	19.0	13–31
<i>Vireo flavifrons</i>	t	100	0.85	0.72–0.95	67	59–75	8.0	6–12
Yellow-throated Warbler,	c	67	0.88	0.73–0.97	114	86–150	3.4	2–6
<i>Setophaga dominica</i>	t	66	0.81	0.60–0.95	85	71–102	3.6	2–7

<sup>a</sup> Effective detection radius exceeded maximum survey radius of 150 m. Maximum survey distance used to estimate species densities.

<sup>b</sup> Effective detection radius not estimated. Maximum survey distance (150 m) used to estimate species densities.

<sup>c</sup> Too few observations for separate estimates within treated and control stands. Estimates are for all surveyed bottomland stands.

Table 3

The influence<sup>a</sup> of hours since dawn (HSD) on the probability of presentation for detection (p) and the influence of treatment (trt), years post-treatment (ypt), basal area (ba), and overstory canopy (os) on probability of stand occupancy (Ψ, SE) by species in stands subjected to wildlife forestry silvicultural treatment (treated) and control stands (control) for bottomland forest on public conservation lands in the Mississippi Alluvial Valley that were surveyed from 2006 to 2012.

Species	p	HSD	Control		Treated		trt	ypt	ba	os
			Ψ	SE	Ψ	SE				
Acadian Flycatcher	0.71	++	0.992	0.008	0.989	0.014	–	+	o	+
American Crow	0.32	---	0.794	0.034	0.792	0.016	–	–	o	–
American Redstart	0.44	++	0.108 <sup>b</sup>	0.034	– <sup>b</sup>		o			
Blue-gray Gnatcatcher	0.53	---	0.797 <sup>b</sup>	0.024	– <sup>b</sup>		o			
Brown-headed Cowbird	0.29	–	0.773	0.031	0.775	0.009	+	o	o	o
Carolina Chickadee	0.43	++	0.944	0.021	0.948	0.013	+	–	++	o
Carolina Wren	0.70	–	0.982 <sup>b</sup>	0.008	– <sup>b</sup>		o			
Downy Woodpecker	0.33	–	0.685	0.057	0.840	0.054	++	–	+	o
Eastern Wood-pewee	0.34	---	0.758	0.039	0.799	0.029	+	---	+	o
Great-crested Flycatcher	0.34	---	0.846	0.049	0.839	0.067	–	++	++	o
Indigo Bunting	0.52	---	0.872	0.027	0.896	0.019	+	+	+	o
Mourning Dove	0.25	---	0.520	0.079	0.565	0.104	+	–	o	+
Northern Cardinal	0.79	++	0.997 <sup>b</sup>	0.003	– <sup>b</sup>		o			
Northern Parula	0.44	++	0.739 <sup>b</sup>	0.028	– <sup>b</sup>		o			
Painted Bunting	0.27	–	0.149	0.045	0.146	0.044	–	o	o	–
Pileated Woodpecker	0.31	–	0.905	0.044	0.926	0.052	+	o	–	o
Prothonotary Warbler	0.61	–	0.949	0.022	0.911	0.043	–	o	–	o
Red-bellied Woodpecker	0.59	–	0.938 <sup>b</sup>	0.014	– <sup>b</sup>		o			
Red-eyed Vireo	0.39	–	0.859	0.035	0.833	0.039	–	o	o	–
Summer Tanager	0.25	–	0.837 <sup>b</sup>	0.027	– <sup>b</sup>		o			
Swainson's Warbler	0.35	–	0.458	0.081	0.764	0.130	+	---	–	–
Tufted Titmouse	0.64	---	0.977 <sup>b</sup>	0.009	– <sup>b</sup>		o			
White-breasted Nuthatch	0.25	–	0.263	0.047	0.302	0.067	+	o	+	o
White-eyed Vireo	0.54	–	0.826	0.065	0.778	0.086	–	o	o	+
Yellow-breasted Chat	0.47	---	0.154	0.050	0.490	0.108	++	–	o	---
Yellow-billed Cuckoo	0.67	o	0.962 <sup>b</sup>	0.011	– <sup>b</sup>		o			
Yellow-throated Warbler	0.27	–	0.495	0.248	0.272	0.210	–	–	o	+

<sup>a</sup> Influence of covariates included in best supported model(s) are denoted as negative (–) or positive (+). Covariates with strong influence, as indicated by the odds ratio on their 95% confidence interval on beta not including 1.0 (equal odds), are denoted as -- or ++. Covariates not included in model(s) with most support are denoted as (o).

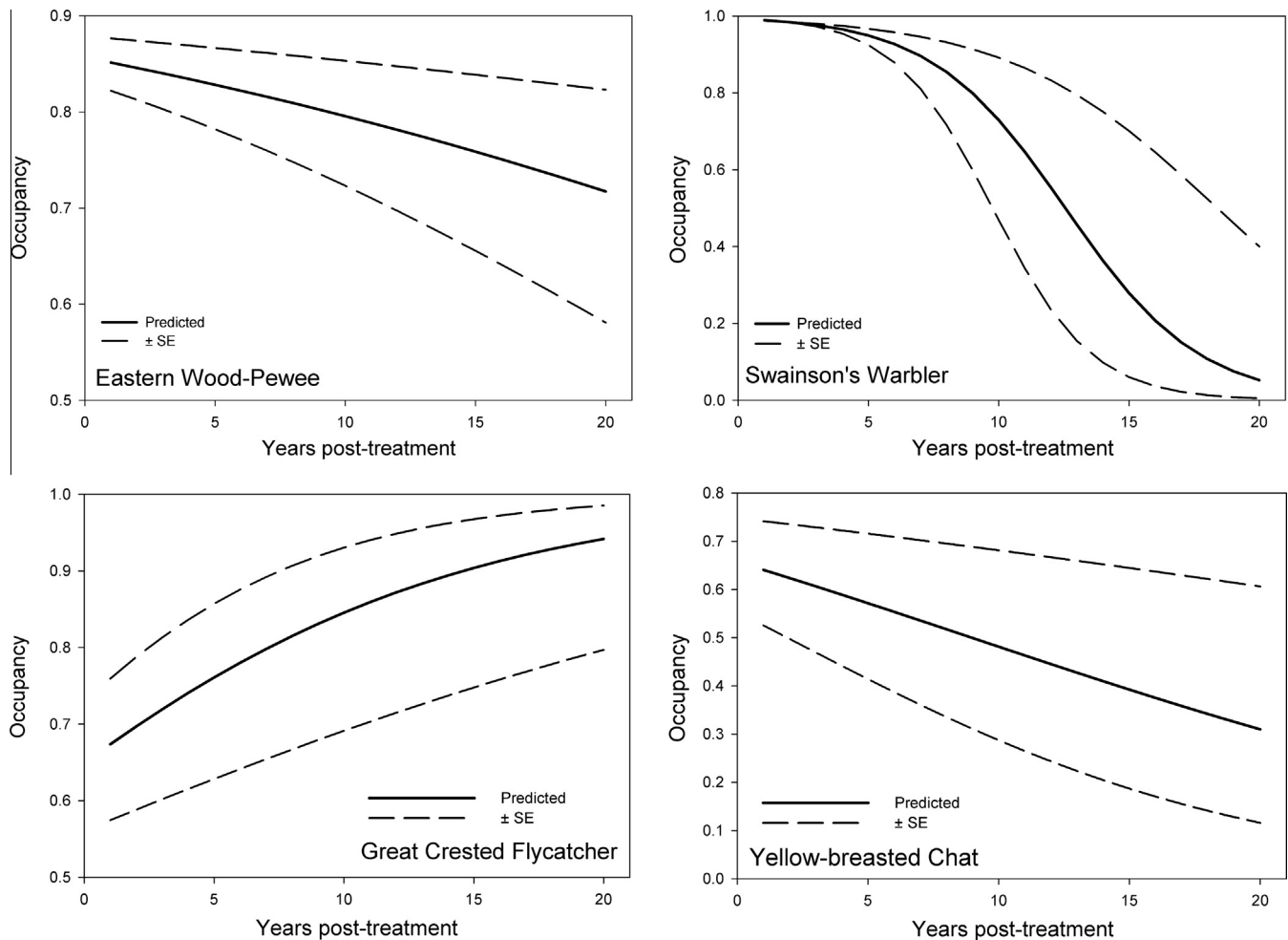
<sup>b</sup> Probability of occupancy (Ψ) did not differ between control and treated stands.

detections on stands subjected to selective timber harvest for 14 of 17 species that differ significantly from unmanaged stands. Finally, [Norris et al. \(2009\)](#) found that of 27 species with significantly different densities for reference and partially harvested stands, 17 species had greater density on harvested stands: 9 species for individual selection harvest, 4 species for group selection, and 4 species for more extensive harvest of >40% of canopy.

Estimated densities of some species, such as Acadian Flycatcher and Blue-gray Gnatcatcher, were relatively high ([Table 2](#)). These

species are fairly ubiquitous within bottomland forests of the Mississippi Alluvial Valley and previously reported densities for both species at Tensas River NWR were similar to estimated densities in this region-wide study (Acadian Flycatcher = 3.10–4.92 birds/ha and Blue-gray Gnatcatcher = 3.27–4.23 birds/ha confidence limits: [Twedt and Somershoe, 2009](#)). Even so, it is possible that our method of estimation may inflate densities of species that have weak vocalizations and therefore are rarely detected at distances >50 m. Notably, the effective detection distance of Blue-





**Fig. 2.** Effect of years post-treatment on occupancy ( $\psi$ ) of bottomland forest stands in the Mississippi Alluvial Valley predicted from the most supported models of treatment effects with other covariates (basal area and overstory cover) held constant at their mean values.

Gray Gnatcatcher within control stands during this study was 26–28 m (Table 2).

In northern hardwood forests, Rankin and Perlut (2015) found stand occupancy increased for four of five species that responded to 18% reduced basal area and 10% reduced canopy cover. For species with significant covariates that explained variation in occupancy, basal area positively influenced three of four species, whereas canopy cover positively influenced four of five species (Rankin and Perlut, 2015). Although the bird community at our bottomland study sites shared few species with the bird community in northern hardwood forests, we similarly found occupancy, for six of nine species, was positively related to basal area and four of nine species had occupancy positively related to canopy cover.

Despite the paucity of species that had increased density on treated stands in our study, probability of stand occupancy was positively related to treatment for 10 of 18 species that included treatment as a covariate in their best predictive model(s). Similarly, the probability of occupancy at a surveyed point within an occupied stand was greater in treated stands for 13 of 24 species that included treatment as a covariate within their best predictive model(s). However, some species, such as Swainson's Warbler, appeared to respond differently to treatments at landscape (i.e., stand occupancy) and local (i.e., within stand occupancy) scales. These differences may be due to greater overall attraction to patchiness of forests resulting from treatments at a landscape scale

(Table 3) and a positive response at a local scale to changing density of understory vegetation where the canopy has recently increased or closed, such as in older harvest or treefall gaps (Table 4). Even though the most supported models of occupancy for many species included treatment as a covariate, the modest differences in estimated occupancy between treated and control stands for many species suggests that treatment may have little ecologically relevant effect on stand occupancy. For example, an increase in occupancy by Indigo Bunting from 0.872 to 0.896 or decreased occupancy by Prothonotary Warbler from 0.949 to 0.911 on wildlife-forestry managed stands compared to control stands probably has few ecological ramifications within the ecosystem.

We included variance of basal area as potential covariate in occupancy models because heterogeneity of forest structure within a treated stand is a desired structural characteristic within bottomland forests (LMVJV Forest Resource Conservation Working Group, 2007). We assumed that the heterogeneous application wildlife-forestry treatment and resultant canopy gaps would increase variance of basal area, but unexpectedly we found that the variance in basal area was reduced on treated stands. Regardless, variation in basal area was not included in the most supported occupancy models for any species that had a detection probability  $>0.25$ , suggesting variance in basal area was not markedly influencing stand occupancy or occupancy at points within stands.

**Table 4**

Probability that surveyed points within occupied stand were occupied (i.e., point occupancy;  $\theta$ , SE) by species in stands subjected to wildlife forestry silvicultural treatment (treated) and control stands (control), and the influence<sup>a</sup> of treatment (trt), years post-treatment (ypt), basal area (ba), and overstory canopy (os) on point occupancy within occupied bottomland forest stands on public conservation lands in the Mississippi Alluvial Valley that were surveyed from 2006 to 2012.

Species	Control		Treated		trt	ypt	ba	os
	$\theta$	SE	$\theta$	SE				
Acadian Flycatcher	0.918	0.027	0.816	0.056	--	-	o	+
American Crow	0.794	0.034	0.792	0.016	-	-	o	-
American Redstart <sup>b</sup>	0.265	0.186	0.087	0.087	-	-	--	o
Blue-gray Gnatcatcher <sup>b</sup>	0.759	0.038	0.727	0.047	-	+	+	o
Brown-headed Cowbird	0.781	0.073	0.787	0.013	+	o	o	o
Carolina Chickadee	0.847	0.065	0.715	0.089	-	+	-	o
Carolina Wren <sup>b</sup>	0.829	0.030	0.838	0.034	+	-	o	--
Downy Woodpecker	0.694	0.074	0.743	0.071	+	--	+	o
Eastern Wood-pewee	0.719	0.078	0.752	0.073	+	-	-	o
Great-crested Flycatcher	0.709	0.064	0.711	0.066	+	-	+	o
Indigo Bunting	0.618	0.043	0.817	0.047	++	--	+	o
Mourning Dove	0.482	0.099	0.436	0.100	-	+	o	-
Northern Cardinal <sup>b</sup>	0.989	0.012	0.811	0.165	--	o	o	++
Northern Parula <sup>b</sup>	0.867	0.036	0.661	0.110	--	--	++	-
Painted Bunting	0.358 <sup>b</sup>	0.123	- <sup>c</sup>		o			
Pileated Woodpecker	0.714 <sup>b</sup>	0.058	- <sup>c</sup>		o			
Prothonotary Warbler	0.763	0.035	0.636	0.051	--	o	++	o
Red-bellied Woodpecker <sup>b</sup>	0.775	0.037	0.794	0.038	+	o	o	--
Red-eyed Vireo	0.782	0.084	0.655	0.095	-	o	o	-
Summer Tanager <sup>b</sup>	0.983	0.037	0.994	0.017	+	o	+	o
Swainson's Warbler	0.525	0.161	0.209	0.137	-	++	-	+
Tufted Titmouse <sup>b</sup>	0.880	0.031	0.902	0.032	+	++	o	+
White-breasted Nuthatch	0.749 <sup>b</sup>	0.135	- <sup>c</sup>		o			
White-eyed Vireo	0.726	0.044	0.744	0.045	+	o	o	--
Yellow-breasted Chat	0.428	0.130	0.573	0.138	+	--	o	++
Yellow-billed Cuckoo <sup>b</sup>	0.809	0.030	0.846	0.032	+	o	-	o
Yellow-throated Warbler	0.206	0.115	0.420	0.204	+	++	o	--

<sup>a</sup> Influence of covariates included in best supported model(s) are denoted as negative (-) or positive (+). Covariates with strong influence, as indicated by the odds ratio on their 95% confidence interval on beta not including 1.0 (equal odds), are denoted as -- or ++. Covariates not included in model(s) with most support denoted as (o).

<sup>b</sup> Species occupancy of stands (Table 3) was not influenced by treatment.

<sup>c</sup> Probability that surveyed points within occupied stand were occupied ( $\theta$ ) did not differ between control and treated stands.

## 6. Management implications

Wildlife-forestry aspires to improve forest habitat for a variety of wildlife species, including threatened species such as the Louisiana black bear (*Ursus americanus luteolus*; LMJV Forest Resource Conservation Working Group, 2007). In the same way, resultant habitat conditions target high priority bird species such as Swainson's Warbler and Prothonotary Warbler (Partners in Flight Science Committee, 2012). Although occupancy of Swainson's Warbler was markedly greater on treated stands, density and occupancy of Prothonotary Warbler were greater on control stands. This is similar to these species temporal response to wildlife-forestry wherein Prothonotary Warbler densities declined for circa 13 years post-treatment but Swainson's Warbler densities began to increase after about five years post-treatment (Twedt and Somershoe, 2009). For other species of moderately high conservation concern such as Orchard Oriole, Red-headed Woodpecker, Wood Thrush, and White-eyed Vireo, overlapping confidence intervals indicated their densities were unaffected by wildlife-forestry treatments. Occupancy for these species was equivocal and only estimated for White-eyed Vireo, which had decreased stand occupancy associated with wildlife-forestry treatment but increased point occupancy within occupied stands.

One explanation for our ambiguous results is that at the time of our surveys most treated stands (74%) had less than 20% reduction in basal area compared to control stands (Table 1). Therefore, differences in forest structure between treated and control stands were not patent. This apparent similarity of forest structures on treated and control stands may have been a function of time since treatment or silvicultural treatments may have removed insufficient volume to achieve marked differences between treated and control stands. If managers desire a significant difference in forest

structure post-treatment, management prescriptions must ensure sufficient volume or canopy removal to achieve this objective.

Notably, current treatments that increase occupancy of birds using early seral stage forest appear to benefit avian conservation in bottomland forests. Indeed, four species that were indicative of treated stands have significant regional (Common Yellowthroat and Yellow-breasted Chat) or continental (Indigo Bunting and Kentucky Warbler) population declines (BBS trend data, Sauer et al., 2014). Presumably, harvest prescriptions for increased canopy removal would similarly benefit this suite of species. However, some of these species (e.g., Indigo Bunting and Yellow-breasted Chat) also occupy early seral stands following afforestation (Twedt et al., 2002) or forestry practices often used on privately owned lands (e.g., shelterwood, seed tree, clear cuts, and patch clear cuts; Kendrick et al., 2015). As these bird species respond favorably to early-seral conditions resulting from forest management on private lands, it may behoove forest managers of public lands to implement wildlife-forestry practices that promote forest structural conditions that more closely resemble late-seral (i.e., older-growth) forests (McClellan, 2004; Bauhus et al., 2009).

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descriptive purposes only and does not imply endorsement by the U.S. Government. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.10.031>. These data include Google maps of the most important areas described in this article.

## References

- Avery, T.E., Burkhart, H.E., 2002. *Forest Measurements*. McGraw-Hill, New York.
- Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. *For. Ecol. Manage.* 258, 525–537.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford University Press, New York, USA.
- Buckland, S.T., 2006. Point-transect surveys for songbirds: robust methodologies. *Auk* 123, 345–357.
- Bugmann, H., 2001. A review of forest gap models. *Climatic Change* 51, 259–305.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference*. Springer, New York.
- Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., White, P.S., 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. For. Res.* 20, 620–631.
- Clatterbuck, W.K., Meadows, J.S., 1993. Regenerating oaks in the bottomlands General Technical Report SE-84. In: Loftis, D., McGee, C.E. (Eds.), *Oak Regeneration: Serious Problems, Practical Recommendations*. Symposium Proceedings, 8–10 September 1992, Knoxville, TN. U.S. Department Agriculture, Forest Service, Southeastern Forest Experiment Station, Asheville, North Carolina, pp. 184–195.
- Colwell, R.K., Chao, A., Gotelli, N.J., Lin, S.Y., Mao, C.X., Chazdon, R.L., Longino, J.T., 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *J. Plant Ecol.* 5, 3–21.
- Doherty, P.F., White, G.C., Burnham, K.P., 2012. Comparison of model building and selection strategies. *J. Ornithol.* 152 (Suppl. 2), S317–S323.
- Dufrenoy, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67, 345–366.
- Eyre, F.H., 1980. *Forest Cover Types of the United States and Canada*. Society of American Foresters, Washington, DC, USA.
- Franklin, J.F., 1990. Biological legacies: a critical management concept from Mount St. Helens. In: McCabe, R.E., (Ed.), *Transaction of the 55th North American Wildlife and Natural Resources Conference*, Denver, Colorado, pp. 216–219.
- Franklin, J.F., Spies, T.A., Pelt, R.V., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manage.* 155, 399–423.
- Gram, W.K., Perneluzi, P.A., Clawson, R.L., Faaborg, J., Richter, S.C., 2003. Effects of experimental forest management on density and nesting success of bird species in Missouri Ozark forests. *Cons. Biol.* 17, 1324–1337.
- Hamel, P.B., Smith, W.P., Twedt, D.J., Woehr, J.R., Morris, E., Hamilton, R.B., Cooper, R.J., 1996. *A land manager's guide to point counts of birds in the Southeast U.S.* Dept. of Agriculture, Forest Service, General Technical Report SO-120. Southern Research Station, New Orleans, Louisiana, p. 39.
- Heltzel, J.M., Leberg, P.L., 2006. Effects of selective logging on breeding bird communities in bottomland hardwood forests of Louisiana. *J. Wildl. Manage.* 70, 1416–1424.
- Hsieh, T.C., Ma, K.H., Chao, A., 2015. iNEXT: An R package for interpolation and extrapolation of species diversity (Hill numbers). <http://chao.stat.nthu.edu.tw/blog/software-download> (Accessed 16.09.13).
- Hunter, W.C., Buehler, D.A., Canterbury, R.A., Confer, J.L., Hamel, P.B., 2001. Conservation of disturbance-dependent birds in eastern North America. *Wildl. Soc. Bull.* 29, 440–455.
- Kendrick, S.W., Perneluzi, P.A., Thompson III, R.R., Morris, D.L., Haslerig, J.M., Faaborg, J., 2015. Stand-level bird response to experimental forest management in the Missouri Ozarks. *J. Wildl. Manage.* 79, 50–59.
- LMJV Forest Resource Conservation Working Group, 2007. Restoration, management, and monitoring of forest resources in the Mississippi Alluvial Valley: recommendations for enhancing wildlife habitat. In: Wilson, R., Ribbeck, K., King, S., Twedt, D. (Eds.), *Lower Mississippi Valley Joint Venture*, Vicksburg, Mississippi, USA, 88 p.
- MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., Franklin, A.B., 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84, 2200–2207.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83, 2248–2255.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2006. *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Elsevier, Burlington, Massachusetts, USA.
- McClellan, M.C., 2004. Development of silvicultural systems for maintaining old-growth conditions in the temperate rainforest of southeast Alaska. *For. Snow Landsc. Res.* 78, 173–190.
- McCune, B., Mefford, M.J., 2011. *PC-ORD. Multivariate Analysis of Ecological Data*. Version 6.08, MjM Software, Gleneden Beach, Oregon, USA.
- McHugh, M.L., 2009. The odds ratio: calculation, usage, and interpretation. *Biochemia Medica* 19, 120–126.
- McShea, W.J., Healy, W.M., Devers, P., Fearer, T., Koch, F.H., Stauffer, D., Waldon, J., 2007. Forestry matters: decline of oaks will impact wildlife in hardwood forests. *J. Wildl. Manage.* 71, 1717–1728.
- Meadows, J.S., Stanturf, J.A., 1997. Silvicultural systems for southern bottomland hardwood forests. *For. Ecol. Manage.* 90, 127–140.
- Meadows, S., Moller, H., Weller, F., 2012. Reduction of bias when estimating bird abundance within small habitat fragments. *N. Z. J. Ecol.* 36, 408–415.
- Moorman, C.E., Guynn, D.C., 2001. Effects of group-selection opening size on breeding bird habitat use in a bottomland forest. *Ecol. Appl.* 11, 1680–1691.
- Nichols, J.D., Bailey, L.L., O'Connell, A.F., Talancy, N.W., Grant, E.H.C., Gilbert, A.T., Annand, E.M., Husband, T.P., Hines, J.E., 2008. Multi-scale occupancy estimation and modelling using multiple detection methods. *J. Appl. Ecol.* 45, 1321–1329.
- Norris, J.L., Chamberlain, M.J., Twedt, D.J., 2009. Effects of wildlife forestry on abundance of breeding birds in bottomland hardwood forests of Louisiana. *J. Wildl. Manage.* 73, 1368–1379.
- Partners in Flight Science Committee, 2012. *Species Assessment Database*, version 2012 <http://rmbio.org/pifassessment> (Accessed 16.04.05).
- Pavlacky Jr., D.C., Blakesley, J.A., White, G.C., Hanni, D.J., Lukacs, P.M., 2012. Hierarchical multi-scale occupancy estimation for monitoring wildlife populations. *J. Wildl. Manage.* 76, 154–162.
- Perneluzi, P.A., Brito-Aguilar, R., Clawson, R.L., Faaborg, J., 2014. Long-term dynamics of bird use of clearcuts in post-fledging period. *Wilson J. Ornithol.* 126 (623–634), 2014.
- Rankin, D.R., Perlut, N.G., 2015. The effects of forest stand improvement practices on occupancy and abundance of breeding songbirds. *For. Ecol. Manage.* 335, 99–107.
- Sauer, J.R., Hines, J.E., Fallon, J.E., Pardieck, K.L., Ziolkowski Jr., D.J., Link, W.A., 2014. *The North American Breeding Bird Survey, Results and Analysis 1966 - 2013*. Version 01.30.2015 USGS Patuxent Wildlife Research Center, Laurel, MD. <http://www.mbr-pwrc.usgs.gov/bbs/> (Accessed 16.07.25).
- Sólymos, P., Matsuoka, S.M., Bayne, E.M., Lele, S.R., Fontaine, P., Cumming, S.G., Stralberg, D., Schmiegelow, F.K.A., Song, S.J., 2013. Calibrating indices of avian density from non-standardized survey data: making the most of a messy situation. *Methods Ecol. Evol.* 4, 1047–1058.
- Sólymos, P., Moreno, M., Lele, S.R., 2014. Detect: An R package for analyzing wildlife data with detection error. <https://cran.r-project.org/web/packages/detect/> (Accessed 16.07.25).
- Symonds, M.R.E., Moussalli, A., 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav. Ecol. Sociobiol.* 65, 13–21.
- Tozer, D.C., Burke, D.M., Nol, E., Elliott, K.A., 2010. Short-term effects of group-selection harvesting on breeding birds in a northern hardwood forest. *For. Ecol. Manage.* 259, 1522–1529.
- Twedt, D.J., 2012. *Wildlife forestry*. In: Okia, C.A. (Ed.), *Global Perspectives on Sustainable Forest Management*, ISBN: 978-953-51-0569-5. Rijeka, Croatia: INTECH, pp. 161–190. <http://www.intechopen.com/books/global-perspectives-on-sustainable-forest-management/wildlife-forestry> (Accessed 15.08.25).
- Twedt, D.J., Loesch, C.R., 1999. Forest area and distribution in the Mississippi alluvial valley: implications for breeding bird conservation. *J. Biogeogr.* 26, 1215–1224.
- Twedt, D.J., Somershoe, S.G., 2009. Bird response to prescribed silvicultural treatments in bottomland hardwood forests. *J. Wildl. Manage.* 73, 1140–1150.
- Twedt, D.J., Somershoe, S.G., 2013. Regeneration in bottomland forest canopy gaps six years after variable retention harvests to enhance wildlife habitat. In: Guldin, J. (Ed.), *Proceedings of the Fifteenth Biennial Southern Silvicultural Research Conference*, U.S. Forest Service, General Technical Report SRS-175, Asheville, North Carolina, pp. 261–269.
- Twedt, D.J., Wilson, R.R., 2016. Data on birds and habitat associated with forest management on public conservation areas in the Mississippi Alluvial Valley. Data in Brief (2016) [submitted for publication].
- Twedt, D.J., Wilson, R.R., Henne-Kerr, J.L., Grosshuesch, D.A., 2002. Avian response to bottomland hardwood reforestation: the first 10 years. *Rest. Ecol.* 10, 645–655.
- Wilson, R., Ribbeck, K., Denman, J., Johnson, E., Blaney, M., Hunter, C., Reinecke, K., 2007. Prospectus for Ivory-billed Woodpecker habitat assessment. In: Wilson, R., Ribbeck, K., King, S., Twedt, D. (Eds.), *Restoration, Management, and Monitoring of Forest Resources in the Mississippi Alluvial Valley: Recommendations for Enhancing Wildlife Habitat*. Lower Mississippi Valley Joint Venture, Vicksburg, Mississippi, pp. 71–76.
- Wu, J., Guan, D., Han, S., Zhang, M., Jin, C., 2005. Ecological functions of coarse woody debris in forest ecosystem. *J. For. Res.* 16, 247–252.