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Long-term responses of disturbance-associated birds after different timber harvests

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ABSTRACT

Timber harvest provides favorable habitat for many species of shrub-dependent birds. Because of historical dominance, effect of clearcutting on early successional birds has been widely studied, but less information is available on alternatives such as shelterwood and group selection, which have become a more dominant means of regenerating pines (*Pinus* spp.) on federal lands of the southeastern US. We compared detection of 12 species of early successional forest birds prior to harvest and at various intervals for 16 years after harvest in stands subjected to clearcutting, shelterwood, single-tree selection, and group-selection harvests. We also compared detection rates of these species between harvested and unharvested control stands. Detection rate for all early successional species combined peaked 5 years after harvest and was greatest in clearcuts 5–12 years after harvest. Clearcuts retained some species for longer periods than other treatments. Hooded warbler (*Setophaga citrine*) and Kentucky warbler (*Oporornis formosus*) benefitted more from partial harvesting than clearcutting; partially harvested areas had increased understory shrub abundance but retained overstory trees. Detections of many species were lower in group selection stands than other harvested treatments, likely because openings were too small for area-sensitive species. Due to the level of overstory removal, shelterwoods likely provided the closest alternative to clearcutting and retained all the species found in clearcuts; shelterwoods also provided habitat to species rare in clearcuts, including hooded and Kentucky warbler. In terms of presence and absence, regeneration methods other than clearcutting provided habitat for most early successional species, but densities of birds are likely lower. Thus, greater expanses of harvesting may be needed to sustain populations of some early successional birds at levels similar to those under even-aged systems that use clearcutting as the primary regeneration method.

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1. Introduction

Many birds are adapted to different forest successional stages for breeding, with some species breeding in mature forests and others breeding in young, regenerating forests dominated by abundant shrubs or young trees (e.g., Titterington et al., 1979; Thompson and Capen, 1988). Birds that breed in disturbed forest take advantage of shrubby, early successional habitats, and are referred to by various authors as shrub specialists, shrubland birds, or early successional birds. These species are undergoing more consistent declines than species that breed in mature forest habitats (Askins, 1993; Hagan, 1993). Part of this decline may be attributed to reductions in habitat. In the last 50 years, the expanse of early successional habitat (including young regenerating forests) has declined throughout many areas of the eastern United States due to fire suppression, farm abandonment, land development, and recolonization by second-growth forests (Askins, 2001; Brooks, 2003; Trani et al., 2001).

Timber harvest may affect bird communities by changing forest structure (e.g., Thompson et al., 1995; King and DeGraaf, 2000), and effects of timber harvest on bird populations has received considerable attention (Sallabanks et al., 2000). Timber harvest can create productive early successional habitat for shrubland birds (e.g., Annand and Thompson, 1997). Different bird species may be associated with the vegetation structure found at different lengths of time after timber harvest or different levels of canopy removal associated with various timber harvest methods (e.g., Crawford et al., 1981; Dickson et al., 1993). For example, hooded warbler (*Setophaga citrine*) and Kentucky warbler (*Oporornis formosus*) may use mature forest stands with dense shrub layers brought about by relatively small reductions in the forest canopy such as partial harvesting (Crawford et al., 1981; Hunter et al., 2001; Heltzel and Leberg, 2006; Robinson and Robinson, 1999; Annand and Thompson, 1997; Thompson et al., 1997). Species such as prairie warbler (*Setophaga discolor*), yellow-breasted chat (*Icteria virens*), and white-eyed vireo (*Vireo griseus*) may occupy areas that have

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undergone greater levels of disturbance, including clearcuts (Dickson et al., 1993; Annand and Thompson, 1997; Thompson et al., 1997; Crawford et al., 1981). Without additional treatments that retard understory succession, such as prescribed burning, the benefits to early successional birds that are derived from timber harvest are ephemeral, and harvested stands usually provide early successional habitat for less than 20 years before canopy closure reduces shrub density (e.g., Conner and Adkisson, 1975; Schlossberg and King, 2009). After substantial disturbance such as clearcutting, early successional birds such as prairie warbler and yellow-breasted chat typically appear in these stands the first or second year after harvest and peak in abundance around 4–8 years after harvest (e.g., Conner and Adkisson, 1975; Dickson et al., 1993; Schlossberg and King, 2009). Thus, a constant supply of areas in the early stages of forest regeneration may be necessary to maintain populations of these species.

Because of its historical dominance as a primary method of forest regeneration, considerable research has been conducted on effects of clearcutting on birds (e.g., Conner and Adkisson, 1975; Dickson et al., 1984, 1993; Thompson et al., 1992; Hagan et al., 1997; Keller et al., 2003). Clearcutting can provide excellent habitat for many early successional, shrub-adapted birds (e.g., Conner and Adkisson, 1975; Titterington et al., 1979; Thompson and Capen, 1988; Wallendorf et al., 2007). However, public opposition to clearcutting has led the US Forest Service to reduce the use of clearcutting in the southeastern US and to rely more on natural-regeneration systems of even- and uneven-aged management. Less is known about effects of these alternative regeneration methods on avian communities, especially in pine-dominated forests of the Southeast (Sallabanks et al., 2000). Although considerable literature has been published on effects of timber harvesting on birds, most studies have been restricted to one or only a few silvicultural practices (Vanderwel et al., 2007).

Herein, we evaluated the long-term response of 12 disturbance-associated species of birds to four different timber harvest methods (clearcut, shelterwood, single-tree selection, and group selection). We compared these treatments with unharvested controls for 2 years prior to harvest and at various intervals for 16 years after harvest. Our goal was to determine how these different regeneration methods affected disturbance-associated forest birds and to determine which alternatives to clearcutting provided reasonable habitat for this suite of species. We included the 9 most abundant species we encountered that were associated with intense forest disturbances (e.g., clearcuts): American goldfinch (*Carduelis tristis*), blue grosbeak (*Passerina caerulea*), common yellowthroat (*Geothlypis trichas*), indigo bunting (*Passerina cyanea*), prairie warbler, northern bobwhite (*Colinus virginianus*), yellow-breasted chat, field sparrow (*Spizella pusilla*), and white-eyed vireo. We also included three relatively abundant species often associated with less-intense disturbances (partial removal of mature forest canopies): northern cardinal (*Cardinalis cardinalis*), Kentucky warbler, and hooded warbler. Finally, we included brown-headed cowbird (*Molothrus ater*), which is a significant nest parasite of shrub-nesting birds. This study represents one of the longest duration studies on bird responses to timber harvest that incorporates rigorous experimental design, including replication and randomization (Sallabanks et al., 2000).

2. Methods

2.1. Study areas

We conducted the study in the Ouachita Mountains of west-central Arkansas and east-central Oklahoma, in the Ouachita National Forest and Magazine District of the Ozark-St. Francis National Forests. The Ouachita Mountains extend from central Arkansas into east-central Oklahoma. Elevations in the region range from 100 to 800 m, mean annual precipitation ranges from 112 to 142 cm, mean annual temperature ranges from 16.0 to 17.0 °C, and the growing season is 200–240 days (McNab and Avers, 1994).

We selected 20 second-growth, mixed pine-hardwood stands, grouped into 4 physiographic blocks (5 stands/block; Baker, 1994). Prior to harvest, each stand was >70 years old with little management history other than fire suppression, >14 ha, and located on southerly aspects with slopes generally <20%. Average total basal area (BA) was 26.0 (SE = ±1.0) m^2/ha. Of this, 17.6 ± 0.9 (range = 13.8–27.5) m^2/ha was pine (*Pinus* spp.) and 8.4 ± 0.6 (range = 4.2–11.5) m^2/ha was hardwood. Stands that met these criteria were randomly selected from those available within randomly-selected townships and ranges (Baker, 1994). Stands were situated throughout the National Forests without regard for conditions in adjacent stands; thus, most stands were imbedded in continuous forests (57%), but some stands were adjacent to (typically bordering on one side) young open forests (24%) and others were adjacent to pasturelands (19%). As a group, the most abundant tree species within study stands were shortleaf pine (*Pinus echinata*), post oak (*Quercus stellata*), white oak (*Quercus alba*), sweetgum (*Liquidambar styraciflua*), and hickories (*Carya* spp.). Prior to harvesting, there were no statistical differences among stands in total pine and hardwood BA or any other habitat variable measured when grouped by future treatment (Thill et al., 1994). Likewise, there were no statistically significant pre-treatment differences ($P > 0.05$) in total bird relative abundance, richness, or diversity among region blocks or among stands when grouped by future treatments (Petit et al., 1994).

2.2. Treatments

Within each of the 4 physiographic blocks, we randomly assigned 1 of 5 treatments to each stand; thus, each treatment was replicated 4 times in a randomized complete-block design. Each block contained 4 harvest treatments, plus an unharvested control. Harvesting was conducted between late May and mid-September, 1993; site preparation occurred the following winter. The overall goal of harvest was to regenerate shortleaf pine. Treatments were:

(1) *Single-tree selection* – some overstory pines and hardwoods were removed uniformly throughout the stand using BDq methods (Baker et al., 1996). Target retained pine BA was 10.3–14.9 m^2/ha and hardwood BA was 1.1–4.6 m^2/ha. Site preparation was performed uniformly throughout the stand, and consisted of felling all hardwoods 5–15 cm dbh with chainsaws.
(2) *Group selection* – all pines and most hardwoods were removed in openings that ranged from 0.04 to 1.9 ha in size; these openings constituted 6–14% of the stand area. Pines within the matrix surrounding the openings were thinned, but no hardwoods were harvested within the matrix. Within group openings, target overstory hardwood retention was 1.1–2.3 m^2/ha, and all hardwoods 5–15 cm dbh were felled; no site preparation was applied in the surrounding matrix.
(3) *Shelterwood* – from 49 to 99 of the largest pines and hardwoods per hectare were retained uniformly throughout the stand, with BA retention targets of 6.9–9.2 m^2/ha pine and 1.1–3.4 m^2/ha hardwood. All other trees (⩾5 cm dbh) were harvested or felled. Site prep consisted of removing all midstory (<15 cm) and non-merchantable trees. Seed trees

were retained and not removed after pine regeneration was present; thus, this treatment is considered a modified shelterwood treatment.

(4) *Modified clearcut* – all merchantable pines and hardwoods were harvested except a few scattered hardwood trees (BA target of 0.5–1.1 m^2/ha) retained for wildlife. Site preparation consisted of injecting all non-merchantable standing trees (except retained wildlife trees–primarily oaks and hickories) with herbicide (Garlon® 3A; Dow AgroSciences, Indianapolis, Indiana). Clearcuts were hand planted with shortleaf pine at 2.4-m intervals within the rips and non-ripped clearcuts were hand planted on a 2.4 × 3-m grid (approximately 1388 seedlings/ha).

(5) *Unharvested control* – these stands consisted of mature, closed-canopy, second-growth, pine-hardwood forests similar to preharvest conditions in all stands (see above).

All stands contained ephemeral stream drainages that typically flowed only during heavy rains. Unharvested buffer strips (or greenbelts) were established for water-quality protection at 15 m on each side of these drains. The total percentage of each stand retained as greenbelt ranged from 4% to 20% and averaged 10.9% across all 16 harvested stands.

2.3. Bird surveys

Prior to harvest, we established 5 permanent bird sampling plots in each stand. Plots were >150 m apart and ⩾90 m from stand boundaries based on limitations in size of stands used. We used 10-min, 40-m fixed-radius point counts, centered on each plot, to survey breeding birds. We sampled each plot three times in 1992 (one year before harvest; Year –1), 1993 (year of harvest; Year 0), and 1994 (1 year after harvest; Year 1), six times in 1996 (Year 3), 1998 (Year 5), 2001 (Year 8), and 2005 (Year 12), and five times in 2009 (Year 16). Surveys in 1992 were prior to harvest and surveys in 1993 were one month prior to harvesting. We used multiple observers for each year of surveys, and each observer generally (with a few exceptions) visited each stand once during a sample year. All surveys were conducted between May 3 and June 12 to correspond with the period of peak breeding activity.

Our goal was to characterize bird responses to stand management under operational conditions encountered throughout national forests of the region, which included retaining greenbelts along drains in harvested stands. Because bird survey plots were established randomly prior to harvest, plots encompassed the mix of habitats and features that were present within stands, including skidder roads, harvested portions of stands, unharvested greenbelts, and both group opening and the thinned matrix surrounding these openings in group-selection stands.

2.4. Habitat measurements

Each sample year, we characterized vertical structure of vegetation in each stand within four 5-m-radius subplots, located at each of the 5 permanent plots. At each subplot, we tallied trees by size class and assigned them to understory (1.1–8.0 cm dbh), midstory (8.1–23.0 cm dbh), and overstory (⩾23.1 cm dbh). To characterize density of vegetation, we raised a telescoping pole and recorded if it touched live vegetation in each vertical 1-m increment (from 0–1 to 9–10 m above the ground). At each subplot, these vertical measurements were taken 4 times (90° apart) along the outer edge of the subplot, with the first location randomly selected. To characterize the cover of vegetation near the ground (shrub and grass layers), we included only the 0–1 and 1–2 m measures in analyses and calculated percent cover in these intervals above the ground by dividing the total number of "hits" in each stand by the total possible (80 total in each stand).

2.5. Statistical analyses

Because individual plots within each stand were not spatially independent, we used stands ($n = 5$ plots/stand; 4 stands/treatment) instead of plots as the experimental unit to avoid pseudoreplication (Hurlbert, 1984); number of bird detections was averaged across all plots, observers, and visits in each stand. Our small sample size ($n = 4$ stands/treatment) was too small to estimate accurate abundance estimates that incorporated detectability (Thompson and La Sorte, 2008). An attempt was made to determine abundance and detectability using N-mixture models (Royle, 2004); however, many species that were analyzed (with either plots or stands as the experimental unit) provided unrealistic estimates of abundance (e.g., >700 birds/plot) and detectability (0.00), especially for rarer species. Therefore, we determined that simple means (naive estimates) were the most reliable estimates to compare bird responses to treatments. Because most detections were based on auditory clues within relatively small plots (40-m radius), we assumed detectability of early successional species was similar among treatments. To reduce potential effects of detection bias, we sampled each plot 3–6 times each season using multiple observers and avoided surveys during moderate-high winds or precipitation.

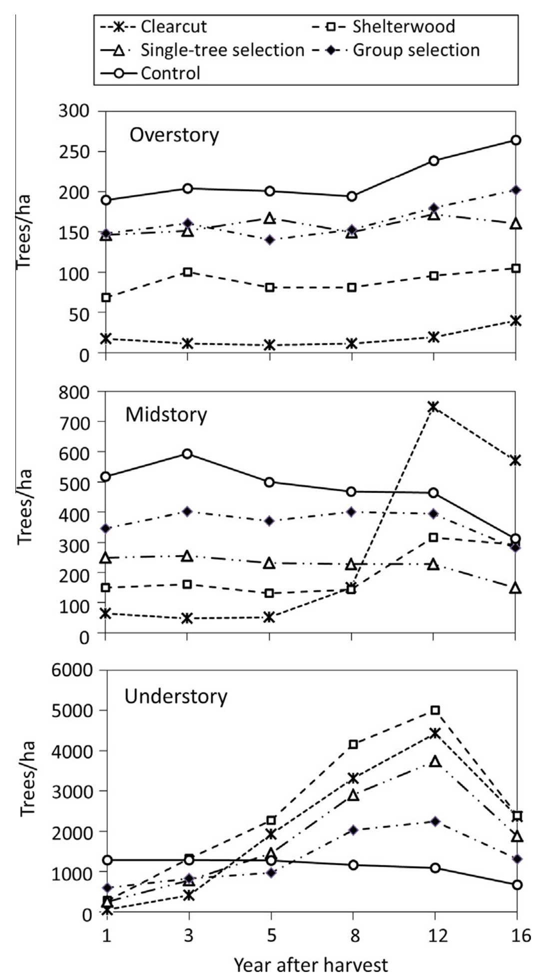

Fig. 1. Mean density (number of stems/ha) of overstory trees (⩾23.0 cm dbh), midstory trees (8.1–23.0 cm dbh), and understory woody plants (1.1–8.0 cm dbh) in four harvest treatments and unharvested controls each year of sampling after harvest (Year) in the Ouachita Mountains of Oklahoma and Arkansas. Sample size was 4 stands per treatment.

We compared treatments (by species and all species combined) using repeated-measures ANOVA in a randomized block design, where stands were repeatedly sampled and block (ecoregion) was considered a random variable (PROC MIXED; Littell et al., 2006). We initially tested each species for a treatment x post-harvest year interaction with this model. When an interaction was not significant, an analysis that incorporated all post-harvest years using repeated measures was included. When significant treatment × year interactions occurred, we analyzed each post-harvest year of sampling separately using one-way ANOVAs. To determine the best covariance matrix to use for repeated-measures analysis, we compared the values of Akaike's information criterion (AIC) among four models that used different covariance matrices (variance components, compound symmetry, Toeplitz, and Huynh-Feldt; Littell et al., 2006; SAS Institute Inc., 2009). A variance components covariance matrix had the best fit for these data. Kenwood–Roger adjustments were used to generalize degrees of freedom for all tests (Littell et al., 2006). Because data were not normally distributed based on Shapiro–Wilk tests (SAS Institute Inc., 2009), analyses were performed on ranked data (Conover and Iman, 1981). We used alpha = 0.10 because we believed the consequences of making Type II errors outweighed those associated with Type I errors, as suggested by Sallabanks et al. (2000) when evaluating effects of timber harvest on bird communities (e.g., Purcell et al., 2005). When ANOVA indicated significant differences among treatments, we conducted pair-wise comparisons of least-squared means and controlled the experiment-wise error rate using the Benjamini-Hochberg method to control the false positive discovery rate (Benjamini and Hochberg, 1995; Waite and Campbell, 2006). We calculated Spearman correlation coefficients between mean number of birds detected per plot in each stand with density (number/ha) of overstory, midstory, and understory woody plants. We also included estimates of percent cover of vegetation 0–1 m and 1–2 m above the ground in these correlations.

3. Results

3.1. Habitat

Density of overstory trees (number of trees/ha ⩾ 23.0 cm dbh) followed a gradient, with clearcuts and shelterwoods having the lowest density and controls having the greatest density; overstory tree density was similar in group selections and single-tree selection stands (Fig. 1). Density of overstory trees generally increased over time in all treatments. Density of midstory trees (8.1–23.0 cm dbh) followed a gradient as well; controls and group selection stands had the greatest midstory densities and clearcuts and shelterwoods had the lowest (Fig. 1). By 12 years after harvest, midstory trees in shelterwoods and clearcuts increased substantially as saplings grew into this size class. In other treatments, midstory trees either declined or remained static, likely due to expansion of overstory crowns and shading mortality. Density of understory woody stems (1.1–8.0 cm dbh) in the most intensively harvested stands (clearcuts, shelterwoods, and single-tree selection stands) surpassed density in controls around 5 years after harvest and peaked around 12 years after harvest (Fig. 1). In years 5–16, single-tree selection, shelterwood, and clearcut stands generally had the greatest density of understory woody plants, whereas group selection and control stands had the least.

Percent cover of live vegetation 1–2 m above the ground (the woody shrub layer) was greatest in controls and least in clearcuts the first year after harvest (Table 1). By the third year after harvest, no difference existed among treatments and controls. In years 5–16 after harvest, clearcuts, shelterwoods, and single-tree selection stands had a greater percent cover of shrubs than controls. By years 12 and 16, all harvested stands had greater coverage of live vegetation 1–2 m above the ground than controls.

3.2. Bird responses

3.2.1. American goldfinch

Detections of American goldfinch generally peaked 3–5 years after harvest in all harvested treatments except clearcuts where detections generally peaked 1–3 years after harvest (Fig. 2). There was not a significant treatment × year interaction ($F = 0.93$, $P = 0.553$). Over all post-harvest years combined, clearcuts and single-tree selection stands had significantly greater detection rates than controls (Table 2).

3.2.2. Blue grosbeak

Blue grosbeak detections peaked 3 years after harvest in shelterwood and single-tree selection stands, 5 years after harvest in group selection stands, and 8 years after harvest in clearcuts; they were never detected in unharvested controls (Fig. 2). There was not a significant treatment × year interaction ($F = 0.99$, $P = 0.480$). Over all post-harvest years combined, clearcuts had significantly greater detection rates than other treatments (Table 2).

3.2.3. Common yellowthroat

Common yellowthroat detections peaked 3 years after harvest in all treated stands except clearcuts, where detections peaked around year 5 after harvest (Fig. 2). Common yellowthroat was never detected in control stands. A significant treatment × year interaction occurred ($F = 3.75$, $P = 0.001$). Clearcuts had significantly greater detection rates than controls the third year after harvest, and clearcut and shelterwood stands had significantly greater detection rates than other treatments the fifth year after harvest (Table 2). By 8 years after harvest, clearcuts had significantly greater detection rates than all other treatments.

3.2.4. Field sparrow

Field sparrows were only detected in clearcuts, shelterwoods, and single-tree selection stands, where their detection rates generally peaked around 3–5 years after harvest (Fig. 2). A significant treatment × year interaction occurred ($F = 2.95$, $P = 0.001$). Clearcuts had significantly greater detection rates than controls or group selection stands the third year after harvest (Table 2). Clearcut and shelterwood stands had significantly greater detection rates than controls or group selection stands the fifth year after harvest.

3.2.5. Hooded warbler

Hooded warbler detections generally peaked in treated stands 12 years after harvest (Fig. 2). Although relatively rare in controls, detections in controls spiked 16 years after harvest. There was not a significant treatment x year interaction ($F = 1.30$, $P = 0.202$). Over all post-harvest years combined, single-tree selection stands had greater detection rates than all other treatments except group-selection stands. They were detected significantly less often in clearcuts than other treatments.

3.2.6. Indigo bunting

Indigo bunting detections generally peaked in harvested stands 3–5 years after harvest, but remained detected in all treatments throughout the study (Fig. 2). There was not a significant treatment × year interaction ($F = 1.11$, $P = 0.351$). Over all post-harvest years combined, clearcuts had significantly greater detection rates than other treatments, followed by shelterwood, single-tree selection and group selection, and finally controls (Table 2). Indigo buntings were only occasionally detected in control stands, and

Table 1
Mean (±SE) percent cover of live vegetation 1–2 m above the ground in unharvested controls and four regeneration harvests surveyed during 6 periods (year after harvest) in the Ouachita Mountains of Oklahoma and Arkansas.

Year	Clearcut	Shelterwood	Single tree	Group selection	Control
1	0.9A ± 0.6[a]	4.1AB ± 1.4	3.4AB ± 1.6	4.7AB ± 1.9	9.4B ± 2.1
3	15.6 ± 5.4	24.4 ± 4.3	13.1 ± 2.5	11.9 ± 2.8	10.0 ± 3.7
5	32.8AB ± 13.0	42.8A ± 7.2	36.3AB ± 11.1	19.7BC ± 3.4	10.6C ± 1.3
8	61.3A ± 12.5	59.4A ± 7.9	56.3A ± 4.5	31.9B ± 4.2	19.4B ± 4.1
12	48.8A ± 6.3	43.4A ± 2.9	50.9A ± 4.7	38.8A ± 4.1	18.4B ± 2.8
16	23.1A ± 4.5	25.3A ± 1.8	23.4A ± 2.4	22.8A ± 0.9	8.4B ± 1.7

[a] Within rows, like letters indicate no significant difference (alpha = 0.10) in means based on ANOVA controlled for experiment-wise error rates using Benjamini-Hochberg control of the false positive rate.

typically around treefalls or where small groups of trees succumbed to lightening or disease.

3.2.7. Kentucky warbler

Detections of Kentucky warbler peaked 8 years after harvest in treated stands and they were rarely encountered in controls (Fig. 2). A significant treatment × year interaction occurred ($F = 2.03$, $P = 0.013$). Five years after harvest, shelterwood and single-tree section stands had significantly greater detection rates than clearcuts or controls, and shelterwood and single-tree selection stands had significantly greater detection rates than controls 8 years after harvest (Table 2). Kentucky warblers were still detected in single-tree selection and group-selection stands 16 years after harvest, but were not detected in other treatments.

3.2.8. Northern bobwhite

Northern bobwhite were only rarely detected in group selection stands and were not detected in controls; however, they were detected relatively often in clearcuts 3–8 years after harvest (Fig. 2). A significant treatment × year interaction occurred ($F = 1.66$, $P = 0.056$). Among years, only year five after harvest showed significant differences among treatments, with clearcuts having significantly greater detection rates than other treatments (Table 2).

3.2.9. Northern cardinal

Northern cardinal detections oscillated among years in group selection stands, but generally peaked in clearcut, shelterwood, and single-tree selection stands around 12–16 years after harvest (Fig. 2). There was not a significant treatment × year interaction ($F = 1.32$, $P = 0.186$). Over all post-harvest years combined, shelterwood stands had significantly greater detection rates than single-tree selection, group selection, or control stands (Table 2). Clearcuts had significantly greater detection rates than single-tree selection or control stands.

3.2.10. Prairie warbler

Prairie warbler detections peaked approximately 3 years after harvest in single-tree selection and shelterwood stands, and 5 years after harvest in clearcuts; they were never detected in control stands (Fig. 2). A significant treatment × year interaction occurred ($F = 6.55$, $P = 0.001$). Three years after harvest, clearcut, shelterwood, and single-tree selection stands had greater detection rates than control or group selection stands (Table 2). In years 5, 8, and 12 after harvest, clearcuts had significantly greater detection rates than other treatments. Prairie warblers were not detected in any stand after 12 years.

3.2.11. White-eyed vireos

Detections of white-eyed vireo peaked 8 years after harvest in all harvested stands, but this species was never detected in control stands (Fig. 2). There was not a significant treatment × year interaction ($F = 1.14$, $P = 0.331$). Over all post-harvest years combined, white-eyed vireo detection rates were significantly greater in clearcut and shelterwood stands than in group selection or control stands (Table 2).

3.2.12. Yellow-breasted chat

Yellow-breasted chat detections peaked approximately 5 years after harvest in harvested stands; they were never detected in control stands (Fig. 2). A significant treatment × year interaction occurred ($F = 3.81$, $P = 0.001$). In years 3 and 5 after harvest, clearcut and shelterwood stands had significantly greater detection rates than control or group-selection stands, and detection rates were significantly greater in clearcuts than other treatments in years 8 and 12 after harvest (Table 2).

3.2.13. Brown-headed cowbird

Detections of brown-headed cowbirds peaked in all harvested treatments 3 years after harvest, with the exception of shelterwoods (Fig. 2). A spike in brown-headed cowbird detections in shelterwoods occurred the first year after harvest, which was attributed to a flock (likely migrants) located in a single stand during a single visit. There was not a significant treatment × year interaction ($F = 0.29$, $P = 0.999$). Over all post-harvest years combined, harvested stands had significantly greater detection rates of this species than control stands (Table 2).

3.2.14. All species combined

Detection rates of all species combined (excluding brown-headed cowbirds) peaked 5 years after harvest in harvested treatments (Fig. 2). There was not a significant treatment × year interaction ($F = 1.36$, $P = 0.163$). Over all post-harvest years combined, detection rates were greatest in clearcuts and least in controls; no difference in detection rates existed between shelterwood and single-tree selection stands (Table 2).

Clearcuts had significantly greater detection rates than all other treatments for blue grosbeak, common yellowthroat (years 5 and 8), indigo bunting, northern bobwhite (year 5), prairie warbler (years 5–12), and yellow-breasted chat (years 8 and 12). Alternatively, clearcuts had significantly lower detection rates than partial harvest treatments for Kentucky warbler (year 5) and hooded warbler. Four species had significantly greater detection rates in shelterwood stands than in single-tree selection stands (common yellowthroat in year 5, indigo bunting, northern cardinal, and yellow-breasted chat in years 3 and 5), and there were 7 species that had significantly greater detection rates in shelterwood stands than in group selection stands (common yellowthroat [year 5], field sparrow [year 5], indigo bunting, Kentucky warbler [year 5], northern cardinal, prairie warbler [years 3 and 5], and yellow-breasted chat [years 3 and 5]).

3.2.15. Bird-habitat relationships

Mean number of birds/plot had a significant negative correlation with overstory tree density (trees/ha) for 12 of the 13 species

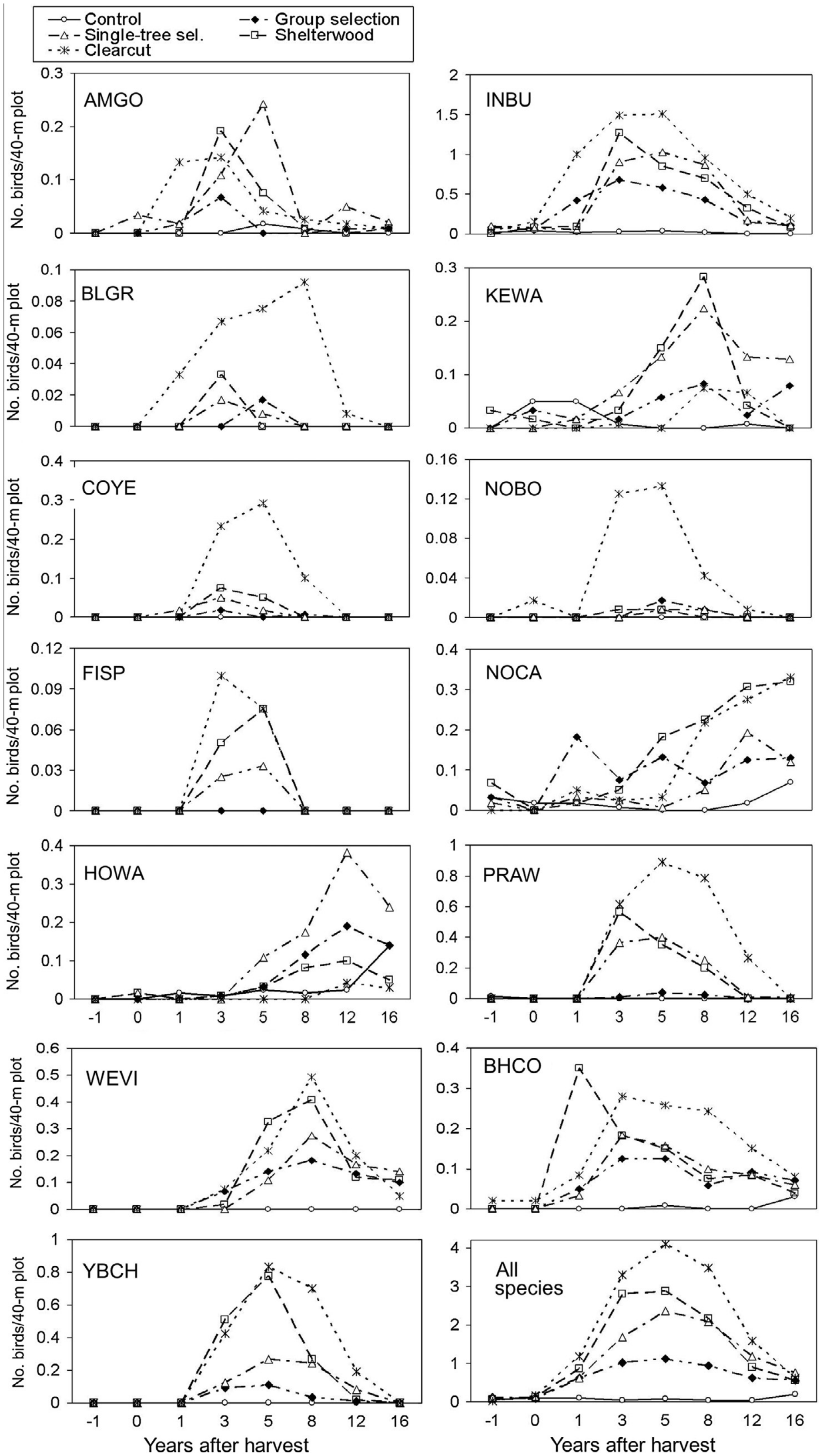

Fig. 2. Mean detections of early successional bird species and all early successional species combined (number of bird detections/plot) in 40-m radius (0.503 ha) plots in 5 forest treatments one year prior to harvest (Year –1) and various years after harvest in mixed pine-hardwoods stands of the Ouachita Mountains of Arkansas and Oklahoma. Harvest year is year 0. Sample size was 4 stands/treatment. AMGO = American goldfinch, BLGR = blue grosbeak, COYE = common yellowthroat, FISP = field sparrow, HOWA = hooded warbler, INBU = indigo bunting, KEWA = Kentucky warbler, NOBO = northern bobwhite, NOCA = northern cardinal, PRAW = prairie warbler, WEVI = white-eyed vireo, YBCH = yellow-breasted chat, BHCO = brown-headed cowbird, ALL = all species combined.

Table 2
Post-harvest (1–16 years after harvest) mean detection rates (number of bird detections/plot) of early successional birds in 40-m radius (0.503-ha) plots in 5 forest treatments and year after harvest (Year) in the Ouachita Mountains of Arkansas and Oklahoma. Only tests with significant differences among treatments are presented.

Year[a]	Species[b]	Clearcut	Shelterwood	Single tree selection	Group selection	Control
ALL	AMGO	0.06A ± 0.02[c]	0.05AB ± 0.02	0.07A ± 0.03	0.02AB ± 0.01	0.01B ± 0.01
ALL	BLGR	0.05A ± 0.02	0.01B ± 0.01	0.01B ± 0.01	0.01B ± 0.01	0.00B ± 0.00
3	COYE	0.23A ± 0.10	0.08AB ± 0.03	0.05AB ± 0.05	0.02AB ± 0.02	0.00B ± 0.00
5		0.29A ± 0.10	0.05B ± 0.02	0.02C ± 0.02	0.00C ± 0.00	0.00C ± 0.00
8		0.10A ± 0.05	0.00B ± 0.00	0.00B ± 0.00	0.01B ± 0.01	0.00B ± 0.00
3	FISP	0.10A ± 0.04	0.05AB ± 0.02	0.03AB ± 0.02	0.00B ± 0.00	0.00B ± 0.00
5		0.08A ± 0.03	0.08A ± 0.04	0.03AB ± 0.02	0.00B ± 0.00	0.00B ± 0.00
ALL	HOWA	0.01A ± 0.01	0.05B ± 0.02	0.15C ± 0.04	0.08BC ± 0.03	0.04B ± 0.02
ALL	INBU	0.94A ± 0.12	0.67B ± 0.09	0.60C ± 0.08	0.39C ± 0.05	0.01D ± 0.01
5	KEWA	0.00A ± 0.00	0.15B ± 0.04	0.13BC ± 0.07	0.06AC ± 0.06	0.00A ± 0.00
8		0.08AB ± 0.04	0.28A ± 0.09	0.23A ± 0.05	0.08AB ± 0.06	0.00B ± 0.00
5	NOBO	0.13A ± 0.06	0.01B ± 0.01	0.01B ± 0.01	0.02B ± 0.02	0.00B ± 0.00
ALL	NOCA	0.16AB ± 0.03	0.18A ± 0.04	0.07C ± 0.02	0.12BC ± 0.03	0.02D ± 0.02
3	PRAW	0.62A ± 0.19	0.57A ± 0.08	0.37A ± 0.09	0.01B ± 0.01	0.00B ± 0.00
5		0.89A ± 0.08	0.35B ± 0.13	0.40B ± 0.11	0.04C ± 0.03	0.00C ± 0.00
8		0.78A ± 0.10	0.20BC ± 0.14	0.25B ± 0.10	0.03CD ± 0.03	0.00D ± 0.00
12		0.27A ± 0.16	0.00B ± 0.00	0.01B ± 0.01	0.00B ± 0.00	0.00B ± 0.00
ALL	WEVI	0.17A ± 0.05	0.16A ± 0.04	0.12AB ± 0.03	0.10B ± 0.04	0.00C ± 0.00
3	YBCH	0.43AB ± 0.14	0.51A ± 0.05	0.13BC ± 0.06	0.09C ± 0.06	0.00C ± 0.00
5		0.83A ± 0.21	0.78A ± 0.12	0.27B ± 0.10	0.11BC ± 0.10	0.00C ± 0.00
8		0.70A ± 0.08	0.27B ± 0.15	0.24B ± 0.15	0.03BC ± 0.03	0.00C ± 0.00
12		0.19A ± 0.06	0.02B ± 0.01	0.08B ± 0.08	0.01B ± 0.01	0.00B ± 0.00
ALL	BHCO	0.18A ± 0.04	0.15A ± 0.04	0.10A ± 0.02	0.09A ± 0.02	0.01B ± 0.01
ALL	ALL	2.38A ± 0.30	1.70B ± 0.21	1.45B ± 0.15	0.83C ± 0.11	0.09D ± 0.02

[a] For Year = ALL, no significant treatment × Year interaction occurred and all post-harvest years were analyzed concurrently using repeated measures.
[b] AMGO = American goldfinch, BLGR = blue grosbeak, COYE = common yellowthroat, FISP = field sparrow, HOWA = hooded warbler, INBU = indigo bunting, KEWA = Kentucky warbler, NOBO = northern bobwhite, NOCA = northern cardinal, PRAW = prairie warbler, WEVI = white-eyed vireo, YBCH = yellow-breasted chat, BHCO = brown-headed cowbird, ALL = all species combined.
[c] Within rows, like letters indicate no significant difference (alpha = 0.10) in means, controlled for experiment-wise error rates using Benjamini-Hochberg control of the false positive rate.

evaluated (Table 3). The exception was Hooded Warbler, which had a significant positive correlation with overstory tree density (Table 3). Although Kentucky warbler had a significant negative correlation with overstory density, this relationship was relatively weak ($r = -0.17$). Eleven species were negatively correlated with density of midstory trees. Six species had positive correlations with number of understory woody stems 1.1–8.0 cm dbh. Ten species had significant positive correlations with percent cover of vegetation 0–1 m above the ground, whereas 9 species had significant positive correlations with percent cover of vegetation 1–2 m above the ground. American goldfinch was the only species whose abundance was not positively correlated with some measure of understory density.

Table 3
Significant (alpha = 0.10) Spearman correlation coefficients (r) between detection rates of early successional bird species (number/plot) and density (number of stems/ha) of overstory trees (⩾23.0 cm dbh), density of midstory trees (8.1–23.0 cm dbh), density of understory woody stems (1.1–8.0 cm dbh), percent cover 0–1 m in height, and percent cover 1–2 m in height in 20 stands under different silvicultural treatments sampled over 16 years in the Ouachita Mountains of Arkansas.

Species[a]	Overstory	Midstory	Understory	Cover 0–1 m	Cover 1–2 m
AMGO	−0.22	−0.31			
BLGR	−0.31	−0.35		0.28	
COYE	−0.39	−0.46		0.42	0.16
FISP	−0.29	−0.43		0.37	
HOWA	0.23		0.39		0.34
INBU	−0.59	−0.63		0.48	
KEWA	−0.17	−0.21	0.52	0.50	0.50
NOBO	−0.34	−0.30		0.17	0.17
NOCA	−0.32		0.44		0.43
PRAW	−0.43	−0.45		0.57	0.38
WEVI	−0.46	−0.34	0.61	0.45	0.65
YBCH	−0.50	−0.44	0.29	0.62	0.48
BHCO	−0.48	−0.29	0.15	0.29	0.25

[a] AMGO = American goldfinch, BLGR = blue grosbeak, COYE = common yellowthroat, FISP = field sparrow, HOWA = hooded warbler, INBU = indigo bunting, KEWA = Kentucky warbler, NOBO = northern bobwhite, NOCA = northern cardinal, PRAW = prairie warbler, WEVI = white-eyed vireo, YBCH = yellow-breasted chat, BHCO = brown-headed cowbird.

4. Discussion

Because of the ephemeral nature of early successional habitats and the relatively quick changes in structure that occur in these areas, time since disturbance was an important factor in the responses of early successional birds to timber harvesting. The length of time a harvested area provides habitat for early successional birds likely depends on a number of factors that affect understory growth, including intensity of tree removal, soil disturbance, climate, number of previous harvest or thinning entries, forest type, and additional treatments such as burning. We found the maximum length of time early successional birds were retained in harvested stands depended on both the type of harvest conducted and the species of bird, with clearcuts retaining many early successional species for longer periods than other treatments. In bottomland hardwood forests of Louisiana, the maximum treatment response to timber harvest (thinning and group selection) among early successional birds was 5–8 years after harvest, and duration of treatment effect was generally <13 years (Twedt and Somershoe, 2009). Numbers of prairie warbler, common yellowthroat, yellow-breasted chat, and indigo bunting may decline around 10 years after harvest, whereas field sparrow may decline after only 5 years (Thompson and DeGraaf, 2001). In pine plantations monitored for 11 years after harvest in east Texas, blue grosbeak was not detected after 7 years and white-eyed vireo was not detected 9 years postharvest (Dickson et al., 1993).

We found the regeneration method used affected when detections of a species peaked, with peak detections differing among treatments for blue grosbeak, common yellowthroat, field sparrow, and northern bobwhite. In other studies examining long-term changes in early successional bird communities after timber harvest, detections of blue grosbeak and indigo bunting tended to peak less than 5 years after harvest, whereas white-eyed vireo, Kentucky warbler, yellow-breasted chat, common yellowthroat, and prairie warbler peaked around 4–9 years (Dickson et al., 1993; Schlossberg and King, 2009; Twedt and Somershoe, 2009).

Clearcuts generally had greater detection rates of early successional species than other treatments 5–12 years after harvest. Clearcuts also retained some early successional species for longer periods, likely because of the more intensive ground disturbance, slower recovery of a shrub layer, and retention of open canopy conditions for longer periods than other treatments. Blue grosbeak, prairie warbler, and common yellowthroat remained in clearcuts 12–16 years after harvest, when they were no longer detected in other harvested stands. Blue grosbeak and northern bobwhite were only rarely detected in stands other than clearcuts. In east Texas, these two species (along with field sparrow and prairie warbler) were detected frequently in even-aged stands in the seedling and sapling stage, but were rarely or never recorded in uneven-aged stands (Thill and Koerth, 2005). Blue grosbeak is associated mostly with open grassland areas with sparse shrubs (e.g., Whitmore, 1977), but may be absent in grasslands lacking shrubs that are subjected to periodic burning (Zimmerman, 1992). Northern bobwhites are associated with grass-forb to grass-shrub stage vegetation (e.g., Dickson and Segelquist, 1979). Although areas that have undergone thinning and midstory removal may provide habitat for northern bobwhite when burned frequently (Cram et al., 2002), we found detection rates were substantially lower in partially harvested stands without periodic burning than in clearcuts, especially the fifth year after harvest. Consequently, clearcutting may provide quality habitat for many early successional species, which may be sustained for longer periods than many other regeneration treatments.

We found all harvested treatments had greater detection rates of brown-headed cowbirds than unharvested controls, but we found no significant differences among these harvested treatments. Other studies suggest brown-headed cowbird densities are often greater in clearcuts or other harvest treatments compared to dense forests (e.g., Annand and Thompson, 1997; Twedt and Somershoe, 2009). Brown-headed cowbird detection rates in our study were similar to those found in other forested landscapes, which are typically less than those in forests fragmented by agriculture (Robinson and Robinson, 1999; Donovan et al., 2000).

Detection of some species was significantly greater in partially harvested stands that retained some mature overstory but had increased understory vegetation. Kentucky warbler and hooded warbler, which were rarely detected in unharvested controls, appeared to benefit less from clearcutting than partial harvesting (shelterwood, single-tree selection, and group-selection stands). Hooded warbler is often found to be most abundant in partially harvested stands or stands with reduced overstory (Crawford et al., 1981; Annand and Thompson, 1997; Heltzel and Leberg, 2006; Robinson and Robinson, 1999), where it may be attracted to dense understories (Morse, 1989). Partially harvested stands may support high numbers of both mature-forests and canopy gap species, but may support lower numbers of early successional species such as prairie warbler and yellow-breasted chat (Annand and Thompson, 1997).

We found blue grosbeak, common yellowthroat, field sparrow, prairie warbler, and yellow-breasted chat were rarely detected in group-selection stands. Although group-selection harvests may retain a substantial proportion of the mature forest bird community (e.g., Annand and Thompson, 1997; Robinson and Robinson, 1999; King et al., 2001; Campbell et al., 2007), openings in group-selection stands are often too small to allow significant abundance of some early-successional species. Studies have found that several shrub-specialist birds that readily use clearcuts are rare in smaller patch cuts created by group-selection management (Annand and Thompson, 1997; Robinson and Robinson, 1999; Costello et al., 2000; Moorman and Guynn, 2001; DeGraaf and Yamasaki, 2003; Alterman et al., 2005), and some species such yellow-breasted chat and prairie warbler, may be absent in group openings <0.56 ha in size (Annand and Thompson, 1997; Robinson and Robinson, 1999; Costello et al., 2000; DeGraaf and Yamasaki, 2003). Some early successional birds may be area sensitive, requiring larger areas of shrub habitat (Rodewald and Vitz, 2005; Alterman et al., 2005), and many shrubland specialists may avoid edges with mature forest (Woodward et al., 2001; Rodewald and Vitz, 2005; Schlossberg and King, 2008). King et al. (2001) concluded that, because group selection stands typically do not provide adequate habitat for early successional birds and the creation of openings disrupts mature forest species, group selection may not be an effective compromise between early successional and mature forest habitats. Original harvest prescriptions in our study called for group openings to be 0.1–0.4 ha in size. However, some openings were uncharacteristically large (e.g., 1.9 ha), which likely contributed to our detections of species such as yellow-breasted chat and prairie warbler that typically are not found in smaller openings. The matrix surrounding group openings was also thinned, which created canopy gaps and increased understory shrub density. Nevertheless, detection rates of many early successional species were significantly lower in group-selection stands than in clearcuts.

In simple terms of presence and absence, regeneration methods other than clearcutting may be used to provide habitat for many early successional species. Shelterwood and single-tree selection stands retained the same species that were found in clearcuts, although detection rates were often significantly less. In the case of blue grosbeak, northern bobwhite, and common yellowthroat, detections in treatments other than clearcut was often substantially less. Thus, these harvest methods may provide habitat for most early successional species, but likely at lower densities than those found in clearcuts. Consequently, greater expanses of these regeneration systems may be needed to sustain early successional birds at population levels similar to that found using clearcutting systems. These partial-harvesting regeneration methods may also provide habitat for species that are rare in both clearcuts and unharvested controls, including hooded warbler and Kentucky warbler.

Although shelterwoods had significantly fewer detections than clearcuts for some species, shelterwoods are likely the closest surrogate for clearcuts in providing early successional habitat for shrub-dependent birds given shelterwoods had the greatest amount of overstory removal among partially harvested stands. However, for most species, detection rates among treatments did not differ between shelterwoods and single-tree selection stands, and detection rates in shelterwoods did not differ significantly from those in single-tree selection stands for all species combined. Compared to group selections, shelterwoods and single-tree selection stands had significantly greater detections of all early successional species combined. Annand and Thompson (1997) found indigo bunting, prairie warbler, white-eyed vireo, and yellow-breasted chat almost exclusively in clearcuts and shelterwoods when compared with other regeneration methods. In hardwood forests, single-tree selection may not provide adequate habitat for some early successional shrubland specialists (King and DeGraaf, 2000). Shelterwoods often have a second entry after seedling establishment to remove the overstory seed trees. However, the modified shelterwood we evaluated in this study did not include this additional entry. This additional harvesting would likely create further disturbance, which could potentially prolong the usefulness of shelterwood stands for providing early successional habitat, but would reduce the overstory conditions that appeared to be important for some species such as hooded warbler.

Not all group-selection, shelterwood, and single-tree selection harvests are the same. Additional treatments such as burning and midstory reduction, and the initial target for retained basal areas may have significant effects on the structure within these stands. For group selection, the size of the openings, thinning of the matrix around openings, and retention of some trees within openings may also affect stand structure. Further, the frequency and total number of entries (additional trees removed in single-tree selection and additional openings added to group selection stands), as well as use of herbicides will also affect structure for breeding birds. Some additional treatments such as burning could prolong the open conditions and retard understory growth, which would prolong the usefulness of these stands for early successional species. Thus, comparisons among studies of bird responses to single-tree selection and group selection among studies may differ based on the individual treatments imposed within these stands.

Although clearcutting provides quality habitat for many early successional bird species, the negative view of clearcutting on public lands necessitates alternatives to clearcutting. When the management objective is to provide habitat for early successional avian species, this can be achieved using regeneration treatments other than clearcutting, although densities of many species may be less under these alternative regeneration methods. In the case of some early successional species, it appears that clearcutting may still be the best approach to maximize densities. Shelterwoods may offer the closest approximation to clearcuts in providing habitat for most early successional birds. In addition, shelterwoods and single-tree selection stands provided habitat to species that were rare in both unharvested controls and clearcuts, such as Kentucky warbler and hooded warbler.

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