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Long-term effects of different forest regeneration methods on mature forest birds

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ABSTRACT

Changes in forest structure that result from silviculture, including timber harvest, can positively or negatively affect bird species that use forests. Because many bird species associated with mature forests are facing population declines, managers need to know how timber harvesting affects species of birds that rely on mature trees or forests for breeding, foraging, and other purposes. We used generalized linear mixed models to determine effects of clearcutting, shelterwood, single-tree selection, and group selection on detection of 18 species of bird associated with mature forests in the Ouachita Mountains of Oklahoma and Arkansas. We surveyed birds for 16 years after harvest. Most species (67%) responded positively to partial harvest that retained some overstory. Less intensive harvests had positive effects on more species and negative effects on fewer species than more intensive harvests, but responses to different treatments varied among species. Five species showed a significant positive response to the most intensive harvest (clearcuts), whereas 2 species showed a negative response. For the second most-intensive harvest (shelterwoods), 7 species showed a significant positive response and 1 species showed a negative response. For the less-intensive harvests, 9 species showed a positive response and no species had negative responses to single-tree selection, whereas 7 species had positive and no species showed negative responses to group selection. Ovenbird (*Seiurus aurocapilla*) and scarlet tanager (*Piranga olivacea*) responded negatively to all timber harvests; ovenbird appeared to be particularly susceptible to timber harvest, especially more intensive harvests such as clearcut and shelterwood. A variety of regeneration methods, including some more intensive treatments, along with maintenance of mature forest stands that retain well-developed midstories can be used to maintain the full suite of forest birds.

1. Introduction

Many bird species are facing population declines and populations of forest-dependent birds have undergone steady declines since 1970, including species that breed in either early successional or mature forests (State of the Birds, 2014). Consequently, forest managers often manage landscapes to maintain populations of forest-dependent species, including both early successional and mature-forest birds. Changes in forest structure that result from silvicultural practices, such as tree harvest and prescribed burning, can positively or negatively affect bird species that use forests (King and DeGraaf, 2000; Perry and Thill, 2013a; Thompson et al., 1995). Therefore, effects of forest management on bird populations have received considerable attention (e.g., Sallabanks et al., 2000).

Various silvicultural systems are used to remove timber, regenerate forests, and create early successional habitat. Even-aged systems include regeneration methods such as clearcut and shelterwood harvests while uneven-aged systems include single-tree selection and group selection harvests. Effects of clearcutting on forest birds have received considerable study (e.g., Conner and Adkisson, 1975; Dickson et al., 1993; Keller et al., 2003; Thompson et al., 1992), and responses of many bird species to clearcutting are predictable. In the short-term (< 10 years after harvest), disturbance-associated species immigrate to or increase use of clearcuts, whereas species associated with mature forest trees may decline or are extirpated (e.g., Annand and Thompson, 1997; Perry and Thill, 2013a). Around 5–8 years after harvest in the southeast U.S., forest canopies begin to close and early successional species are slowly replaced by species associated with mature trees

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(e.g., Conner and Dickson, 1997). However, less is understood about responses of mature-forest birds to forest harvests that retain some mature trees (Sallabanks et al., 2000). Although a substantial number of studies have investigated the effects of different silvicultural systems on forest birds, most of these studies were short duration, only examining bird responses immediately after harvest or for periods of < 5 years after harvest. Few studies have examined long-term (> 10 years) responses of forest birds after harvest. Long-term studies can provide information that is lacking in short-term studies, such as how long species utilize or are extirpated from a forest stand after harvest.

The Ouachita National Forest is consistently among the top 5 national forests in annual timber output in the U.S. (U.S. Forest Service, 2017) and managers need information on how forest harvesting affects forest birds, especially those associated with mature forests. Our goal was to determine the long-term (16 years after harvest) responses of mature-forest species to different regeneration methods in shortleaf pine (*Pinus echinata*)-dominated stands to determine which methods positively or negatively affected birds known to require mature trees or mature forests. This study represents one of the longest duration studies of forest bird responses to timber harvest in the eastern U.S. We modeled responses of 18 bird species associated with mature forests or mature trees (Table 1) to 4 regeneration methods; one method (clearcut) that removed most overstory trees, and 3 methods (shelterwood, group selection, and single-tree selection) that removed only a portion of the mature overstory. We also compared bird responses in these treated stands to untreated mature forest stands. We hypothesized that detections of most species associated with mature trees would be similar or increase after partial harvests (single-tree selection, group selection, and shelterwood), and all would decrease after clearcutting. We also predicted some species such as ovenbird (*Seiurus aurocapilla*) and scarlet tanager (*Piranga olivacea*), would decrease or disappear in stands subjected to intensive regeneration method such as clearcut.

2. Methods

2.1. Study areas

We conducted the study in the Ouachita Mountains of west-central Arkansas and east-central Oklahoma, within 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 geographic blocks (5 stands/block; Baker, 1994). Prior to harvest, stands had little management history other than fire suppression. These stands developed after most of the region was heavily logged in the early 1900s (Smith, 1986). Each stand was > 70 years, > 14 ha, and located on southerly aspects with slopes generally < 20%. As a group, stands were dominated by shortleaf pine (*Pinus echinata*), but also contained numerous hardwood species including post oak (*Quercus stellata*), white oak (*Q. 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).

Table 1
Bird species associated with mature forests or mature trees and total number of detections for each species modeled for effects of timber harvest on birds over time in the Ouachita Mountains of Arkansas and Oklahoma, 1992–2009.

Species	Scientific name	Total detections
Black-and-white warbler	*Mniotilta varia*	846
Blue-gray gnatcatcher	*Polioptila caerulea*	386
Carolina chickadee	*Poecile carolinensis*	338
Downy woodpecker	*Dryobates pubescens*	82
Eastern wood-pewee	*Contopus virens*	158
Great crested flycatcher	*Myiarchus crinitus*	187
Ovenbird	*Seiurus aurocapilla*	281
Northern flicker	*Colaptes auratus*	47
Pine warbler	*Setophaga pinus*	2415
Pileated woodpecker	*Dryocopus pileatus*	217
Red-eyed vireo	*Vireo olivaceus*	1223
Scarlet tanager	*Piranga olivacea*	155
Summer tanager	*Piranga rubra*	522
Tufted titmouse	*Baeolophus bicolor*	327
White-breasted nuthatch	*Sitta carolinensis*	99
Worm-eating warbler	*Helmitheros vermivorum*	54
Yellow-billed cuckoo	*Coccyzus americanus*	83
Yellow-throated vireo	*Vireo flavifrons*	70

2.2. Treatments

We randomly assigned 1 of 5 treatments to each stand within each of the 4 geographic blocks (north, south, east, and west); thus, each treatment was replicated 4 times in a randomized complete-block design (Fig. 1). Each block contained 4 regeneration methods, plus an unharvested control. Harvesting was conducted between late May and mid-September 1993; site preparation occurred the following winter.

Four regeneration methods were implemented; single-tree selection, group selection, shelterwood, and clearcut. Clearcuts were planted with shortleaf pine seedlings, but all other methods relied on natural regeneration. Clearcut treatments were modified to retain scattered overstory hardwoods with 0.5–1.1 m^2/ha of basal area (BA) and snags were created (mean density of 24.8 ± 1.4 snags/ha, Perry and Thill, 2013b) by injecting non-merchantable trees with herbicide. Shelterwoods retained 49–99 overstory pines and hardwoods per hectare with retained BAs of 6.9–9.2 m^2/ha pine; all other trees were felled or removed. Group selections had all pines and most hardwoods removed in openings (0.04–1.9 ha in size) with openings constituting 6–14% of the stand area. Pines within the matrix surrounding the openings were thinned and openings retained 1.1–2.3 m^2/ha of BA in hardwoods. Single-tree selection stands had some overstory pines and hardwoods removed uniformly throughout the stand, with target retained pine BA of 10.3–14.9 m^2/ha and hardwood BA of 1.1–4.6 m^2/ha. Most midstory trees (< 15 cm dbh) were felled in shelterwood, single-tree selection, and openings of group-selection stands. Unharvested buffer strips, or greenbelts (also commonly referred to as stringers, or inclusions), were established for water-quality protection at 15 m on each side of stream drains (30-m total width) in most stands, including clearcuts. Total percentage retained in each stand as greenbelt was 4–20% (mean = 10.9%) across all 16 harvested stands. For more specific details on each harvest treatment, see Perry and Thill (2013a).

2.3. Bird surveys

We established 5 permanent bird sampling plots in each stand prior to harvest. Plots were > 150 m apart and ≥ 90 m from stand boundaries based on limitations in the size of our stands. We used 10-min, 40-m-radius point counts, centered on each plot to survey breeding birds. We sampled each plot three times in 1992 (one year before harvest), 1993 (year of harvest), and 1994 (1 year after harvest); six times in 1996 (3 years after harvest), 1998 (5 years after harvest), 2001 (8 years after harvest), and 2005 (12 years after harvest); and five times in 2009 (16 years after harvest). Survey effort was increased in each stand in 1996 to reduce potential variability in detection and only 5 surveys were conducted in each stand in 2009 due to scheduling conflicts. Surveys in 1993 were conducted approximately one month prior to harvesting. We conducted surveys between May 3 and June 12 to

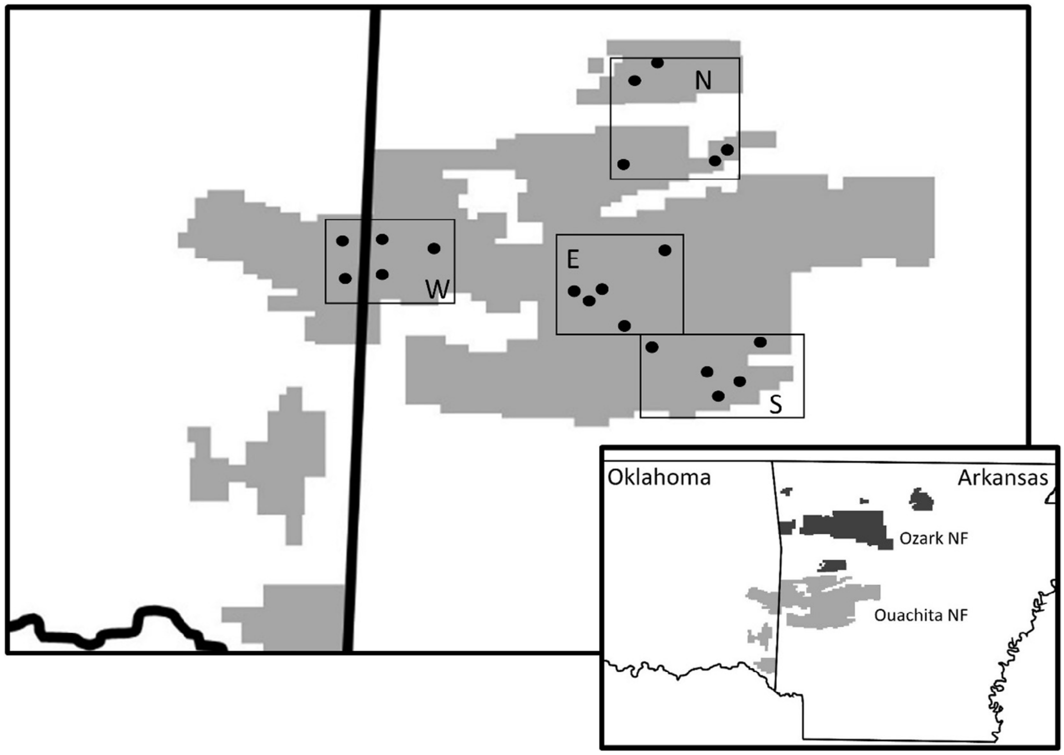

Fig. 1. Map of 20 study stands (black circles) distributed across the Ouachita National Forest and southern most district of the Ozark National Forests of Oklahoma and Arkansas where forest birds were surveyed from 1992–2009. Stands were selected randomly from 4 geographic blocks (north = N, south = S, east = E, and west = W); each stand in each block was randomly assigned 1 of 4 treatments (clearcut, shelterwood, single-tree selection, and group selection) or unharvested control.

correspond with the period of peak breeding activity and avoided surveying during moderate–high winds or precipitation to maximize detectability. Our goal was to characterize mature-forest bird responses to stand management under operational conditions encountered throughout national forests of the region. Because plots were established prior to harvest, portions of some sample plots included retained greenbelts along stream drains and skidder roads in harvested stands.

2.4. Statistical analyses

We evaluated effects of forest treatments on the relative abundance of 18 bird species (Table 1). We chose these 18 species because all had ≥47 total detections (range 47–2415), they use overstory trees for nesting, or they have pole timber or saw timber listed as suitable or optimal habitat in mixed pine-hardwood forests of the Southeast (Hamel, 1992). We did not include detectability in our modeling because the small fixed-radius plot design and lack of distance data did not allow us to meet assumptions of closure for N-mixture models incorporating detectability (Royle, 2004). Initial tests using open population N-mixture models produced highly improbable detectability and abundance results (Dail and Madsen, 2011). Therefore, we used generalized linear mixed models (Bates et al., 2015; R Core Team, 2015) in an information theoretic framework (Burnham and Anderson, 2002) to model detections over time among treatments. We calculated the mean and maximum count for each species per year. We evaluated the use of gamma (mean annual count at each plot) and Poisson (maximum annual count at each plot) distributions for the response variable (number of birds detected in a plot) and selected the Poisson distribution for improved model convergence. All overdispersion values were close to 1.

We included a random effect of stand nested within block to account for the blocked study design and to account for non-treatment related differences among stands. We also included a random effect of year to account for variation in observers. We calculated interclass correlation coefficients (ICC) for each random variable. If models did not converge with all random effects, we dropped block and reported its ICC (McDonald et al., 2000).

Generalized linear mixed models were based on 800 sampling occasions per species (8 sample years × 5 plots per stand × 5 stands × 4 physiographic blocks). We hypothesized that the effects of different regeneration methods (TRT) would vary with year since treatment (YST; 0, 1, 3, 5, 8, 12, 16), and that the response over time may not be linear. We standardized YST ($x - \bar{x}/SD$) for purposes of model convergence. Our model set included 3 models: an intercept only (null) model, a model with fixed effects of TRT × YST with the separate effects of TRT and YST, and a model of TRT × YST^2 with the separate effects of TRT and YST^2. We used the second-order Akaike's information criterion (AICc) for model selection and calculated differences in AICc values and model weights to evaluate relative support for candidate models (Burnham and Anderson, 2002). We conducted 10-fold cross-validation to evaluate fit of the top model for each species and report the mean Spearman rank between predicted and observed values (Boyce et al., 2002). We report coefficient effects and 95% confidence intervals for the top supported model of each species. We did not report coefficients for models where the null model was indisputably best. However, if the top model was the null model and a treatment model was within 2.0 AICc of the null model, we report coefficients and 95% confidence intervals for the treatment model. We considered an effect to be significant if the 95% confidence interval for the parameter

Table 2
Comparison of models evaluating treatment effects over time for mature forest birds in the Ouachita Mountains, including number of parameters in each model (K); difference between each model's second-order Akaike's Information Criterion (AICc) value and the lowest AICc value in the candidate set (ΔAICc); Akaike weight of each model in relation to the entire candidate set (*w*); and sum count of each species across the study (*n*). Fit = mean Spearman's rank correlation from 10-fold cross validation; TRT = treatment (regeneration method) and YST = year since treatment.

Model[a]	K	logLik	AICc	ΔAICc	w	Fit
Black-and-white warbler (*n* = 525)						
TRT × (YST + YST^2)	18	−748.92	1534.71	0.00	0.51	0.34
TRT × YST	13	−754.41	1535.28	0.58	0.39	
Null	4	−764.98	1538.01	3.30	0.10	
Blue-gray gnatcatcher (*n* = 333)						
TRT × (YST + YST^2)	18	−587.43	1211.74	0.00	1.00	0.47
TRT × YST	13	−598.68	1223.82	12.07	0.00	
Null	4	−615.93	1239.92	28.17	0.00	
Carolina chickadee (*n* = 491)						
TRT × (YST + YST^2)	18	−840.70	1718.28	0.00	1.00	0.29
Null	4	−860.84	1729.74	11.46	0.00	
TRT × YST	13	−853.30	1733.07	14.79	0.00	
Downy woodpecker (*n* = 88)						
TRT × (YST + YST^2)	18	−261.80	560.48	0.00	0.75	0.19
Null	4	−277.32	562.69	2.21	0.25	
TRT × YST	13	−272.08	570.63	10.15	0.00	
Eastern wood-pewee (*n* = 136)						
TRT × (YST + YST^2)	18	−308.32	653.51	0.00	0.47	0.41
TRT × YST	13	−313.54	653.54	0.03	0.47	
Null	4	−324.85	657.74	4.23	0.06	
Great crested flycatcher (*n* = 172)						
Null	4	−436.35	880.74	0.00	0.57	0.25
TRT × YST	13	−427.60	881.66	0.92	0.36	
TRT × (YST + YST^2)	18	−423.99	884.86	4.12	0.07	
Northern flicker (*n* = 40)						
Null	4	−147.52	303.08	0.00	0.74	0.17
TRT × YST	13	−139.42	305.30	2.22	0.24	
TRT × (YST + YST^2)	18	−137.03	310.93	7.85	0.01	
Ovenbird[b] (*n* = 179)						
TRT × YST	12	−359.54	743.48	0.00	0.99	0.49
Null	3	−373.46	752.96	9.48	0.01	
TRT × (YST + YST^2)	15	NA	NA	NA	NA	
Pine warbler (*n* = 1223)						
TRT × (YST + YST^2)	18	−1098.35	2233.58	0.00	1.00	0.49
TRT × YST	13	−1121.35	2269.17	35.59	0.00	
Null	4	−1136.23	2280.51	46.94	0.00	
Pileated woodpecker (*n* = 145)						
Null	4	−397.49	803.04	0.00	0.95	−0.04
TRT × (YST + YST^2)	18	−386.28	809.43	6.39	0.04	
TRT × YST	13	−393.37	813.20	10.16	0.01	
Red-eyed vireo (*n* = 729)						
TRT × YST	13	−873.86	1774.19	0.00	0.86	0.42
Null	4	−885.51	1779.07	4.88	0.07	
TRT × (YST + YST^2)	18	−871.25	1779.39	5.19	0.06	
Scarlet tanager (*n* = 180)						
TRT × YST	13	−441.15	908.77	0.00	0.59	0.23
Null	4	−450.76	909.57	0.80	0.40	
TRT × (YST + YST^2)	18	−439.90	916.68	7.91	0.01	
Summer tanager (*n* = 498)						
TRT × YST	13	−772.63	1571.72	0.00	0.55	0.28
TRT × (YST + YST^2)	18	−768.18	1573.24	1.52	0.26	
Null	4	−782.92	1573.89	2.17	0.19	
Tufted titmouse (*n* = 340)						
TRT × (YST + YST2)	18	−634.31	1305.50	0.00	0.86	0.35
TRT × YST	13	−641.34	1309.15	3.65	0.14	
Null	4	−660.88	1329.81	24.30	0.00	
White-breasted nuthatch (*n* = 108)						
TRT × (YST + YST^2)	18	−288.10	613.07	0.00	1.00	0.30
TRT × YST	13	−299.55	625.57	12.50	0.00	
Null	4	−312.93	633.91	20.84	0.00	
Worm-eating warbler (*n* = 88)						
TRT × YST	13	−244.49	515.44	0.00	0.94	0.28
Null	4	−256.65	521.36	5.92	0.05	
TRT × (YST + YST^2)	18	−243.49	523.85	8.41	0.01	
Yellow-billed cuckoo (*n* = 88)						
Null	4	−265.27	538.59	0.00	0.92	0.27
TRT × YST	13	−259.07	544.60	6.01	0.05	
TRT × (YST + YST^2)	18	−254.21	545.30	6.71	0.03	
Yellow-throated vireo (*n* = 61)						
TRT × (YST + YST^2)	18	−191.49	419.85	0.00	0.51	0.19
Null	4	−206.62	421.29	1.44	0.25	
TRT × YST	13	−197.45	421.36	1.50	0.24	

[a] Block, stand nested within block, and year were included as random variables in each model.
[b] For ovenbird, models did not converge with nested effects; therefore, results are shown for models with a random effect of year and stand only. The quadratic interaction model (TRT x (YST + YST^2) also did not converge.

coefficient did not include zero. We did not model-average coefficients since our models included random effects and quadratic terms (Symonds and Moussalli, 2011); instead, we modeled predictions based on each model and averaged those predictions based on model weights for each species (Burnham and Anderson, 2002; Mazerolle, 2016).

3. Results

Models converged with all random effects for 17 of 18 bird species. The null and linear YST model for ovenbird converged after the random effect of block (ICC = 0.03) was removed. The quadratic YST model for ovenbird did not converge for any mixed model tested and was removed from the ovenbird model set. K-fold cross validation of TRT models (excluding null models) ranged from 0.19 to 0.49 (Table 2), and model fit increased when birds were more numerous. We found strong support for models containing TRT effects over time for 12 of the 18 species (null model > 2AICc from top model; Table 2). For great crested flycatcher, scarlet tanager, and yellow-throated vireo, we found weak support for TRT effects over time (null model within 2AICc from the top model; Table 2, Fig. 2). We did not find support (null model was indisputably best) for pileated woodpecker, yellow-billed cuckoo, and northern flicker (Table 2, Fig. 2).

Counts of 10 species showed a positive effect from at least one regeneration method (Table 3; Fig. 2; Appendix A). All 4 regeneration methods had a significant positive effect on detections for blue-gray gnatcatcher, eastern wood-pewee, great crested flycatcher, summer tanager, and white-breasted nuthatch (Table 3). Compared to unharvested stands, predicted counts of blue-gray gnatcatcher ranged from 8 times greater in group selections to 20 times greater in shelterwoods and predicted counts of eastern wood-pewee were 2.5 times greater in clearcuts and 8.5 times greater in single-tree selection stands during the eighth year after harvest. For some species, overall treatment effects were not significant, but we found significant linear or quadratic trends associated with treatments. We found a significant increase over time in response to shelterwood harvests by worm-eating warbler but no significant response to other treatments (Fig. 2; Appendix A). Positive effects of one or more treatments were short-lived (< 10 years) for some species. Predicted counts of blue-gray gnatcatcher, Carolina chickadee, eastern wood-pewee, and yellow-throated vireo peaked around 8 years after harvest in most treatments, but declined thereafter (Fig. 2).

For 8 species, main effects of TRT were negative for at least 1 regeneration method, but only two species (pine warbler and ovenbird) had a significant negative response to at least one regeneration method

(Table 3; Fig. 2; Appendix A). Four additional species (Carolina chickadee, scarlet tanager, tufted titmouse, and white-breasted nuthatch) showed significant trends over time in one or more regeneration methods (Table 3; Appendix A). In the case of tufted titmouse, predicted counts in all treatments increased significantly over time (Fig. 2; Appendix A). Based on model-averaged predictions, clearcuts negatively affected counts of pine warbler, red-eyed vireo, tufted titmouse, and worm-eating warbler, but less intensive methods either increased or did not affect their abundances over time (Fig. 2). Predicted counts of pine warbler ranged from 4 times greater (in controls) to 7 times greater (in single-tree selection) than in clearcuts eight years after harvest, but rebounded to levels similar to other treatments by the 16th year after harvest. For worm-eating warbler, predicted counts in shelterwoods were almost 30 times greater than in clearcuts and almost 10 times greater than in unharvested stands by the 16th year after harvest.

Less intensive regeneration methods had positive effects on more species and negative effects on fewer species than more intense methods. Based on model parameters, 5 species showed significant positive TRT effects in the most intensive method (clearcuts), whereas 2 species showed a significant negative response (Table 3). For the second

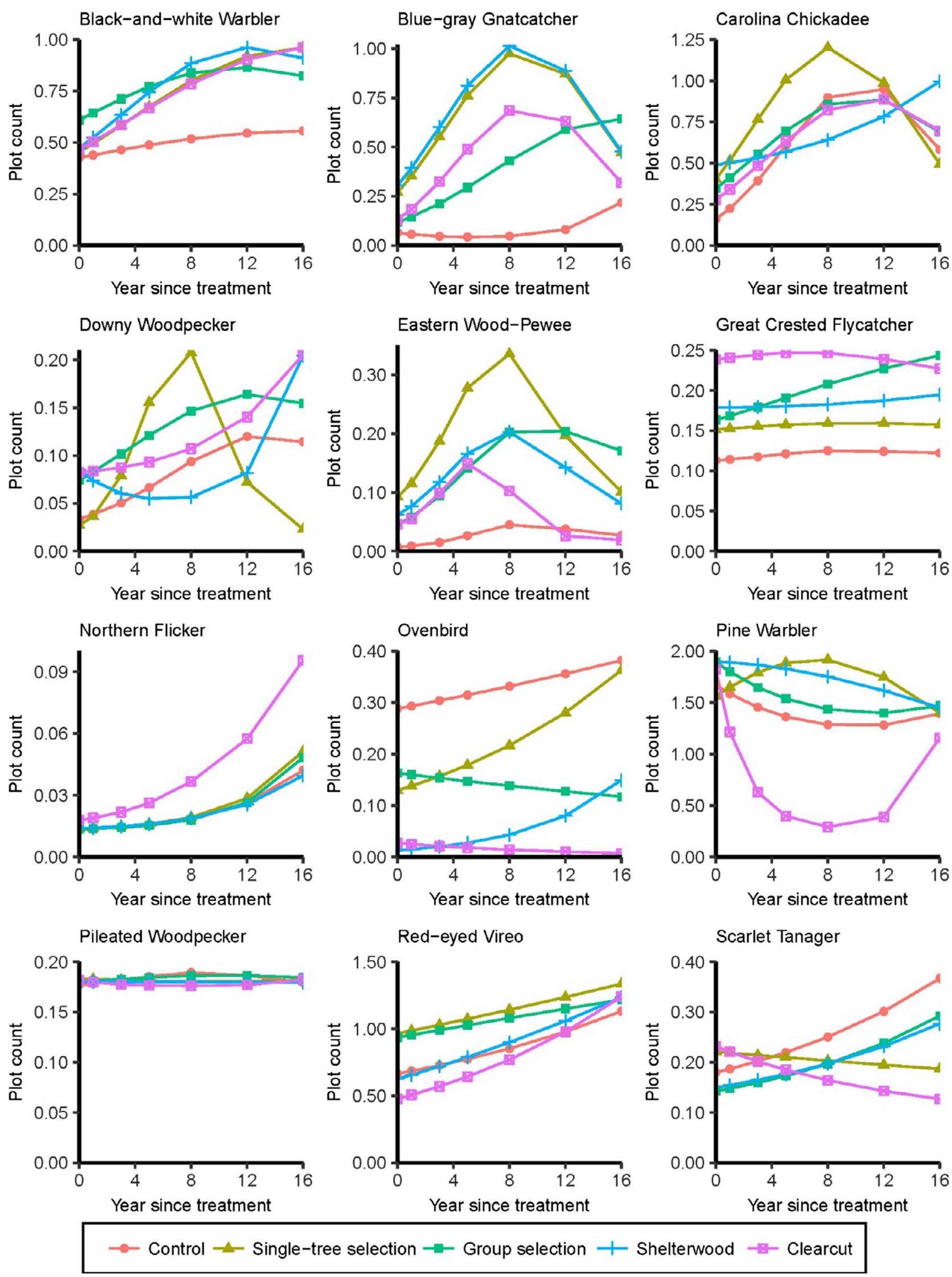

Fig. 2. Predicted counts (number of birds/40-m radius plots) averaged from models of 4 regeneration methods (clearcut, shelterwood, single-tree section, and group selection) and unharvested forest (control) sampled over 16 years after harvest in the Ouachita Mountains of Oklahoma and Arkansas, 1992–2009.

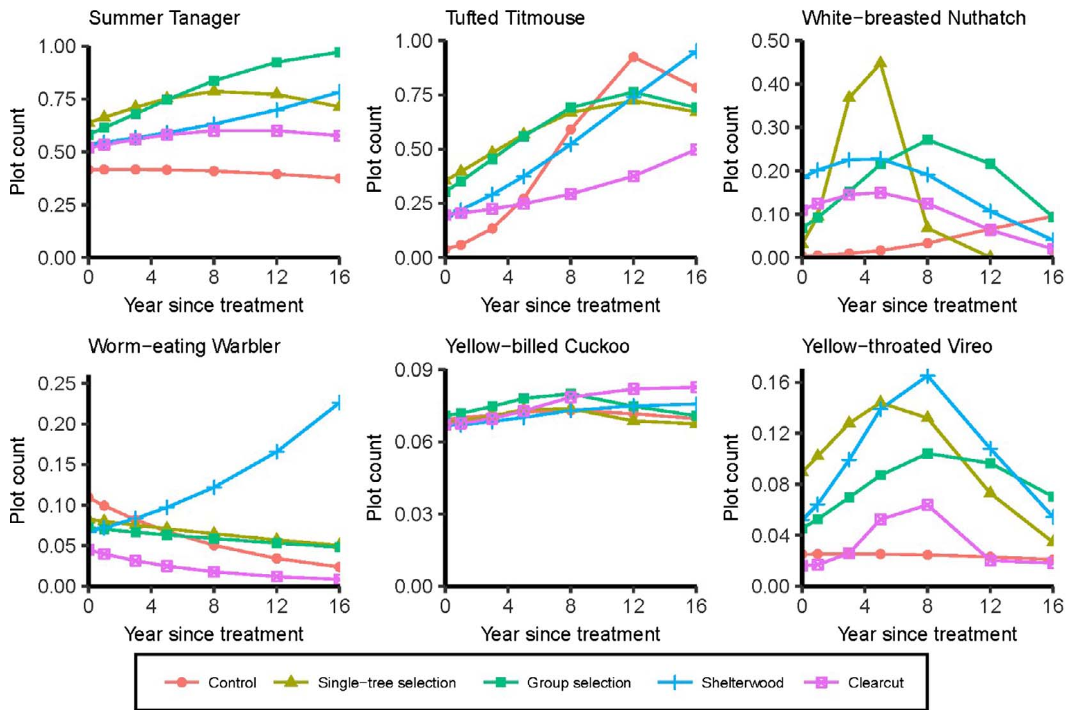

Fig. 2. (*continued*)

Table 3
Summary of TRT effects predicted by models of counts for 18 species of mature-forest birds in 4 regeneration methods compared to unharvested controls in the Ouachita Mountains of Arkansas and Oklahoma, 1993–2009. Sign indicates positive (+) or negative (−) effects of each treatment on a species. Significant linear and quadratic effects are not included. Blanks indicate the null model was best and no TRT models were within 2.0 AICc, or the model parameter estimates were negligible (e.g., ± 0.01).

Species	Clearcut	Shelterwood	Single-tree selection	Group selection
Blue-gray gnatcatcher	*+	*+	*+	*+
Eastern wood-pewee	*+	*+	*+	*+
Great crested flycatcher	*+	*+	*+	*+
Summer tanager	*+	*+	*+	*+
White-breasted nuthatch	*+	*+	*+	*+
Yellow-throated vireo	+	*+	*+	+
Black-and-white warbler	+	*+	+	*+
Tufted titmouse	−	+	*+	*+
Pine warbler	*−	+	*+	+
Red-eyed vireo	−		*+	+
Worm-eating warbler	−	+	+	
Carolina chickadee	−	−	+	+
Downy woodpecker	+	−	+	+
Ovenbird	*−	*−	−	−
Scarlet tanager	−	−	−	−
Northern flicker				
Pileated woodpecker				
Yellow-billed cuckoo				

* = significant effect of treatment in models; 95% confidence interval for parameter estimate did not include zero.

most-intensive method (shelterwoods), 7 species had significant positive TRT effects and 1 species showed a significant negative response. For the least-intensive methods, 9 species had significant positive TRT effects in single-tree selection and 7 species showed significant positive responses to group selection, whereas no species showed a significant negative TRT effect in either of these methods.

4. Discussion

Most species (12 of 18) responded positively to partial timber harvest that retained mature overstory trees, and modeled counts of most mature forest birds increased after low-intensity harvests compared to unharvested stands. From a bird community perspective, less-intensive harvests maintained a larger number of mature-forest species than did intense treatments such as clearcuts. From an individual species perspective, no harvest method appeared to be optimal for all mature-forest birds, and responses of individual species to different treatments should be taken into consideration when certain species are a priority (species of concern).

Our results mirror shorter-term studies whereby some species associated with mature forests (e.g., black-and-white warbler, eastern wood-pewee) increased after harvest regardless of the harvest method, whereas other species (e.g., ovenbird) declined, regardless of harvest method (Kellner et al., 2016; Kendrick et al., 2015; Morris et al., 2013; Twedt and Somershoe, 2009). Surprisingly, counts for 5 mature-forest species (blue-gray gnatcatcher, eastern wood-pewee, great crested flycatcher, summer tanager, and white-breasted nuthatch) were significantly greater in clearcuts that in unharvested stands, and previous studies have also found some of these species more abundant in clearcuts than unharvested stands (e.g., Annand and Thompson, 1997; Campbell et al., 2007; Costello et al., 2000; King and Degraaf, 2000; Thompson and Fritzell, 1990). We included each species in our "mature forest" suite based on information presented in management guides, such as Hamel (1992). Our results and those of other studies on forest management suggest some species (black-and-white warbler, eastern wood-pewee, Carolina chickadee, great-crested flycatcher) may occur across a range of forest conditions, including mature, mid-successional, and younger regenerating forests (e.g., Conner et al., 1979; Dickson et al., 1993; Kellner et al., 2016). Thus, all the species we included in our study may not be mature-forest obligates and some may instead be forest generalists.

Contradictory responses of individual species to similar regeneration methods among studies may result from differences in how treatments are implemented. Differences in residual tree densities and differences in site preparation such as midstory removal likely affect species responses. It should be noted that clearcuts in this study retained low densities of residual mature trees, along with numerous created snags. Retaining unharvested greenbelts in harvested stands, including clearcuts, is a standard operational component of timber harvesting on national forests in the region, and including these buffers in our sampling (along with the scattered mature trees that were retained) likely increased counts of mature-forest birds that otherwise may have not occurred in those stands. We found summer tanagers significantly more abundant in clearcuts than unharvested stands, but species such as summer tanager may be absent in clearcuts without these residual trees (Strelke and Dickson, 1980; Thompson and Fritzell, 1990). Therefore, detailed descriptions of treatments may be important for interpreting bird responses to prescriptions.

Our results suggest that effects of regeneration treatments are relatively short-lived (< 16 years) for many mature-forest species. Four species (tufted titmouse, pine warbler, red-eyed vireo, and worm-eating warbler) had their lowest predicted counts in clearcuts, but were not negatively affected by other regeneration methods. These four species are often rare or absent for several years following clearcut harvests (Annand and Thompson, 1997; Strelke and Dickson, 1980; Thill and Koerth, 2005; Thompson and Fritzell, 1990). However, predicted counts of pine warbler and tufted titmouse rebounded in clearcuts by the 16th year after harvest and rebounded by the 12th year after harvest for red-eyed vireo. Temporal patterns of abundance for 5 species (blue-gray gnatcatcher, Carolina chickadee, eastern wood-pewee, pine warbler, and red-eyed vireo) suggested the effects of timber harvest generally lasted around 16 years after harvest, as predicted counts for these species converged to similar levels (with some exceptions) in that year. Temporal patterns of predicted counts for other species (black-and-white warbler, great crested flycatcher, scarlet tanager, and summer tanager) suggested that longer time periods may be required for some species to recover to similar levels among treatments.

We found ovenbird was most sensitive to timber harvests, regardless of the level of disturbance. Ovenbird disappeared after clearcutting and were rare in shelterwood harvests; predicted counts in single-tree selection and group-selection stands were half of those found in unharvested stands. Similarly in Missouri, detections of ovenbird in unharvested mature forests were nearly twice that of forests subjected to single-tree selection and nearly seven times that found in shelterwoods (Annand and Thompson, 1997). Ovenbird may be absent or less abundant in young, even-aged stands or stands that have been partially harvested compared to unharvested mature forests across their breeding range (e.g., Baker and Lacki, 1997; Rodewald and Smith, 1998; Wallendorf et al., 2007; Yahner, 1987). Predicted counts of ovenbird slowly increased over time in single-tree selection and shelterwood stands, likely due to redevelopment of midstories that were removed during site preparation. By the 16th year after harvest, predicted counts of ovenbird in single-tree selection stands was similar to that in unharvested controls. Thus, ovenbird declines in the least-intensive treatment (single-tree selection) appear to be relatively short lived, whereas ovenbird numbers in other treatments may take substantial time to recover.

We relied on numbers of birds detected for our analysis, which may have been influenced by our ability to detect birds. We attempted to use N-mixture models that incorporate detectability (Royle, 2004) based on multiple observers, but these models produced highly improbable abundance (e.g., > 500 birds/plot) or detectability (0.00) results (Dail and Madsen, 2011). Nevertheless, our methods were initially designed to minimize potential detection differences; most detections were based on auditory clues within relatively small plots (40-m radius) which reduced the potential for detection differences among treatments. We also sampled each plot 3–6 times each sample year using multiple observers and avoided surveys during moderate to high winds or during precipitation. Although detection differences among treatments may have occurred, they likely affected our findings minimally.

Multiple goals are associated with timber harvest, including regenerating new trees and creating early successional forest habitats. At the forest-stand level, no method appeared optimal for the entire mature forest bird community, but single-tree selection had the most species with significant positive responses and the least number of species with a negative response. However, the effectiveness of each method at regenerating new trees is important and methods may differ in effectiveness based on forest type. For example, single-tree selection may not be an effective method for regenerating shade-intolerant Southern pines without the use of herbicides or fire (e.g., Cain and Shelton, 2002; Jensen and Kabrick, 2008; Shelton and Cain, 2000), and incurs more frequent site disturbance and a more permanent road network to support frequent harvesting with this system (Rudolph and Conner, 1996). Therefore, managers have to balance wildlife needs with the effectiveness of different regeneration methods at regenerating new forests.

5. Management implications

Species associated with mature forest had diverse responses to forest regeneration methods and many responded positively to tree harvest. Managers wishing to maintain diverse bird communities of forest birds can use a diversity of regeneration methods, such as those studied here, to provide habitat for the full suite of mature-forest birds. Furthermore, managers should also consider the benefits different regeneration methods provide to early-successional or disturbance-dependent birds (Perry and Thill, 2013a), and the habitat requirements of mature-forest birds outside the nesting season, such as their extensive use of early successional forest during the post fledgling period (Chandler et al., 2012; Stoleson, 2013). For species of concern or focal species, managers may consider the effects of regeneration methods reported here to tailor management to benefit those species over others.

Because some species, especially ovenbird, appear negatively affected by treatments that reduce or remove midstories of mature forests, some mature stands with well-developed midstories could be maintained to provide habitat for these species. Alternatively, recolonization by species such as ovenbird may take as little as 16 years after initial single-tree selection harvests in the absence of additional disturbance. However, given the increased use of prescribed fire for encouraging natural regeneration of pines and oaks in the years following timber harvest, research is still needed on the interaction among these treatments and bird use. For example, additional treatments such as fire may set back development of midstories needed for ovenbird.

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Appendix A

Parameter coefficients (β) with upper and lower 95% confidence intervals (95% CI) for the top supported model for each species. Significant effects (95% CI for β does not include zero) are marked with *. Unharvested controls (TRT_CO) were used as the intercept. Model parameters are not shown for species in which the null model was best.

Species/model parameter	β	95% CI	
		Lower	Upper
Black-and-white warbler			
(Intercept)*	−0.70	−1.06	−0.35
TRT_ST[a]	0.44	−0.02	0.89
TRT_GS*	0.55	0.10	1.01
TRT_SW*	0.58	0.13	1.03
TRT_CC	0.41	−0.05	0.87
YST	0.15	−0.15	0.46
YST^2	−0.06	−0.34	0.22
TRT_ST × YST	0.29	−0.12	0.69
TRT_GS × YST	0.08	−0.30	0.47
TRT_SW × YST	0.32	−0.08	0.72
TRT_CC × YST	0.25	−0.16	0.65
TRT_ST × YST^2	−0.12	−0.48	0.24
TRT_GS × YST^2	−0.09	−0.45	0.26
TRT_SW × YST^2	−0.22	−0.58	0.14
TRT_CC × YST^2	−0.09	−0.45	0.27
Blue-gray gnatcatcher			
(Intercept)*	−3.14	−4.24	−2.05
TRT_ST*	2.95	1.76	4.13
TRT_GS*	2.01	0.79	3.23
TRT_SW*	3.01	1.82	4.19
TRT_CC*	2.53	1.33	3.73
YST	0.04	−0.77	0.85
YST^2	0.44	−0.25	1.13
TRT_ST × YST	0.57	−0.28	1.43
TRT_GS × YST	0.74	−0.18	1.65
TRT_SW × YST	0.52	−0.34	1.38
TRT_CC × YST	0.77	−0.13	1.67
TRT_ST × YST^{2*}	−0.93	−1.66	−0.20
TRT_GS × YST^2	−0.66	−1.42	0.10
TRT_SW × YST^{2*}	−0.91	−1.65	−0.18
TRT_CC × YST^{2*}	−1.02	−1.79	−0.26
Carolina chickadee			
(Intercept)*	−0.39	−0.76	−0.03
TRT_ST	0.46	−0.02	0.94
TRT_GS	0.09	−0.42	0.59
TRT_SW	−0.15	−0.67	0.37
TRT_CC	0.01	−0.50	0.52
YST*	0.90	0.53	1.26
YST^{2*}	−0.52	−0.80	−0.24
TRT_ST × YST	−0.42	−0.86	0.03
TRT_GS × YST	−0.42	−0.88	0.04
TRT_SW × YST*	−0.69	−1.13	−0.24
TRT_CC × YST	−0.32	−0.79	0.16
TRT_ST × YST^2	0.04	−0.32	0.41
TRT_GS × YST^2	0.25	−0.12	0.62
TRT_SW × YST^{2*}	0.56	0.20	0.93
TRT_CC × YST^2	0.22	−0.16	0.60
Downy woodpecker			
(Intercept)*	−2.68	−3.65	−1.71
TRT_ST	1.13	−0.05	2.30
TRT_GS	0.73	−0.42	1.87
TRT_SW	−0.42	−1.81	0.96
TRT_CC	0.37	−0.83	1.58

YST	0.97	0.00	1.95
YST^2	−0.35	−1.05	0.35
TRT_ST × YST	0.23	−1.22	1.67
TRT_GS × YST	−0.50	−1.61	0.62
TRT_SW × YST	−1.07	−2.27	0.12
TRT_CC × YST	−0.69	−1.82	0.45
TRT_ST × YST^{2*}	−1.55	−3.00	−0.10
TRT_GS × YST^2	0.16	−0.68	1.00
TRT_SW × YST^2	0.89	−0.05	1.83
TRT_CC × YST^2	0.45	−0.41	1.31
Eastern wood-pewee			
(Intercept)*	−3.09	−4.72	−1.46
TRT_ST*	2.37	1.02	3.72
TRT_GS*	1.64	0.25	3.02
TRT_SW*	1.81	0.43	3.19
TRT_CC*	1.74	0.31	3.17
YST	1.65	−0.48	3.77
YST^2	−1.43	−3.21	0.35
TRT_ST × YST	−0.83	−2.81	1.14
TRT_GS × YST	−0.68	−2.69	1.33
TRT_SW × YST	−0.89	−2.89	1.11
TRT_CC × YST	−1.60	−3.96	0.76
TRT_ST × YST^2	0.21	−1.47	1.88
TRT_GS × YST^2	0.64	−1.02	2.31
TRT_SW × YST^2	0.44	−1.24	2.12
TRT_CC × YST^2	−1.31	−3.96	1.34
Great crested flycatcher			
(Intercept)*	−2.85	−3.58	−2.13
TRT_ST*	0.91	0.03	1.79
TRT_GS*	1.35	0.50	2.20
TRT_SW*	1.27	0.42	2.13
TRT_CC*	1.77	0.95	2.60
YST	0.14	−0.51	0.79
TRT_ST × YST	−0.10	−0.84	0.63
TRT_GS × YST	0.12	−0.56	0.81
TRT_SW × YST	−0.08	−0.79	0.62
TRT_CC × YST	−0.17	−0.84	0.51
Ovenbird			
(Intercept)*	−1.14	−1.98	−0.30
TRT_ST	−0.54	−1.73	0.65
TRT_GS	−0.79	−1.99	0.42
TRT_SW*	−2.39	−3.86	−0.91
TRT_CC*	−2.97	−4.58	−1.36
YST	0.10	−0.19	0.39
TRT_ST × YST	0.26	−0.06	0.59
TRT_GS × YST	−0.21	−0.63	0.21
TRT_SW × YST*	0.77	0.08	1.46
TRT_CC × YST	−0.57	−1.66	0.51
Pine warbler			
(Intercept)*	0.29	0.01	0.58
TRT_ST*	0.35	0.02	0.68
TRT_GS	0.12	−0.22	0.46
TRT_SW	0.30	−0.03	0.63
TRT_CC*	−1.32	−1.79	−0.85
YST	−0.13	−0.34	0.08
YST^2	0.08	−0.12	0.28
TRT_ST × YST	0.20	−0.03	0.43
TRT_GS × YST	−0.02	−0.25	0.21
TRT_SW × YST	0.06	−0.16	0.29
TRT_CC × YST*	−0.68	−0.97	−0.40
TRT_ST × YST^2	−0.21	−0.43	0.02
TRT_GS × YST^2	−0.01	−0.23	0.21
TRT_SW × YST^2	−0.11	−0.33	0.11
TRT_CC × YST^{2*}	0.69	0.40	0.98

Red-eyed vireo			
(Intercept)	−0.24	−0.48	0.01
TRT_ST*	0.33	0.01	0.66
TRT_GS	0.28	−0.04	0.60
TRT_SW	0.01	−0.33	0.34
TRT_CC	−0.20	−0.54	0.15
YST*	0.20	0.01	0.39
TRT_ST × YST	−0.08	−0.30	0.14
TRT_GS × YST	−0.10	−0.33	0.12
TRT_SW × YST	0.06	−0.18	0.29
TRT_CC × YST	0.16	−0.08	0.41
Scarlet tanager			
(Intercept)*	−1.42	−1.91	−0.92
TRT_ST	−0.12	−0.74	0.49
TRT_GS	−0.40	−1.04	0.24
TRT_SW	−0.36	−1.00	0.27
TRT_CC	−0.37	−1.01	0.28
YST	0.36	−0.00	0.73
TRT_ST × YST*	−0.46	−0.89	−0.02
TRT_GS × YST	0.06	−0.37	0.48
TRT_SW × YST	−0.01	−0.44	0.42
TRT_CC × YST*	−0.77	−1.27	−0.26
Summer tanager			
(Intercept)*	−1.00	−1.31	−0.70
TRT_ST*	0.70	0.31	1.08
TRT_GS*	0.73	0.35	1.11
TRT_SW*	0.51	0.11	0.90
TRT_CC*	0.41	0.02	0.81
YST	−0.04	−0.32	0.24
TRT_ST × YST	0.11	−0.22	0.43
TRT_GS × YST	0.26	−0.06	0.58
TRT_SW × YST	0.20	−0.12	0.53
TRT_CC × YST	0.10	−0.24	0.44
Tufted titmouse			
(Intercept)*	−1.06	−1.47	−0.66
TRT_ST*	0.56	0.05	1.07
TRT_GS*	0.57	0.06	1.07
TRT_SW	0.17	−0.36	0.71
TRT_CC	−0.30	−0.91	0.32
YST*	1.71	1.08	2.35
YST^{2*}	−0.71	−1.09	−0.33
TRT_ST × YST*	−1.35	−2.05	−0.65
TRT_GS × YST*	−1.24	−1.94	−0.53
TRT_SW × YST*	−1.06	−1.79	−0.33
TRT_CC × YST*	−1.43	−2.18	−0.67
TRT_ST × YST^{2*}	0.53	0.07	1.00
TRT_GS × YST^{2*}	0.48	0.02	0.94
TRT_SW × YST^{2*}	0.59	0.12	1.07
TRT_CC × YST^{2*}	0.75	0.23	1.27
White-breasted nuthatch			
(Intercept)*	−3.96	−5.55	−2.38
TRT_ST*	2.98	1.24	4.73
TRT_GS*	2.51	0.79	4.22
TRT_SW*	2.47	0.73	4.20
TRT_CC*	2.05	0.27	3.83
YST	1.43	−0.69	3.56
YST^2	−0.31	−1.60	0.99
TRT_ST × YST*	−3.52	−6.47	−0.56
TRT_GS × YST	−0.82	−2.99	1.36
TRT_SW × YST	−1.63	−3.80	0.53
TRT_CC × YST	−1.62	−3.82	0.58
TRT_ST × YST^{2*}	−4.17	−7.07	−1.27
TRT_GS × YST^2	−0.28	−1.65	1.08

TRT_SW × YST^2	−0.08	−1.48	1.33
TRT_CC × YST^2	−0.17	−1.65	1.31
Worm-eating warbler			
(Intercept)*	−2.77	−3.67	−1.86
TRT_ST	0.10	−0.61	0.81
TRT_GS	−0.01	−0.73	0.72
TRT_SW	0.50	−0.16	1.16
TRT_CC	−1.09	−2.19	0.01
YST	−0.57	−1.43	0.30
TRT_ST × YST	0.39	−0.35	1.12
TRT_GS × YST	0.42	−0.33	1.17
TRT_SW × YST*	1.00	0.33	1.67
TRT_CC × YST	−0.16	−1.32	1.01
Yellow-throated vireo			
(Intercept)*	−3.94	−5.76	−2.13
TRT_ST*	2.40	0.52	4.29
TRT_GS	1.86	−0.07	3.79
TRT_SW*	2.45	0.57	4.33
TRT_CC	1.52	−0.63	3.66
YST	−0.05	−1.62	1.51
YST^2	−0.10	−1.59	1.39
TRT_ST × YST	0.14	−1.54	1.82
TRT_GS × YST	0.62	−1.13	2.36
TRT_SW × YST	0.75	−0.98	2.48
TRT_CC × YST	1.64	−1.63	4.91
TRT_ST × YST^2	−0.67	−2.31	0.97
TRT_GS × YST^2	−0.41	−2.03	1.21
TRT_SW × YST^2	−0.88	−2.52	0.76
TRT_CC × YST^2	−3.38	−8.28	1.51

[a] TRT_ST = single tree selection, TRT_GS = group selection, TRT_SW = shelterwood, TRT_CC = clearcut, YST = year since treatment.

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