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Author(s): Melissa C. Roach, Frank R. Thompson, III, and Todd Jones-Farrand
Source: The Condor, 120(3):543-556.
Published By: American Ornithological Society
https://doi.org/10.1650/CONDOR-17-189.1
URL: http://www.bioone.org/doi/full/10.1650/CONDOR-17-189.1

THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 120, 2018, pp. 543–556
DOI: 10.1650/CONDOR-17-189.1

RESEARCH ARTICLE

Songbird nest success is positively related to restoration of pine–oak savanna and woodland in the Ozark Highlands, Missouri, USA

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Submitted September 24, 2017; Accepted March 28, 2018; Published June 13, 2018

ABSTRACT

Savanna and woodland are transitional vegetation communities that have largely disappeared while many early-successional bird species have simultaneously declined in abundance. Pine savanna and woodland are being restored in the Midwest through prescribed fire and tree thinning to create their characteristic open canopy, dense ground layer, and variable shrub cover. Ideally, these restoration strategies for vegetation should also facilitate bird conservation objectives. We determined daily nest survival (DSR) for 6 songbird species, representing both shrub-nesting and canopy-nesting species, in southern Missouri, USA, in 2014 and 2015. We evaluated support for hypotheses relating temporal, vegetation, and management factors to DSR. We predicted that nest survival of the 3 shrub-nesting species (Eastern Towhee [*Pipilo erythrophthalmus*], Yellow-breasted Chat [*Icteria virens*], and Prairie Warbler [*Setophaga discolor*]) would show positive relationships with thinning and fire, but only Yellow-breasted Chat DSR was positively related to tree thinning. However, pooling species into a shrub-nesting guild resulted in a positive relationship of nest survival with tree thinning and a weak relationship with fire. For canopy-nesters, Eastern Wood-Pewee (*Contopus virens*) and Summer Tanager (*Piranga rubra*) DSR was negatively related to mean canopy cover, and Pine Warbler (*Setophaga pinus*) DSR was weakly related to tree density by size class. The canopy-nesting guild had higher DSR in thinned areas with lower basal area and less canopy cover. Our results demonstrate that pine savanna–woodland restoration in Missouri is providing high-quality breeding habitat for both shrub-nesting and canopy-nesting species, some of which are species of conservation concern.

Keywords: nest success, management, savanna–woodland, restoration, early-successional, prescribed fire, thinning, canopy cover

El éxito del nido de un ave canora está positivamente relacionado a la restauración de la sabana de pino-roble y del bosque en las Tierras Altas de Ozark, Missouri

RESUMEN

La sabana y el bosque son comunidades vegetales de transición que han mayormente desaparecido mientras que muchas especies de aves de estadios sucesionales tempranos han disminuido simultáneamente en abundancia. La sabana de pino y los bosques están siendo restaurados en el Medio Oeste a través de la prescripción de fuego y el raleo de árboles para crear su característico dosel abierto, una capa inferior densa y una cobertura variable de arbustos. Idealmente, estas estrategias de restauración de la vegetación también deberían facilitar los objetivos de conservación de las aves. Determinamos la supervivencia diaria del nido (SDN) para seis especies de aves canoras, representando especies que anidan en arbustos y en el dosel, en el sur de Missouri en 2014 y 2015. Evaluamos el apoyo a las hipótesis relacionando factores temporales, de vegetación y de manejo con la SDN. Predijimos que las tres especies que anidan en arbustos (*Pipilo erythrophthalmus*, *Setophaga discolor* y *Icteria virens*) deberían mostrar relaciones positivas con el raleo y el fuego, pero solo la SDN de *I. virens* estuvo positivamente relacionada con el raleo. Sin embargo, juntando las especies en un gremio de aves que anidan en arbustos se obtuvo una relación positiva de la supervivencia del nido con el raleo de árboles y una relación débil con el fuego. Para los individuos de *Contopus virens* y de *Piranga rubra* que anidan en el dosel, la SDN estuvo negativamente relacionada con la cobertura media del dosel. La SDN de *Setophaga pinus* estuvo débilmente relacionada con la densidad de tamaños de los árboles. El gremio de aves que anidan en el dosel tuvo una SDN más alta en las áreas raleadas con menor área basal y menor cobertura del dosel. Nuestros resultados demuestran que la restauración de la sabana de pino y del bosque en Missouri está brindando hábitat de anidación de alta calidad tanto para las especies de aves que anidan en arbustos como en el dosel, algunas de las cuales son especies de preocupación para la conservación.

Palabras clave: éxito de nido, cobertura del dosel, fuego prescripto, manejo, raleo, restauración, sabana-bosque, sucesión temprana

INTRODUCTION

Savannas and woodlands are transitional vegetation communities characterized by a variable but open canopy, sparse understory, and dense herbaceous ground layer consisting of grasses, forbs, and shrubs (McPherson 1997, Nelson 2002). These ecotonal communities contain characteristics of both open grasslands and closed forests, creating a vegetation gradient that can support bird species from distinct habitats (Temple 1998, Grundel and Pavlovic 2007, Barrioz et al. 2013). Savannas (<30% canopy closure) and woodlands (30–90% canopy closure) both have sparse understories, historically maintained by natural and anthropogenic fire, grazing by native ungulates, and other natural disturbances (McCarty 1993, Nelson 2002, Dey and Kabrick 2015). Both communities are now considered endangered (Noss et al. 1995) and have been drastically reduced in the Midwestern U.S. within the past century due to timber harvest, conversion to agricultural land, and succession to closed-canopy forest following extended periods of fire suppression (Schroeder 1981, Nuzzo 1986, Cutter and Guyette 1994, Cunningham 2007). Prescribed burns are a critical component in restoring and maintaining the characteristic open quality of these communities (Lorimer 2001, Peterson and Reich 2001, McCarty 2002, Cunningham 2007). Land managers are increasing their efforts to restore lost or degraded savanna–woodland toward historical conditions in order to promote floristic and biological diversity (The Nature Conservancy, Ozarks Ecoregional Assessment Team 2003, Hedrick et al. 2007).

State and federal agencies in Missouri, USA, are restoring areas of pine savanna–woodland because shortleaf pine (*Pinus echinata*) was historically common, covering nearly 2.7 million ha of the Ozark Plateau (Liming 1946, Nelson 1997). Shortleaf pine was often associated with open forests, which resulted in an Ozark landscape dominated by pine savanna–woodland interspersed through mature hardwood forest (Martin and Presley 1958, Batek 1994, Nelson 1997). Prescribed fire and tree thinning are the primary management practices used to restore pine savanna and woodland in the Ozark Highlands (Mark Twain National Forest 2011). Selectively removing mature trees, usually hardwood species, effectively opens the canopy, promoting growth at the ground layer (Figure 1). A regimen of low-intensity prescribed burns inhibits maturation of hardwood saplings and stimulates regeneration of pine trees. It is unclear how this pine savanna–woodland restoration will affect the breeding bird community in the region because most bird studies have focused on oak savanna–woodland restoration (Artman et al. 2001, Hartung and Brawn 2005, Brawn 2006, Reidy et al. 2014). Many early-successional and woodland generalist species are more abundant in restored pine savanna–woodland than in unrestored areas in Missouri (Roach 2017), but breeding productivity in these restored areas is largely unknown.

We examined the effects of nest site- and territory-level characteristics on nest survival in areas that had received varying amounts of prescribed fire and tree thinning in the last 10 yr. We hypothesized that restored savanna and woodland would serve as breeding habitat for disturbance-dependent, early-successional species, while generalist species would also benefit but to a lesser degree (Davis et al. 2000, Hunter et al. 2001, Askins et al. 2007, Vander Yacht et al. 2016). We selected 3 shrub-nesting species, the Eastern Towhee (*Pipilo erythrophthalmus*), Yellow-breasted Chat (*Icteria virens*), and Prairie Warbler (*Setophaga discolor*), all of which are species of concern, to represent early-successional species, and 3 canopy-nesting species, the Eastern Wood-Pewee (*Contopus virens*), Pine Warbler (*Setophaga pinus*), and Summer Tanager (*Piranga rubra*), to represent woodland generalists. We purposely selected species that allowed us to examine nest survival from the ground to the high canopy. We used an information-theoretic approach to evaluate support for hypotheses that nest survival would be positively related to fire, thinning, and shrub cover but negatively related to tree density and canopy cover. For shrub-nesting species, dense ground cover provides necessary vegetation for nesting sites. While these factors may seem less important for canopy-nesting species, the canopy-nesters in this study are generally associated with woodlands and could benefit from treatments that create and maintain woodlands.

METHODS

Study Area

We worked in sections of the Ozark Highlands, Missouri, USA undergoing pine savanna and woodland restoration. This region is characterized by rolling to rugged terrain with diverse karst landscapes, resulting in an abundance of exposed rock, caves, and spring systems amid the steep hills and valleys (The Nature Conservancy, Ozarks Ecoregional Assessment Team 2003, Missouri Department of Natural Resources 2016). The Ozark Highlands are dominated by oak–hickory, pine–oak, and mixed-oak woodland and forest communities (Nelson 2012). Common upland tree species include post oak (*Quercus stellata*), blackjack oak (*Q. marilandica*), white oak (*Q. alba*), northern red oak (*Q. rubra*), hickory (*Carya* spp.), shortleaf pine (*Pinus echinata*), and flowering dogwood (*Cornus florida*), with open woodland and savanna containing bluestem grasses (*Andropogon gerardii, Schizachyrium scoparium*), sedges (*Cyperaceae* spp.), saplings, and woody shrubs such as fragrant sumac (*Rhus aromatica*) and blackberry (*Rubus* spp.; Nelson 2012). This study was done in conjunction with the Collaborative Forest Landscape Restoration Project (CFLRP) and conducted on

FIGURE 1. Examples of (**A**) untreated, closed-canopy forest and (**B**) pine–oak woodland in the process of restoration after tree thinning and prescribed fire in the Ozark Highlands, Missouri, USA.

139,903 ha in the Mark Twain National Forest (MTNF) in Missouri (Mark Twain National Forest 2011). While management is occurring throughout the CFLRP area, treatments are scattered and varied in intensity. We selected 4 70-ha plots within the CFLRP that were accessible by road, known to have moderate detections of our focal species based on point count surveys completed the year prior to our study, and not scheduled for treatment during the study period. Selected plots had received restoration treatment(s), but the extent of management and local site features varied, resulting in a heterogeneous vegetation gradient that spanned a continuum from open savanna–woodland to mature, closed-canopy forest.

Nest Searching and Monitoring

We searched for and monitored nests of the Eastern Wood-Pewee, Eastern Towhee, Yellow-breasted Chat, Pine Warbler, Prairie Warbler, and Summer Tanager between early April and mid-August of 2014 and 2015. We selected these 6 species because they are more abundant in savanna and woodland than nearby forest (Brawn 2006, Kendrick et al. 2013, 2015, Reidy et al. 2014, Roach 2017). We selected species with differing natural histories to cover a range of nest placement heights from ground level to high canopy, resulting in 2 guilds, shrub-nesters (Eastern Towhee, Yellow-breasted Chat, and Prairie Warbler) and canopy-nesters (Eastern Wood-Pewee, Pine Warbler, and Summer Tanager).

We monitored nests during daily visits to 2 plots per year. We located nests using a combination of parental behavior and systematic searching across the entire plot (Martin and Geupel 1993). Each nest was marked with weather-resistant flagging placed $\geq$5 m away. Nests were monitored every 1–3 days, dependent on nest age or stage, until the nest fledged or failed. We used mirror poles or parental behavior to determine nest stage and nest contents, including Brown-headed Cowbird (*Molothrus ater*) eggs or nestlings. We limited disturbance to nests by completing checks as quickly as possible and with little or no alteration to the surrounding vegetation. We avoided checking nests if Blue Jays (*Cyanocitta cristata*), American Crows (*Corvus brachyrhynchos*), or Brown-headed Cowbirds (hereafter, cowbirds) were present. We determined nest fate using the expected fledging date in conjunction with observations made during the final nest check or subsequent visits. We confirmed successful fledging by observing at least one nestling leave the nest or through a combination of other cues such as adults carrying food repeatedly to the same area (and subsequently leaving without food), begging calls, and trails of fecal sacs or feces leading away from the nest. Visual observations of fledglings were always attempted but we limited disturbance to adults and recently fledged young. If we found no evidence of fledglings, we monitored the territory for any immediate renesting attempts, which suggested nest predation. Nests with unknown final fates were included in analysis without the final monitoring interval.

Habitat, Landscape, and Management Variables

We measured vegetation structure at each nest shortly after it fledged or failed using a modified BBIRD protocol (Martin et al. 1997). We recorded point-level canopy cover, ground cover composition, and tree density centered on each nest. We measured point-level canopy cover as the average of 4 spherical densiometer readings facing each cardinal direction. We visually estimated the percentage of grass–forb cover, shrub cover, leaf litter, and bare ground in 4 quadrants within a 5-m radius of the nest and calculated the mean for each category. The sum of ground cover percentages in each quadrant was allowed to exceed 100 because cover types could be multilayered. Within an 11.3-m radius of each nest, we measured diameter at breast height (DBH) of all trees with DBH $\geq$2.5 cm, recording trees as deciduous, evergreen, or snag. We later converted these measurements to the density of saplings (2.5–12.5 cm DBH), pole timber (13.0–27.5 cm DBH), and saw timber ($>$27.5 cm DBH). We calculated deciduous and evergreen tree basal area by summing the area estimated from DBH values.

We examined landscape structure and composition by calculating mean canopy cover and percent evergreen forest cover within a 150-m radius of each nest using the 2011 National Land Cover Dataset (NLCD; Homer et al. 2015) in ArcMap 10.1 (ESRI, Redlands, California, USA). In all cases, evergreen forest cover encompassed shortleaf pine and eastern redcedar (*Juniperus virginiana*), although cedar was uncommon in our sites. We obtained the management history for all 4 plots for the 10 yr prior to the final year of our study. We calculated the total number of prescribed burns that a nest location had received and whether the location had been mechanically thinned at least once. For landscape-scale factors, we used a 150-m buffer around the nest as an arbitrary estimate of territory size. We did not consider larger-scale landscape factors known to affect songbird nesting success in the region (Robinson et al 1995, Thompson et al. 2002, Cox et al. 2012b) because the 4 nest-searching plots occurred in a similar landscape context.

Data Analysis

We used the logistic exposure method (Shaffer 2004, Shaffer and Thompson 2007) to estimate the daily survival rate (DSR) of nests in relation to temporal, vegetation, and management factors using the GENMOD procedure in SAS (SAS Institute, Cary, North Carolina, USA). We only considered active nests with confirmed contents, which excluded intervals in the building or prelaying stage. We defined nest intervals as successful (success = 1) if the nest was still active with contents or fledging had been confirmed, or as unsuccessful (success = 0) if the nest had failed for any reason since the previous check. We first determined the most-supported temporal model by examining singular and additive combinations of stage (Stage), year (Year), and linear, quadratic, and cubic forms of ordinal date (day of year: DOY, DOY^2, DOY^3). We considered laying, incubation, and nestling stages for shrub-nesters, but omitted the laying stage for canopy-nesters as we were typically unable to confirm that a nest was active with contents until incubation had been initiated. We ranked models based on Akaike's Information Criterion for small sample sizes (AIC_c) and used effective sample size (n_{eff}) to calculate AIC_c (Rotella et al. 2004). We used covariates from the most-supported temporal model in all models with vegetation and management factors (hereafter vegetation models). We standardized all continuous vegetation covariates.

We first examined linear vs. quadratic vegetation models for mean canopy cover, basal area, and percent evergreen forest because we hypothesized that these relationships could be linear or quadratic. Only a quadratic relationship was supported, and subsequently carried forward, for mean canopy cover for Summer Tanagers. We then examined point-level canopy cover vs. shrub cover and basal area vs. tree density and used the top-ranked covariate from each comparison in the final model set below. This approach allowed us to create species-specific model sets while eliminating redundancy among covariates and reducing the total number of candidate models.

We constructed 18 vegetation models for our final model set consisting of singular and additive combinations of point-level canopy cover or percent shrub cover, hardwood and evergreen basal area or tree density by size class, mean canopy cover (150 m), percent evergreen forest (150 m), total number of burns, and thinned vs. not thinned. We ranked all vegetation models, the most-supported temporal model, and the null (intercept-only) model using AIC_c and evaluated goodness-of-fit using the Pearson χ^2 statistic (Burnham and Anderson 2002). Because of low sample sizes for some species, we also analyzed nest survival by guild and tested for an effect of species in each guild (to account for differences in DSR among species). We calculated DSR as a function of the most-supported covariate(s) while holding other covariates at their mean (Shaffer and Thompson 2007). We calculated period nest survival by expanding the DSR to each species' specific nesting cycle (laying, incubation, and nestling) observed in this study: 25 days for Summer Tanager, 26 days for Eastern Towhee and Yellow-breasted Chat, 27 days for Prairie Warbler, 29 days for Pine Warbler, and 33 days for Eastern Wood-Pewee. We report DSR and period survival predictions conditional on the most-supported model but report covariate coefficients for all competing models with $\Delta\text{AIC}_c < 2$. We did not consider models that only added an uninformative parameter to a more parsimonious model (Arnold 2010). We did not model average parameter estimates or predictions because there were either no competing models or they captured similar hypotheses with different covariates, and averaging in a zero effect for a covariate absent from a model when trying to understand specific covariate effects may not be appropriate in these circumstances (Burnham and Anderson 2002). While we only drew inferences from models with $\Delta\text{AIC}_c \leq 2$, we provide a complete ranking of models in Supplemental Material Table S1.

Spatial correlation in nest success can bias DSR standard error estimates. The logistic exposure model fit with PROC GENMOD in SAS does not permit spatial random effects, so we examined the residuals from the top model for the shrub and canopy guilds for spatial autocorrelation. We failed to reject the null hypothesis of zero spatial autocorrelation based on Moran's I statistic ($P > 0.10$; PROC Variogram; SAS Institute, Cary, North Carolina, USA) and concluded that spatial correlation was not a problem.

RESULTS

We monitored 462 nests for 2,875 intervals between nest checks in 2014 and 2015 combined. These included 57 Eastern Towhee nests ($n_{\text{eff}} = 559$), 133 Eastern Wood-Pewee nests ($n_{\text{eff}} = 2{,}725$), 65 Pine Warbler nests ($n_{\text{eff}} = 880$), 53 Prairie Warbler nests ($n_{\text{eff}} = 532$), 56 Summer Tanager nests ($n_{\text{eff}} = 684$), and 98 Yellow-breasted Chat nests ($n_{\text{eff}} = 1{,}089$), totaling 208 nests in the shrub-nesting guild ($n_{\text{eff}} = 2{,}180$) and 254 nests in the canopy-nesting guild ($n_{\text{eff}} = 4{,}289$). Vegetation characteristics varied greatly among nests, with the exception of mean canopy cover that ranged from 57% to 76% canopy closure (Table 1). Management covariates also varied greatly among nests, from 0 burns and no thinning up to 8 burns.

We observed 215 nests (47%) successfully fledge at least 1 host young and only 1 nest fledge a cowbird only (0.2%). The majority of the 225 nest failures were attributed to predation (217; 47%), but 3 nests were abandoned for unknown reasons (0.6%), 3 nests were abandoned in response to cowbird parasitism (0.6%), and 2 nests were lost due to severe weather events (0.4%). The final fates of 21 nests were unknown (5%); we were unable to conclusively determine nest fate for 9 nests, and 12 nests were still active at the conclusion of the study seasons. We confirmed that 25 nests (5%) were parasitized by cowbirds; however, we were unable to determine the contents of canopy nests until they reached the mid-to-late nestling stage when nestlings were visible from the ground. Due to this constraint, it is possible that canopy nests that failed before nestlings were visible could have contained cowbird eggs or nestlings. We did not observe cowbird nestlings in Eastern Wood-Pewee or Pine Warbler nests. We observed 2 Summer Tanager nests with 1 cowbird nestling each. Cowbirds parasitized 5% of Eastern Towhee, 9% of Yellow-breasted Chat, and 21% of Prairie Warbler nests. Within the shrub-nesting guild, 5% of nests were parasitized.

Tolerance values <0.4 for all variables in our global model indicated no excessive multicollinearity among covariates (Allison 1999; PROC REG, SAS Institute, Cary, North Carolina, USA). The overdispersion parameter (Pearson χ^2 test statistic/df; Burnham and Anderson 2002) did not indicate lack of fit of the top model for any species or guild. Period nest survival ranged from 0.24 to 0.45 for the 6 species (Table 2). The most-supported temporal model varied among species and guilds. Eastern Towhee, Yellow-breasted Chat, and Pine Warbler DSR was not related to stage, year, or linear, quadratic, or cubic DOY (Table 2). DSRs of Eastern Wood-Pewee, Prairie Warbler, Summer Tanager, shrub guild, and canopy guild were all related to ≥ 1 temporal variables (Table 2, Appendix Table 3). Eastern Wood-Pewee DSR was related to DOY^2 and stage (Table 2), with greater nest survival during incubation (Appendix Table 3). Prairie Warbler DSR was greater in the nestling stage than during either laying or incubation and decreased with DOY (Appendix Table 3). Summer Tanager DSR was lower in 2014 than 2015 and was positively related to DOY^3 (Table 2, Appendix Table 3). Shrub guild DSR was greatest during incubation and lowest during the laying stage (Table 2, Appendix Table 3). Canopy guild DSR was related to species, DOY^3, and stage, with greater DSR during incubation (Table 2, Appendix Table 3).

Overall, we found little support for vegetation structure or management treatment influencing nest survival of individual shrub-nesting species. There was no support for relationships between DSR and vegetation or management for the Eastern Towhee or Prairie Warbler (Table 2). Yellow-breasted Chat DSR showed a weak positive relationship with tree thinning, but the 95% confidence interval for this covariate overlapped zero and the AIC_c value and Akaike weight of this model were nearly identical to those of the null model (Table 2, Appendix Table 3). When species were pooled into the shrub guild, however, there was a strong positive relationship between DSR and tree thinning (Figure 2, Table 2, Appendix Table

TABLE 1. Descriptive statistics for vegetation and landscape characteristics and management activity at nest locations in managed savanna–woodlands in the Ozark Highlands, Missouri, USA, 2013–2015.

Covariate	Abbreviation	Mean	SD	Min	Max
Point-level canopy cover (%)	Canopy	64.62	20.84	4.75	95.00
Shrub cover (%)	Shrub	35.96	24.31	2.25	98.75
Mean canopy cover (150-m radius)	Canopy150	67.76	3.52	56.90	76.31
Saplings ha^{-1}	Treesize density	40.94	99.52	0.00	825.00
Pole timber ha^{-1}	Treesize density	91.96	109.33	0.00	775.00
Saw timber ha^{-1}	Treesize density	174.30	85.51	0.00	425.00
Evergreen basal area m^2 ha^{-1}	Basal	17.14	10.70	0.00	50.11
Hardwood basal area m^2 ha^{-1}	Basal	4.62	6.00	0.00	35.56
Evergreen forest (150-m radius, %)	Everg150	50.50	24.98	0.00	100.00
Total prescribed burns in 10 yr	Burns	3.96	0.69	0.00	8.00
Thinned vs. Not thinned	Thin	0.78 thinned			

3). The second-ranked model for the shrub guild included thinning and the number of burns but, while this model had $\Delta AIC_c = 0.69$, the confidence interval for both effects overlapped zero. Nevertheless, while only marginally supported based on AIC_c, nest success nearly tripled as prescribed burns increased from 0 to 8. There was no support for a species effect on DSR within the shrub guild (Table 2).

In contrast to the shrub-nesting species, we found support for relationships between DSR and vegetation structure for all 3 canopy-nesting species. Eastern Wood-Pewee DSR was negatively related to mean canopy cover within 150 m of the nest (Table 2, Appendix Table 3). Pine Warbler DSR was positively related to sapling and pole timber density and negatively related to saw timber density, but all confidence intervals overlapped zero (Table 2, Appendix Table 3). Summer Tanager DSR showed a quadratic relationship with mean canopy cover within 150 m of the nest, with the highest nest survival in intermediate canopy closure. Summer Tanager DSR was also negatively related to evergreen basal area, hardwood basal area, and percent evergreen forest within 150 m of the nest (Table 2, Appendix Table 3). Canopy guild DSR was negatively related to evergreen and hardwood basal area, mean canopy cover, and percent evergreen forest (Figure 3, Table 2, Appendix Table 3). There was support for a species effect on DSR for the canopy guild, with the Eastern Wood-Pewee having the greatest DSR and Pine Warbler the lowest.

DISCUSSION

Demography

Our nest survival estimates, as measured by DSR, demonstrated relationships between nest survival and tree thinning, prescribed fire, and management-driven vegetation structure for both shrub- and canopy-nesting species in restored pine savanna–woodlands. We found support for positive effects of thinning and prescribed fire and no support for negative effects of savanna–woodland restoration. Our study species showed positive relationships directly with management treatments or indirectly with vegetation patterns resulting from treatments. We had low sample sizes for some species, which made it difficult to detect relationships at the species level. Grouping species into shrub and canopy guilds, however, resulted in stronger support for relationships.

Our DSR estimates differed slightly from other studies in Midwestern savanna–woodland. The Eastern Wood-Pewee had the highest DSR of our 6 focal species, consistent with other studies that have also reported high DSR for this species (Knutson et al. 2004, Brawn 2006, Kendrick et al. 2013). Few studies have examined Pine Warbler and Summer Tanager nest success, but our estimates were similar to those for Pine Warblers in southern pine forests (Barber et al. 2001) and for Summer Tanagers in restored savannas in Illinois, USA (Brawn 2006). Our estimates of Eastern Towhee and Yellow-breasted Chat DSR were higher than estimates from other recent studies (Krementz and Powell 2000, Woodward et al. 2001, Brawn 2006, Shake et al. 2011, Novak et al. 2016). The Prairie Warbler was the only species for which other

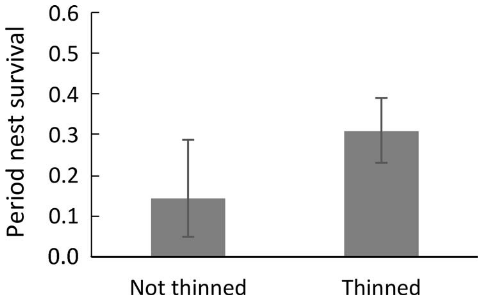

FIGURE 2. Period nest survival ± 95% confidence intervals for the shrub guild in relation to thinning activity in managed woodlands in the Missouri Ozarks, USA, 2014–2015. Period nest survival was estimated from predicted daily nest survival based on a mean nesting period of 26.33 days.

TABLE 2. Most-supported nest survival models with informative parameters and a difference in Akaike's Information Criterion adjusted for small sample sizes (ΔAIC_c) <2, effective sample size (n_{eff}), number of parameters (K), Akaike weight (w_i), log likelihood ($-2LogL$), and daily survival rate (DSR) and period survival rate (PSR) with 95% confidence limits (LCL, UCL) for birds in managed savanna–woodland in the Ozark Highlands, Missouri, USA, 2014–2015. See Table 1 for definitions of vegetation and management model terms. Temporal model terms include stage of the nesting period (Stage), year (Year), and linear, quadratic, and cubic forms of ordinal date (day of year: DOY, DOY^2, DOY^3).

Models by species	n_{eff}	K	ΔAIC_c	w_i	$-2LogL$	DSR (LCL, UCL)	PSR (LCL, UCL)
Eastern Wood-Pewee							
Stage + DOY + DOY^2 + Canopy150	2,725	5	0.00 [a]	0.33	−213.88	0.97 (0.96, 0.98)	0.35 (0.22, 0.49)
Eastern Towhee							
Null	559	1	0.00 [b]	0.19	−86.07	0.95 (0.93, 0.97)	0.28 (0.16, 0.41)
Yellow-Breasted Chat							
Thin	1,089	2	0.00 [c]	0.13	−140.33	0.96 (0.95, 0.97)	0.36 (0.25, 0.47)
Null	1,089	1	0.00	0.13	−141.33		
Pine Warbler							
Treesize density	880	4	0.00 [d]	0.22	−117.22	0.96 (0.94, 0.97)	0.26 (0.15, 0.38)
Null	880	1	1.38	0.11	−120.93		
Prairie Warbler							
Stage + DOY	532	4	0.00 [e]	0.22	−85.02	0.95 (0.93, 0.97)	0.24 (0.13, 0.38)
Summer Tanager							
Year + DOY + DOY^2 + DOY^3 + Canopy150^2	684	7	0.00 [f]	0.19	−75.35	0.97 (0.94, 0.98)	0.45 (0.21, 0.67)
Year + DOY + DOY^2 + DOY^3 + Basal + Everg150	684	8	1.62	0.09	−75.14		
Year + DOY + DOY^2 + DOY^3	684	5	1.79	0.08	−78.28		
Shrub guild							
Stage + Thin	2,180	4	0.00 [g]	0.22	−312.10	0.95 (0.94, 0.96)	0.29 (0.22, 0.36)
Stage	2,180	3	1.62	0.10	−313.92		
Canopy guild							
Species + Stage + DOY + DOY^2 + DOY^3 + Basal + Canopy150	4,289	10	0.00 [h]	0.22	−418.66	0.96 (0.95, 0.97)	0.32 (0.21, 0.43)
Species + Stage + DOY + DOY^2 + DOY^3 + Canopy150	4,289	8	0.05	0.21	−420.70		
Species + Stage + DOY + DOY^2 + DOY^3 + Basal + Everg150	4,289	10	1.48	0.10	−419.40		

[a] $AIC_c = 437.78$.
[b] $AIC_c = 174.14$.
[c] $AIC_c = 284.67$.
[d] $AIC_c = 242.49$.
[e] $AIC_c = 178.12$.
[f] $AIC_c = 164.87$.
[g] $AIC_c = 632.22$.
[h] $AIC_c = 857.37$.

studies have consistently reported higher DSR (Woodward et al. 2001, Shake et al. 2011, Novak et al. 2016).

DSRs of shrub-nesting species were not influenced by vegetation covariates, a somewhat counterintuitive result. Eastern Towhee DSR was not related to any covariates, and Prairie Warbler DSR was only related to temporal variables. Yellow-breasted Chat nest survival was greater in thinned areas, but no other covariate showed an effect. This lack of support for vegetation or management effects for shrub-nesters likely stems from both specialized nesting requirements and small sample sizes. These species are dependent on disturbance (Eckerle and Thompson 2001, Nolan et al. 2014, Greenlaw 2015) and nested almost exclusively in areas that had received management treatment; all shrub-guild nests were in areas that had been burned, and 87% were in thinned areas. Sample sizes for the Eastern Towhee and Prairie Warbler were also among the lowest of our focal species. These factors resulted in reduced variability across vegetation and management covariates, making it difficult to detect

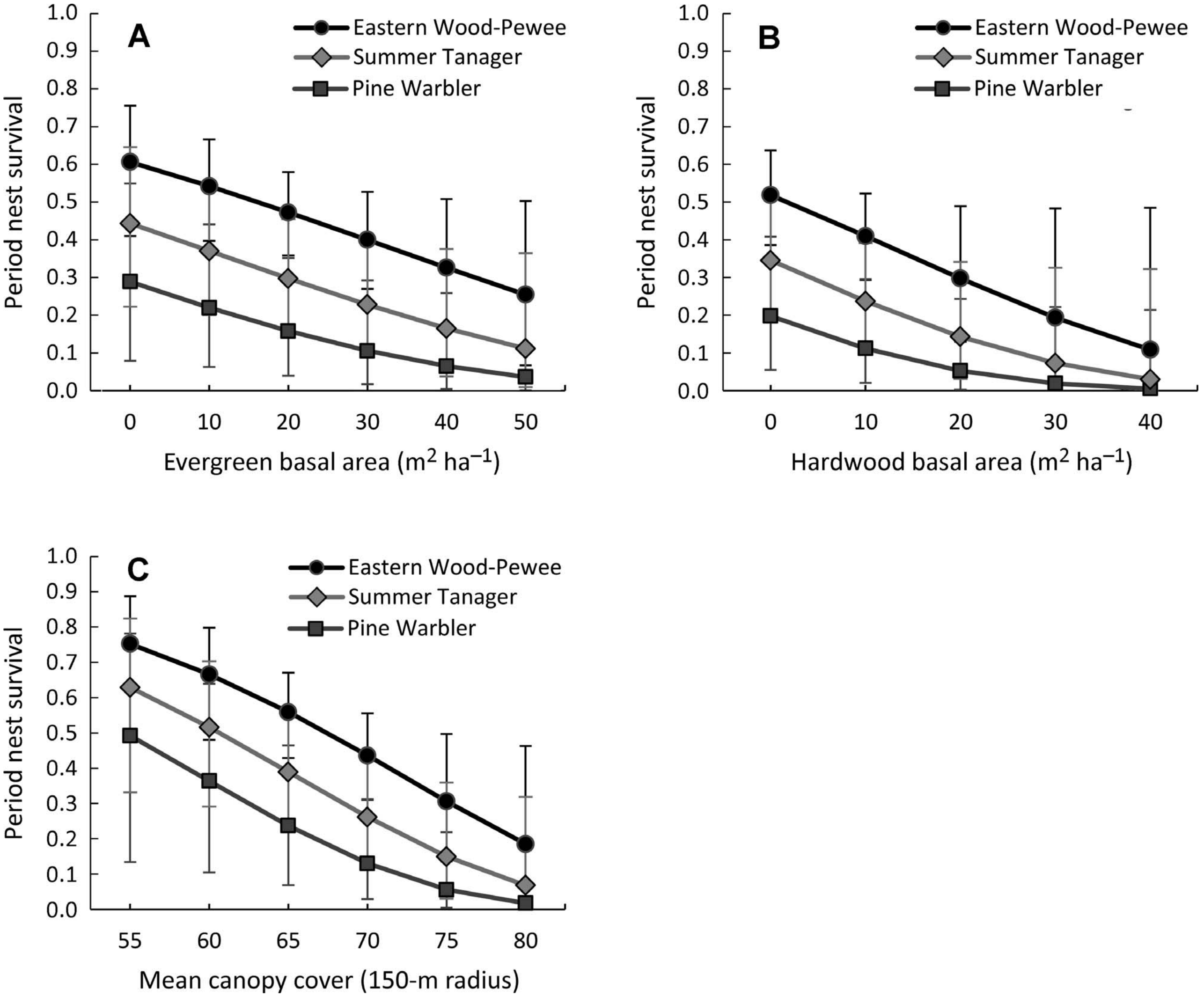

FIGURE 3. Period nest survival ± 95% confidence intervals for the canopy guild in relation to (**A**) evergreen basal area, (**B**) hardwood basal area, and (**C**) mean canopy cover in managed savanna–woodland in the Missouri Ozarks, USA, 2014–2015. Period nest survival was estimated from predicted daily nest survival based on a nesting period of 33 days for Eastern Wood-Pewee, 29 days for Pine Warbler, and 25 days for Summer Tanager.

relationships with nest survival. Combining these 3 species into one guild, however, produced a strong positive relationship of nest survival with thinning activity (Figure 2) and also revealed a positive relationship with the number of burns, although the 95% confidence interval overlapped zero (Appendix Table 3). Tree thinning is typically applied to areas that will also be burned, but we found no support for an interaction between burns and thinned areas. It is likely that both management treatments contribute to higher DSR for shrub-nesters, but that thinning has a stronger effect because it more drastically alters canopy coverage and, in turn, the development of a dense ground layer.

Our 3 canopy-nesting species showed no direct relationships between nest survival and tree thinning or prescribed fire but had clear relationships with vegetation covariates affected by management. Eastern Wood-Pewee DSR was higher in areas with less canopy cover. Fewer mature trees is a direct result of thinning and is often maintained by prescribed burns. Eastern Wood-Pewees are aerial insectivores that use conspicuous perches in the canopy to sally out to catch prey (Watt et al. 2017). Moderate tree densities and open canopies may provide an ideal mix of perching sites and foraging space to maximize foraging efficiency. Summer Tanager DSR showed a quadratic relationship with mean canopy cover, with the highest survival at intermediate levels of canopy closure, a classic woodland characteristic. Like Eastern Wood-Pewees, Summer Tanagers primarily forage by catching insects on the wing but will also readily eat items such as caterpillars, beetles, and fruit (Robinson 2012). Pine Warbler DSR was weakly related to tree density by size class; DSR was positively related to sapling and pole timber density but negatively related to saw timber (all confidence intervals overlapped zero). Pine Warblers do not sally for prey as a primary foraging strategy (Rodewald et al. 2013), so they likely do not benefit from open woodland structure in the same manner as Eastern Wood-Pewees and Summer Tanagers. However, the Pine Warbler was our only pine specialist and should have benefited from pine woodland restoration. As a guild, canopy-nesting DSR was negatively related to tree basal area and mean canopy cover (Figure 3). The increased structural diversity of woodlands likely creates a diverse and abundant prey base for breeding birds, and may also decrease nest predation as potential predators take advantage of an abundance of alternative prey. As expected, nest survival of the canopy guild was less influenced by ground vegetation and, instead, was related to overall community structure (i.e. tree density).

In addition to nesting success being generally high and positively affected by savanna–woodland restoration, it was likely sufficient for positive population growth. Only Prairie Warblers had period nest survival $<30\%$. The finite rate of population increase of a migrant songbird will generally be >1 for species with multiple nesting attempts, adult survival >0.6, and juvenile survival >0.3, if period nest survival is ≥ 0.25 (Donovan and Thompson 2001). Therefore, we suggest that this is additional evidence that tree thinning and prescribed fire are not negatively affecting, and may be benefiting, these species. Previous research has shown that this region is likely a population source for some Midwestern songbirds, but did not focus on areas managed to restore woodland or savanna (Donovan et al. 1995).

Management Implications

Nest predation is responsible for the vast majority of nest failures in our and other studies (Stake et al. 2005, Thompson 2007, Cox et al. 2012a), but multiple factors affect the predator community and, thus, the likelihood of a predation event occurring. Savanna and woodland restoration drastically alters the ground layer, promoting dense shrubs and grasses, which could have a significant effect on nest detection by predators within the shrub layer (Borgmann and Conway 2015). This dense shrub layer may not only decrease nest detectability but could also provide more potential nest sites, thus forcing predators to increase their foraging efforts while decreasing the chance of any single nest being found (Bowman and Harris 1980, Martin 1993). Some studies have suggested that habitat fragments increase predation rates due to the negative effect of contrasting vegetation edges (Paton 1994, Tewksbury et al. 2006), but restoration may be at a large enough scale in this system to offset any fragmentation effects. Additionally, the transition from savanna–woodland to forest, such as in our study sites, is typically less harsh than the more-studied forest to agricultural land transition, thus reducing the chance of significant edge effects. The heavily forested landscape around our study sites may also lower cowbird parasitism rates compared with those in systems with more agriculture.

Our results show that the combination of tree thinning and prescribed fire is effectively creating the necessary vegetation structure to attract focal species, and that these species are then able to reproduce successfully. DSR relationships with vegetation and management covariates were similar to density relationships found within the same study area (Roach 2017). Similar responses to management as measured by both abundance and nest success provide strong evidence that these species are benefiting from restoration. Postfledging survival, however, remains unknown, and further research examining responses of nest predators and arthropod prey important to breeding birds could reveal mechanisms driving our results.

Restored savannas and woodlands in the Missouri Ozarks are small to moderately sized patches within a heavily forested landscape and, while this restoration reduces the nesting area usable by forest-nesting species such as the Ovenbird (*Seiurus aurocapilla*) and Worm-eating Warbler (*Helmitheros vermivorum*), it does not necessarily create a tradeoff between early-successional and forest-interior species. Recent research suggests that a heterogeneous landscape with varying habitat types can actually increase nestling and fledgling survival, as both adults and fledglings use multiple vegetation types for foraging and cover (Mazerolle and Hobson 2003, Streby et al. 2012, King and Schlossberg 2014, Jenkins et al. 2016, Burke et al. 2017). Land managers can use this approach to create a varied, heterogeneous landscape that will benefit important species of concern from different habitats.

ACKNOWLEDGMENTS

We thank William Dijak for assistance with GIS analysis and Jane Fitzgerald, Brian Davidson, and the Missouri Department of Conservation for project planning and various forms of support. We also thank Jennifer Reidy, Lisa Webb, and John Kabrick for review of the manuscript. We are grateful to Sarah Kendrick, Joel Kutylowski, Laura Makielski, Vinnie Johnson, Philip Turner, Michael David, Danielle Blick, and Elizabeth Matseur for assistance with data collection.

Funding statement: Financial support was provided by the U.S. Department of Agriculture Forest Service Mark Twain National and Northern Research Station (agreement 13-CR-11242311-047). The U.S. Department of Agriculture Forest Service Northern Research Station reviewed and approved this manuscript but suggested no modifications to it.

Ethics statement: This study was purely observational and no ethics protocols were required to be followed.

Author contributions: M.C.R. led and worked on all aspects of this study; F.R.T. contributed to the conception and design of the study, data analysis, and manuscript writing; and T.J.-F. helped to conceive and design the study and provided input into the manuscript.

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APPENDIX TABLE 3. Coefficients (Coeff.), standard errors (SE), and 95% confidence limits (LCL, UCL) for covariates in nest survival models with informative parameters and $<2\ \Delta\mathrm{AIC}_c$ (Table 2) in managed savanna–woodland in the Ozark Highlands, Missouri, USA, 2014–2015.

Species model, covariate	Coeff.	SE	LCL	UCL
Eastern Wood-Pewee (EAWP)				
Stage (incubation)	0.671	0.301	0.081	1.261
Stage (nestling)	0.000	0.000	0.000	0.000
DOY	−0.548	0.186	−0.912	−0.184
DOY^2	0.002	0.001	0.001	0.003
Canopy150	−0.415	0.139	−0.687	−0.143
Eastern Towhee (EATO)				
Intercept	2.985	0.194	2.605	3.365
Yellow-breasted Chat (YBCH; model 1)				
Thin	0.607	0.403	−0.184	1.398
Yellow-breasted Chat (YBCH; model 2)				
Intercept	3.205	0.154	2.903	3.506
Pine Warbler (PIWA; model 1)				
Sapling	0.613	0.333	−0.040	1.266
Pole timber	0.076	0.173	−0.263	0.415
Saw timber	−0.087	0.188	−0.455	0.281
Pine Warbler (PIWA; model 2)				
Intercept	3.161	0.168	2.832	3.490
Prairie Warbler (PRAW)				
Stage (incubation)	−0.643	0.453	−1.530	0.244
Stage (laying)	−1.681	0.588	−2.834	−0.528
Stage (nestling)	0.000	0.000	0.000	0.000
DOY	−0.030	0.015	−0.059	−0.002
Summer Tanager (SUTA; model 1)				
Year (2014)	−0.592	0.471	−1.515	0.332
Year (2015)	0.000	0.000	0.000	0.000
DOY	−3.273	2.192	−7.569	1.023
DOY^2	0.016	0.012	−0.007	0.040
DOY^3	0.000	0.000	0.000	0.000
Canopy150	−0.353	0.280	−0.902	0.196
Canopy150^2	−0.413	0.211	−0.826	0.000
Summer Tanager (SUTA; model 2)				
Year (2014)	−0.543	0.469	−1.461	0.375
Year (2015)	0.000	0.000	0.000	0.000
DOY	−4.265	2.259	−8.691	0.162
DOY^2	0.022	0.012	−0.002	0.047
DOY^3	0.000	0.000	0.000	0.000
Evergreen basal	−0.212	0.258	−0.718	0.294
Hardwood basal	−0.461	0.192	−0.837	−0.085
Everg150	−0.487	0.292	−1.060	0.086
Summer Tanager (SUTA; model 3)				
Year (2014)	−0.866	0.441	−1.730	−0.002
Year (2015)	0.000	0.000	0.000	0.000
DOY	−3.803	2.157	−8.030	0.424
DOY^2	0.020	0.012	−0.004	0.043
DOY^3	0.000	0.000	0.000	0.000
Shrub guild (model 1)				
Stage (incubation)	0.089	0.219	−0.340	0.517
Stage (laying)	−1.038	0.339	−1.703	−0.373
Stage (nestling)	0.000	0.000	0.000	0.000
Thin	0.520	0.261	0.009	1.031
Shrub guild (model 2) *				
Stage (incubation)	0.093	0.218	−0.335	0.521
Stage (laying)	−1.043	0.340	−1.709	−0.377
Stage (nestling)	0.000	0.000	0.000	0.000
Burns	0.210	0.187	−0.156	0.576
Thin	−0.496	0.261	−1.008	0.016

APPENDIX TABLE 3. Continued.

Species model, covariate	Coeff.	SE	LCL	UCL
Shrub guild (model 3)				
Stage (incubation)	0.053	0.217	−0.373	0.479
Stage (laying)	−0.991	0.338	−1.653	−0.329
Stage (nestling)	0.000	0.000	0.000	0.000
Canopy guild (model 1)				
Species (EAWP)	0.811	0.253	0.315	1.308
Species (PIWA)	−0.266	0.334	−0.921	0.388
Species (SUTA)	0.000	0.000	0.000	0.000
Stage (incubation)	0.438	0.201	0.044	0.832
Stage (nestling)	0.000	0.000	0.000	0.000
DOY	0.579	0.313	−0.035	1.193
DOY^2	−0.004	0.002	−0.008	0.000
DOY^3	0.000	0.000	0.000	0.000
Evergreen basal	−0.218	0.122	−0.457	0.021
Hardwood basal	−0.186	0.101	−0.385	0.012
Canopy150	−0.254	0.110	−0.469	−0.039
Canopy guild (model 2)				
Species (EAWP)	0.781	0.253	0.286	1.276
Species (PIWA)	−0.247	0.329	−0.892	0.398
Species (SUTA)	0.000	0.000	0.000	0.000
Stage (incubation)	0.438	0.200	0.046	0.831
Stage (nestling)	0.000	0.000	0.000	0.000
DOY	0.588	0.312	−0.023	1.199
DOY^2	−0.004	0.002	−0.008	0.000
DOY^3	0.000	0.000	0.000	0.000
Canopy150	−0.336	0.101	−0.533	−0.139
Canopy guild (model 3)				
Species (EAWP)	0.813	0.251	0.321	1.305
Species (PIWA)	−0.297	0.338	−0.959	0.364
Species (SUTA)	0.000	0.000	0.000	0.000
Stage (incubation)	0.409	0.200	0.017	0.801
Stage (nestling)	0.000	0.000	0.000	0.000
DOY	0.601	0.316	−0.019	1.221
DOY^2	−0.004	0.002	−0.008	0.000
DOY^3	0.000	0.000	0.000	0.000
Evergreen basal	−0.246	0.121	−0.483	−0.008
Hardwood basal	−0.308	0.097	−0.498	−0.119
Everg150	−0.210	0.107	−0.419	0.000

* Shrub guild model 2 contains an uninformative parameter (Burns).